# SUBLIMINAL PERCEPTION IN THE BRAIN: HDERP AND FMRI DATA

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**Tesis Doctoral**

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# SUBLINIMAL PERCEPTION IN THE BRAIN: HDERP AND FMRI DATA

# *(PERCEPCIÓN SUBLIMINAL EN EL CEREBRO: DATOS DE HDERP Y fMRI)*

Tesis Doctoral presentada por **María Ruz Cámara** en el *Departamento de Psicología Experimental y Fisiología del Comportamiento*, para aspirar al grado de Doctor en Psicología, en el programa de doctorado de *Psicología Experimental y Neurociencias del Comportamiento*, de la Universidad de Granada.

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# PREFACE

The research described in this dissertation is part of the work that I have carried out during the last five years at the Departamento de Psicología Experimental in the Universidad de Granada and also at the Sackler Institute for Developmental Psychobiology of Weill Medical College of Cornell University. Our central goal in this investigative project was to take advantage of the new research possibilities afforded by modern neuroimaging techniques to shed some light on a classic field of inquiries in Experimental Psychology: Is our behavior guided only by the aspects of our mental life to which we have conscious access or do unconscious and inattentive processes also have an impact?

The exposition begins with a defense of the necessity of incorporating brain data in theoretical models in Psychology that try to explain how the human mind works. The discussion then focuses on the cognitive system of Attention as a model research field in which the incorporation of biological information has been highly beneficial. We next frame our research project by relating the concepts of attention and consciousness and discussing the main pitfalls that investigations of unconscious and inattentive processing share. We then introduce the three studies that comprise the present thesis. The first investigates the existence of unconscious semantic priming at objective detection levels and the other two characterize word encoding in an inattentional blindness task that represents a high attentional load situation. Brain activity is measured by means of High Density Event Related Potentials (HDERP) in the first two articles and by Functional Magnetic Resonance Imaging (fMRI) in the final study.

Results suggest that words are unconsciously analyzed at the objective detection threshold of consciousness and that they are also processed in a demanding high attentional load task. Conclusions highlight the idea that unconscious and unattended information can influence cognitive processing in a way that is objectively quantifiable via brain activity measures and stress the essential contribution of neuroimaging techniques for reaching these conclusions.

# INTRODUCTION:

## PHILOSOPHICAL FOUNDATIONS OF COGNITIVE NEUROSCIENCE

# 1. WHY SHOULD THE MIND CARE ABOUT THE BRAIN?

We humans are conscious rational agents and, at the same time, we are physical and biological entities shaped by evolution. This dual vision of human nature has helped to draw the borders among disciplines that study the human being. The mind, which drives our rational behavior, has been investigated in disciplines such as Philosophy of Mind and Cognitive Psychology. The study of the human body, on the other hand, has been left to biological sciences. Along our history, the way in which the mind and body have been separated has stressed the notion that the two are somewhat incompatible. In the last decades, however, the development of techniques suitable for the study of high-level cognitive processes in the human brain has generated a conceptual revolution that in the not so distant future may blur the dichotomy between mind and brain.

The main goal of this conceptual introduction is to consider the implications that the inclusion of brain data has on investigations of the human mind. We first note some basic investigative assumptions in Functionalism and Cognitive Science to then question the independence among levels of analysis of human cognition. Next we describe some of the ways in which data from the brain help in explaining the human mind. Finally, we take the cognitive system of Attention as an example to show how the consideration of brain data has boosted our knowledge about the components and working mechanisms of this system. The conclusions highlight the essential role that brain knowledge will play in the scientific quest for a unified and accurate understanding of the human mind.

## 1.1. FUNCTIONALISM IN PHILOSOPHY OF MIND

Philosophy of mind has been one of the main disciplines interested in describing the intentions and desires most basic to human behavior. In brief, a functional description of any complex processing device (such as a soda can vending machine) contains the *inputs* to the machine (e.g., inserting a coin), the series of the *internal operations* generated by those inputs as well as the relations among them, and finally the *outputs* of the machine (e.g., can delivery), which in turn are dependent on the inputs and the series of internal operations. This description contains the *functions* that the different states have on the economy of the system. Similarly, Functionalism in Philosophy of Mind claims that mental states are to be characterized by their functional properties, that is, for the role they have in the mind of agents or the inputs that cause them, the outputs that result from them and the whole system of causal transactions among the different states. Specifying the nature of a mental state consists of describing its functional role.

Putnam (1975) originally introduced the Computational Functionalism doctrine (or Functionalism of the Turing Machine), in which mental states are understood in the same manner as the internal states of a computational program. Scientific Functionalism, on the other hand, contends that functional roles must be ascribed to mental states in light of scientific psychological data. The key aspect in either of these variants is the distinction between the function of a mental state and its *physical realizer*. Describing a mental state involves determining its role on the tasks specified by the psychological theory or the computational program. In turn, the physical realizer is the physical state that implements the specific function.

This distinction between function and realizer leads to the *multiple realizability* argument, a core notion in the functionalist doctrine. Computations are multiply realizable in the sense that the same functions can be implemented in very different physical substrates. Consider a key as a simplified example. A key, as any mental state, is defined by its function, which is to open or close a lock. However, this function can be realized by different physical means, because a key can be made out of metal shaped in a particular form or by a plastic card with a magnetic code. Thus, the important characteristic in defining a key is not its physical substrate but rather its causal role. In the same manner, a mental state is not defined by its material constitution but rather by its role in the net of inputs, internal states and outputs in the computational organization of the system proposed by the psychological theory. That is, as there is no one-to-one mapping between a mental state and a physical feature, mental states and computations must be defined by their functions in the whole system and not by its material realization in a specific device. Thus, talking about minds is studying material systems at a higher level, abstracting from whatever physical constituents realize them. High-level mental terms designate properties that are different from properties of the material substrate that implements them, and thus mental states are not identifiable with, or reducible to, the material states they are realized in.

The independence among levels of analysis is shown in Turing's machine, a demonstration that the same operations can take place in very different substrates (Turing, 1950). This abstract machinery, known as the Universal Machine (UM), is able to imitate the behavior of any other formally specifiable computer, hence demonstrating that the very same computation can be performed by different kinds of material devices. Computation and implementation seem not to be directly linked to each other, and therefore it is possible to ignore the material composition of a system when studying it as a computational and algorithmic machine. From this perspective, biology of the brain plays no significant role in the search for the mental states that constitute the human mind. A typical functionalist assertion is that when psychological theories are mature enough, perhaps it will be possible to *translate* the discoveries made into the actual substrate that corresponds to such mental states in the human brain. Furthermore, when such a translation is possible, and perhaps this will never be the case, adding biological data to the picture will not bring explanatory power to the mentalistic accounts, but will only describe how mental states are materially realized in the brain (e.g. Fodor, 1999).

The investigative approach in Functionalism, however, lacks an experimental strategy to confirm or disprove the facts it proposes about the mind. Folk Psychology may be partially wrong in the intentions and desires it supposes to be at the basis of human behavior (Dennett, 1981). Defining mental states and their functions in an aprioristic manner needs some kind of experimental feedback in order to evaluate whether the operations proposed to explain the human behavior are actually causally efficient. Otherwise, the proposed concepts might be fictional accounts not at all related to the actual causes of behavior. Therefore, a complement to theorizing in Philosophy of Mind is the experimental approach in Cognitive Psychology. During its history, psychology has joined other disciplines in related fields trying to gain an integrated and coherent knowledge about how the human mind works. Cognitive Science and Cognitive Neuroscience are the two multidisciplinary enterprises that have worked toward this goal. Although many conceptual and methodological tools are shared by both paradigms, they differ in some basic assumptions and in the role they ascribe to biological data when explaining the mind.

## 1.2. COGNITIVE SCIENCE

By the end of the behaviorist era around the 1950s, when only observable stimuli and responses were open to scientific inquiry, the appearance of Cognitive Psychology recovered the interest in the internal representations and processes that constitute the human mind (see Tudela, 2004). This change in theoretical thinking came together with the advent of digital computers, and has come to be known as the *information processing revolution*. Its foundational basis was the acknowledgment that a parallel could be drawn between a computer and a human mind (the so-called *mind-computer analogy*). Both minds and computers could be understood as complex information processing systems that receive external stimulation (input) and emit a response (output) thanks to diverse internal representations and processes that manipulate symbols in task-specific ways (Newell, Rosembloom and Laird, 1989). Therefore, Cognitive Science was defined as the study of intelligence and its computational processes in humans (and other animals), in computers and in the abstract (Simon and Kaplan, 1989). Its main contributing disciplines are Cognitive Psychology, Artificial Intelligence, Linguistics and Logic. The development of computational models able to perform complex tasks emulating human behavior (e.g. Anderson, 1983) was the main tool to describe and explain how intelligence works in different complex systems.

A basic assumption in Cognitive Science is that the human mind can be viewed as a complex information-processing machine, and thus it can be decomposed into different functional modules, each specialized in the performance of a set of basic cognitive processes such as perception, memory, language, attention or emotion (see Cummins, 1983). These sets of cognitive systems are further recursively decomposed into more detailed representations and processes, up to the point of elementary mental operations (see Posner and Rothbart, 1994). Research in Cognitive Psychology offers feedback to prove or disconfirm the utility of the proposed concepts at different levels of abstraction (i.e., from general function to specific elementary processes).

David Marr (1982) described the idea that there are different epistemic points of view from which complex processing information systems can be studied. This author noted that there is no single view of a complex system that explains everything about it. To obtain a complete understanding of a system, it must be explained at different levels. In the first place, a *computational theory* has to be developed, which explains what the system computes and why it does so. The second level corresponds to the *representation and algorithms*, which details the representations of the input, the output and the algorithms that transform these representations. Finally, the *implementation* describes the physical device that actually realizes the system.

One of the central tenets in Cognitive Science involves building functional theories at the level in which it is supposed that minds and computers are equivalent, given that this correspondence can take place at many levels of description (see Pylyshyn, 1989). Obviously these two systems hold little correspondence at the implementation level, given that they are constituted by different physical materials that are arranged in different ways. Both systems, however, can be thought to correspond at the computational level, because they execute the same input–output function but by different means (a case of *weak* equivalence). For example, the same problem of addition (input – output function) is solved in completely different steps (or algorithms) depending on whether it is done by an abacus or by a modern computer. On the other hand, if we assume a *strong* equivalence, both systems also use the same algorithms or processes in order to fulfill their function, being thus correspondent at both the computational and the algorithmic levels. For Cognitive Science to be useful in discovering the principles by which human minds process information, the assumption of correspondence must be taken in its strong version (Pylyshyn, 1989). That is, for a computational system to be a model of cognitive processes active in the human mind, the model not only has to generate the same output given the same input, but it has to do so by using the same internal operations that the human mind employs. Otherwise the model only mimics human behavior and suggests a plausible way by which the task could be solved, but it does not explain how humans actually do so.

Similar to the multiple realizability argument in Functionalism, a key proposal of Marr's philosophy is the autonomy of levels of analysis. Although responses at the three levels must be obtained in order to gain a complete understanding of the whole system, each of them has a unique area of inquiry, in the sense that research can be done at any level without knowledge of results in the others. This is because questions asked and issues explained at each of the levels are fundamentally different and therefore autonomous.

This independence assumption is adopted in Cognitive Science as well. The same functions and computations can be carried out by very different physical substrates and for this reason knowing about the implementation of a given process is not needed to be able to obtain a complete understanding at the computational and algorithmic descriptions. Thus, a model describing certain computations in the human mind can be devised with no data at all on the physical system that implements the device. Moreover, adequate theories at the computational and algorithmic levels can be complete in Cognitive Science even when the specific material substrate that implements the system is unknown. Again, this line of theorizing maintains the long-standing distinction between mind and body.

### 1.3. QUESTIONING THE INDEPENDENCE ASSUMPTION

In the fifties, it was very useful for research in Cognitive Science to acknowledge that the study of cognitive processes has its own level of analysis independent of biological data. Talking about minds was different from talking about brains. Techniques available at that time were not able to measure brain activity during performance on the cognitive task of interest. Thus, the existence of a level of theorizing unique for cognitive processing was needed in order to investigate how humans represent and process information. Years of research in this discipline have shown that in fact it is possible to learn about how the human mind works without paying attention to its biological reality.

However, technical developments in the last years have offered the possibility of measuring brain activity while humans are performing complex cognitive tasks. Different techniques, such as fMRI, PET or TMS, enable the localization of brain activations that correspond to specific computations, while it is also possible to study the time course at which these areas come into play by the use of HDERP (see Posner and Raichle, 1994; Mazziotta and Toga, 1996)[1]. Moreover, electrophysiological recordings offer insights into the mechanisms of neural cognitive processing (see, for example, Miller, 1999) and, together with brain imaging techniques, they suggest the kind of representations that a specific region may support (Naccache and Dehaene, 2001). These facilities are providing data on how the brain actually performs the computations that have been studied in Cognitive Psychology for a long while (see Gazzaniga, Ivry and Mangun, 1998; Gazzaniga, 2000, 2004). The conceptual approach in Cognitive Neuroscience is different from classical concepts in biology (i.e., it is not 'pure biology', see Stoljar and Gold, 1998). The sort of questions that are asked about the primate brain in Cognitive Neuroscience are aimed at learning about its cognitive functioning rather than about the physical properties of its constituents.

Since the technological and conceptual revolution that Cognitive Neuroscience has brought about, a central question remains: How important are data obtained from the brain in theorizing about mental phenomena? In other words, now that we are starting to acquire knowledge about cognitive brain functioning, can we still consider the three level of analysis proposed by Marr as independent? One crucial point in answering this question involves setting the central goals of the research endeavor. If we want to explain how any computational system might process information (regardless of whether it is an animal, a computer, an abstract device or even a Martian), data from human brains could be treated as any other source of relevant information. However, if we are interested in discovering how humans actually represent and process information, we must consider results in Cognitive Neuroscience in order to develop theories that properly answer our research questions. If not, it is likely that the theory deals with computations

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[1] PET: positron emission tomography. TMS: transcranial magnetic stimulation.

and algorithms that, although plausible mechanisms of cognitive processing, are not the ones that human brains actually employ.

Although the same computation or general function can be performed by very different material substrates, as Turing's UM shows, the physical structure of a specific device impacts how the function is performed. That is, the kind of physical composition and material structure constrains to a great extent the sort of algorithms, or representations and processes, that are used to implement the function the system has to fulfill. The UM devised by Turing performs the same computations as any other formally structured device by generating the same output state from the same input. However, the kind of steps or algorithms that this machine employs to resolve the task can be rather different than those of the system being emulated. This is because its internal structure constrains how the task is decomposed, represented and processed; that is, how the output pattern is actually obtained from the input the device receives (Pylyshyn, 1989; Sejnowski and Churchland, 1989). Think again about a key as example. Although the same function (to open or close a lock) can be performed by very different physical substrates (i.e., metal or plastic), how the function is performed depends on the specific material the key is constructed from. A key made out of metal must have a specific shape to fit into the lock. However, a plastic card key opens the lock with the magnetic code it contains. The operations by which the key performs its function are completely different in both cases, and it is the material arrangement that constrains the operations. In general, how a system is materially arranged constrains its internal operations to a specific set. Therefore, we must know about how the human brain works in order to explain how we humans process information, which is the goal of Cognitive Psychology.

Investigative strategies in Functionalism or Cognitive Science cannot offer a complete picture to explain how the human mind actually works. Here, mental states and their functions, processes and representations, are described a priori and their implementation is left as a posteriori problem of translation, just as a description at a different level of analysis. However, theorizing about mental states or mental computations as something that does not need to be informed by the human brain is a severely limited enterprise nowadays. As stated above, this strategy has the serious risk of constructing psychological theories that describe plausible ways of how a cognitive system may function but that are far from how the human mind actually works. Research on cognitive processing in the brain will constrain which explanatory concepts are useful and which ones are not.

Knowledge at the three levels of analysis is neither independent nor autonomous. The interchange of information across levels will bring an adjusted view on how cognition is carried out in the human brain. Researchers in the field of Cognitive Neuroscience are investigating the human mind from this perspective.

## 1.4. COGNITIVE NEUROSCIENCE: INSIGHTS FROM COGNITION IN THE BRAIN

Cognitive Neuroscience is a multidisciplinary scientific effort aimed at studying the cognitive functioning of the human brain. Its emergence, in the 1980s, was driven by two separate achievements (see Posner and Raichle, 1994). First, the development of non-invasive brain imaging techniques allowed the recording of brain activity while humans engaged in different cognitive tasks. Second, a broad spectrum of theories of mental processes and of tasks suitable for the study of human cognitive processes were provided by more than half a century of Cognitive Psychology. These tasks, so well studied within the realm of Cognitive Psychology, can now be used to study how the brain performs these cognitive computations.

By merging techniques, data and theories at the cognitive and biological level of explanation (Marr, 1982), research on Cognitive Neuroscience tries to provide a coherent and integrated explanation of the biological basis of human cognitive behavior (Posner and Raichle, 1994). Its main goals can be described as explaining how the brain enables the mind (Gazzaniga et al., 1998), translating the phenomenology of cognition to biological processes (McIntosh, Fitzpatrick and Friston, 2001), localizing cognitive processes in the brain (Posner and Raichle, 1994; Posner and Rothbart, 1994; Corbetta, 1998; Humphreys, Duncan, and Treisman, 1999) and discovering the cognitive functions of brain regions (Naccache and Dehaene, 2001).

The recording of brain activity while humans perform carefully designed tasks allows researchers to probe the dynamics of the neural networks implementing cognitive processes under scrutiny. During the last decade, a great deal of progress has been made in the mapping of perceptual, mnemonic, linguistic, emotional, learning and attentional processes onto different brain networks (see Gazzaniga, 2004, for a comprehensive overview). Research in this new discipline is starting to integrate questions of human cognition from neurons through behavior (Posner and DiGirolamo, 2000). Here, the independence between levels claimed by the functionalist doctrine breaks down; the continuous interplay of questions and answers among levels is driving an integration of theoretical concepts among them.

Years of research in Cognitive Psychology offer the conceptual tools necessary to study how cognition works in the brain, by focusing research questions and providing experimental paradigms and task analyses (Humphreys et al., 1999; Posner and DiGirolamo, 2000). Questions asked in this discipline by different research paradigms are not about the physical mechanisms by which the brain works (as the nature of neurotransmitters, ionic currents or action potentials), but about the neural mechanisms of cognitive information processing (for example, how different sorts of information are coded and stored in the brain or how attention to a selected representation changes the pattern of activity in the cells coding those representations). Thus, the role left for biology is not just *descriptive* (as it was in Cognitive Science and Functionalist doctrine) but *explicative*; the way in which the human brain is designed helps to explain the algorithms that are used to process information.

A simplistic view of research in this discipline argues that the localization of already described cognitive processes brings no hints on the nature of those processes (Fodor, 1999). However, most theorists in the field of Cognitive Neuroscience support the opposite view: results in this field are starting to change theoretical ideas on major psychological issues (Humphreys et al., 1999; Posner and DiGirolamo, 2000; Driver, 2001). That is, theories on cognitive processes are being modified or even generated by results derived from research in Cognitive Neuroscience.

## 1.5. HOW DOES THE BRAIN HELP IN EXPLAINING THE MIND?

As noted above, until quite recently most investigations on human cognition have been shaped by the notion that mind and body-related concepts belong to completely different levels of description. Although in the present descriptions at a 'pure cognitive' or a 'pure biological' level are still possible, research in the fast growing field of Cognitive Neuroscience may be starting to blur the boundaries between our minds and our brains. Here, classical cognitive concepts such as object recognition, memory consolidation or decision-making, together with tasks designed to study them are being used to ask how our neural tissue performs the relevant operations. At the same time, brain data can be used in a feedback manner to consolidate, refine or modify how existing theories describe or analyze mental operations (Churchland, 1986; Posner and DiGirolamo, 2000). Thus, this endless interchange of information from cognition to brain functioning drives the inclusion of 'biological' concepts into theories of cognition while at the same time organizes our knowledge of brain functioning into cognitive dimensions. The results are theories in which it is difficult to find the distinctions between the mind and body side of human cognition (see Gazzaniga Ivry and Mangun, 1998, for a comprehensive overview).

Although the field of Cognitive Neuroscience is admittedly young, the incorporation of data from the brain for studying the human mind is starting to show several advantages over previous approaches, some of which are outlined below.

### 1.5.1. MULTIDIMENSIONAL DATA SETS ARE OBTAINED FROM EACH TASK.

Behavioral research in Cognitive Psychology faces the problem that only a few data points are derived from each trial in an experiment. In this discipline, analyses are usually made on the basis of reaction times and/or accuracy to respond to stimuli. The whole chain of internal processes that takes place from a stimulus to a response is measured with only one or two markers per trial, which may not even be sensitive to some of the internal operations needed to perform the task. However, brain imaging shows activations and deactivations in different parts of the brain as well as the temporal ordering of these processes (see Cabeza and Kingstone, 2001), and this can be obtained even in the absence of a behavioral response (see Leopold and Logothetis, 1999).

For example, Lumer and Rees (1999) studied the brain correlates of human consciousness in a binocular rivalry paradigm. Using knowledge of the temporal profile of the binocular rivalry of the participants in the study, they were able to infer the brain activity associated with conscious experience without the participants generating an overt response about the content of their consciousness. These authors found that consciousness was related to functional interactions of coordinated activity between different brain areas such as visual and prefrontal cortices, linked in previous studies to visual perceptual analyses, working memory and control of attention processes. Thus, the multidimensionality of data obtained by means of neuroimaging can be used to analyze the brain as a whole, to study how some areas activate in concert with others (what is called *functional brain dynamics*) and the constraints anatomy imposes on these interactions. This is a very useful approach for studying the dynamics of a complex system such as the human brain (see, for example, Sporns, Tononi and Edelman, 2000), which was not available for research until the advent of neuroimaging techniques.

### 1.5.2. RESOLUTION OF LONG STANDING QUESTIONS IN COGNITIVE PSYCHOLOGY.

For a long time there have been debates in the field of Cognitive Psychology that have framed important parts of the research and for which no clear answers have been found. One of them is the locus of selection of information (Broadbent, 1958, Posner and DiGirolamo, 2000). Theorists argue about whether attentional selection operates at early stages of information processing at the perceptual level of analyses (Broadbent, 1958; Posner, 1980) or whether this selection only takes place at later stages such as response selection or access to conscious representations (Deutsch and Deutsch, 1963; Pashler, 1994). Research with brain imaging techniques has shown that selection of information can take place at both early and late stages of processing. In brain dynamics, paying attention to a stimulus causes the amplification in the firing of the neurons that code for that stimulus (Corbetta et al., 1991; Desimone and Duncan, 1995). This enhanced activity helps the neural representation of the attended stimulus to win the competitive processes for the control of action that takes place between brain areas (Desimone and Duncan, 1995; see Geraint, Frackowiak and Frith, 1997). Research with neuroimaging techniques has revealed that this attentional amplification in neural signals can take place both early (Hillyard, Vogel and Luck, 1998; Posner and Gilbert, 1999) and late in time after the stimulation is presented (see, for example, Driver and Vuilleumier, 2001). Therefore, the answer from Cognitive Neuroscience to the old research question is that attentional selection can take place at several levels of processing (Luck and Hillyard, 2000). The question for research now is which task characteristics drive the brain to select information at different levels of representation (Luck and Hillyard, 2000; Lavie, 2000).

Another area of research illuminated by brain imaging has been that of conscious vs. unconscious processing of information (see Merikle and Daneman, 2000). For a long time it was not clear whether stimuli not consciously perceived are processed at all (Holender, 1986). However, by measuring brain activity after unconscious stimulation it has been shown that a great deal of cerebral processing takes place even when participants lack the subjective experience of the stimulation (see Dehaene and Naccache, 2001; Kanwisher, 2001, for an overview) both in normal and in neuropsychological patients. Neuroimaging data show that unconscious stimuli such as words or faces activate to a great extent the extrastriate areas in the cortex specialized for high-order visual analysis (see Dehaene et al., 2001; Rees, 2001). Now, the research question has turned to understanding which characteristics of brain dynamics are related to conscious awareness. Multiple results indicate that consciousness is associated with covariation of activity in multiple extrastriate ventral, parietal, and prefrontal cortical areas, suggesting that the interchange of information between areas involved in visual perceptual analyses and those related to attentional selection and cognitive control may contribute to conscious awareness. These results, in turn, support models that depict consciousness as a high-level stage in brain processing where information from multiple sources is integrated and used in the control of explicit behavior (i.e., Baars, 1988; Dehaene and Naccache, 2001). Thus, results in the field of Cognitive Neuroscience are helping to solve old questions that had found no clear answers from traditional methods. At the same time, data obtained from neuroimaging are generating new questions, which in turn will look at the brain dynamics to find answers to them.

