

Université de Montréal

Effects of Emotional Salience and Semantic Domain on Cross-form Priming

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Université de Montréal
Faculté des études supérieures

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Résumé

La mémoire implicite est révélée par des tâches indirectes (par exemple, l'amorçage) qui ne nécessitent pas de récupération consciente. L'amorçage constitue une augmentation de l'efficacité de traitement d'un stimulus ou d'un concept suite à une exposition au même stimulus ou concept. L'amorçage d'identité trans-forme (AITF) est un paradigme dans lequel seule la nature conceptuelle du stimulus est répétée entre les phases d'étude et de test. À ce titre, cette forme d'amorçage est liée à la mémoire implicite conceptuelle.

Motivés par une perspective évolutionniste, nous avons utilisé un paradigme d'AITF (amorçage des mots par des images) dans le but d'évaluer si certaines variables ayant des effets sur la mémoire explicite et la mémoire sémantique ont également des effets sur la mémoire implicite. En se basant sur les atteintes catégorielles sémantiques observées de façon sélective chez certains patients cérébrolésés, nous avons comparé, dans l'Étude #1, l'AITF pour des items appartenant aux catégories objets "vivants" et "non-vivants". D'autre part, le rappel en mémoire à long terme semble meilleur pour les stimuli ou évènements chargés émotionnellement. Dans l'Étude #2 nous avons investigué si la charge émotionnelle exerce un impact sur l'AITF. Enfin, dans l'Étude #3, nous avons investigué le substrat neuronal de l'AITF subliminal en utilisant l