### 1.5.3. GENERATION OF NEW HINTS ON THE PARALLELISM BETWEEN DIFFERENT SIDES OF COGNITION.

As neuroimaging results accumulate, an increased amount of knowledge is gained about the cognitive functions of different brain areas and networks (see Cabeza and Nyberg, 2000; Naccache and Dehaene, 2001). The finding that a certain behavior activates a set of cerebral regions may help to elucidate the cognitive processes that the task recruits by inferring this from other studies that find overlapping brain activations. Therefore, parallelisms as well as dissociations among different tasks can be found by comparing their respective patterns of activations (Humphreys et al., 1999). For example, measurements of brain activity while persons are performing tasks that require the generation of internal visual images have shown that the brain areas recruited overlap to a great extent with those regions that respond when persons are actually perceiving visual stimuli in their environment (Thompson and Kosslyn, 2000). This result suggests that the act of imagining a situation is performed by internally activating a subset of the brain areas that are used to construct a percept when the stimulation comes from the external world.

The work of Lieberman (2000) is another example of this strategy. This author proposes that social intuition skills have their basis in knowledge obtained by means of implicit learning processes (see also Adolphs, 2003). Apart from the conceptual similarities that can be drawn between these two domains of cognition, it has been shown that they both depend on similar structures in the brain, in particular on normal basal ganglia functioning. Because of the basal ganglias's location and projections, it is an ideal candidate to subserve brain mechanisms to unconsciously detect subtle relevant regularities in the environment. Thus, intuition could be the subjective experience associated with the use of knowledge obtained trough implicit learning processes (Lieberman, 2000). Hence, data from Cognitive Neuroscience can be used as a source of insights in order to draw parallels, as well as dissociations, among conceptual domains that could seem unrelated when examined only by purely behavioral methods.

### 1.5.4. VALIDATION OF GENERAL ASSUMPTIONS IN THEORIES ABOUT THE MIND.

The information processing approach in Cognitive Psychology divides cognitive tasks into constituent operations and uses mental chronometry to measure these elementary processes (Posner, 1978). In the same vein, results in Cognitive Neuroscience are showing that complex brain functions can be decomposed into simpler processes which can be anatomically localized and that correlate with simple behavioral processes (Posner and Rothbart, 1994; Posner and DiGirolamo, 2000). For example, some cognitive theories on how visual perception is accomplished state that the input from the environment is decomposed into several dimensions (lines, orientation, motion, form, color and the like) and then arranged to form a complex object in higher levels of analyses (Marr, 1982). The study of visual perceptual regions in the brain has shown that there are different areas devoted to representing the attributes in which the perceptual input is decomposed and that other areas represent objects as a whole (see Zeki, 1993). Therefore, brain analysis has validated a group of theories developed in the field of Cognitive Psychology because it has shown that the primate brain is organized in the same dimensions as the theory postulates. Another assumption held for a long time by several theories in the field of visual perception was that of hierarchical processing along modules containing encapsulated information, in which higher-level modules depend on the lower-level ones but not vice versa (e.g. Marr, 1982). However, it has been shown that perceptual information is processed in the brain in a recurrent and interactive fashion instead of in an encapsulated manner (see Churchland, Ramachandran and Sejnowski, 1994; Lamme and Roelfsema, 2000), a discovery that invalidates the hierarchical assumption held by several models. Therefore, part of the assumptions that have driven research in Cognitive Psychology for a long time are now being validated by functional brain imaging and others are being proven to be wrong, thus forcing models to be reconsidered in the light of results from Cognitive Neuroscience.

### 1.5.5. CLARIFICATION OF THE ADEQUATE LEVEL OF ANALYSIS FOR THEORIZING ABOUT THE MIND.

The behavior indeterminacy claim states that by using behavioral data alone it will never be possible to find a strong equivalence between a model and the psychological reality in the human brain (see Pylyshyn, 1989).

Different theories describe the same psychological phenomena by using concepts at different levels of abstraction. Discovering the right level at which a certain problem has to be explained is a key factor for success in research (Ramachandran and Hirstein, 1997). In a not so distant future, results in Cognitive Neuroscience may provide invaluable insights into the adequate level of analysis to study how brain process information. The appropriate ontological level for the analysis of cognition in the brain may depend on the specific problem under study. For example, while attentional selection may be explained at the level of competition among neuronal groups coding for different stimuli, it might be more useful to study the interactions among different brain regions in order to explain memory consolidation or conscious awareness phenomena. In any case, research in Cognitive Neuroscience will be a reference point to elucidate which theories and concepts are useful in explaining how the human mind works.

## 2. ATTENTION THEORY BEFORE AND AFTER NEUROIMAGING

As a second step to stress the relevance of neuroscience data to cognition, we describe how research in the field of Attention has been benefited enormously by the consideration of the brain as a valuable source of information. First, Cognitive Neuroscience has supported models affording Attention the status of a cognitive system by showing how it is composed by three attentional networks that map into a set of reliable brain regions linked to specific neurotransmitters, separable genetic bases and developmental courses. In this way, in the last decades attention has changed from being mainly a variable used to explain several research problems to being an autonomous system that has the right to be explained on its own. Second, brain data has facilitated a change in the focus of research from the attentional effects on behavior to the study of the attentional mechanisms or the processes by which attention biases the flow of information in other processing systems.

## 2.1. ATTENTION AS A MODEL OF THE USEFULNESS OF KNOWING ABOUT THE BRAIN

Certainly it is not an easy task to develop an accurate taxonomy of mental processes. And if such a quest were truly impossible as some authors claim, incorporating fallible new technologies and brain data would do nothing but add confusion to the story (Uttal, 2001). Many authors, however, do not agree with the previous conclusions. First, science is a self-corrective enterprise. Theories and taxonomies of the mind proposed nowadays are in early stages and are not definitive but subject to continuous revisions (e.g. Bechtel, 2002; Hubbard, 2003). Second brain data, far from being useless to the cognitive domain, is one of the relevant sources that can be used to support, modify or falsify proposed mental taxonomies and can even offer insights for devising brand new dissections of mental processes (Churchland, 1986; Posner and DiGirolamo, 2000). Moreover, the limitations of individual research methodologies can be made much less conspicuous by appealing to the convergence of evidence from multiple sources. And this is precisely the most powerful strength of the Cognitive Neuroscience approach to the study of the human mind and brain (Gazzaniga, Ivry and Mangun, 1998). This convergent discipline is being successfully applied to many research fields such as perception, memory, learning, executive functions and consciousness (see Gazzaniga, 2004). Within these, the study of attention has been one of the fields that have benefited most from this approach (Posner, 2004), due to several reasons outlined bellow.

## 2.2. THREE NETWORKS AS A TAXONOMY OF ATTENTION

Attention is a word that pervades our daily vocabulary. The Oxford English dictionary defines it as 'the act or state of attending especially through applying the mind to an object of sense or thought' or as 'a condition of readiness for such attention involving especially a selective narrowing or focusing of consciousness and receptivity'. In 1890, William James proposed a psychological definition of attention that appealed to the subjective knowledge of the reader and that has become a reference point in the literature:

> Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several

> simultaneously possible objects or trains of thought. Focalization, concentration, or consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state (...) [James, 1890, p. 404]

A century later, however, Harold Pashler (1998) captured the confusion in the field when he wrote that:

> No one knows what attention is, and (…) there may even not be an "it" there to be known about (although of course there might be). [Pashler, 1998, p. 1]

The tension between these two affirmations exemplifies the difficulty of finding a scientific definition of attention to which everyone agrees. The fact that attention is a concept incorporated into science from folk psychology does not help, but the core problem arises from the fact that attention, as a psychological process, is not a unitary phenomenon (e.g. James, 1980; Posner and Boies, 1971). Trying to define attention as a whole, and attempting localize it as such in the brain, is a potentially fruitless approach. However, using a decomposition strategy (Bechtel, 2002) to develop a taxonomy of attention at the appropriate level of explanation (Posner and Rothbart, 1994) may be extremely useful for suggesting provisional definitions of what attention may be. The attentional networks proposed by Posner and collaborators represent an example of a taxonomy of a cognitive process that nowadays receives support from several converging methodologies. Here knowledge about brain areas related to attention acts not only as the backbone of the proposal but has also been used to constrain, redefine and suggest new ideas for organizing the attentional networks.

Attention can be conceptualized as a system of different anatomical areas that is composed by three distinct and specialized modules (see Posner and Fan, 2004, for an extended description). The achievement and maintenance of an alert state is mediated by the alerting network; the orientation to sensory objects is carried out by the orienting network and finally the executive network is responsible for monitoring and resolving conflicts between computations taking place in different brain areas.

The *alerting network* generates changes in the preparatory state of the organism in expectation of an incoming stimulus. The paradigms employed to study it involve vigilance tasks and the use or warning signals. Anatomically, it comprises areas of the right parietal and frontal hemispheres, and it is mainly related to the norepinephrine (NE) neurotransmitter that arises from the locus coeruleus. Lesions to these brain regions generate deficits in alerting and drugs modulating NE levels affect its functioning while leaving other attentional dimensions intact (see Posner and Fan, 2004). The selection of stimuli from sensory input is the role of the *orienting network*, which has been mainly studied using 'costs and benefits' paradigms (Posner, 1980). Voluntary changes in the allocation of attention are mediated by areas in the superior parietal lobe, together with the frontal eye fields, superior colliculus and some nuclei in the thalamus. Reflexive or automatic changes in attention generated by the appearance of unexpected stimuli at novel locations seem to be resolved by activations in the temporo-parietal junction (TPJ). The neurotransmitter acetylcholine (Ach) originating in the basal forebrain is the main chemical regulating the orienting function, as drugs affecting this transmitter modify indices of orienting with no impact on alerting. Most neglect patients, who suffer a deficit in orienting to and detecting events appearing contralateral to their brain lesions, have damage affecting their right TPJ. Finally, the *executive network* monitors and resolves conflict between different representations in the control of behavior. This usually happens in situations requiring action planning, decision making, error detection, novel or difficult situations or when overcoming a habitual response is needed. The use of a model task to study executive attention, the Stroop task, has shown the relevance of lateral prefrontal regions, the anterior cingulate cortex (ACC) and basal ganglia in mediating this function. The neurotransmitter most relevant in this case is the dopamine (DA) of the ventral tegmental system, and its imbalances are known to affect executive functions. Lesions in these brain areas can lead to deficits in voluntary behavior, loss of planning capabilities or lack of appropriate social behavior.

In the last years there has been extensive research aimed at supporting this mental taxonomy with converging evidence coming from different domains. As described above, the three networks have been associated with different psychological functions and brain regions that use distinct neurotransmitters as signals. This is supported by several lines of research including neuroimaging experiments, studies of differential functional loss after focal brain damage and dissociations using drugs targeted at specific neurotransmitters in alert monkeys and humans (see Posner and Fan, 2004). The ANT (Attention Network Testing; Fan, McCandliss, Sommer, Raz and Posner, 2002) task was specifically devised to obtain behavioral indices of the functioning of the three networks in different populations (children, healthy and neuropsychological adults, psychiatric patients and non-human primates). Using this tool as a model to both operationalize and quantify attention processes, it has been shown that reaction time and accuracy measures of each network are uncorrelated with one another, in the sense that the same individuals can have differential efficiency in the three functions, which strengthens the idea that they are differentiable. Also, the combination of this testing tool with genetic methods suggests that the three networks are linked to distinct genes and have independent heritability, which stands in agreement with the data supporting their different developmental courses in infancy and their separable involvement in some psychiatric pathologies (see Posner and Fan, 2004).

Thus, this differentiation of attention in three distinct but interrelated networks can be used as a model taxonomy of a complex mental phenomenon that relies on brain structure and functioning (psychological) as a essential backbone. In this case, knowledge of localization of cognitive functions in the brain was not added only after the processes of the mind had been described. Partial biological information from neuropsychology and animal neurophysiology was used to help build the taxonomy from the beginning (Posner and Petersen, 1990). With time, the acquisition of new behavioral and brain data pushed the modification and improvement of the categories proposed for attention. This has led to a refining of their alleged computational functions (mainly of the executive and orienting networks) and of its constituent parts (Posner and Fan, 2004). This represents a true example of how bi-directional cross talk between data and constructs of cognitive psychology and neuroscience can be used to build a taxonomy of a cognitive function that is supported from several different domains of knowledge.

### 2.3. The mechanisms of attention

Brain data can be used as a driving force in building taxonomies of the mind. But this is not the only way neuroscience helps cognitive theories. One of the critiques to brain research is that it is of no use in understanding cognitive processes. From this perspective, these cognitive processes can be explained and understood a priori and neuroimaging could be used in a second step just to localize in the brain previously described cognitive phenomena, but this brings no new information about these processes (e.g. Fodor, 1999). However, Cognitive Neuroscience can also help in understanding the processes *per-se*. That is, rather than just *translating* to brain previously discovered phenomena, brain data has a crucial role in *explaining* how those cognitive mechanisms work.

For many years, behavioral research was the principal source of investigation in cognitive psychology. During all this time, the field of attention was populated with a vast list of valuable information about the behavioral effects of manipulating attention in different ways and about attention-related phenomena. In the last decades, however, the inclusion of electrophysiological recordings in awake monkeys aided in the last years with neuroimaging technology applied to humans, have boosted our knowledge on the mechanisms by which attention operates in the brain. Here it is highly useful to differentiate between the brain *sources* of attention modulation and the *sites* that are affected by this attentional modulation.

One of the oldest ideas about attention concerns its selective nature. We are surrounded by a myriad of stimuli and the system is in need of selecting only a few of them to control our behavior. Why is this so? Although the teleological nature of this is still unknown, in the last years we have gained some knowledge concerning why this happens (see Desimone and Duncan, 1995; Duncan, 2004). Electrophysiological recordings in monkeys showed that stimuli compete for representational resources in the brain by mutually suppressing their respective neural responses. This basic effect is observed when the response of a neuron, which is maximal after the presentation of an effective stimulus in its receptive field, is significantly reduced by the presentation of a second stimulus within the same field. That is, the addition of the second stimulus suppresses the effective response of the cell to the first stimulus. In contrast, the discharge of the neuron is not affected if the competing stimulus is presented outside its receptive field, showing that the suppression is driven by mutual interactions within the region of space in which the cell is interested. This effect has been shown in several different places in the brain, suggesting that it is not an isolated phenomenon but a general one. However, when attention is directed to the attribute that the neuron represents, this suppressive influence from other stimuli is eliminated and the cell gives its maximal response even in the presence of competing stimuli. That is, attention biases the competition between stimuli and favors that the relevant attribute (either a kind of stimuli, a specific spatial location or an attribute such as motion) gains representational resources and dominates the neural response. These attentional modulations have been shown for monkeys and humans in many locations of the brain, including both the dorsal (occipito-parietal) pathway representing spatial locations and the ventral (occipito-temporal) route affecting representations of objects (see Kastner, 2004).

So far we have described the mechanisms operating at the *sites* of attentional modulation; those mechanisms by which attention affects processing by biasing competitions throughout the brain. At the same time, there have been models devised to explain how the putative attention regions, the so-called *sources* of attention, operate to be able to bias processing in other brain systems. The theory of Cohen and collaborators (Cohen, Dunbar and McClelland, 1990; Cohen, Aston-Jones and Gilzenrat, 2004) on cognitive control (i.e. executive attention) is a good example of such a model. The *guided activation theory of cognitive control* proposes that this control is achieved by means of the activation of the neurons in prefrontal cortex (PFC) representing the appropriate goal for the situation. These goal representations, or task-demand units, generate a bias that guides the flow of activity in the system along the pathway of its associated units and attenuates processing in another paths not relevant to perform the goal. The theory of Cohen and collaborators specifies the functional requirements that such goal representations must fulfill to be effective and how these are achieved in the brain.

First, the goal representations have to be actively maintained in PFC in absence of environmental support while the relevant action is performed, avoiding distraction by resisting perturbation from stimuli irrelevant for the task. This function is achieved by means of self-excitatory recurrent connections that give rise to attractor dynamics. These connections allow the appropriate goals to be activated and to bias processing in the relevant systems until the intended action is finished. Secondly, however, the task-demand units must also be able to avoid perseveration. That is, the representations have to be adaptatively updated once the outcome has been achieved and the action is no longer appropriate. This relies on an adaptative gating mechanism mediated by DA from the ventral tegmental area, also involving structures in the basal ganglia. Here, a transient gating signal renders the task-units temporally sensitive to inputs from other neurons that activate the representation of new goals. Due to reinforcement learning, the system knows when to produce a gating signal, by using the DA release as a learning cue that reinforces those associations that predict a better reward. Finally, the system needs a means to know in which situations control is needed and how much of it is required. The theory proposes that the ACC is the structure responsible for detecting the degree of conflict between different goals. The higher the conflict, the more control is needed and PFC representations must be activated more strongly. Hence, whereas the ACC is responsible of conflict detection, the PFC and basal ganglia are the centers responsible of allocating control resources to the brain pathways able to realize the desired outcomes.

The notion that the paragraphs above try to convey is that asking how the brain works by means of different technologies is useful for understanding and theorizing about the mechanisms by which cognitive processes operate. The ideas presented are informed mainly from neurophysiological recordings in monkeys, neuroimaging techniques in humans and biologically-driven computational models, all of them aided by tasks devised during many years of behavioral research in cognitive psychology. This convergent brain imaging effort has brought work on the mechanisms to the fore of attention research, a move that would have been much more difficult with behavioral methods alone.

## 3. MIND THE BRAIN

Some decades ago, the main goal of Cognitive Science was to determine the computations of intelligent systems. Thanks to the acknowledgement of a specific level of analysis for cognition, research in this area considerably advanced our knowledge on how humans represent and process information. The independence assumption stemming from the Functionalist doctrine was adopted in Cognitive Science and thus the role for biological data was left as a posteriori description of already described mental phenomena. More than fifty years later, technological developments allow us to translate questions on cognition to the human brain. Cognitive Neuroscience is turning out to be a main source of knowledge regarding the neural mechanisms of cognitive processing. It offers multidimensional data sets from each task, which helps to study cognitive processes in the brain as a whole. Moreover, it is useful in the resolution of long standing questions in Cognitive Psychology and in the generation of new hints on the parallels between different sides of cognition. At the same time, results in this discipline are a tool for the validation of general assumptions in Cognitive Psychology about how to explain human cognition, as well as a means to find out the adequate level of analysis for theorizing about the mind. The fast development of Cognitive Neuroscience is offering an explanation of human cognitive functioning where Marr′s levels of analysis, or function and realizer, are no longer autonomous. Thinking of the human mental operations and their functions as completely independent of their material substrate does not take profit from the technological and conceptual developments in the last years. Indeed, in a not-so-distant future, theories explaining human cognition may use concepts in which mind and body are no longer understood as independent phenomena.

We have described how neuroscience data has been a crucial source of information for developing a taxonomy separating attention in three independent networks; how biological knowledge has boosted research on the mechanisms operating at the sites of attentional influence, and also at brain sources of attention. We are aware that the models and ideas presented here are far from being definitive. Understanding what attention means, how to properly dissect it and which set of brain structures and mechanisms are responsible for the myriad of attentional effects described in the literature will be a long-term pursuit. However, advances obtained so far in the cognitive neuroscience of attention suggest that it is actually possible to devise a taxonomy of a high-level system that is supported from many different sources of investigation, in spite of limitations in current technology and the non-linearity of brain dynamics. Moreover, in doing so they show that taking into account brain functioning is essential. Even when different levels of analyses may be independent, they need to inform each other. Time will tell whether this integration of knowledge will eventually take us to a complete and coherent understanding of human cognition in the brain. Hopefully the discussion presented in this introduction can be taken as an indication that we are on the right path.

# JUSTIFICATION AND GOALS:

## SUBLIMINAL PERCEPTION IN THE BRAIN

We humans experience a vast array of information coming from the environment and decide about the contents of such experiences by attending to what is of interest to us. We feel in control of our behavior as conscious rational agents. But is this feeling caused by a real conscious agency or is it just an illusion? Do our attention and conscious contents drive our behavior or there are other mental processes that help to explain our actions? Put other way, does our brain represent and analyze information that does not receive attention and/or is unconscious? Obtaining scientific evidence that bears on these questions will significantly advance our knowledge of how the brain is built to give rise to the human mind. In the long run, this knowledge will also be important for the layperson to gain a better understanding of the nature of the mechanisms that guide our lives.

Conclusions derived from research conducted for more than a century have claimed the existence of high-level processing of information outside consciousness and attention. In both cases however there have been theorists who contend that results are not due to pure subliminal perception but to the effects of residual consciousness or to some level of attention being applied to the information. The main goal of the present chapter is to draw a parallel between research on unconscious and inattentive information processing, and to suggest that both are true phenomena. For this, we first analyze the various theoretical positions on the relation between consciousness and attention. Next we describe the behavioral and neuroimaging methods that can be employed to differentiate between conscious vs. unconscious and attentive vs. inattentive processing. Finally, we outline the research projects that compose the present dissertation. The three of them combine rigorous behavioral paradigms of unconsciousness or inattention with neuroimaging measures, to conclude that pure unconscious and inattentive processing can influence brain activity in specific ways separable from their conscious and attentive counterparts.

## 1. ATTENTION AND CONSCIOUSNESS

The relationship between attention and consciousness has been extensively debated, and theorist can be divided between two basic camps: those who claim that both are intimately related (James, 1890; Baars, 1988;

Posner, 1994; Dehaene and Changeux, 2004) and those who accentuate those grounds in which they can be separated (Wolfe, 1999; Lamme, 2003; Block, 2005).

In a popular sense, we are conscious of the contents we can talk about, and attending to something brings this content into a conscious state. The human cognitive system can be understood as composed by two different kinds of processors. On the one hand we have a set of encapsulated modules that deal with specific kinds of information in an efficient way, and on the other hand there is a general broadcast system, which is used as a means to share the information among all the specialized processors (Fodor, 1983). Baars (1988, 2002) was one of the first authors to use this conception to theorize about consciousness. According to him, consciousness is linked to the activity of a Global Workspace (GW) that allows the information to be integrated, combined in novel ways and broadcasted to the rest of modular processing systems in the brain. The GW is closely related to Working Memory (WM) processes, and information represented in this GW is used to coordinate and exchange information between modules. Within this framework, selective attention is the mechanism that enables representations the access to a conscious state (see also Posner, 1994); that is, focusing attention on a given content boosts it to conscious state. This conscious information corresponds to high levels of representation and is used in the voluntary control of behavior. On the other hand, there is extensive unconscious processing taking place in the brain but it is limited to modular regions.

Stanislas Dehaene (Dehaene and Naccache, 2001; Dehaene and Changeux, 2004) extended this framework and proposed a biologically inspired computational model that detailed how such a system could work. Initially (Dehaene and Naccache, 2001) the GW was related to the activity of long-range corticocortical connections between distant brain areas, and implicated the lateral prefrontal cortex and anterior cingulate as crucial nodes in the system. In the last years there has been a great deal of evidence that relates the coordinated activity in dorsolateral prefrontal cortex and bilateral parietal areas with the brain *mechanisms* that allow the generation of a conscious state (see Rees, Kreiman and Koch, 2002). Whereas the integrity of extrastriate regions processing relevant attributes seems to be *necessary* for a *content* to become conscious, this is not *sufficient* as activity in the fronto-parietal network is crucial as well (e.g. Driver and Vuilleumier, 2001; Kanwisher, 2001). Moreover, neuroimaging results show that regions related to the mechanisms of consciousness overlap to a great extent with those brain areas previously linked to the source of attention control and working memory processes (Corbetta and Shulman, 2002; Rees, Kreiman and Koch, 2002; Naghavi and Nyberg, 2005). Therefore, from this perspective, the relationship between attention and consciousness seems straightforward: attention is the mechanism used to bring a stimulus into conscious awareness by selecting among potential conscious contents.

The conception of consciousness as our reportable phenomenological experience, tightly linked to attention, is close to the definition of *access consciousness* provided by Ned Block (1990, 2005), which is the content information that is broadcast in the GW and thus is globally available. However, this and other authors (Wolfe, 1999; Lamme, 2003) argue for the existence of a conceptually separate type of consciousness named *phenomenal consciousness* (Block, 1990). This kind of consciousness refers to the subjective or qualitative flavor of different mental states, such as the red or orange qualia. Phenomenal consciousness proceeds without the participation of attention. Its characteristics would be close to iconic memory processes (Lamme, 2003), in the sense that the duration of its contents is extremely short and are quickly erased from the system and forgotten, and thus are hardly reportable (i.e. they are subject to inattentional amnesia, see Wolfe, 1999). The contents represented in this preattentive state or phenomenal consciousness are not yet identified and may not be fully analyzed by the system. They compete among them to be selected by the GW in a winner-takes-all manner, to dominate the pattern of activation and to accede to a reportable status. Recently, this phenomenal experience has been related to the activation of extrastriate areas coding for specific attributes of vision (such as motion, faces or other objects; Block, 2005), whose integrity we know is necessary for conscious awareness of the relevant stimuli (Kanwisher, 2001; Rees, Kreiman and Koch, 2002). Phenomenal consciousness is thus a prerequisite for access consciousness. In principle, the existence of any discriminative behavior above chance between two stimulus states is taken as evidence for phenomenal experience, even when the person confidently denies that he/she perceives anything (Holender, 1986). In this way, we should accept that neglect or blindsight patients are indeed conscious of the stimulation that they are denying to see because we can obtain experimental evidence that their brain is in someway processing the stimuli. Therefore, from this point of view consciousness is not to be equated with the reportable contents of experience because we are conscious of things that we are not able to report due to lack of attention.

Hence, the relationship proposed between attention and consciousness depends on the theoretical framework preferred. For those authors equating consciousness to access to the GW, these two phenomena are tightly related as attention is the means used to boost content into a conscious state. Alternatively, those who differentiate between access and phenomenal awareness understand that consciousness and attention are independent of each other. In the next section, we turn to explore the possible parallels between research on unconscious and inattentive information processing. This analysis show that both fields are related at the practical research level as they both have the problem of measuring whether or not a certain content is conscious versus unconscious or has or has not been attended to.

## 2. Is subliminal perception possible?

More than a century ago, Freud (1900/1961) claimed the existence of a whole realm of processes that guide our behavior outside our conscious experience. Unconscious perception has been a subject of study since the beginning of experimental psychology (see Greenwald, 1992; Merikle, Smilek and Eastwood, 2001, for reviews), and the history of this line of research has been closely linked to the methods employed to assay the conscious or unconscious quality of stimuli. The *dissociation* paradigm is among the procedures that have been more extensively employed. Here two different measures are obtained, the *direct* index is supposed to tap conscious processing in an exhaustive and exclusive manner whereas the *indirect* index must capture the results of unconscious information processes. Initially the direct measure were subjective reports (e.g. Sidis, 1898), as the participant was supposed to know whether he had consciously perceived a certain stimuli or not. However, as subjective reports were susceptible to contamination from response biases and expectations, Eriksen (1960) proposed the use of an Objective Threshold (OT) for consciousness. This threshold was defined as the maximum presentation time in which the forced-choice discrimination detection behavior of participants was at chance. Using this OT, for example Marcel (1983) showed that unconscious words activated their semantic representation in memory to facilitate processing of other words related in meaning (see also Allport, 1977; Fowler, Wolford, Slade y Tassinary, 1981; Balota, 1983). Some years later, however, the dissociation paradigm was criticized because of its methodological characteristics (see Holender, 1986) and research logic (Cheesman and Merikle, 1984). In the first place, Holender (1986) argued against claims of unconscious perception on the grounds that such research could not rule out the possibility of some sort of residual consciousness of the stimulation. In opposition, Cheesman and Merikle (1984; see also Reingold and Merikle, 1988) claimed that the dissociation paradigm was not appropriate to test unconscious perception because it was impossible to find a pure measure of conscious processing, that is, a direct index that reflected all aspects of consciousness in an exhaustive and exclusive manner. Instead, they proposed to use a Subjective Threshold (ST) of consciousness, defined as the maximal stimulus presentation conditions at which participants claimed not being aware of the stimuli.

As a reaction to these critiques, some authors tried to improve the dissociation paradigm (e.g. Greenwald, Draine and Abrams, 1996; although see criticisms by Dosher, 1998) whereas others proposed alternatives such as the *qualitative differences* approach (e.g. Reingold and Merikle, 1988). This paradigm no longer tries to obtain direct indices of conscious processing, but aims at showing qualitative differences on behavior from the effects of conscious and unconscious processing. For example, they showed how a variant of the Stroop task with only two color alternatives and a high proportion of incongruent trials generated benefits on RT for congruent trials when primes were briefly presented and thus unconscious to participants and the opposite costs for consciously perceived congruent trials (see also Debner and Jacoby, 1994). Hence, with this methodology a direct measure of conscious perception is not calculated but it is shown that conscious and unconscious perception has opposite effects on behavior. However, some authors (Holender, 1986; Holender and Duscherer, 2004; Snodgrass, 2002) argue that it is difficult to interpret a qualitative difference as the existence of unconscious influences when they could be due to the mere addition of another conscious process (see also Visser and Merikle, 1999).

After many years of research, the existence of pure unconscious effects is still a matter of debate (i.e. Hannula, Simons and Cohen, 2005). Although it is accepted that information presented bellow the subjective threshold for consciousness has the capability to affect our behavior (Merikle, Smilek and Eastwood, 2001), many authors contend that rather than reflecting unconscious influences these effects are coming from weak conscious percepts rapidly forgotten (Holender, 1986; Snodgrass, 2002). When objective thresholds are used instead, complaints focus on the difficulties associated with unequivocally demonstrating a null effect on a direct variable (Holender, 1986; Reingold and Merikle, 1988). It seems then that for theorists that support a single-conscious perception model (e.g. Holender and Duscherer, 2004) there may never be a demonstration of a pure unconscious effect.

Something similar happens in the field of inattentive information processing. Manipulating attention allocation is one of the means used to supposedly prevent consciousness of stimuli (Merikle and Joordens, 1997; Merikle, Smilek and Eastwood, 2001). In this line, some authors have shown how the degree of masking is modified by attention (e.g. Ramachandran and Cobb, 1995; Shelley-Tramblay and Mack, 1999; DiLollo, Enns and Rensik, 2000). Others relate the attentional blink to a momentary lack of attention (Raymond, Shapiro and Arnell, 1992). Also, Mack and Rock (1988) devised an influential research paradigm in which they showed inattentional blindness to stimuli presented outside the focus of attention when participants were engaged in a demanding task elsewhere. In all these cases it has been shown that information that participants reported not being conscious of, supposedly because they were not attending to it, affected behavior in several ways. Again, some authors claimed that stimuli in these situations are actually consciously perceived but soon forgotten (Wolfe, 1999).

Regardless of whether information presented in these situations is consciously perceived or not, it has proven very hard to find a demonstration that these stimuli had actually not been attended to[2]. For some authors, the existence of preattentive vision is an illusion (e.g. DiLollo, Kawahara, Zuvic and Visser, 2000) and any measurable effect of a stimulus on behavior is considered as evidence that it has captured attention (see Ruz and Lupiañez, 2002, for a review) rather than the demonstration that unattended information has the capacity of affecting performance. Consider the Stroop effect as a prototypical example. In this situation, the irrelevant meaning of a color word interferes with the task of naming the ink of the stimuli in those incongruent trials in which word and ink refer to different colors. For theorists who believe in the existence of automatic or inattentive information processing (e.g. Posner, 1978), these data show how highly automatic stimuli, such as words, are able to influence behavior even when they are not attended to. Instead, for those who argue that all processes demand at least some degree of attention (e.g. Kahneman and Treisman, 1984; Cohen, 2004), the Stroop effect is an example of how a highly practiced task such as word encoding captures attention and thus competes for the response with the less practiced task of naming the ink of a stimulus. Hence, authors coming from different theoretical backgrounds use the same set of data to support either the existence of automatic processing or the capacity of some stimuli to capture attention and thus affect behavior. Such a situation reveals a fundamental ambiguity that sometimes arises when trying to use only behavioral data to resolve debates over the functional organization of cognitive processes.

There have also been demonstrations of qualitative differences on the effects of attended and ignored information. For example, in a negative priming paradigm, attended stimuli (i.e. those that are responded to) generate facilitation in consecutive trials, whereas ignored ones (i.e. those

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[2] Note that the dissociation paradigm is not well suited to be used in research on inattentive processing. Obviously, obtaining a direct index to show that information has not been attended is impossible given that a stimulus must be attended to in order to be able to respond to any aspect related to it.

that are not responded to) generate a slowing in response (that is, a negative priming effect). Positive and negative semantic priming effects have also been shown for attended stimuli presented at fixation and ignored ones appearing in the periphery of the visual field (e.g. Fuentes and Ortells, 1993; Fuentes, Carmona, Agis and Catena, 1994; see also Merikle and Joordens, 1997, for additional evidence of qualitative differences that depend on attention). Again, the inhibitory effects supposedly due to ignoring certain stimuli could be caused by an additional attentional process that inhibits the stimuli that generate the interference because even when it is not relevant for responding, it is capturing attention resources (e.g. Lavie and Fox, 2000; Tipper, 2001). Note, just as in the literature on unconscious processing, the crucial issue in demonstrating automatic information processing then comes to being able to measure attention allocation and to show that ignored information is not actually being attended to.

In summary, providing conclusive evidence that subliminal perception effects are linked to nonconscious processes has proven to be a tough battle. From the previous analyses, it seems that one of the means to accomplish this would be to combine rigorous quantifiable measures of consciousness and attentive processing with convincing evidence of unconscious and inattentive effects. This has been the goal of the investigation program that shapes the present dissertation. In the next section we describe three experiments that have combined strict unconscious and inattentive processing situations with a powerful means to demonstrate information processing and process-dissociations: neuroimaging tools.

## 3. NEUROIMAGING DATA: DISSOCIATING CONTRIBUTIONS TO UNCONSCIOUS AND INATTENTIVE INFORMATION PROCESSING

The possibility of employing non-invasive techniques to obtain indices of brain activity while adults perform carefully designed cognitive tasks has opened a wide spectrum of possibilities to advance in the psychological study of the human mind and brain. In the field of subliminal perception, this improvement is due to several reasons. First, neuroimaging allows to measure brain activations in response to unconscious or unattended information without the need of imposing a behavioral response that could contaminate results by driving the attention of participants to information they should not care about. Also, the patterns of brain activations in conscious or attentive and unconscious or inattentive situations should be very informative about the existence of either single or multiple processes at the basis of these effects. Usually the overlap in effects between two conditions (whether effects are localized in the same ERP component or in the same brain area as measured by fMRI) is taken to suggest that the same set of processes is responsible for both phenomena. Conversely when two experimental conditions correlate with non-overlapping or partially separable brain markers, the conclusion derived is that the cognitive processes at the basis of such effects are not the same. Note however that this second conclusion has more validity than the first. Two partially distinct processes could correlate with the same ERPs or BOLD activations and still constitute different computations coming from separable kinds or sets of neurons localized so close to each other that the resolution of current techniques would not be able to resolve the difference (e.g. Ffytche, 2002).

Since the advent of neuroimaging techniques, several investigations have been aimed at uncovering the cerebral basis of unconscious perception (see Hannula, Simons and Cohen, 2005, for a review) and some studied the neural fate of ignored stimuli (Rees and Lavie, 2001; Yi, Woodman, Widders, Marois, and Chun, 2004). Results in the last years seem to support the claim that unconscious perception is based on the low-level activity of extrastriate regions dealing with different stimulus attributes (Rees, Kreiman and Koch, 2002; Hannula, Simons and Cohen, 2005), although most of these studies have been criticized for not obtaining careful enough objective measures of awareness (Hannula, Simons and Cohen, 2005). In this way, the observed extrastriate effects could actually correspond to activations related to phenomenal awareness, as argued by some authors (Block, 2005).

Most neuroimaging studies looking at the fate of ignored stimuli support the idea that attention is needed for a stimulus to be analyzed. The majority of these experiments have been inspired by the Perceptual Load framework by Nilli Lavie (Lavie and Tsal, 1994; see Lavie, 2005, for a review). Her theory proposes that when the perceptual/attentional load of a task is low, spare resources spill over to allow irrelevant stimuli to be analyzed and thus to affect responses. However, when the experimental setting is very difficult all resources are invested in the task, so ignored information is not processed and thus it does not affect responses. Although at the beginning the theory was supported exclusively by behavioral evidence suggesting that distracters no longer interfere with behavior in high load situations (Lavie, 1995), more recently neuroimaging data have shown how attentional high load also obliterates distracter representations in their relevant brain areas (e.g. MT/V5, Rees, Frith and Lavie, 1997; LGN, O'Connor, Fukui, Pinsk, and Kastner, 2002; V4 and TEO, Pinsk, Doninger and Kastner, 2004; V1, Schwartz et al., 2004; PPA, Yi et al., 2004). Hence, there seems to be strong evidence to support the notion that when attention is fully withdrawn from a stimulus, the brain areas normally activating in its presence no longer respond to it.

In the next section we will present the three studies composing the present dissertation. They all employed neuroimaging techniques together with carefully designed experimental manipulations. The first one shows that it is possible to obtain unconscious priming even at objective detection threshold levels and that the electrophysiological correlates of this effect are qualitatively different from those of conscious priming. This supports the notion that pure subliminal information actually affects brain responses and that conscious and unconscious computations are separable to some extent. The second and third studies use HDERP and fMRI data respectively to show that highly practiced stimuli such as words are processed by the brain even in a high attentional load situation. Results suggest that not all computations in the brain are dependent on attention resources and provide clear evidence, in the form of observable brain activity, for inattentive or automatic information processes active during perception.

# DISCUSSION

## 1. UNCONSCIOUS PRIMING

To explore the existence of purely unconscious semantic priming, we combined a careful measurement of consciousness at the strictest level possible (Holender, 1986), the objective detection threshold (OT), with a semantic priming paradigm similar to the one used by Marcel (1983). Also, in an effort to show that the unconscious priming found was not due to residual consciousness of the prime we used a HDERP recording system to study the cerebral basis of priming effects and their separability (Ruz, Madrid, Lupiáñez and Tudela, 2003; see Appendix I).

This experiment was composed of two phases. In the first, we measured the ST and OT of consciousness for each participant by means of a descending staircase methodology. The ST corresponded with the stimulus quality at which each participant reported not being conscious of whether a word had been presented or not. The OT was established, on the other hand, when the absence-presence word detection performance of each participant was at chance levels. To allow for stabilization of d prime measurements, we recorded 120 trials at each of the three detection levels employed: conscious (CO), ST and OT. In the second phase of the experiment, the semantic priming generated by primes presented at CO, ST and OT levels was measured concurrently with its HDERP signatures. Care was taken that the stimulus presentation conditions were the same in both threshold setting and priming phases. We also measured the OT again for each participant after the finalization of the priming experiment to make sure that thresholds did not change with practice.

Behavioral results showed that conscious primes benefited their semantic associates by speeding their responses in 52 ms on average. There was also a significant priming effect for words presented at the OT, although of smaller magnitude (19 ms). This semantic facilitation was not present at the ST. The electrophysiological indices showed the non-overlapping nature of these conscious and unconscious effects. When words were consciously perceived, priming was indexed by a centroparietal N400 effect and a later LPC. However, none of these effects were present when primes appeared at the OT. Instead, the unconscious priming at OT was indexed by a modulation of the posterior N2 and also of activity measured in electrodes at left frontal areas.

This study demonstrates a pure unconscious perception effect at the strict OT. Note that both the behavioral and electrophysiological results are inconsistent with an explanation in terms of residual consciousness of the prime. In the first place, if this residual consciousness of the prime was the cause of the priming effects, we should expect that the better the perceptual quality of the prime (i.e. the longer prime-target SOA[3]), the larger the size of the facilitation effect. However, primes presented at the ST had a better perceptual quality than those at the OT (36 vs. 1 ms in average of prime-mask SOA in ST and OT situations, respectively). Still, whereas there was no priming at the ST this effect was significant at the OT (see Snodgrass, Bernard and Shevrin, 2004a, 2004b, for a detailed argumentation in the same line and review of supporting evidence). It could still be argued that the lack of priming at the ST does not necessarily rule out the possibility that residual conscious perception was generating the effects at the OT, as some other factor might prevent priming in the ST condition. Thus one might turn to d prime analyses for additional evidence. The residual consciousness hypothesis would lead to the expectation that d prime correlates with priming size, as the better the discriminative capacities the higher the residual consciousness and hence the size of the effect. Again, though, the correlation between individual d prime at the OT and the priming effect was non-significant and nominally had a negative value (-0.2), thereby failing to support the residual consciousness account and suggesting instead that subthreshold priming effects were actually caused by unconscious processes.

We find converging evidence from the electrophysiological results in support of an unconscious processing interpretation. If effects at the OT were due to residual activity of processes at work when information is consciously perceived, we should have obtained unconscious modulations in at least a subset of the components that are sensitive to conscious semantic facilitation. However, neither the N400 nor the LPC effects were significant at the OT.

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[3] Stimulus Onset Asynchrony.

Conversely, none of the effects found to correlate with unconscious semantic priming, such as the N2 and left frontal modulations, were found significant when primes were consciously perceived. Thus we have a double dissociation between the cerebral markers of conscious and unconscious priming, indicating that the processes at the basis of these effects are rather different. So, the combination of behavioral and neuroimaging evidence supports first that pure unconscious information analysis is the likely source of our subliminal facilitatory effects and also that conscious and unconscious priming are generated by qualitatively separable brain mechanisms.

## 2. UNATTENDED INFORMATION PROCESSING IN HIGH ATTENTIONAL LOAD TASKS

High attentional load tasks are very strict paradigms to test the processing of unattended information. Several behavioral and neuroimaging experiments (see Lavie, 2005) seem to support the notion that when attention is fully occupied by a highly demanding task, irrelevant information is no longer processed. These experiments aside, words seem to be a good candidate for stimuli that do not need attention to be analyzed, at least to a certain extent, given our extended practice with this kind of items (e.g. Posner, 1978; Dehaene et al., 2001). There is also a longstanding tradition of research on the automaticity of word processing (e.g. Carr, 1992). Therefore, we studied the fate of ignored words presented in a high attentional load task by means of two neuroimaging methods. The experiments measuring HDERPs are described in the Appendix II (Ruz, Worden, Tudela, and McCandliss, 2005) and the experiments measuring fMRI responses are described in the Appendix III (Ruz, Wolmetz, Tudela and McCandliss, *under review*).

We used a high attentional load inattentional blindness task (Mack and Rock, 1998) originally devised by Rees, Russell, Frith and Driver (1999). The display presents a rapid series of stimuli (lasting 250 ms each with a stimulus-onset asynchrony of 500 msec) consisting of overlapping drawings and letter strings (words or nonwords). In different blocks, task instructions direct attention to either the drawings or the letters to detect the immediate repetition of items in the attended dimension. As stated by Lavie (Lavie, 2005; see also Rees et al., 1999; Rees and Lavie, 2001), this paradigm fulfills the requirements of a high perceptual load task. The difficulty of the repetition detection task that is implemented in the design forces the full focusing of attention in the attended dimension (Rees et al., 1999), and this difficulty is reflected in the accuracy rates (around 70%) that are above chance yet significantly below ceiling. In addition, the pattern of behavioral interference and brain activity markers obtained also accord with previous results using high attentional load tasks, as it is described bellow. Our results, however, provide a critical point of departure from previous research as they show unattended information is indeed processed in this high attentional load situation.

In two different research projects, we used HDERP and fMRI to record brain activity while participants were engaged in the inattentional blindness high attentional load task described above. In both studies, the contrasts of interest were brain activation differences between words and nonwords in the two conditions of attention and inattention to letters. These are markers of word processing when attention is directed to the letter domain and also when attention is fully withdrawn from it by its engagement in the overlapping drawings. Crucially, although participants were not required to respond to the lexicallity of letters on any grounds, we were able to use repetition detection responses as behavioral indicators of word-nonword differential processing. Finally, at the end of each experiment a surprise explicit memory test was used to explore the effects of attention on memory consolidation for attended and ignored words.

Behavioral results were similar in the two experiments. When the strings of letters were the targets of the repetition detection task, d prime indices were better for words than nonwords and there was also a difference in RT between both kinds of items. In contrast, when drawings were attended to and thus words and nonwords were subject to a complete attention withdrawal, none of the behavioral indices differentiated between these two classes of stimuli. Note that in a long series of behavioral reports, this very lack of interference from the unattended dimension has been taken as evidence that irrelevant stimuli were not being analyzed due to lack of attention resources (Lavie and Tsal, 1994; Rees and Lavie, 2001; Lavie, 2005). Results from the surprise memory test seemed to point in the same direction, given that in both studies whereas memory for attended words was very good (around 80% of hits), participants were not able to differentiate ignored words from foils. Thus all the behavioral results suggest that ignored words were not processed. The HDERP and fMRI markers of brain activity, however, uncover a challenge for this account, by demonstrating that unattended stimuli in this high attentional load task are indeed processed but they do not affect behavioral indices of performance.

In two different experiments, the HDERP differentiated between attended words and attended nonwords in left frontal, left posterior and medial scalp locations, and modified the N400 component. These results are in accord with previous reports about the ERP markers of word encoding. Crucially, the brain measures also differentiated between ignored words and ignored nonwords, as indexed in left posterior, medial and frontal scalp locations. These differences were of smaller magnitude and appeared later in time than attended ones, and they took place in both overlapping and separate ERP components.

Results of the fMRI experiment are consistent with the previous electrophysiological report, and provide additional information regarding the brain areas that support word processing in absence of attention. Overall, behavioral results were similar across the fMRI and HDERP experiment. Regarding brain responses, attended words activated left frontal, left temporal and parietal areas, again in agreement with previous fMRI literature on the brain regions responsible for word encoding and replicating results using the same paradigm (Rees et al., 1999). On the other hand, the word vs. nonword contrast when drawings were attended and thus letters were ignored indicated the involvement of several regions including left insula, right cerebellum and bilateral pulvinar. Interestingly, there was no common neural region activated for both attended and ignored items, which suggests a change in processing pathways when attended and ignored words are presented in a high attentional load task.

Our HDERP and fMRI results indicate that highly practiced items such as words are indeed processed even in high load situations that completely withdraw attention from them. In parallel to the unconscious processing study presented in the previous section, the present results are difficult to reconcile with an interpretation in terms of residual attention to ignored items. If words were capturing some amount of attention when participants were responding to drawings, we should expect at least moderate levels of interference from this word dimension, as this is the usual result obtained in paradigms that superimpose a relevant and an irrelevant stimulus (e.g. Stroop tasks). No such interference was found in any of the behavioral indices when participants responded to drawings, as responses in this condition were not affected by the lexical quality of the ignored strings of letters. It could be argued though that the task used is not sensitive enough to capture this interference. However, such a view would be at odds with neuroimaging results. If words were somehow capturing attention when participants responded to drawings, we should find activations in at least some of the same brain regions that are activated when attention is directed to letters. In direct contradiction prediction, removing attention from letters completely obliterated responses in brain regions usually activated by this kind of items, a common result found in high attentional load situations like the present one (see Lavie, 2005). The current study suggests an additional finding that bears on the issue of word encoding under inattention. Our results demonstrate that a different set of regions responded to the word-nonword contrast in attentive and inattentive conditions, which supports the idea that processing occurring in this inattentive situation is not mediated by attention to the letters but it is due to mechanisms that do not rely on the availability of attention resources.

# CONCLUSIONS

The quest for proof of processing without consciousness and/or without attention started more than a century ago and has still received no definitive answers. One of the main pitfalls to this enterprise is the complex issue of how to measure in a precise manner the absence of conscious appreciation of a stimulus or the lack attention to it. The research presented here has specifically chosen careful experimental paradigms that address this issue combined with the powerful advantages brought by neuroimaging technology to be able to conclude that pure subliminal perception (unconscious and inattentive) is possible.

In all experiments presented, unconscious and inattentive processing have been related to qualitatively different neural substrates than conscious and attentive ones. Most likely this is due to the extreme conditions employed in the experimental paradigms used to test these effects. Presenting words at the objective detection threshold or in a high attentional load task was chosen because both represent situations designed for strict subliminal processing, which would give us the highest confidence that results represent true examples of unconscious and inattentive information processing. However, the fact that in these extreme cases conscious and unconscious or attentive and inattentive processing recruit different brain systems does not necessarily mean that this is also true in more common settings. There is a quite a bit of evidence suggesting that conscious and unconscious information processing overlap in several brain regions (Rees, Kreiman and Koch, 2002) and that attending to a stimulus heightens the neural responsivity of a brain region that can also respond to that stimulation when attention is not explicitly directed to it (e.g. Posner and Petersen, 1990; Kastner, 2004). Therefore, in normal situations conscious, attentive, unconscious and inattentive processing may activate both overlapping and separable brain regions that together collaborate to shape our behavior in an adaptive manner.

Our results lay in the extremities of unconscious and inattentive processing. However, there seems to be a theoretical disagreement on whether processing taking place at more intermediate levels (such as information presented at the subjective level of consciousness or the irrelevant dimension in the Stroop task) represent examples of unconscious or inattentive processing (e.g. Dehaene and Changeaux, 2004) or are actually due to residual consciousness or to some level of attentional capture (Snodgrass, 2002; Cohen, Aston-Jones and Fitzenrat, 2004). Resolving between these two alternatives may need many more years of research and theoretical debate in which neuroimaging promises to be one of the main sources of relevant information. In contrast, the research described in the present dissertation project has avoided these intermediate situations and instead has used rigorous situations of unconscious and inattentive information processing to show that even in these extreme settings subliminal perception is possible.

The addition of brain recording techniques to classical behavioral measurements in the experiments presented has been a key point to explore whether unconscious and unattended information processing had taken place. In the inattention paradigm, brain markers were the only indication that unattended information had been analyzed, given that behavioral indices obtained were no sensitive to this. Importantly, in all cases neuroimaging data indicate that the neural generators of the effects found are separable, which further suggests that they have different nature (conscious vs. unconscious and attentive vs. inattentive). Therefore, we hope that the research carried out for the present project represents an example of the utility of listening to the brain when thinking about the mind, in this specific case to support the notion that truly unconscious and inattentive information processing is a reality in the human brain.

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# APPENDICES I TO III

# APPENDIX I

Ruz, M., Madrid, E., Lupiáñez, J. and Tudela, P. (2003) High density ERP indices of conscious and unconscious semantic priming. *Cognitive Brain Research, 17*, 719–731.

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Research report

# High density ERP indices of conscious and unconscious semantic priming

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## Abstract

The existence of differential brain mechanisms of conscious and unconscious processing is a matter of debate nowadays. The present experiment explores whether conscious and unconscious semantic priming in a lexical decision task at a long prime-target stimulus onset asynchrony (SOA) correlate with overlapping or different event related potential (ERP) effects. Results show that the N400 effect, which appeared when words were consciously perceived, completely disappeared when primes were masked at a level where the ability of participants to detect the prime was near chance. Instead, a rather different set of ERP effects was found to index unconscious semantic priming. This suggests that the processes at the basis of conscious and unconscious semantic analyses can under some circumstances be rather different. Moreover, our results support the notion that conscious and unconscious processes are at least partially separable in the brain.

*Theme:* Neural basis of behaviour

*Topic:* Cognition

*Keywords:* Consciousness; Unconscious priming; N400

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## 1. Introduction

The extent to which unconscious stimuli are able to modulate our behavior has been a recurrent topic of research since the beginning of experimental psychology (i.e., Refs. [39,54]). Among the vast amount of studies exploring unconscious information processing there are those showing that semantic information can be accessed without conscious awareness of stimuli. For example, Marcel [51] proved in his now classic studies that undetectable masked words were able to semantically prime other words presented afterwards in a lexical decision task (LDT), thus showing that the meaning of stimuli can be accessed without conscious experience of these words (see also Refs. [3,33]).

One of the main concerns in the study of unconscious processing was how to make sure that reported effects were not actually due to residual consciousness of the stimulation [38]. Although in the early studies subjective reports were accepted as good estimators of awareness (e.g., Ref. [71]), it was soon noted that more rigorous measures of consciousness were needed in order to prove that participants had indeed been unconscious of the stimuli [32]. Therefore, the objective threshold of consciousness was defined as the maximum stimulus duration at which participants are at chance in discriminating between alternative stimulus states [32]. Although those alternative states can refer to several stimuli dimensions (such as its lexical or semantic status), the most conservative measure of consciousness tests the ability participants have in detecting whether or not a stimulus has been presented [38]. The subjective threshold, on the other hand, is the maximum stimulus duration at which participants report lack of awareness of the stimulation [13].

Nowadays, several studies using different paradigms have shown semantic priming effects with both subjective and objective thresholds of consciousness (e.g., Refs. [25,35,58]). Usually, the mechanism postulated at the basis of this unconscious processing is the automatic activation

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of word meaning, in contrast to those effects caused by conscious expectation [65] (see Ref. [59] for an overview of the processes at the basis of semantic priming effects). Some authors have argued, however, that instead of being caused by an automatic separate mechanism, unconscious semantic processing could be explained by residual effects of strategic conscious processing of the prime (e.g., Ref. [38]). One of the means to study this issue is to record brain activity during both conscious and unconscious semantic processing. If brain correlates of unconscious semantic priming are the same as those of conscious priming, it could be claimed that the same kind of mechanism is involved in both cases. On the other hand, the separate processes hypothesis would be supported if conscious and unconscious semantic analyses correlate with different brain markers [16].

For a long time, event related potentials (ERPs) have been a fruitful tool for studying the mechanisms of cognitive processing in several domains (see, for example, Refs. [49,68]). The high-temporal resolution they provide for measuring brain activity allows researchers to obtain a detailed index of the processing chain from stimulation to response that isolated response time (RT) data cannot offer. Language comprehension tasks are one of those suitable for study with this methodology, and one of the most studied ERP components in this field is the N400, which is a negative-going deflection that appears around 400 ms after stimulus onset.

The N400 is an ERP generated by any content word, and it is sensitive to the ease by which a stimulus is integrated with its preceding semantic context [49], possibly reflecting concept activation. It is not unique to the visual modality of stimuli presentation [37]. The distribution and magnitude of the effect may be dependent on the specific task subjects are performing and the recording reference employed [49]. Kutas and Hillyard [48] were the first authors to describe the N400. In their original reading experiments, sentences that ended with semantically anomalous words generated a more negative N400 component than those ending in a congruent manner. The N400 effect, i.e., the amplitude difference between these two conditions, soon was found in other language tasks. Bentin et al. [7] were the first to show this effect in a semantic priming paradigm. In a lexical decision task, word targets that were related to their primes generated a N400 of smaller amplitude than unrelated ones. Since then, the sensitivity of the N400 to conscious semantic relatedness has been replicated in several studies (see Ref. [49] for an overview). Regarding the cognitive processes the N400 reflects, a debate exists on whether it is sensitive either to both strategic and automatic factors in language processing [59] or only to the former.

On the one hand, the N400 modulation by attentional instructions, or controlled conscious processing, has been proven several times. One of the first researchers to show this was Holcomb [36]. In a lexical decision task, this author manipulated at the same time both the percentage of prime-target related pairs and the instructions to either attend or ignore the primes. A N400 effect was evident in both low and high proportion of related pairs, but its magnitude was larger under instructions to attend to the prime. Therefore, it seemed that the N400 was sensitive to automatic propagation of activation, although this effect was enhanced by attention. In a similar way, Kutas and Hillyard [47] showed that even in tasks in which it was not needed to process the meaning of words (i.e., where attention should be paid to the orthographic structure of stimuli) the N400 effect appeared (see also Ref. [5]).

However, those studies did not prove the sensitivity of the N400 to purely automatic processes, given that the tasks used did not prevent the conscious semantic analysis of stimuli. Indeed, the insensitivity of the N400 component to the automatic component of semantic processing was suggested in another series of studies. For example, Bentin et al. [6] presented two lists of related and unrelated words and pseudowords, one in each ear, in a dichotic listening task. Participants had to attend to and remember words presented in one ear while ignoring words in the other ear. A clear N400 effect appeared for stimuli presented in the attended channel, but this effect was missing in the unattended one. Two post-hoc tests (a comparison between false alarms to attended and unattended semantically related words and a repetition priming task) proved that the meaning of unattended stimuli had been processed. Hence, the N400 was insensitive to whatever mechanism was generating this non-controlled analysis of word meaning. In a similar line, Chwilla et al. [14] showed that when attention was not directed to the meaning of stimuli, the N400 was insensitive to semantic relatedness between words (see Refs. [42,55] for converging results). Thus, from these studies it seemed that the N400 amplitude is not modified by an automatic semantic analysis that is not contaminated by controlled strategies.

Masking has been another technique used to study the sensitivity of the N400 to the automatic mechanisms of semantic processing. With this masking procedure it has been proven several times that stimuli that are rendered unconscious by means of a mask are still able to prime responses to another words semantically related to them (e.g., Refs. [25,35,51]). Brown and Hagoort [9] reported that masked semantic priming did not modify the amplitude of the N400, while unmasked priming did. These authors set the threshold where recognition performance for masked words was near chance and then used this value to measure semantic priming for unconscious words. Although both conscious and unconscious words facilitated responses to semantically related stimuli, the N400 amplitude was only modified by primes consciously perceived. However, null results in this study could be questioned given that recognition threshold setting and behavioral semantic priming measures took place in a different group of participants than those from whom ERP were recorded. Thus, it is possible that between group threshold variability made subjects in the ERP group not to show semantic priming at all, which is reinforced by the fact that neither the N400 effect nor any other correlate of semantic analysis appeared. As no behavioral priming was measured in this ERP group, this is an open question.

Indeed, recent investigations have questioned this early masking result. Deacon et al. [21] measured the semantic priming effect in the N400 generated by words preceded by two more words, the second of which could be either masked or not and could be semantically related with the third word or not. ERP results revealed a N400 effect that had the same magnitude and topographical distribution in both conscious and unconscious semantic priming (see also Ref. [69]). Kiefer and Spitzer [44] results corroborated the sensitivity of the N400 to masked semantic priming. These authors showed that primes that could not be identified did modify the N400 amplitude at a short prime-target stimulus onset asynchrony (SOA; 67 ms). On the other hand, when targets followed masked primes after 200 ms of SOA, the N400 was not modulated by semantic relatedness, as in Deacon et al.'s [21] experiment (see also Ref. [43]).

However, neither of the previous reports investigated any other possible correlates of unconscious semantic priming in those conditions in which the N400 was not modulated by this effect. Although in Brown and Hagoort's [9] study there was no correlate of unconscious semantic priming, Kiefer and Spitzer [44] found a frontal ERP modulation in the long SOA condition when semantic priming did not modify the N400. Therefore, in those cases where the brain processes indexed by the N400 are not at the basis of unconscious semantic priming, other electrophysiological markers could signal the activity of the brain regions in charge of such unconscious semantic analysis. Pilot results in our laboratory [77] as well as brief reports in previous literature (e.g., Refs. [44,61,72]) led us to the hypothesis that unconscious semantic analysis could correlate with electrophysiological markers with a more left frontal topography and earlier time course than those of conscious semantic priming.

Therefore, the present study was aimed at studying the differential electrophysiological correlates of conscious and unconscious semantic priming. As previous results in the literature have shown that the prime-target SOA plays a crucial role in determining the N400 sensitivity to unconscious priming [44], we decided to adopt the long SOA interval Marcel [51] used in his study, given the similarity between this paradigm and ours. The finding of differential electrophysiological correlates of semantic priming would suggest that under certain circumstances conscious and unconscious semantic analyses are supported by *partially* distinct brain mechanisms, thus adding support to those theories proposing different mechanisms for conscious and unconscious semantic priming [59,65] in the brain.

With this goal we measured high density ERP (HDERP) correlates of masked and unmasked semantic priming after setting for each participant the subjective (ST) and objective thresholds (OT) of consciousness (see Refs. [13,38]). Moreover, the same stimulus display, materials and subjects were used in both threshold setting and priming phases, and the OT was measured again after the priming phase to ensure individual threshold did not change during the session. This all warranted that perceptual stimulation was the same in both phases and that our results at the OT were due to purely unconscious semantic analysis instead of residual conscious processing of the prime [38].

## 2. Materials and methods

### 2.1. Subjects

Forty-five students from introductory courses in psychology (33 female) gave consent for participating in the experiment in exchange for course credits. They all had Spanish as their first language and had normal or corrected to normal vision. All subjects participated in both phase 1 and phase 2 of the experiment.

### 2.2. Material

A total of 45 associatively related pairs of Spanish words[1], from four to seven letters, were used as stimuli. These words, extracted from a database [73], were used to construct nine different experimental lists. In order to do so, the 45 pairs were divided into three groups, which had similar length and familiarity [12]. From each group three variants were obtained, the first of it by maintaining the pairs semantically related, the second by intermixing words in pairs for them not to be semantically related and the last one by constructing a pseudoword from the second word in pairs not semantically related. Pseudowords were created by changing one vowel or consonant in each word following orthographic normative restrictions in Spanish. Nine sublists were obtained by mixing these three variants, taking five related pairs from one variant, five unrelated from the other and five pseudoword pairs from the variant left. For each participant, three different sublists were used to create the experimental word lists. All participants saw all words, which where counterbalanced across conditions between subjects. Thus, words were repeated eight times for each participant in the whole experiment. In practice

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[1] Mean word familiarity was 5.86. This index represents subjective familiarity as estimated by a Likert rating scale ranging from 1 (poorly familiar) to 7 (highly familiar). The associative strength was calculated by asking a group of participants to generate the first word that comes to mind after reading a prime word (see Ref. [12]). All target words used in this experiment were generated within the first three positions, the average generation position being 1.4.

trials, a different set of words was presented with similar length and familiarity as experimental stimuli. All participants viewed the same words in practice trials.

Each trial was composed of the following stimuli, all white colored in a gray background. A fixation point 5 mm high by 5 mm wide (0.5°), a prime word made up of four to seven uppercase letters each 8 mm high (0.8°) by 5 mm wide (0.5°) presented between brackets (8 mm high by 1 mm wide, 0.8°) or the same brackets without a prime inside but separated by the same distance as if they had a prime word inside. Four different compound masks were formed by 12 uppercase letters, each 8 mm high (0.8°) by 5 mm wide (0.5°). Finally, a target word with the same characteristics as the primes was presented.

All stimuli were presented on a 17 inch Apple Multiple Scan 1075 monitor, connected to a Power Macintosh 8100/100 AV computer running EGIS [63]. This computer was connected by a serial port to a second computer, same model, recording continuous EEG.

## 2.3. Design

The experiment comprised two phases. In the first, ST and OT of consciousness were individually estimated for each participant, by means of a descendent methodology (see Ref. [20]). This was done by shortening in a staircase manner the time from prime onset to mask onset. Once each threshold was established, 120 trials were run. Therefore, phase 1 comprised 360 trials [120 where the prime was conscious (CO), 120 presented at the ST and 120 at the OT] plus the trials needed to find those thresholds (variable among participants, with a range of 64–126 trials). Half of trials in phase 1 presented a prime between the brackets and in the other half the brackets were presented alone. In trials where the prime was presented, prime and target were related in meaning in one third of them, in another third they were unrelated and in the remaining trials the target was a pseudoword. Phase 2 followed the same structure as phase 1 except that primes were presented in all trials between the brackets. The proportion of related, unrelated and pseudoword pairs was kept the same as in phase 1. Again in a descendent manner, primes were presented consciously in the first block, and at ST and OT in the second and third block, respectively. Each threshold phase comprised 120 trials.

## 2.4. Procedure

### 2.4.1. Phase 1

Subjects carried out a detection task on prime words. After a 500 ms fixation point, a prime was presented into brackets for 13 ms on half of the trials and on the other half only the brackets appeared during the same temporal interval. The time from prime offset to mask onset (ISI or inter stimulus interval) varied depending on blocks. After 1486 ms from prime offset (1500 ms of prime-target SOA), a target word was presented and its offset, 500 ms afterwards, signaled participants they had to respond whether the prime was either present or not by pressing either the X or the M key (see Fig. 1). Each threshold block comprised 120 trials, being the prime present in half of them. In the first block (CO), prime-mask ISI was 483 ms. When this block was finished, the ISI was shortened in a staircase manner, in miniblocks of 18 trials, in order to reduce perceptual quality of the prime (following the sequence 250, 78, 52, 39, 26 and 13 ms). At the end of each miniblock, participants were questioned about the consciousness they had on the prime words. This was achieved by means of a Lickert type scale that varied from 1—prime fully unconscious, to 10—prime fully conscious. The ISI at which participants ranked their consciousness with a 3 or below in this scale was defined as the ST. After this, the ST detection block started, in which participants performed another 120 prime detection trials with the ST ISI. When it was finished, ISI was reduced again in a staircase manner. The experimenter checked the detection

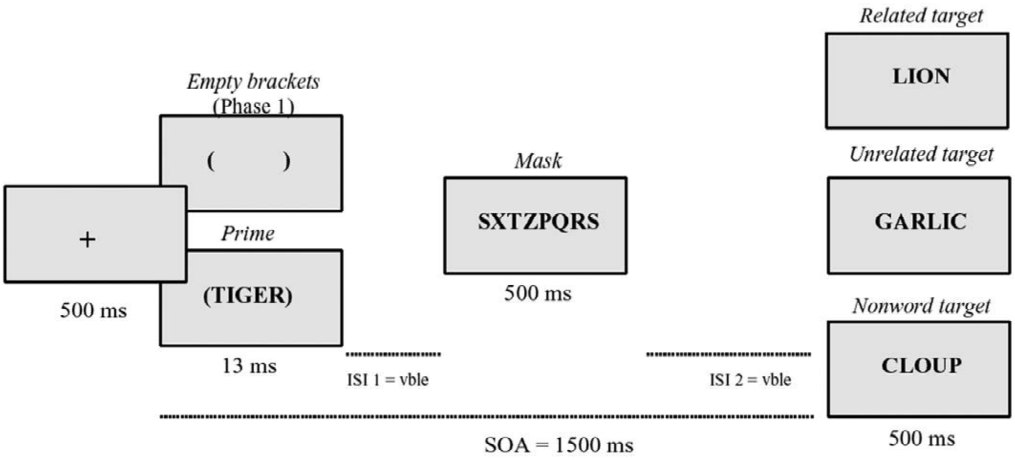

Fig. 1. Experimental procedure in phases 1 and 2.

performance of participants on-line. The criterion for setting one SOA as the OT was either when detection performance was near to chance (i.e., approximately 50% accuracy in the binary detection task) or when the interval could not be shortened anymore (i.e., the SOA was 0 ms). Then, the OT block proceeded for the last 120 trials in phase 1. Participants performed 18 practice detection trials at the beginning of the session with the same structure as CO trials but with a different set of words.

#### 2.4.2. Phase 2

After 2 or 3 weeks from the first session (variable among participants), phase 2 took place. The stimuli display sequence was exactly the same as in phase 1 except that the prime was present in all trials (see Fig. 1). Subjects were to respond, as fast and accurately as possible, to the target with a lexical decision by pressing either the X or the M key depending on whether this stimulus was a real word in Spanish or not. In one third of trials prime and target were semantically related, they were not related in another third and in the trials left the target was a pseudoword. Participants performed 18 lexical decision practice trials with the same structure as the CO block but with a different set of words. As in phase 1, consciousness of the prime was decreased in a descendent manner along blocks. In the first threshold (CO) the ISI was 486 ms. The individual ST was used in the second block for each subject and the OT in the last block. In total there were 360 trials. At the end of the session, participants performed a 120 trials OT detection block, which served as an index of their prime detection in phase 2.

### 2.5. EEG recording and data analysis

Subjects seated in front of the computer monitor in an electrically shielded room and were instructed to avoid eye blinks and movements during stimulus presentation. Scalp EEG was collected with a 128-channel Geodesic Sensor Net [75] (see Fig. 2) connected to an AC-coupled, 128-channel, high-input impedance amplifier (200 MΩ). Individual electrodes were adjusted until impedances were less than 50 kΩ, as recommended for the Electrical Geodesics high-input impedance amplifiers. Amplified analog voltages (0.1 to 100-Hz band pass) were digitized at 250 Hz (12 bits A/D converter and 0.02 μV minimum resolvable voltage). Recorded voltages were initially referenced to a vertex channel. The EEG was segmented 200 ms before the target word and 800 ms after it and then

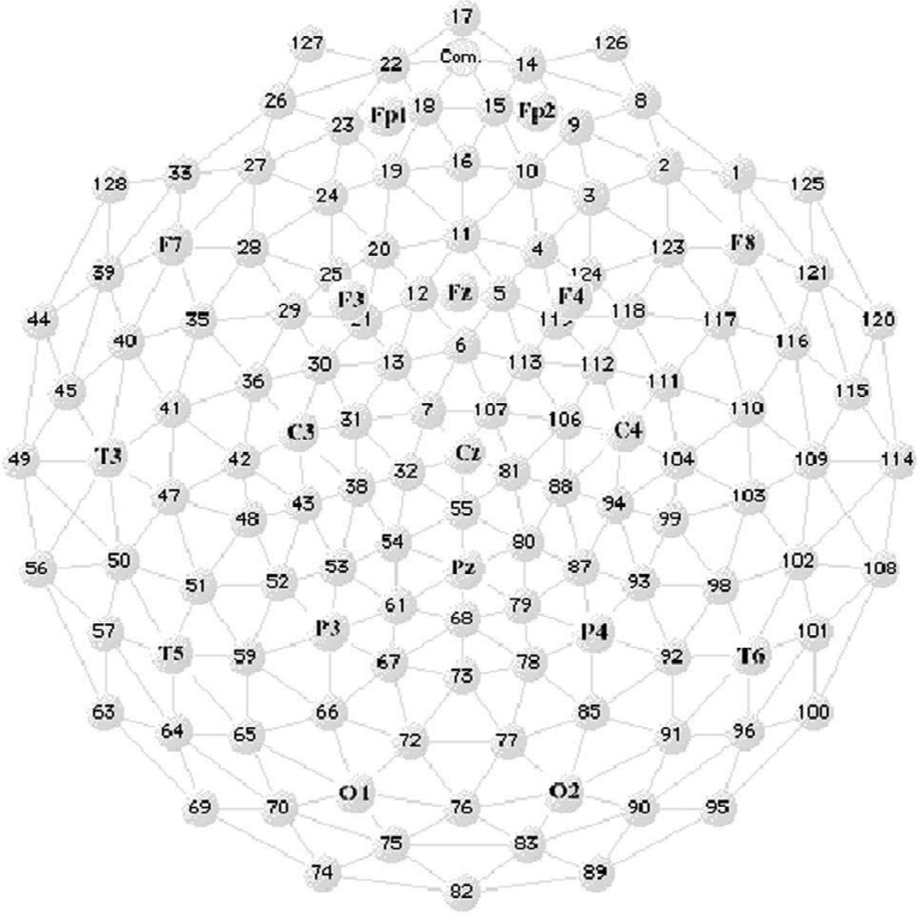

Fig. 2. Layout of the 128-electrode Geodesic Sensor Net.

submitted to software processing for identification of artifacts. Trials containing eye blinks or eye movements (vertical or horizontal electro-oculogram channel differences greater than 70 μV) or more than 7% of bad channels (changing more than 100 μV from one sample to the next, or reaching amplitudes over 200 μV) were not included in the ERPs. Data from individual channels that were consistently bad for a specific subject were replaced using a spherical interpolation algorithm. After incorrect trials and trials containing artifacts were rejected, the mean number of good trials retained for ERP averaging per experimental condition per subject was 32.7 (an average of 18.25% rejected trials). ERPs were re-referenced off-line into an average reference to eliminate the effects of reference-site activity and generate an accurate estimation of the scalp topography of the recorded electrical fields [28,76]. ERPs were baseline-corrected for the 200-ms interval prior to the presentation of the target and digitally band pass filtered from 0.5 to 30 Hz. A final grand average was obtained by averaging across the subject's averages for each experimental condition.

## 3. Results

### 3.1. Behavioral results

In phase 1, mean ISI value for the ST block was 36.4 ms (with a range of 52–13 ms) and 0.57 ms for the OT block (all participants but one had 0 as ISI in OT). Participants responses were classified as hits, misses, false alarms and correct rejections and then transformed to a $d'$ index (see Table 1; $d'$ range was $-0.54-0.75$; 0.39 S.D.). Those values, for each participant and threshold, were introduced into a one-way analysis of variance (ANOVA) (Threshold: CO, ST and OT). $d'$ values were different among thresholds, $F(1,44)=111.47$, $P<0.001$. Moreover, CO d′ was different from d′ in the ST block [$F(1,44)=27.38$, $P<0.001$] and $d'$ in the ST differed from $d'$ in OT [$F(1,44)=73.35$, $P<0.001$]. The mean $d'$ in the OT in phase 1 did not differ significantly from zero (single-sample $t=1.85$, $P>0.05$) and it did not differ either from the $d'$ measured in the detection block that took place after the lexical decision task in phase 2, $F<1$.

In phase 2, only trials in which the probe was a word were analyzed. Furthermore, trials containing a wrong response (1.19%) or those in which RT was shorter than 200 ms or longer than 1065 ms (the mean plus two standard deviations, 3.1% of trials) were rejected from analyses. The mean RT for each participant in the remaining trials (see Table 2) was introduced into a three (Threshold: CO, ST and OT)×2 (semantic relationship: Related and Unrelated) two-way repeated measures ANOVA. There was a main effect of Threshold, $F(1,44)=12.67$, $P<0.001$, a main effect of Semantic relationship, $F(1,44)=12.31$, $P<0.001$ and an interaction between the two factors, $F(1,44)=5.85$, $P<0.005$. The semantic priming effect was significant in the CO threshold (52 ms), $F(1,44)=17.60$, $P<0.001$ and in the OT (19 ms), $F(1,44)=4{,}32$, $P<0.05$, but not in the ST, $F<1$. The priming observed in the CO threshold (52 ms) was significantly greater than that in the OT (19 ms), $F(1,44)=4.13$, $P<0.05$. The same analysis was performed on error rates. No significant effects were found (all $F$ values$<1$).

Table 1
Mean $d'$ for participants in CO, ST and OT blocks in phase 1 and in the detection block after TDL in phase 2

| | Mean $d'$ |
|---|---|
| CO block | 2.47816 |
| UT block | 1.63214 |
| OT block | 0.30762 |
| OT after phase 2 | 0.23576 |

### 3.2. Electrophysiological results

Only ERP data from phase 2 are reported in this article. Data from three participants were rejected from analyses due to too many bad channels all over the recording. ERP amplitudes from the rest of participants were first analyzed by means of a sample by sample two-tailed $t$-test and those ERP sections showing modulation by semantic priming were further analyzed with ANOVAs. Bonferroni corrected degrees of freedom were used in all cases in which no previous hypothesis existed regarding the site of the ERP semantic priming modulations. In order to facilitate comparisons, the same time windows and electrodes were used in the three thresholds of consciousness.

#### 3.2.1. CO threshold

Related and unrelated primes first differed in the time range of the N400 component, starting 352 ms after target onset, in centroparietal electrodes (see Fig. 3; in all the ERP figures, positive is plotted upward). In order to evaluate the statistical significance of the N400 effect, a one-way ANOVA (Semantic relation: Related and Unrelated targets) was performed on the averaged amplitudes of the parietal electrodes noted in Table 3, in a time window spanning from 352 to 492 ms.

The N400 effect was significant in this spatio-temporal window, $F(1,41)=20.64$, $P<0.001$. Related and unrelated ERPs also differed in the LPC over right posterior channels (listed in Table 3), from 556 to 588 ms, $F(1,41)=6.676$, $P<0.05$. No other significant effects were found.

Table 2
Mean RT (in ms) of each experimental condition in phase 2

| | CO | UT | OT |
|---|---|---|---|
| Related targets | 632.71 | 618.08 | 604.74 |
| Unrelated targets | 684.384 | 623.96 | 623.63 |
| Pseudoword targets | 747.02 | 683.37 | 694.50 |

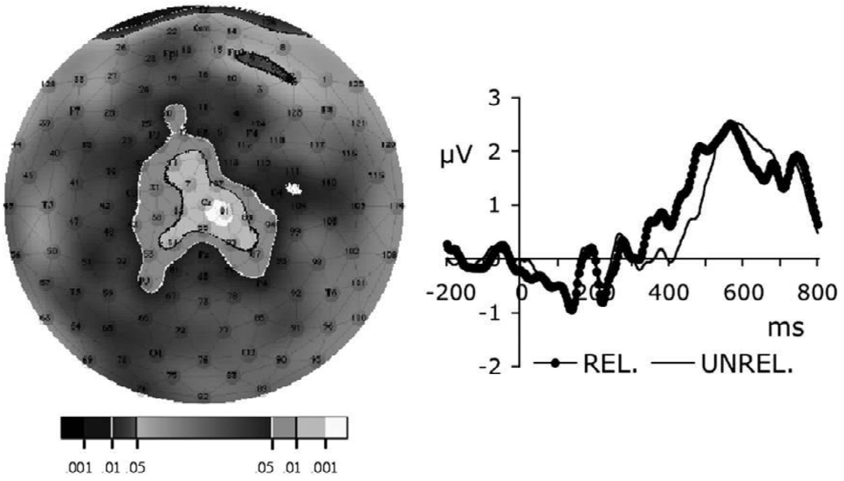

Fig. 3. *t*-Test interpolated map at 484 ms after target onset in CO block. Both the N400 effect topographical distribution and all the epoch (averaged across channels) are shown.

Table 3
Electrodes selected for the ANOVA in CO and OT blocks

| | | |
|---|---|---|
| CO block | N400 | 6, 7, 13, 31, 32, 38, 43, 53, 54, 55, 60, 80, 81, 88, 94, 107 129 |
| | LPC | 72, 73, 76, 77, 78, 83, 84, 85, 86, 90, 91, 92 |
| OT block | N200 | 54, 55, 61, 62, 67, 68, 72, 73, 76, 77, 78, 79, 80 |
| | Left frontal | 12, 20, 21, 24, 25, 28, 29, 35 |
| | Right frontal | 1, 3, 4, 5, 6, 11, 12, 105, 106, 112, 113, 118, 119, 122, 123, 124 |

### *3.2.2. ST*

Neither the N400 effect nor the LPC were significant (as spatio-temporally defined in the CO threshold; both $F$ vaules$<$1). No other significant effect was found.

### *3.2.3. OT*

Related and unrelated waveforms differed from 212 to 248 ms after target onset in posterior medial electrodes (Table 3). This is because the peak of the N200 component is more negative for related targets than for unrelated ones, $F(1,41)=5.52$, $P<0.05$; see Fig. 4.

From 280 to 320 ms after target onset, unrelated targets become more negative in left frontal electrodes (Table 3), $F(1,41)=9{,}19$, $P<0.005$; see Fig. 5.

Finally, related and unrelated waves differ in right frontal electrodes from 316 to 500 ms (see Table 3),

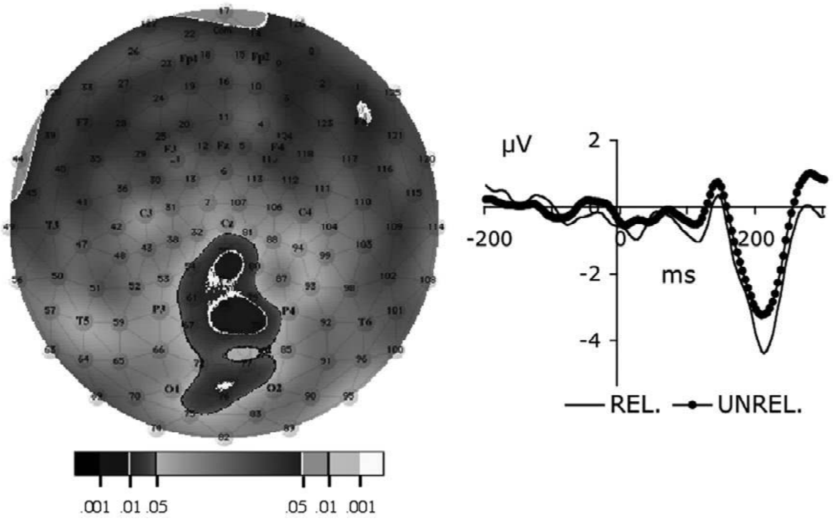

Fig. 4. *t*-Test interpolated map at 220 ms after target onset in OT block. The map shows the distribution of the modulation in the N200 component, and all the epoch is shown averaged across channels showing the effect.

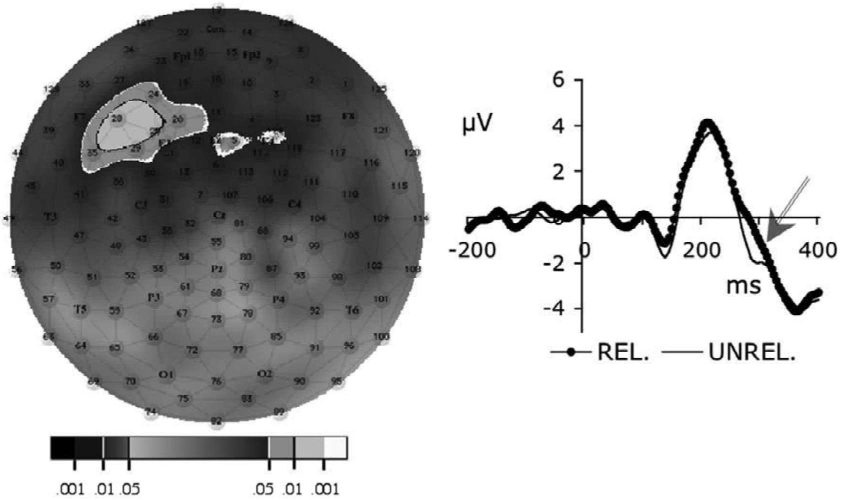

Fig. 5. *t*-Test interpolated map at 292 ms after target onset in OT block. Both the topographical distribution of the left frontal effect and all the epoch averaged across channels are displayed.

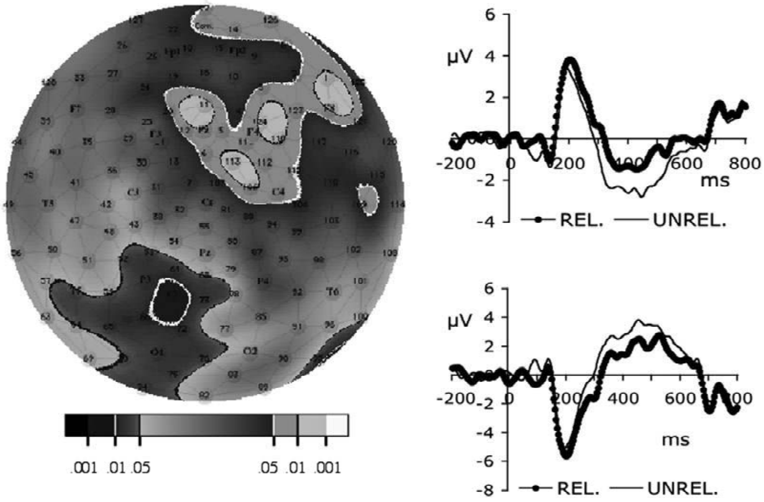

Fig. 6. *t*-Test interpolated map at 332 ms after target onset in OT block. The distribution of the modulation in right anterior and left posterior electrodes is shown, as well as all epoch activity averaged across channels that show the effect.

$F(1,41)=8.13$, $P<0.01$, with a reversed amplitude effect at left posterior electrodes, $F(1,41)=7.47$, $P<0.01$, see Fig. 6. The N400 effect, as defined in the CO threshold, was not significant ($F<1$)[2] as neither was the LPC, $F(1,41)=3.31$, $P>0.08$. The interaction in the spatiotemporal window of the N400 between the CO and OT is significant; $F(1,41)=3.96$, $P<0.05$. In order to assess whether the right frontal effect in the OT block had the same of different scalp distribution as the N400 in the CO block, the interaction between Threshold, Semantic Relation and Topographic distribution (i.e., sensor group) was computed on normalized ERP data as proposed by McCarthy and Wood [56][3]. The ANOVA shows a significant second order interaction between Semantic Relation, Consciousness Threshold and Sensor Group, $F(1, 40)=9.6$, $P<0.005$.

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[2] As noted by one of the reviewers, it may be possible that a small N400 effect was present in the OT condition but was masked by our high pass 0.5 filtering. However, the same ANOVA performed on 0.1–30 Hz band pass filtered ERPs showed this was not the case ($F<1$).

[3] For each participant, experimental condition and time point, the minimum and maximum value across right frontal and central groups of electrodes (see Table 3) were determined and the normalized value $n$ at each electrode group $j$ was computed according to:

$$n_j(t) = \frac{x_j(t) - \min}{\max - \min}$$

where $x_j(t)$ is the mean potential at sensor group $j$ and time point $t$.

## 4. Discussion

The goal of this investigation was to study the extent to which conscious and unconscious semantic priming are supported by overlapping or differential brain mechanisms at a long prime-target SOA. We obtained a behavioral semantic priming effect for both conscious and unconscious priming. Moreover, these two effects correlated with different ERP markers depending on consciousness of the prime. In the first place, our results are in line with previous behavioral research on semantic priming. Conscious stimuli that are presented at a long prime-target SOA are able to semantically prime speeded responses to other words. In addition, unconscious masked words presented at the OT of consciousness are still able to prime words presented after a 1500 ms delay. Although some authors characterize automatic or unconscious effects as decaying fast in time (e.g., Refs. [23,65]), our results show that, at least under certain circumstances, unconscious effects can persist more than one second (see Ref. [22], for converging results). Indeed, early reports of unconscious semantic priming that employed the LDT used a long prime-target SOA (e.g., Refs. [3,33,51]). Therefore, although unconscious semantic priming in the OT is smaller in magnitude (19 ms) than priming in the conscious threshold (52 ms), our results add to the wealth of studies showing that unconscious words, even when presented under strict masking conditions, are able to prime other words related in meaning.

The lack of unconscious priming at the ST, although puzzling, is in the same line as some previous results showing that $d'$ and amount of priming do not correlate or are even negatively correlated in some masked semantic priming procedures [18,30,40,43,46]. That is, it is not always the case that a better perceptual quality leads to a deeper processing of word meaning. There are, indeed, some theories devised to explain phenomena like this one. The center-surround mechanism by Dagenbach and Carr [18] is perhaps the most well known (see also Ref. [30]). These authors proposed an attentional mechanism that helps stimulus recognition by the inhibition of related representations in circumstances in which the experimental setting renders recognition hard to accomplish (like, for example, stimuli masked at the subjective threshold of awareness [19] or very infrequent words whose semantic representations are not well established in memory (see Ref. [18] for more details). Following Dagenbach and Carr [18]), it may be possible that the descendent testing methodology used in this study led participants to narrow down the attentional focus to help identifying the stimuli, and this may have inhibited the semantic associates of word targets and thus make the semantic priming benefit disappear. The fact that this attentional center-surround mechanism does not operate in all circumstances but only when information retrieval is difficult but still possible [18] could explain why semantic priming was found in both CO and OT blocks. However, our investigation was not aimed at exploring this specific question and thus cannot prove this to be the right explanatory mechanism for the lack of priming effects at the ST. Hence, more investigations will be needed in order to shed light on this issue.

On the other hand, our study replicates and extends previous results on the ERP correlates of conscious and unconscious semantic priming. When primes were consciously perceived, ERP to target words show a N400 effect at parietal locations in the scalp together with a later modulation on the LPC. On the other hand, when primes were masked at the OT, the N400 effect disappeared. Instead of it, a posterior N200 effect together with later modulations in left frontal and right fronto-central waves appeared. Our results are in accord with those of Brown and Hagoort [9] who showed a masked priming effect that was not indexed by an N400 effect. Since then, several studies have reported that the N400 can in fact be modulated by the meaning of unconsciously perceived words, given that the SOA between words is short enough [44] (see Refs. [21,43], although see Ref. [24]). This modulation in the N400 is taken to prove that this component is sensitive to automatic mechanisms leading to semantic facilitation effects, which have a fast decay rate after unconscious presentation conditions. However, the N400 is not sensitive to the unconscious semantic priming effect found in our study, although its amplitude was modulated by consciously perceived primes. This means that whatever mechanism is generating our semantic priming effects, it is at least partially different from the one involved in Refs. [21] and [43].

There are some variations among the procedures of the experiments that could be at the basis of the divergence in the results. In the first place, the prime-target SOA used in our study was longer than the SOA in previous reports showing N400 modulation by unconscious semantic priming [22,43,44]. As a matter of fact, Kiefer and Spitzer [44] results suggest the length of the SOA may be the main variable determining the N400 sensitivity to unconscious effects. In their experiment they showed that when prime-target SOA was really short unconscious semantic priming modify the N400 whereas this effect was not found when the SOA was long enough. In order to explain why the SOA at which the N400 is no longer modified by unconscious words varies among studies, these authors claim that the duration of unconscious automatic semantic activation depends on the specific procedure employed [44]. For example, in an attentional blink paradigm [50] this activation must last longer because the N400 is modified even at a 583 ms prime-target SOA [66] whereas in the paradigm employed in [44] it had decayed at 200 ms prime-target SOA.

Another difference is the task employed to set the OT of awareness. In our study, performance of participants was driven near to chance in a stimuli detection task, whereas the other studies used different criteria (recognition of words, [21]; forced discrimination in Ref. [43]), which some authors have characterized as being less stringent that a pure detection task [38]. Finally, in our paradigm all stimuli were repeated several times for each participant whereas previous studies presented words only once. Thus, although the most likely cause for the absence of unconscious N400 modulation is the long prime-target SOA, we cannot reject the other details as contributors to our results.

On the other hand, our experiment was not designed to explore which are the causes of a lack of N400 modification by unconscious semantic priming. Instead, our aim was to study the electrophysiological markers that do indeed correlate with the unconscious priming that actually appears in those situations in which the N400 is not modulated by unconscious words that still prime other words.

### *4.1. Novel correlates of unconscious semantic priming*

The use of a HDERP recording system allowed us to obtain a more exhaustive sampling of the electrical signal on the scalp and thus to find some novel correlates of unconscious semantic priming. When primes are unconsciously processed, semantically related targets generate a N200, peaking at 212 ms, of larger amplitude than that generated by unrelated targets. Moreover, prime-target semantic relation also modulates ERPs at left frontal electrodes around 280 ms and at right frontal and left posterior locations starting at 316 ms. Although language related left frontal modulations in ERP have been reported several times (e.g., Refs. [8,60–62,79]), the same is not true for the other two ERP modulations revealed by our data. The use of a HDERP recording system with our specific experimental paradigm allowed us to detect some ERP effects which may be harder to find with other ERP recording techniques and references (see Refs. [17,28]).

The modulation in the amplitude of early posterior components by language variables has been reported before. The N170 component, as well as the Recognition Potential [52,67] amplitude, differs depending on whether stimuli are words or pseudowords (see Ref. [79]), and its likely generators have been located in a posterior fusiform area, the so-called visual word form area (VWFA [15,53]). Moreover, Martín-Loeches et al. [53] showed that the Recognition Potential can be modified by semantic factors, which is in line with our results and with other reports of early semantic activation (Dien et al. [29]). This N170 component is also modified by manipulations outside language, like orientation of human faces (e.g., Ref. [31]), and it is also sensitive to the degree of practice participants have with stimuli [74]. Although the maximum peak and topographical distribution of the N200 we measured is slightly different from previous reports [8,15,17], it is likely that its generators are in the VWFA or in close regions, given its sensitivity to language variables. The repetition of words that took place through the experimental sessions could be considered as a sort of practice, what could have boosted this early N200 component sensitive to semantic variables (see Refs. [29,70]).

On the other hand, the modulation of left frontal electrodes is common in different language paradigms (e.g., Refs. [8,61,62,79]), being the N3 the component focus of research. Some authors [60,64] claim that this early frontal effect signals lexical process while later and more posterior ones (i.e., the N400) reflect discourse integration [49]. These frontal ERP modulations could be generated by frontal left hemisphere regions related to language processing [8]. Specifically, there are some regions that seem to be involved in semantic tasks and that show semantic repetition priming in several neuroimaging studies [10,11,26,41,57] as well as ERP studies [64,72]. Moreover, these activations remain in amnesic patients [34], what drives some authors to relate these regions with implicit recollection of semantic information [78]. All this together suggests that the negative deflection that appears for semantically related targets in our ERP data could be generated by modulations in the activity of these frontal left regions involved in semantic processing.

Finally, right frontal electrophysiological effects elicited by language variables although less common than left lateralized effects have been previously reported (e.g., Refs. [1,45]). This right scalp effect we have found may be driven either by some specific characteristic of our lexical decision task or by a more general semantic process, but this issue should be addressed in future research.

### *4.2. Conscious vs. unconscious semantic priming*

The electrophysiological indices of semantic priming in our study were qualitatively different depending on whether primes were either consciously or unconsciously perceived. Targets preceded by conscious primes generated a N400 effect at centroparietal scalp locations. However, when the same targets were primed by unconscious stimuli, the N400 effect completely disappeared and instead of it the N200 and frontal sites were modulated. It may be important to note that perceptual stimulation was exactly the same in both conscious and unconscious target related ERPs (as all the targets words are presented during the same amount of time and after the same prime-target SOA in all conditions), and therefore electrophysiological differences could only be generated by differential consciousness of the prime. The electrophysiological markers of conscious and unconscious priming in our study show that, al least in a long prime-target SOA procedure, the mechanism at the basis of these effects are *partially* dissociable. Therefore, it is not likely that unconscious effects in our procedure are generated by residual conscious expectative but rather by unconscious mechanisms. In general, our results raise more general issues on the relation between conscious and unconscious processing in the human brain.

The fact that electrophysiological indices of semantic facilitation are, at least, partially dissociable suggests that conscious and unconscious processes differ to some extent. Contrary to models which claim that a certain cognitive representation is unconscious because its level of activation has not reached the threshold for consciousness (e.g., Refs. [4,27]), our results rather support those theories that relate conscious and unconscious processes to partially separable brain anatomy and different functions in the cognitive system [2,16,23]. The finding that consciousness of a stimulus qualitatively changes the pattern of ERP effects suggest that, instead of a mere raise in the level of activation of a set of representations, consciousness of stimulation recruits a unique set of brain areas and processes to perform the cognitive functions that are uniquely tied to conscious information processing [16,23].

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# APPENDIX II

Ruz, M., Worden, M.E., Tudela, P. and McCandliss, B. (2005) Inattentional amnesia to words in a high attentional load task. *Journal of Cognitive Neuroscience, 17*, 768–776.

# Inattentional Amnesia to Words in a High Attentional Load Task

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Pío Tudela[2], and Bruce D. McCandliss[1]

## Abstract

■ We investigated the dependence of visual word processes on attention by examining event-related potential (ERP) responses as subjects viewed words while their attention was engaged by a concurrent highly demanding task. We used a paradigm from a previous functional magnetic resonance imaging (fMRI) experiment [Rees, G., Russel, C., Frith, C. D., & Driver, J. Inattentional blindness vs. inattentional amnesia for fixated but ignored words. *Science, 286*, 2504–2506, 1999] in which participants attended either to drawings or to overlapping letters (words or nonwords) presented at a fast rate. Although previous fMRI results supported the notion that word processing was obliterated by attention withdrawal, the current electrophysiological results demonstrated that visual words are processed even under conditions in which attentional resources are engaged in a different task that does not involve reading. In two experiments, ERPs for attended words versus nonwords differed in the left frontal, left posterior, and medial scalp locations. However, in contrast to the previous fMRI results, ERPs responded differentially to ignored words and consonant strings in several regions. These results suggest that fMRI and ERPs may have differential sensitivity to some forms of neural activation. Moreover, they provide evidence to restore the notion that the brain analyzes words even when attention is tied to another dimension. ■

## INTRODUCTION

The dependence of information processing on attentional resources has been an issue of central importance in the field of selective attention (for reviews, see Luck & Vecera, 2002; Driver, 2001). However, research has not offered a clear answer to the question of whether the brain is able to process information without attending to it. Early selection theorists have marshaled substantial evidence that information can indeed be selected at an early perceptual processing stage (e.g., Hillyard, Teder, Saelejaervi, & Muente, 1998), whereas many other reports (e.g., Ruz, Madrid, Lupiañez, & Tudela, 2003; Luck, Vogel, & Shapiro, 1996) suggest that ignored or unconscious stimuli can have access to high-level nonperceptual analyses, supporting late selection theories. In recent years, Lavie (1995) (see Lavie & Tsal, 1994, for a review) proposed an integrative approach that potentially accounts for many of the disparate results obtained in experiments examining the locus of selection. Her perceptual load framework states that the presence or absence of automatic processing of unattended irrelevant stimuli may be accounted for by assuming that there is limited capacity for perceptual processing. When task demands are low, resources are available to allow perceptual processing to be applied to ignored information. Under such conditions, the processing of unattended stimuli can be described as automatic in the sense that the processes are initiated and progress without intentional control of the individual. However, when perceptual task demands increase to the point at which these resources are no longer available, irrelevant stimuli are not processed.

Research on the fate of irrelevant stimuli encountered under different processing demands has traditionally faced some methodological limitations such as clearly distinguishing whether ignored information was processed and quickly forgotten (a case of *inattentional amnesia*) or never processed at all (*inattentional blindness*; see, e.g., Wolfe, 1999; Holender, 1986). Whereas behavioral tests present fundamental limitations in differentiating between these two outcomes, neuroimaging techniques afford the possibility of recording brain activation at the time information processing is taking place without the need for an overt response, proving invaluable in helping to solve this debate. Indeed, in recent years functional magnetic resonance imaging (fMRI) reports have stressed the relevance of task demands on the resources devoted to ignored information. For example, Rees, Frith, and Lavie (1997) reported that blood oxygen level dependent (BOLD) activation in V5 generated by irrelevant moving stimuli was modulated by the degree of perceptual load on a different task. When task demands were low, irrelevant background

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motion generated a large BOLD response in area V5. However, in blocks where task demands were high, motion-related activation in this area was absent. Crucially, a study by Rees, Russell, Frith, and Driver (1999) suggested that word reading, a process thought to become highly automatic due to extensive training (e.g., Dehaene et al., 2001; Posner, 1978; Deutsch & Deutsch, 1963), was obliterated when fully focusing attention in another dimension. In this study, participants saw overlapping drawings and letter strings and, in different blocks, they were asked to attend either to the drawings or to the letters and to simply detect stimulus repetitions in the attended domain. The stimuli were shown at a fast presentation rate, which maximized the attentional load associated with encoding and evaluating the attended stimuli. The design involved blocks of nonwords versus blocks that were mixed containing 60% words plus 40% nonwords, and the critical question involved how this stimulus contrast was modulated by attention. When the task required attention to letters, word stimuli activated several language-related areas, such as the left inferior frontal, left posterior temporal, and left posterior parietal regions, providing evidence that the lexical and semantic status of words had been processed. However, when participants attended to drawings, the stimulus contrast of word blocks versus nonword blocks demonstrated no such activations, leading the authors to conclude that when attention is fully withdrawn, ''word processing is not merely modulated, but is abolished'' (Rees et al., 1999).

These results made a strong case for the dependency of word recognition on attentional resources and thus argued against the automatic nature of this highly practiced skill. Taken at face value, the fact that the fMRI BOLD response did not differentiate blocks with and without words under the drawings focus condition suggests that words are not processed in absence of attention. This conclusion, however, rests very strongly on the assumption that a lack of any effect in the BOLD measure *necessarily* indicates a lack of neural sensitivity to this contrast. Indeed, it is possible that perceptual mechanisms respond differentially to familiar words versus novel consonant strings when attention is directed elsewhere, yet these transient responses fall below the sensitivity range of the BOLD response. It may also be possible that other imaging techniques that are more sensitive to rapid transient information are more effective in detecting such signals.

Event-related potentials (ERPs) have been fruitfully used to study the effects of attention on word processing. Looking specifically at contrasts between words and consonant strings, several reports have demonstrated sensitivity to the N200, P300, and N400 components (i.e., Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; McCandliss, Posner, & Givon, 1997; Compton, Grossenbacher, Tucker, & Posner, 1991). These ERP effects have been further examined with respect to attentional modulation, varying, for example, the depth of processing applied to the stimuli (i.e., Bentin et al., 1999; McCandliss et al., 1997; Bentin, Kutas, & Hillyard, 1995; Holcomb, 1988). In terms of detecting neural responses, the high temporal resolution of ERP complements the fMRI approach to attentional modulation of visual word processing. The addition of ERP opens the possibility of uncovering rapid, transient automatic activations to visual words that were not found in the Rees et al. (1999) study. To date, no ERP study has examined the degree to which responses thought to be automatic might be negated under conditions in which attention is occupied with another highly demanding task.

The central issue of the current study was whether fully engaging attention to a different stimulus dimension obliterates ERP effects commonly found for visual words. Such a finding would provide an important replication of the previously reported fMRI result, and together these findings would limit previous claims concerning the automaticity of processes associated with word recognition. Conversely, to the extent that results demonstrate visual word processing under conditions in which attention is engaged in a demanding task, such results would call into question the conclusions of Rees et al. (1999). In order to investigate these issues, we recorded high-density ERP (HDERP) correlates of words in the paradigm Rees et al. devised as is illustrated in Figure 1.

## RESULTS

### Behavioral

Mean repetition detection was 74.8% when participants attended to letter strings and 76.2% when they re-

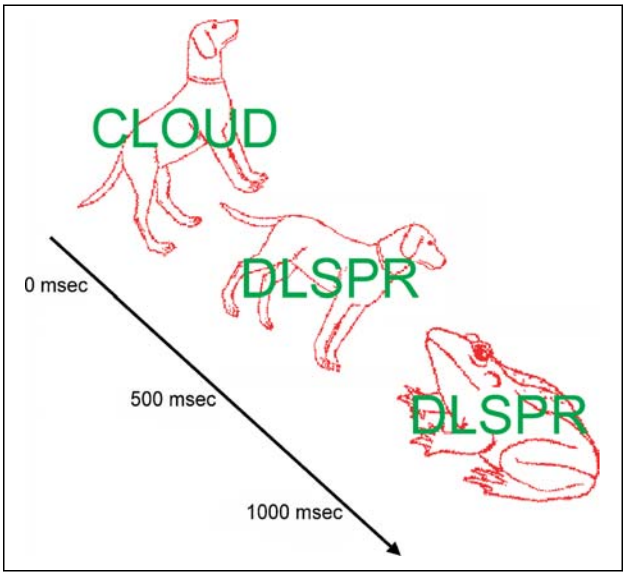

**Figure 1.** Representation of the stimulus display in the repetition detection task.

sponded to drawings. An ANOVA with factors for Attention (attended letters vs. attended drawings) and Lexical Status (words vs. nonwords) showed no effect of Attention, $F(1,11) = 1.501, p > .244$, or Lexical Status, $F < 1$, and a lack of interaction between the two factors, $F(1,11) = 1.255, p > .286$. Furthermore, mean response time (RT) was 398.7 msec for letter strings and 403.4 msec for drawings. When the same ANOVA as above was calculated for RT, the variable Attention had no effect ($F < 1$), but both Lexical Status and the interaction between Attention and Lexical Status were significant, $F(1,11) = 12.37, p < .005$; $F(1,11) = 8.7, p < .05$. In explanation, RT for words (426.2 msec) was longer than for nonwords (371.1 msec) when letter strings were attended, $F(1,11) = 11.24$; $p < .01$ and this was not true when participants attended to drawings (401.2 vs. 405 msec), $F < 1$. Finally, in the surprise memory test, word recognition accuracy was high for attended words (78% of "yes" responses; *MSE*, 0.18) and significantly different from that of ignored words (12%), *MSE*, 0.16; $F(1,11) = 117.27, p < .001$, or Foils (12%), *MSE*: 0.09; $F(1,11) = 155.9, p < .001$. Responses to ignored words and foils were the statistically equivalent, $F < 1$ (see Figure 2).

### Electrophysiological

Attentional instructions generated widespread and long lasting effects in several areas of the scalp topography (see Figure 3). Attended drawings generated more positive ERPs at medial scalp locations than attended words, from 30 to 210 msec, $F(1,11) = 24.6, p < .001$, and the reverse was true from 100 to 300 msec in the left and right posterior scalp, $F(1,11) = 14.18, p < .01$, and in left and right anterior locations from 175 to 275 msec, $F(1,11) = 34.3, p < .001$ (see Figure 3).

When attention was directed to letters, ERPs for words and nonwords differed in several scalp locations. Words were more negative than nonwords in left frontal channels from 120 to 190 msec, $F(1,11) = 12.48, p < .01$, and in left posterior locations from 195 to 300 msec, $F(1,11) = 9.06, p < .01$. Also, the peak of the N170 component was more negative for nonwords than words in medial posterior electrodes, $F(1,11) = 11.6, p < .01$. From 240 to 315 msec, words were more positive than nonwords in anterior medial scalp sites, $F(1,11) = 12.47$, $p < .01$, and the reverse was true from 250 to 350 msec in left posterior electrodes, $F(1,11) = 12.44, p < .01$. An N400 effect was present from 350 to 425 msec, $F(1,11) = 8.23$, $p < .05$. Finally, words were more positive than nonwords from 460 to 690 msec in left medial locations, $F(1,11) = 15.18$, $p < .001$, and more negative in left frontal electrodes from 450 to 750 msec, $F(1,11) = 21.5$, $p < .001$ (see Figure 4).

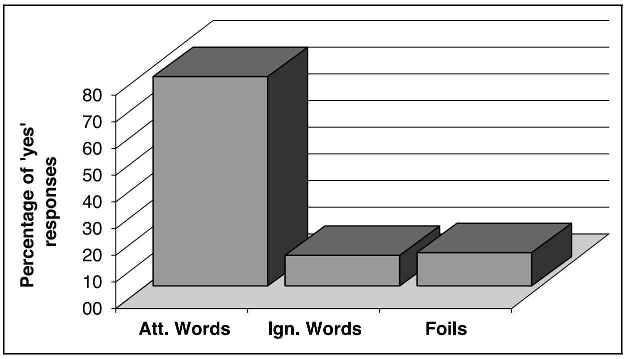

**Figure 2.** Percentage of "yes" responses to words presented during the surprise memory test in the Experiment 1. Whereas word recognition accuracy was very high for attended words, responses to ignored words were the same as responses to foils.

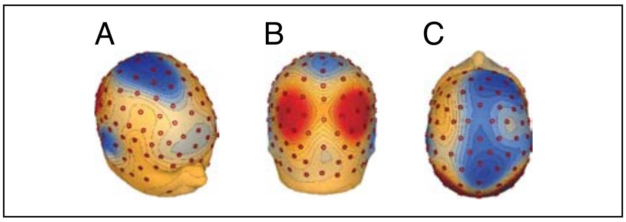

**Figure 3.** 3-D current source density maps of the main effects of Attentional instructions. (A) Attended drawings generated more positive ERPs at medial scalp locations than Attended words from 30 to 210 msec, (B) and the reverse was true from 100 to 300 msec in the left and right posterior scalp, (C) and in the left and right anterior locations from 175 to 275 msec.

When these same contrasts (with the same groups of electrodes and temporal windows) were applied to ignored words versus ignored nonwords, the ANOVAS showed words more positive than nonwords from 460 to 690 msec in left medial locations, $F(1,11) = 10.80, p < .01$. This difference held for left frontal electrodes as well, from 450 to 750 msec, $F(1,11) = 6.5, p < .03$ (see Figure 5). Moreover, when additional contrasts were performed on ignored words versus nonwords, words were more positive than nonwords in left posterior sites from 350 to 550 msec, $F(1,11) = 7.31, p = .02$, and more negative in anterior medial electrodes in the same temporal window, $F(1,11) = 9.33, p = .01$ (see Figure 5).[1]

## DISCUSSION

The fundamental result of this experiment is that words, in contrast to consonant strings, produce distinct patterns of ERP responses even under conditions in which attention is directed away from such processing by a highly demanding task. Using a nearly identical design as that of Rees et al. (1999) yet achieving different findings for unattended words might raise questions about whether the current instantiation of the paradigm was equivalent to the one originally employed. Several facts suggest that this replication effort was successful. These data tightly replicated the initial pattern of behavioral

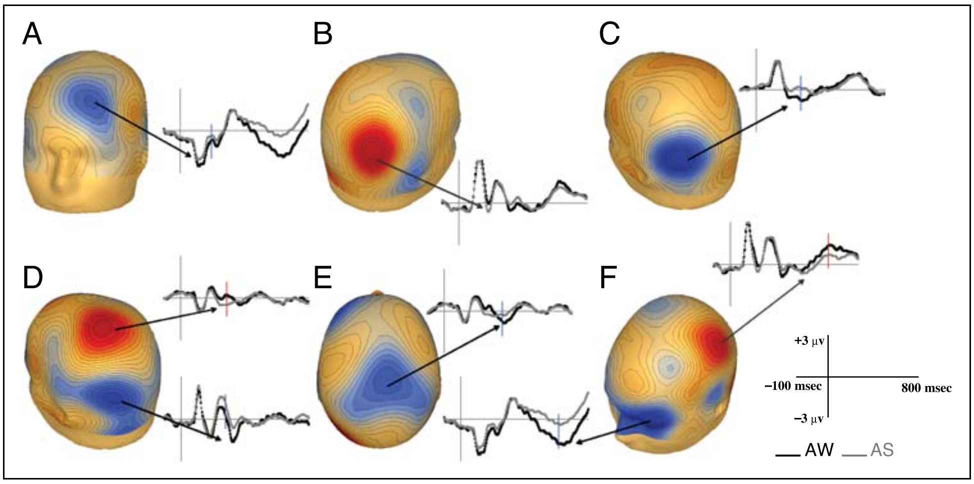

**Figure 4.** 3-D current source density maps of attended words versus attended nonwords effects. When letters were attended to (A) words were more negative than nonwords in left frontal channels from 120 to 190 msec (C) and in left posterior locations from 195 to 300 msec. (B) Also, the peak of the N170 component was more negative for nonwords than words in medial posterior electrodes. (D) From 240 to 315 msec, words were more positive than nonwords in the anterior medial scalp sites and the reverse was true from 250 to 350 msec in left posterior electrodes. (E) A N400 effect was present from 350 to 425 msec. (F) Words were more positive than nonwords from 460 to 690 msec in left medial locations, and more negative in left frontal electrodes from 450 to 750 msec. AW = attended words; AS = attended strings.

data. Results from the surprise memory test show that participants remembered more than 75% of the attended words, whereas the percentage of yes responses to ignored words (12%) was the same as that to foils. Furthermore, the HDERP results demonstrated a main effect of instructions, which provides further support that our instantiation of the paradigm was effective in directing participants' attention to the letter and the drawings modality.

When letters were attended, ERP responses to words and nonwords differed in several regions, including left frontal, left posterior, and medial scalp locations, consistent with the Rees et al. (1999) results and replicating previous reports in the literature of ERP word processing (e.g., Bentin et al., 1999; Badgaiyan & Posner, 1997; Kutas & Hillyard, 1987). When participants attended to drawings, ERP responses were dramatically influenced by this difference in attentional focus, yet, crucially, we still found ERP differences between unattended words and nonwords in left posterior, anterior medial, left medial, and left frontal sites (see Figure 5). Therefore, this stimulus contrast lends support to the notion that

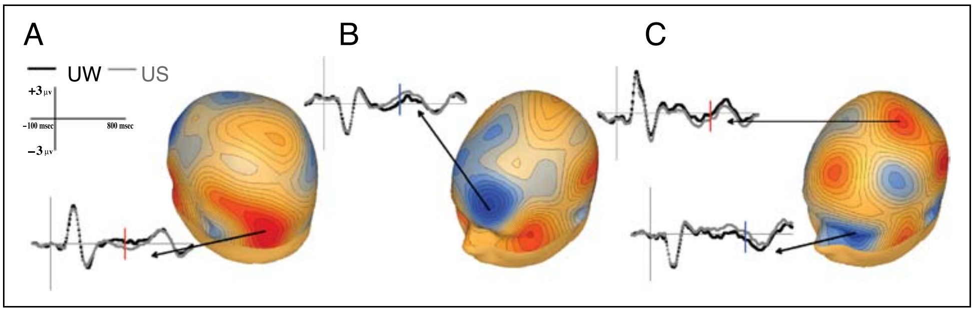

**Figure 5.** 3-D current source density maps of unattended words versus nonwords. (A) Words were more positive than unattended nonwords in left posterior sites from 350 to 550 msec (B) and more negative in anterior medial electrodes in the same temporal window. (C) In addition, in the same way as in blocks where letters were attended, ignored words were more positive than nonwords from 460 to 690 msec in left medial locations. This difference was also true in left frontal electrodes from 450 to 750 msec. UW = unattended words; US = unattended strings.

even under conditions of high attentional load, words engage a form of processing that differentiates them from nonword letter strings.

Interestingly, the difference between words and consonant strings was not identical under the two attentional conditions, suggesting that at least some of the observed ERP effects are dependent on attentional processes. Much of the activity extant in blocks where letters were attended was missing in blocks where participants focused on the drawings, whereas some remained. Moreover, unattended words produced activations at different times than attended ones. Taken together, this suggests that performing a highly demanding task substantially modifies the way in which the brain registers differences between words and nonwords. We will discuss these results together with Experiment 2 in the General Discussion section.

## Experiment 2

Results from Experiment 1 show that even in conditions in which attention is engaged in a separate highly demanding task, the brain detects some difference between irrelevant words and nonwords. However, it is unclear from these data whether item repetition, a key manipulation in Experiment 1, is needed in order to observe this effect. That is, it could be the case that only when ignored items are repeated several times does the brain detect them. To rule out this scenario, we ran a second experiment in which letter strings were presented only once during the repetition detection task. In addition, in contrast to Experiment 1 in which some blocks of trials contained 60% words and some blocks contained 100% nonwords, in Experiment 2 all blocks contained 50% words and nonwords randomly intermixed to prevent any strategic effects due to block composition predictability. Finally, this new experiment represented a replication effort of findings in Experiment 1.

## Results

### *Behavioral*

When participants attended to letter strings, mean repetition detection was 71.5% and 68.5% when they responded to drawings. An ANOVA with the factors Attention (attended letters vs. attended drawings) and Lexical Status (words vs. nonwords) showed no effect of Attention, $F < 1$, or Lexical Status, $F(1,11) = 1.827, p > .2$, and a lack of interaction between the two factors, $F < 1$. Mean response time was 388 msec for letter strings and 324 msec for drawings. The ANOVA yielded Attention as the only significant variable, $F(1,11) = 20.66, p < .001$. In the surprise memory test, word recognition accuracy for attended words (37% of yes responses, *MSE*: 0.17) was significantly higher than that of ignored words (31%; *MSE*: 0.18; $F(1,11) = 8.555, p < .05$) or Foils (30%; *MSE*: 0.18; $F(1,11) = 12.09, p < .01$). Responses to ignored words and foils were the same, $F < 1$.

### *Electrophysiological*

Attention to drawings generated more negative deflections at left and right posterior areas from 250 to 350 msec, $F(1,11) = 6.8, p < .05$. In addition, in the same temporal window attended drawings ERPs were more positive at anterior locations, $F(1,11) = 9.4, p = .01$. When letters were attended, words were more negative in left posterior locations from 275 to 325 msec, $F(1,11) = 18.127, p < .001$, and more positive than nonwords in left frontal channels from 300 to 550 msec, $F(1,11) = 6.515, p < .05$. The N400 effect was significant from 350 to 425 msec, $F(1,11) = 7.28, p < .05$. Finally, words were more positive than nonwords from 350 to 450 msec in left medial locations, $F(1,11) = 9.36, p = .01$. Unattended words, on the other hand, were more negative than nonwords in left posterior channels from 275 to 325 msec, $F(1,11) = 5.18, p < .05$, and more positive in left frontal areas from 300 to 550 msec, $F(1,11) = 7.83, p < .05$. In addition, unattended words were more negative than nonwords in left posterior channels from 625 to 725 msec, $F(1,11) = 14.33, p < .005$.

## Discussion

Experiment 2 replicates the previous experiment in showing that unattended words are differentiated from nonwords when attention is engaged in a demanding task in another dimension. Similar to Experiment 1, attention to different modalities modulated the ERPs at left and right anterior and posterior locations. When participants attended to letters, lexical category of stimuli produced effects at left posterior and frontal sites, as well as an N400 effect, together with modulations in left medial areas. Most crucially, unattended words once again modulated left posterior and frontal channels although parietal effects (N400 and left medial) were missing. Behavioral results replicated the original memory effect for attended words that was absent for ignored ones, although the size of this effect was small (7%). Presumably presenting a large set of words only once during the task decreases the likelihood of incidental learning.

# GENERAL DISCUSSION

The current ERP findings show that the brain differentiates between lexical and nonlexical stimuli even in conditions in which attention is focused in a highly demanding task unrelated to language. This takes place when words are repeated several times as in Experiment 1 as well as when items are briefly presented only once, as is the case in Experiment 2.

Attention had a large effect in the ERP waveforms. Instructional main effects manifested as widespread and long-lasting modulations of the ERP signal in both posterior and anterior scalp locations. These effects accord well with the Rees et al. (1999) results and add to many others supporting the notion that attentional focus substantially modulates the brain regions recruited to perform a task, a phenomenon that has been demonstrated in several domains (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). On the other hand, attention substantially modulated word processing in both experiments by changing some of the regions responding differentially to words and nonwords and the timing of their activations.

In both Experiments 1 and 2, attention to letters was associated with word–nonword differences in left posterior, frontal, and medial areas, as well as an N400 effect. Based on previous evidence (e.g., Abdullaev & Posner, 1998), left posterior effects could reflect activations of the posterior region of the reading network, potentially fusiform and middle temporal areas known to be selective for visual word forms (McCandliss, Cohen, & Dehaene, 2003). Frontal modulations may result from activity in left prefrontal areas known to tap syntactic and semantic codes of words (e.g., Luke, Liu, Wai, Wan, & Tan, 2002) and left medial effects may reflect activations near Wernicke's area (Abdullaev & Posner, 1998). When attention was focused on the drawings (and thus letters were ignored), some of the abovementioned ERP effects were missing, whereas some remained and others underwent a temporal shift. For instance, in both experiments the classical N400 effect appeared when letters were attended and was not present in inattention conditions, which is consistent with previous literature (i.e., McCarthy & Nobre, 1993) The sensitivity of the N400 to attentional manipulations has been previously documented (i.e., Holcomb, 1988; see Kutas & Van Petten, 1994, for a review) and several reports have shown N400 effects absent when attention is directed away (i.e., Bentin et al., 1995; McCarthy, & Nobre, 1993; although see Kiefer, 2002). In contrast, left posterior and left frontal effects persisted in the inattention conditions of both experiments, suggesting that brain regions generating these modulations, arguably left fusiform and frontal areas, still detect word–nonword differences when attention is focused away from letters.

Intriguingly, unattended word–nonword differences appear late in time in both experiments. Although the onset and time course of ERP effects differs between the two (most likely due to massive item repetition in Experiment 1), both experiments exhibit late unattended contrast effects (at 350 and 275 msec in Experiments 1 and 2, respectively). Although some relevant studies describe unattended unconscious processing early in time (e.g., Dehaene et al., 2001), this is not the case in the present experiments. However, the specially challenging characteristics of the present task (composed of a highly rapid succession of complex stimuli requiring attention focused in one modality and suppression of foveated stimuli in the other modality), which was not designed to investigate word processing per se, offer a plausible explanation for this temporal peculiarity. As previous reports have shown (McCann, Remington, & Van Selst, 2000), language-related features such as word frequency can be delayed in time in conditions in which processing is occupied by another task. In inattention conditions of the present task, participants were responding to drawings presented at a very fast rate and letters were completely irrelevant. This would put differential pressure on the cognitive system, giving priority to certain processes over others, causing word–nonword differential activations to be delayed in time—an effect similarly reported for processes sensitive to word frequency in the experiment of McCann et al. (2000), which were delayed by several hundred milliseconds when attention was occupied in a unrelated task.

As discussed, our central finding—word processing enduring attention withdrawal—is in conflict with the results of Rees et al. (1999), who demonstrated no such effect. Although several incidental disparities between the two studies cannot be ruled out as the source of departure, a likely explanation for the contradictory result is the differential sensitivity of fMRI and ERPs to certain kinds of brain activity. Indeed, some authors (e.g., Logothetis, 2003; Logothetis et al., 2001; Nunez & Silberstein, 2000) note differential sensitivity of various neuroimaging techniques to different types of brain activity, which could lead to contradictory results when using more than one methodology to study the same cognitive process. Furthermore, Nunez and Silberstein (2000) argue that there are some cases in which either technique could offer a positive result while the other one shows no brain activation. One of the factors driving these different measurement outcomes is related to the temporal sensitivity of the measured responses. ERPs can show stimulus-specific brain responses less than 100 msec after stimulus onset, whereas BOLD response usually needs 4 to 6 sec to reach its maximum levels. These temporal factors are especially important when dealing with block fMRI, in which brain activity is collapsed over blocks lasting several seconds (40 sec in the case of Rees et al., 1999).

The present study shows that HDERP data can provide positive evidence of transient processing of ignored or unattended words in a high attentional load task. Our results indicate that the brain processes to some extent stimuli associated with some forms of extensive visual expertise, such as words, automatically. Indeed, recent behavioral investigations have shown that certain kinds of biologically relevant stimuli, such as human faces, may be processed regardless of task demand (Jenkins et al., 2003; Lavie, Ro, & Russell, 2003; see also Mack, Pappas, Silverman, & Gay, 2001). Whether this form of automaticity is associated with general properties of stimuli for which humans have obtained advanced levels of perceptual expertise or is specific to a special class of stimuli with adaptive significance is a matter of debate (i.e., Gauthier & Nelson, 2001). In any case, both faces and words are extensively processed throughout life and elicit distinct patterns of activity in extrastriate regions.

Results from the present study show that word processing can take place under conditions in which attention is tied to a different dimension. However, the focus of attention on a different task modified the set of effects indexing word processing, as well as their temporal onset, raising the question of whether our results can be taken as a proof of automatic word processing. Since the early days of the automatic controlled dichotomy (Shiffrin & Schneider, 1977; Posner, 1975), several authors have noted the nonunitary nature of processes labeled as automatic (e.g., Bargh, 1992; Logan & Cowan, 1984), in the sense that most of them do not fulfill all criteria that have been suggested as indexes of this kind of processes such as being nonintentional, uncontrollable, unconscious, and impervious to attention. Even when it can be assumed that in the present experiments participants did not have the intention to process the letters when they were attending to drawings, and thus it is unlikely that they had any conscious control over it, attention had the marked effect on ERP effects and their latency. This suggest that the kind of automaticity that our results point to is one in which word processing is influenced by the allocation of attention but unintentionally persists in an unconscious manner even in conditions of high attentional demands in another dimension.

## METHODS

### Experiment 1

*Subjects*

Twelve paid subjects (5 men, mean age, 23) gave written consent to participate in the study. All were right-handed, reported normal or corrected-to-normal vision and had English as their first language.

*Stimuli and Apparatus*

Sixty five-letter words were selected from the Kucera and Francis (1967) database (60 mean frequency), 70 strings of five consonants were created, and 100 drawings were selected from the Snodgrass and Vanderwart (1980) set. Words were divided into four lists matched in mean frequency that were used as attended words, ignored words, and foils for the recognition memory test. The same stimuli (drawings, words, and nonwords) were presented 11.5 times, on average, across the repetition detection task. All material was counterbalanced across subjects and conditions.

Participants saw a rapid stream of sequentially presented stimuli which were presented for 250 msec every 500 msec (with a jitter of ±100 msec between presentations), each consisting of red drawings and overlapping green uppercase letters of approximately 5° of visual angle (see Fig. 1). Between-modality uncorrelated stimulus repetition occurred in both drawings and letters once every six items, on average. Four pseudorandom stimulus orderings were generated to use in the four blocks of the experiment and were counterbalanced across subjects and attention conditions. Drawings were randomly rotated 30° clockwise or counterclockwise from trial to trial and they were always shown in a different orientation when an immediate repetition took place. Stimulus presentation was done using a PC running E-Prime v1.0 (PST, Pittsburgh, PA) with a screen refresh rate of 60 Hz.

EEG was continuously recorded during the repetition detection task with a 128-channel geodesic sensor net (Tucker, 1993) connected to an AC-coupled high-impedance amplifier (EGI, Eugene, OR). Individual electrode impedances were adjusted until they were below 50 m$\Omega$. Amplified analog voltages (0.1–100 Hz band pass) were digitized at 250 Hz and recordings were initially referenced to Cz. To improve signal-to-noise ratio, EEG was low-pass filtered off-line from 30 Hz and then segmented 300 msec before stimulus onset and 800 msec afterward, according to the Attention condition (attended letters or ignored letters) and the syntactic category of the letter (words or nonwords). Segments containing artifacts were rejected off-line. Individual segments were averaged by condition to create ERPs and were then baseline corrected with reference to a −200- to 0-msec interval. An average-reference transformation was then applied to more accurately estimate the distribution of activity on the scalp (Bertrand, Perrin, & Pernier, 1985). Mean voltages were calculated for each group of channels and conditions showing potential effects and then introduced into ANOVAS comparing words versus nonwords in each Attention condition (attended letters and attended drawings). Bonferroni-corrected degrees of freedom were used in all those cases in which there were no a priori predictions regarding the site of ERP modulations.

*Procedure*

In four different blocks lasting 4 min 48 sec each, participants were instructed to attend either to the drawings or to the letters and to press a button every time a stimulus repeated in the attended dimension. Each block was composed of eight 36-sec interleaved task and rest periods. Half of the task periods contained only nonwords, whereas the other half had 60% words and 40% nonwords in the letter dimension. In all cases, the first eight trials always contained nonwords. Immediately after the repetition detection task, participants performed a surprise memory test. Sixty words (attended and unattended words together with 30 foils) were presented in the center of the computer screen after a 1000-msec fixation point and participants were asked to respond by a button press whether they thought they had seen that word during the repetition detection task or not. The response of the participant erased the word from the screen and initiated the next trial.

## Experiment 2

The following sections describe differences between Experiment 1 and 2. All other methodological details were the same.

### *Subjects*

Twelve participants (5 men; mean age, 21.9) gave written consent to participate in the study.

### *Stimuli and Apparatus*

Four hundred words of from 4 to 5 letters were selected from the Kucera and Francis (1967) database (67.7 mean frequency) and 264 consonant strings (from 4 to 5 letters) were created. Four hundred drawings were used from the Snodgrass and Vanderwart (1980) database. Words were divided into four lists matched in mean frequency, which were counterbalanced across attention conditions and tasks.

### *Procedure*

The repetition detection task was composed of 544 trials divided into eight blocks of 68 trials lasting 32 sec each. The first eight trials in every block were composed of nonwords. During the surprise memory task, 320 words were presented to the participants in the same way as in Experiment 1. Half of them were new and the other half had appeared in the previous task. From the old ones, half of them had been attended and the other half were ignored words. Only words not repeating in the previous phase were included in the memory test. Participants performed 16 blocks of 20 words each.

## Acknowledgments

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## Note

1. As pointed out by one of the reviewers, the short ISI (500 msec) used in this study, together with the fact that the words and nonwords proportion was different (60% vs. 40%) in Experiment 1, raises the question of whether late effects observed in the unattended condition are due to lexical interactions between pairs of word stimuli or to processing of the first stimulus per se. We performed an additional analysis eliminating word–word pairs from the average ERPs to answer this question. When the same ANOVAS as before were carried out in the unattended letters condition, all effects remained significant: left medial effect, $F(1,11) = 5.632$, $p < .05$; left frontal electrodes, $F(1,11) = 24.798$, $p < .001$; left posterior sites, $F(1,11) = 10.776$, $p < .01$; anterior medial electrodes, $F(1,11) = 21.698$, $p < .001$. Thus, these effects are due to genuine word processing rather than to lexical interactions between items.

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# APPENDIX III

Ruz, M., Wolmetz, M., Tudela, P. and McCandliss, B. (*under review*) Two brain pathways for attended and ignored words. *NeuroImage*.

# Two Brain Pathways for Attended and Ignored Words

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**The dependency of word processing on spare attentional resources has been debated for several decades. Recent research in the study of selective attention has emphasized the role of task load in determining the fate of ignored information. In parallel to behavioral evidence, neuroimaging data shows that the activation generated by unattended stimuli is eliminated in task-relevant brain regions during high attentional load tasks. We conducted an fMRI experiment to explore how word encoding proceeds in a high load situation. Participants saw a rapid series of stimuli consisting of overlapping drawings and letter strings (words or nonwords). In different blocks, task instructions directed attention to either the drawings or the letters, and subjects responded to immediate repetition of items in the attended dimension. To look at the effect of attention on word processing we compared brain activations for words and nonwords under the two attentional conditions. As compared to nonwords, word stimuli drove responses in left frontal, left temporal and parietal areas when letters were attended. However, although the behavioral measures suggested that ignored words were not analyzed when drawings were attended, a comparison of ignored words to ignored nonwords indicated the involvement of several regions including left insula, right cerebellum and bilateral pulvinar. Interestingly, word-specific activations found when attended and ignored words were compared showed no anatomical overlap, suggesting a change in processing pathways for attended and ignored words presented in a high attentional load task.**

## INTRODUCTION

The focus of attention has a fundamental impact on brain dynamics. When attention is focused on a spatial location, an object, or certain features of a stimulus, a set of frontal and parietal regions initially code for the appropriate attentional template (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002). In many cases, this top-down focus generates an enhancement of pre-target activation in brain areas coding for task-relevant information (Luck, Chelazzi, Hillyard and Desimone, 1997; Kastner, Pinsk, De Weerd, Desimone and Ungerleider, 1999), preparing the system to respond when the relevant target stimulus arrives (Corbetta, Miezin, Dobmeyer, Shulman and Petersen, 1991; see also Chawla, Rees and Friston, 1999). This set of neural processes help the organism prioritize and respond to the specific dimensions of the environment selected as relevant from among the many distractions competing for the control of behavior. Accordingly, during any given act of perception, attentional focus may act to exclude many irrelevant items from the available set.

Considerable debate spanning several years has centered on the fate of ignored information and questions concerning whether ignored information might gain access to high-level processing (see Lavie and Tsal, 1994; Driver, 2001), with evidence supporting both early and late selection theories. One of the fields in which this question has been extensively investigated is word encoding, a classical example of automatic processing (see for example Driver, 2001). Although several behavioral studies have suggested that attention is needed for some forms of word processing (e.g. Fuentes, Carmona, Agis and Catena, 1994; Besner and Stolz, 1999; Naccache, Blandin and Dehaene, 2002), many others indicate that unattended and/or unconscious words do access high-level lexical and semantic analyses (e.g. Fuentes and Ortells, 1993; Merikle, Mack and Rock, 1998; Smilek and Eastwood, 2001; Catena, Fuentes and Tudela, 2002; Ortells, Daza and Fox, 2003; Ruz, Madrid, Lupiáñez and Tudela, 2003). Investigations using ERP have shown that removing attention from words eliminates (McCarthy and Nobre, 1993; Bentin, Kutas and Hillyard, 1995; Ruz, Worden, Tudela and McCandliss, 2005) or attenuates (Holcomb, 1988; Bentin, Kutas and Hillyard, 1993) components such as the N400, an index of semantic processing. For example, using a dichotic listening task, Bentin et al. (1995) reported that both the N400 and explicit memory were absent for ignored words, whereas implicit indexes such as false recognition of semantic associates and repetition priming remained for unattended items. This class of results can be taken to support the conclusion that although words only reach high-level controlled processing when they are attended to, evidence of more automatic processing can be observed by means of implicit measures.

In the more general literature on attention and automaticity, one currently prevailing view holds that perceptual task load is the main determinant of the fate of ignored stimuli (Lavie, 2000). The Perceptual Load theory by N. Lavie (1995) assumes that perceptual processing proceeds in an automatic, but limited, manner and this determines the resources available for task-irrelevant stimuli. When the task is easy, perceptual load is low and the spare resources spill over to irrelevant ignored items, which are then processed and able to affect the ongoing behavior. In contrast, when the perceptual load of the task is high enough, all resources are occupied and information not directly relevant to the task does not gain access to high-level processing.

Neuroimaging results have added to the wealth of research supporting this view. In the first such study, Rees, Frith and Lavie (1997) reported that blood-oxygen level dependent (BOLD) response in V5 generated by irrelevant moving stimuli was modulated by the degree of perceptual load on an unrelated task. When task demands were low (e.g. case decision on a letter string), irrelevant background motion generated a large BOLD response in area V5. However, in blocks where task demands were high (e.g. a challenging syllabic decision on a letter string), motion related activation in this area was absent. This attenuation of neural response to irrelevant stimuli during high attentional load has also been shown in brain regions early in the processing stream, including Lateral Geniculate Nucleus (O'Connor, Fukui, Pinsk, and Kastner, 2002) and V1 (Schwartz et al., 2004). Similarly, Yi and colleagues (2004) showed that BOLD response to task-irrelevant places measured in the Parahippocampal Place Area (PPA) was obliterated when perceptual demands of a task performed on faces presented at fixation increased (see also Pinsk, Doninger and Kastner, 2004).

Given the potential impact of these developments for studies of automaticity in word recognition, a few investigations have devised high attentional load paradigms to examine word responses in attended versus unattended conditions. Rees, Russell, Frith and Driver (1999) used fMRI to measure the BOLD response in a high attentional load task manipulating attention either to letters or drawings presented in overlapping spatial positions. Results showed that those regions differentially activating words and nonwords when attention was focused on letter stimuli were silent to this same contrast when attention was 'fully withdrawn' from the letter domain (Rees et al., 1999). Therefore, the authors suggested that within a high perceptual load task, attention to other stimuli eliminates irrelevant processing of even highly practiced words.

Most fMRI studies investigating stimulus processing in high load situations employ the strategy of identifying specific brain regions typically associated with processes of interest and demonstrating a lack of responsiveness under high attentional load conditions when attention is otherwise engaged (Rees et al., 1997; O'Connor et al., 2002; Yi et al., 2004; although see Schwartz, 2004). However, whereas this 'selective region-of-interest (ROI) strategy' has the advantage of higher statistical power and is consistent with some a priori predictions, it carries the risk of missing effects that might arise in regions not expected to be relevant for a given task. This drawback is particularly relevant in the field of selective attention, because unattended information may not be processed in the same fashion or through the same pathways as attended items. For example, previous work (e.g. Raichle et al., 1994) has reported that when the same task and stimuli are presented in situations that pose either high or low attentional demands on processing, different brain pathways are recruited to perform the task. Thus, it could be the case that in situations of high load, different sets of structures are sensitive to information when ignored, as opposed to when attended, due to compensatory strategies. In this case, an approach covering the whole brain might be more useful in revealing regions important for the analysis of task-irrelevant information. Several lines of evidence suggest this alternate-pathway option to be plausible.

Recent electrophysiological research in our lab (Ruz et al., *in press*) indicates that irrelevant ignored words are indeed processed in the high attentional load task devised by Rees et al. (1999) to investigate inattentional blindness. Results of this electrophysiological study show that both late anterior and posterior electrophysiological components differentiated between ignored words and ignored nonwords when attention was fully focused on overlapping drawings. This outcome resonates with previous studies suggesting that participants' own names are able to capture attention when presented in this same inattentional blindness paradigm (Mack, Silverman and Pappas, 2001; see also Mack and Rock, 1998; Wolfe, 1999) and is in agreement with a large literature establishing, in many aspects, an automaticity of visual word encoding (i.e. Posner, 1978; Dehaene et al., 2001).

The goal of the present study was to investigate potential brain regions sensitive to unattended word processing in the high attentional load paradigm originally devised by Rees and colleagues (1999; see Lavie, 2005). This paradigm demonstrated a form of inattentional blindness for ignored words by manipulating whether attention was directed to words versus superimposed drawings. We used fMRI to obtain whole-brain images while participants were engaged in these two contrasting high attentional load conditions. Guided by results in the original study (Rees et al., 1999) and later research extensions (Ruz et al., *in press*), we expected that withdrawing attention from the letter dimension would reduce or even eliminate activation in brain regions responding to attended words. At the same time, we hypothesized that other brain areas would support some level of word encoding in inattention situations (e.g. Raichle et al., 1994), a result which would be in agreement with previous reports (Mack et al., 2001; Ruz et al., *in press*). In this way, we expected to extend the knowledge on the effect of attention on brain dynamics related to word encoding in high attentional load situations.

## METHODS

### *Subjects*

Twelve paid subjects gave written consent to participate in the study. All reported right-handedness, normal or corrected to normal vision, and were monolingual English speakers. The Institutional Review Board of the Weill Medical College of Cornell University approved the protocol of the study.

### *Stimuli and apparatus*

Sixty five-letter words were selected from the Kucera and Francis (1967) database (60 mean frequency), 70 strings of five consonants were created and one hundred drawings were selected from the Snodgrass and Vanderwart (1980) set. Words were divided in four lists matched in mean frequency that were used as attended words, ignored words and foils for the recognition memory test. The same stimuli (drawings, words and nonwords) were presented 11.5 times on average across the repetition detection task. All material was counterbalanced across subjects and conditions.

Participants saw a rapid stream of sequentially presented stimuli (each lasting 250 ms presented every 500 ms with a jitter of +/- 100 ms between presentations)[1], consisting of green drawings and overlapping red letters of approximately $5^{o}$ of

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[1] This jitter was used to make the paradigm compatible with an electrophysiological study using the same task (Ruz et al., 2005, *J Cog Neurosc*, 17, 768-776) and not for event-related fMRI purposes.

visual angle (see Fig. 1). Stimulus presentation was done using a PC running E-Prime v1.0 (PST, Pittsburgh, PA) with a screen refresh rate of 60 Hz.

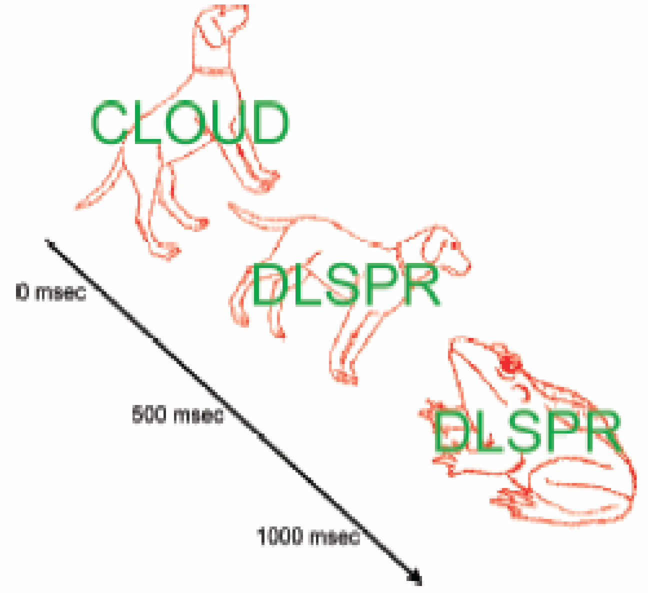

**Figura 1.** Experimental procedure for the repetition detection task. Stimuli were presented foveally for 250 msec as subjects monitored for a repetition in the attended dimension (letters or pictures).

### *Procedure*

During four separate runs, lasting 4 minutes 48 seconds, alternating instructions directed the attention to either letters or pictures. Participants were instructed to attend either to the drawings or to the letters and to press a button every time a stimulus repeated in the attended dimension. Each run was composed of eight 36-second interleaved task and rest blocks. Half of the blocks contained only nonwords whereas the other half had 60% words and 40% nonwords in the letter dimension. In all cases, the first eight trials always contained nonwords. Immediately after the repetition detection task, participants performed a surprise memory test. Sixty words (attended and unattended words together with 30 foils) were presented in the center of the computer screen after a 1000 ms fixation point. Participants were asked to respond by a button press as to whether they thought they had seen that word during the repetition detection task or not. The response of the participant erased the word from the screen and initiated the next trial.

### *fMRI acquisition*

We used a 3 Tesla whole body fMRI system for the acquisition of a T2*-weighted gradient echo planar imaging (EPI) sequence sensitive to the BOLD contrast [TR=4000, TE= 35 ms, flip angle 90º, with a matrix of 64 x 64 and field of view (FOV) of 200 mm (voxel size of 3.125 x 3.125 mm)]. We acquired 42 3.5 mm thick contiguous axial slices along the AC-PC plane as determined by the mid-saggital section. T1-weighted anatomical high-resolution structural images were acquired (TR= 2300, TE= min full, flip angle 20º, matrix of 256 x 160 matrix and FOV of 240 mm; 124 contiguous axial slices of1.5 mm thickness) for each participant. Also, T2-weighted anatomical images in the same orientation as the functional images (TR = 3.3 sec, TE = 68 ms, data matrix 256 x 192) were obtained for individual coregistration of functional scans with high-resolution structural data.

### *Image preprocessing and statistical analyses*

Image processing was performed with SPM2 (Welcome Department of Imaging Neuroscience, University of London, London, UK). Functional images were realigned using a least squares approach and a six parameter (rigid body) spatial transformation to correct motion artifacts. EPI images were registered to each participant's T1-weighted structural images and then transitively to the high-resolution images. For group analysis purposes, the high-resolution structural images were normalized to MNI space and the resultant transformation parameters were then applied to the functional images. Voxels were resampled to a 2 $mm^3$ size for normalization, and a 8 $mm^3$ full width at half maximum Gaussian kernel was used to smooth the EPI images.

Statistical analysis was performed with a General Linear Model for each participant with regressors for each of the four conditions (attended words, attended nonwords, unattended words, and unattended nonwords) convolved with the standard hemodynamic response function, and covariates for the six motion realignment parameters. High-pass filtering (128 seconds) for low frequency variation was applied and global changes in signal intensity were removed by proportional scaling. The weighted sums of the beta weights for the four conditions for each subject (resulting from the combination of the factors of Attention and Lexical category of strings) were used as inputs to a random-effects ANOVA. Thresholds of $p<0.001$ (uncorrected) were imposed except where specified. To avoid false-positives, only clusters with more than 20 contiguous voxels were considered.

## RESULTS

### *Behavioral results*

Participants responded to 69.3% immediate letter string repetitions while under attend letter instructions, and to 72.9% of picture repetitions while under attend drawings instructions. A within-subjects ANOVA performed on these data including factors for Attention (Attended Letters vs. Attended Drawings) and Lexical Status (Words vs. Nonwords), showed no effect of Attention, $F(1,11) = 1.099$, $p>0.316$ or Lexical Status, $F(1,11) = 1.883$, $p>0.19$, and demonstrated no interaction between the two factors, $F<1$. Although the interaction was not significant for d prime ($F(1,11) = 2.533$, $p>0.13$), based on our a-priori predictions we conducted simple comparisons that revealed higher sensitivity in word blocks (3.5) than in nonword blocks (2.7) when letters were attended, $F(1,11) = 6.87$, $p<0.05$, whereas this was not true when letters were ignored (4.3 vs. 4.6, $F<1$). To ensure that all participants were accurate in following the attention instructions in every block, we conducted an 'inverse d prime' analysis for each participant in which hits were defined as responses to repetitions in the unattended domain and false alarms as responses in all trials in which there was no repetition in the unattended stream. The average of this measure across blocks was -0.13 (range –0.73 to 0.6), showing that in no block did any participant respond to the unattended modality. Reaction time (RT) was 531 ms for letter strings and 509 ms for drawings. The same ANOVA as before revealed that neither Attention ($F(1,11) = 1.97$, $p<0.19$) nor Lexicallity ($F(1,11) = 3.32$, $p>0.09$) were significant, although the interaction between the two variables was, $F(1,11) = 6.66$, $p<0.05$. This was so because whereas words and nonwords differed in RT when they were attended, 548 ms. vs. 513 ms, $F(1,11) = 5.67$, $p<0.05$, they did not differ when they were ignored (506 vs. 511, $F<1$). Finally, in the surprise memory test, word recognition accuracy was high for attended words (81% of 'yes' responses, MSE: 0.11) and significantly different from that of ignored words (20%; MSE: 0.11; $F(1,11) = 152.5$, $p<0.001$) or foils (18%; MSE: 0.13; $F(1,11) = 135.4$, $p<0.001$). Responses to ignored words and foils were statistically equivalent, $F<1$ (see Figure 2).

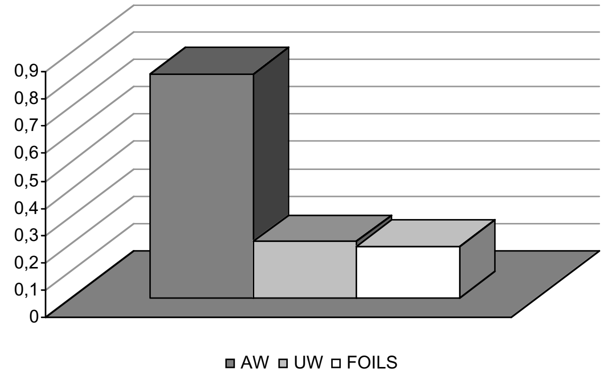

**Figura 2.** Results of the unexpected recognition memory test following the experiment, displayed as percentage of endorsements for recognized words ('yes' responses) for stimuli previously presented attended words (AW), unattended words (UW) and foils. Words previously encountered in the AW condition were correctly recognized a high proportion of trials, whereas words presented under unattended conditions produced no measurable memory trace above the false alarm rate of the foils.

### *fMRI results*

The top-down focus of attention, as manipulated by the letter versus picture instructions, had a profound impact on BOLD response. When attention was focused on letters, bilateral frontal regions and the left inferior parietal lobule recorded greater activity than when participants attended to drawings (see Table 1, Figure 3). Alternatively, when pictures were task-relevant, more posterior and sub-cortical regions were recruited, including the fusiform gyrus, insula, and superior temporal

Table 1. Main Effect of Attention Letters > Drawings

| Anatomical Area | Cluster Peak (xyz) | | | z | k |
|---|---|---|---|---|---|
| Cingulate Gyrus | 10 | 29 | 28 | 4.15 | 194 |
| R Medial Frontal Gyrus | 6 | 35 | 33 | 3.86 | |
| L Medial Frontal Gyrus | -6 | 33 | 30 | 3.59 | |
| R Superior Frontal Gyrus | 42 | 48 | 22 | 3.57 | 23 |
| | 32 | 42 | 27* | 3.28 | |
| L Inferior Parietal Lobule | -55 | -35 | 46* | 2.65 | 22 |
| L Middle Frontal Gyrus | -53 | 19 | 27* | 2.53 | 82 |

p < .001 uncorrected * denotes p < .01
Talairach coordinates. L = Left R = Right (for all tables)

Table 2. Main Effect of Attention Drawings > Letters

| Anatomical Area | Cluster Peak (xyz) | | | z | k |
|---|---|---|---|---|---|
| R Cuneus | 20 | -86 | 21 | 4.40 | 60 |
| L Postcentral Gyrus | -40 | -36 | 59 | 3.43 | 35 |
| L Hippocampus | -22 | -18 | -9 | 3.39 | 84 |
| L Precentral Gyrus | -16 | -8 | 69 | 3.36 | 77 |
| R Middle Occipital Gyrus | 50 | -57 | -4 | 3.22 | 45 |
| R Fusiform Gyrus | 44 | -65 | 10 | 2.76 | |
| L Superior Temporal Gyrus/Insula | -46 | -14 | 1 | 3.10 | 126 |
| L Precuneus | -8 | -59 | 23 | 3.10 | 28 |
| R Superior Temporal Gyrus | 51 | 0 | 2 | 3.05 | 382 |
| R Insula | 38 | -17 | 3 | 3.04 | |
| R Hippocampus | 30 | -20 | -9 | 2.87 | |

p < .005 uncorrected

Table 3. Attention by lexicality interactions

| Anatomical Area | Cluster Peak (xyz) | | | z | k |
|---|---|---|---|---|---|
| R Globus Pallidus | 24 | -8 | -1 | 4.38 | 245 |
| | 20 | -14 | -4 | 3.74 | |
| R Hippocampus | 30 | -14 | -8 | 3.38 | |
| L Thalamus | -24 | -19 | 8 | 4.03 | 311 |
| L Pulvinar | -10 | -27 | 9 | 3.87 | |
| L Claustrum | -36 | -18 | -4 | 3.63 | 130 |
| L Lentiform Nucleus | -30 | -8 | 0 | 3.40 | |
| R Superior Parietal Lobule | 26 | -49 | 60 | 3.35 | 20 |
| R Insula | 28 | -25 | 9 | 3.34 | 24 |
| R Precuneus | 6 | -68 | 38 | 3.75 | 184 |
| R Supramarginal Gyrus | 59 | -49 | 23 | 3.63 | 197 |
| L Superior Parietal Lobule | -38 | -54 | 49 | 3.45 | 138 |
| L Inferior Parietal Lobule | -38 | -51 | 38 | 3.43 | |

p < .001 uncorrected

gyrus bilaterally (see Table 2, Figure 3). Table 3 shows the regions sensitive to the attention by lexicality interactions.

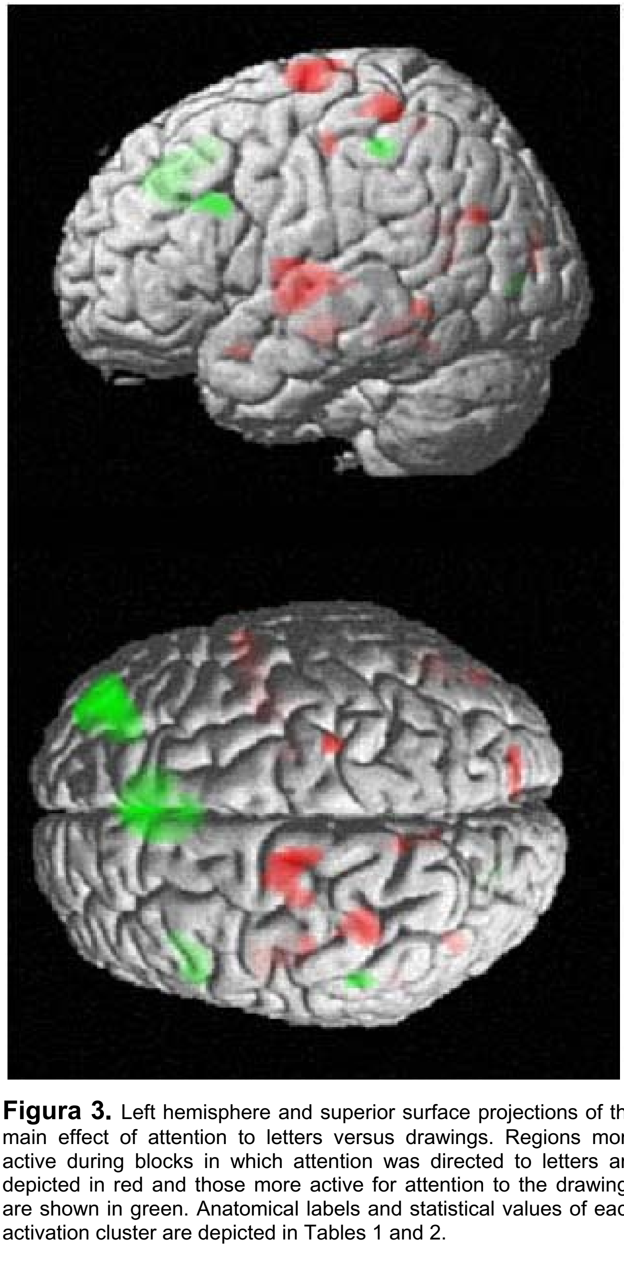

**Figura 3.** Left hemisphere and superior surface projections of the main effect of attention to letters versus drawings. Regions more active during blocks in which attention was directed to letters are depicted in red and those more active for attention to the drawings are shown in green. Anatomical labels and statistical values of each activation cluster are depicted in Tables 1 and 2.

Attending to blocks containing words, in contrast to nonwords, resulted in greater activity in left inferior frontal and superior/middle temporal regions, as well as the right precuneus extending to the right posterior cingulate (see Table 4, Figure 4). A smaller cluster than the specified threshold (19 voxels) was also observed in the right inferior frontal gyrus. To investigate the possibility of the involvement of any of these regions in the ignored word vs. the ignored nonword blocks, we created a mask including those areas above p=0.01 (uncorrected) for the attended words greater than attended nonword contrast and used this to look for voxels showing greater response to unattended words over unattended nonwords. Not a single voxel was activated in these masked areas, even when the threshold was lowered to p<0.05 (uncorrected). To account for individual variability we repeated the procedure but masked the data on an individual subject level, with the same lack of overlap for attended and ignored word-related activation.

In the critical contrast of the study, when a whole brain volume search was conducted unattended words yielded clusters of activation in many other regions, mainly subcortical, when compared to unattended nonword blocks (see Table 5, Figure 4). The left insula, bilateral pulvinar and superior temporal gyri, together with the right cerebellum and putamen were more active during the presentation of unattended words. None of these regions were present in the contrast showing voxels greater for attended words than attended strings (AW>AS). Furthermore, an additional conjunction analysis was run to examine voxels that conjointly activated in this contrast as well as the contrast between UW and fixation[2]. Two sets of activations, the left insula and bilateral pulvinar, passed this additional test, providing further evidence that not only do such regions demonstrate sensitivity to the lexicality of ignored strings but also reflect increased responsiveness to ignored words.

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[2] Activations found for UW>US could be a result of increases in UW activation relative to baseline, or deactivations of US relative to baseline. To identify the regions specifically tied to UW-related increases, an implicit mask generated from UW>baseline, p<.01 (uncorrected) was used to query UW>US, p<.001.

**Table 4.** AW>AS sensitivity regions

| **Anatomical Area** | **Cluster Peak (xyz)** | | | **z** | **k** |
|---|---|---|---|---|---|
| L Inferior Frontal Gyrus | -42 | 21 | 27 | 3.75 | 239 |
| L Superior/Middle Temporal Gyrus | -57 | -46 | -13 | 3.06 | 61 |
| | -53 | -62 | 12 | 2.96 | |
| R Precuneus | 14 | -51 | 32 | 3.03 | 129 |

p < .005 uncorrected

**Table 5. UW>US sensitive regions**

| **Anatomical Area** | **Cluster Peak (xyz)** | | | **z** | **k** |
|---|---|---|---|---|---|
| L Insula | -42 | 4 | -2 | 4.36 | 207 |
| | -38 | -10 | 0 | 3.39 | |
| L Superior Temporal Gyrus | -52 | -2 | -2 | 3.40 | |
| R Cerebellum (Culmen) | 14 | -45 | -3 | 3.78 | 241 |
| L Pulvinar | -8 | -25 | 5 | 3.53 | |
| R Lingual Gyrus | 4 | -33 | -2 | 3.37 | |
| R Putamen | 30 | 0 | -8 | 4.21 | 47 |
| R Superior Temporal Gyrus | 48 | 9 | -7 | 3.43 | 35 |
| R Thalamus | 10 | -4 | 0 | 3.50 | 23 |

p < .001 uncorrected

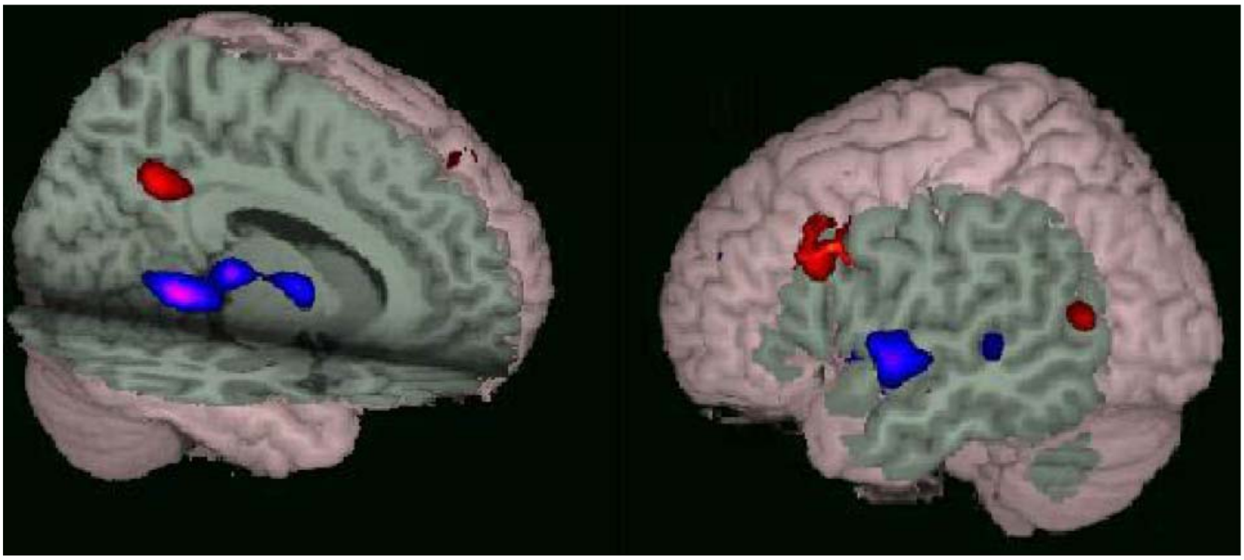

**Figura 4.** Cutaway image depicts the right and left hemisphere activations in cortical and subcortical regions for the words vs nonwords contrast within the attend letters condition (displayed in red) and words vs. nonwords contrast within the attend drawings condition (displayed in blue). Anatomical labels and statistical values of each activation cluster are depicted in Tables 4 and 5. The coloring of regions is due to contours and not a representation of significance.

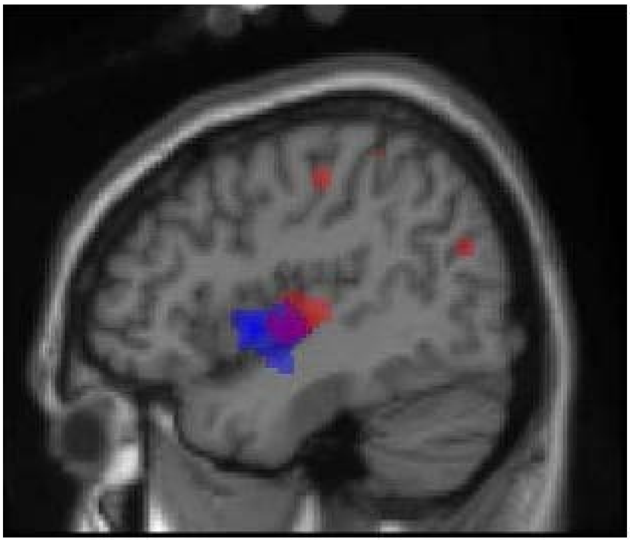

**Figura 5.** Mid-saggital image (x = -45) showing the partial overlap between the global contrast of attention to drawings > attention to letters (in red) and the specific contrast of words > nonwords under the attend drawings condition (=in blue). Note the main region of overlap between these two findings lies in insular regions.

## DISCUSSION

The present study shows the dramatic effect of the focus of attention on patterns of BOLD response during high attentional load tasks. Despite identical stimulus presentations, attention to letters generated activations in frontal and parietal regions whereas attention to drawings uniquely restricted activation to occipital and temporal regions (see Figure 4). The interaction between the attended dimension and the lexical status of letter strings involved many areas that responded differentially to words and nonwords, depending on the focus of attention. When letters were attended to, a set of language-relevant areas including left inferior prefrontal, left superior temporal and right precuneus differentiated words from nonwords. When the same items were ignored, these areas were no longer activated by this stimulus contrast and instead a completely different set of brain structures, including left insula, right cerebellum, thalamus and putamen, differentiated words from consonant strings. These results suggest that fully removing attention from letters may lead to some form of suppression of word-specific responses in typically activated areas and the involvement of supplementary brain regions influential in modulation of information processing and sensitive to word stimuli[3].

Behavioral results support the successful manipulation of attention and the high load nature of this task. On-line indices of performance show that word-nonword differences were evident when attending to letters, in the sense that participants were more sensitive to repetitions of words than nonwords (d prime 3.5 vs. 2.7). However, when participants were attending to drawings, the presence of words or nonwords in the unattended letter dimension had no effect in performance, as assessed by either response latency or d prime. This lack of interference from unattended items is a common pattern for ignored information in high perceptual load situations (Lavie, 1995) and has previously been used as evidence for absence of irrelevant item processing in this kind of tasks (e.g. Rees and Lavie, 2001; Lavie, 2005). Similarly, results point to the important role of attention in memory formation, in the sense that recognition of attended words was high (80% of 'yes' responses) whereas ignored words were no different from foils (20 vs. 18% of 'yes' responses). Thus, both behavioral and brain activation indices suggest that the instructional manipulation was effective in directing participants' attention to the two different stimulus dimensions and that this had the effect of fully withdrawing attention from the ignored domain.

Results of the present study are consistent with previous effects showing that attention has a large

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[3] Eye-movements are not a likely source of differences between conditions given the anatomy of the results. Furthermore, although they were not monitored during the fMRI session, a previous ERP study using the same paradigm (Ruz et al., *in press*) showed that eye movements were minimal in all conditions (less than 3% of trials for every participant). In addition, the short stimulus presentation time (250 ms) and short ISI were selected in part to discourage eye movement during each presentation, and to reduce the likelihood that such eye movements could provide a strategic benefit for the repetition detection task.

impact on brain dynamics in high attentional load situations. Previous neuroimaging results have shown that brain regions sensitive to the presence of irrelevant information during low-demand conditions cease to respond when perceptual demands are high (Rees et al., 1997; Rees et al., 1999; O'Connor et al., 2002; Pinsk et al., 2004; Yi et al., 2004). Among investigations suggesting that high load prevents processing of ignored information, one particular study (i.e. Rees et al., 1999) is especially relevant to the present investigation. Although a large subset of the current findings replicate the results of this previous study, the partial volume approach used by Rees et al. (1999, see note 18) may have restricted their analysis of ignored word vs. ignored nonword activations to only those regions first demonstrating sensitivity to attended words vs. attended nonwords. However, such a restriction rests on the implicit assumption that any word-specific activity under the attended pictures condition should belong to the set of areas involved in word processing when letters are attended.

In our study, attending to letters generated more activation for words than nonwords in a set of brain areas previously shown to be related to language processing (for reviews see Price, 2000; Martin, 2003). The role of left inferior frontal areas in semantic retrieval has been shown several times (i.e. Cabeza and Nyberg, 2000) and there is some consensus on the association of this area with effortful semantic processing (Price, 2000; Pugh et al., 2000). Phonological processes have been linked to the resonsiivity in the superior temporal regions (Pugh et al.,2000). The precuneus is activated in many situations requiring attention to phonology (e.g. McDermott, Petersen, Watson and Ojemann, 2003), phonological working memory (Zurowski et al., 2002), detection of accents (Berman, Mandelkern, Phan and Zaidel, 2003) or auditory word priming (Kotz, Cappa, von Cramon and Friederici, 2002) and imagery of letters (Raij, 1999).

From previous literature, it would be expected to obtain basal temporal activations for this contrast. The Visual Word Form area is a fusiform region that is tuned to respond to the regularities of written words in a bottom-up manner (McCandliss, Cohen and Dehaene, 2001) and has been shown to be responsive even to unconscious words (Dehaene et al., 2001)[4]. However, the present task was not designed to study word encoding per se and thus it is not suited to draw strong inferences about bottom-up word related activation in normal reading conditions. For example, letters appeared in light green and overlapped with red drawings to prevent automatic capture by salient items. This spatial overlap could have led to competition for resources between letters and drawings, given the closeness of the representation of these items in fusiform regions (e.g. Gathers and Piper, 2003). Moreover, higher saliency of red colored drawings could have given advantage in the competition with the green letters and result in a lack of availability of resources for letters in these regions. Additionally, previous research has shown that the rate of item presentation modifies the pattern of language-related activations (Price, Moore and Frackowiak, 1996; Mechelli, Friston and Price, 2003), and the fast rate in our study was not optimized to activate all word encoding areas. Indeed, unpublished results from our laboratory show that participants performing the same one-back task but with items presented at a slower pace and without the distracting drawings do show VWFA activation as expected, in agreement with published results (e.g. Pugh et al., 2000).

Regions found in the current experiment more active for words as compared to nonwords when attention was focused on drawings have been implicated in many language studies, although their specific roles remain less clear. For example, left insular activations have been reported in practiced verb generation (Raichle et al., 1994), second language learning (Raboyeau et al., 2004) and proficiency in a second language (Chee, Soon, Lee and Pallier, 2004), low frequency word processing (Fiebach, Friederichi, Muller and von Cramon, 2002), verbal working memory (Derrfuss, Brass and von Cramon, 2004), and

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[4] Indeed, we do find liberal threshold activation in fusiform regions for the attended word-nonword contrast. At $p<0.03$, uncorrected, we find activation peaking at the -40, -54, -8 Talairach coordinates encompassing 48 voxels.

Chinese character reading (e.g. Lee et al., 2004; Zhang et al., 2004). The right hemisphere of the cerebellum, connected to left cerebrum hemisphere, is also found in many studies related to language learning (Raboyeau et al., 2004) word generation (Raichle et al., 1994), memory retrieval (Andreasen et al., 1995; Buckner, Raichle, Miezin and Petersen, 1996), lexical-semantic tasks (Roskies et al., 2001) and verbal fluency/lexical retrieval (see Justus and Ivry, 2001). The activation of the thalamus in language paradigms in not uncommon (i.e. Fiebach et al., 2002) and has been linked to acquisition of semantic information (Maguire and Frith, 2004) and language learning (Jarvis, 2004). The putamen, on the other hand, has been activated in word generation tasks (Crosson et al., 2003), language-based counting (Hinton et al., 2004), and is sensitive to semantic priming (Rossell, Bullmore, Williams and David, 2001) and syntactic violations (Friederici, Ruschemeyer, Hahne and Fiebach, 2003). Note, however, that these regions may subserve different roles outside language that could be relevant to explaining our results. For example, the insula has been found activated in several tasks involving cognitive control (Wager and Felman-Barret, unpublished manuscript) and also when the expected trial type changes (Casey et al., 2000). The pulvinar nucleus, on the other hand, is a key structure in attentional deployment and it seems to be especially relevant in situations in which attended and ignore information overlap or compete (e.g. Danzinger, 2004; and for full discussion see Michael and Desmedt, 2004).

The present study directly tested the possibility of an alternative pathway involved in word processing when letters are ignored. Our experiment, which represents a close implementation of the Rees et al. (1999) inattentional blindness paradigm, shows a similar outcome when a partial search volume is conducted, in the sense that any of the regions activated by the attended word-nonword contrast is influenced by lexicality in the attention to pictures condition. However, when a whole brain search strategy is employed instead, a set of regions is found to be involved in differentiating between unattended words and nonwords. Therefore, our results do not support the conclusion derived from the original study that visual word recognition is fully dependent on attentional resources. Instead, results suggest that word-related information modulates different pathways according to attention allocation and generates differential effects on performance depending on task context.

While the critical contrast between unattended words vs. nonwords provides compelling evidence of some sensitivity to lexical status under these high attentional load conditions, deriving precise links between the specific brain regions implicated and the particular cognitive processes engaged by these two different conditions is limited however by a number of considerations. The current paradigm does not allow us to resolve whether the activations observed in response to ignored words reflect lexical processes triggered by these items or rather the impact that lexical activation might have on picture matching, such as a general effect of processing in the face of irrelevantly activated information, or even more specific competition between semantic entries activated by the simultaneous presence of words and pictures. For example, the activation of an attention-related nucleus such as the pulvinar specifically related to the presentation of unattended words could be indicating a higher need to resolve competition, semantic or otherwise, due to the presence of ignored words.

Some aspects of the current results, however, are not consistent with the notion that ignored lexical information led to increased competition or increased task difficulty for the matching condition First, if responding to drawings requires that the representations of words are inhibited, the areas that need to be suppressed are those that differentially process words and nonwords when these are attended to (that is, it makes no sense to inhibit an area that is not activated when responding to words). Hence, we would expect to find inhibition-related activation in the same areas that were activated by this contrast during attention to letters. Results show, however, that there is no region overlap for this contrast between the two attention conditions. On the other hand, there is no reason to suspect that words were generating interference when they were ignored as any of the performance indices obtained is sensitive to this word-nonword variable when attention was focused on drawings. That is, accuracy, RT and d prime (and conversely false alarm rate) were statistically equivalent for the attend drawings condition regardless of the lexical nature of the ignored letter strings. Such findings fail to support an explanation of the critical UW>US activation contrast in terms of differential interference or semantic competition upon the primary task.

There are other considerations relevant to further interpretation beyond evidence of lexical sensitivity for ignored letter strings. The use of a block design, compelled by our replication strategy, leaves open the question of the time-course of the effects. For example, it is currently unknown whether our results are specifically induced by each ignored word or represent more tonic processes present throughout the block, perhaps related to overall differences in block context (see Chawla et al., 1999 for discussion). Although the current fMRI design cannot resolve such issues, our previous ERP study using the same task however, demonstrated rapid processing differences time-locked to stimulus onsets of ignored words and nonwords presented during the same block (Ruz et al., in press). On the other hand, nonwords are harder to process than words. This pattern confirmed by behavioral data when letters were attended. Note, however, that when attention was tied to drawings the presentation of words vs. nonwords did not affect any behavioral index of performance. Thus, differences in difficulty between the two kinds of stimuli could be contributing to attended word vs. nonword BOLD differences but not to those revealed when letters were ignored. Another consideration for interpreting the neuroimaging results is that the paradigm required the items to be repeated frequently (but see Ruz et al., *in press*, Experiment 2). Stimulus repetition is known to enhance explicit memory of attended items and to change brain activations in several ways (see Henson, 2003), and thus this manipulation should be relevant to our results. However, stimulus repetition was constant across our variables, so it does not represent a source of contamination.

More generally, the finding of different brain pathways in performing a task under conditions that manipulate effortful versus automatic processing is not unprecedented, as similar effects have been frequently demonstrated in learning situations (see Petersen, van Mier, Fiez and Raichle, 1998). For example, practice-related effects in the verb generation task described by Raichle and colleagues (1994) are paradigmatic in the field. In this landmark study, participants were asked to verbally generate uses for common nouns (versus a control task of reading the nouns aloud). Brain regions recruited in during the initial unpracticed state included left inferior prefrontal and cerebellum. However, after a few minutes of practice, overt responses became faster and stereotyped, and BOLD indices in these regions were no longer sensitive to the instructional manipulation (i.e. generate versus read), yet other regions including the left insula demonstrate increased sensitivity to verb generation. Similar practice related changes in brain pathways have been replicated several times in other learning paradigms (e.g. van Mier et al., 1998; Korman, Raz, Flash and Karni, 2003). Explanations for this phenomenon rely on differences in computations used when performing an attention-demanding novel task and the easier automatic processing that takes place after practice. When participants are not skilled with a task, a set of effortful processes is employed to cope with the situation. With practice, however, a more automated processing strategy is adopted, which leads to more accurate and faster performance. This processing shift is accompanied by a change in neural pathways recruited to support the altered processing strategy.

In the present study, practice levels were the same in the two attention conditions. However, attention was tightly focused in the letter domain in one situation and fully withdrawn from it in the other. The fact that both letters and drawings were presented in overlapping spatial positions in a highly demanding task most likely led to strong competition between the two dimensions

(Desimone and Duncan, 1995). This competition could have been heightened by the foveal position of items, as it has been previously shown that suppression of information in inattentional blindness paradigms is much more pronounced when items are presented at fixation relative to more peripheral locations (see Mack and Rock, 1998). In our experiment, attention to letters and drawings directed resources to different brain regions to successfully perform the task. This distribution of resources could be responsible for allowing only a set of brain regions to respond to the word-nonword contrast, in the sense that only regions activated by the attention task would have available resources to differentiate between words and nonwords. Results provide some support for this notion, given that there was a partial overlap between the regions more activated when attention was directed to drawings and those more active for ignored words than nonwords in this attention condition (see Figure 5). The reverse is also true, although to a lesser extent, when attention was focused on letters. This hypothesis is reinforced by the fact that even when the threshold was reduced to $p<0.05$ uncorrected, none of the regions more active for attended letter blocks was involved in the unattended word-nonword contrast, and vice versa when drawings were the focus of attention.

Our results suggest that in conditions of high attentional load, brain resources route to different pathways in response to task demands. The analysis of word stimuli by these different processing pathways produces different behavioral and neural effects. In the present study, attention to letters activated a set of language-relevant areas, partially overlapping with those more activated for words than nonwords. This generated more efficient responses to words than nonwords and allowed a consolidation in explicit memory for attended words[5]. In contrast, when attention was directed to drawings, the competition with letters directed resources to a different set of brain regions and this allowed a different and non-overlapping subset of areas to respond differentially to words and nonwords, although these activations did not have any effect on behavioral measures, most likely because in that condition behavior was being guided by regions related to the processing of the drawings.

In summary, the present study adds to previous literature suggesting the existence of some level of word processing even in strict inattention situations that lead to symptoms of inattention amnesia. Critically, we find that pathways responsive to word processing may change depending on the focus of attention. Future research will need to show whether this dramatic effect of attention on brain dynamics and performance is limited to the fast presentation parameters and stimulus contrasts (words vs. nonwords) of the present experiment or can be generalized to other high perceptual load task paradigms dealing with domains outside language.

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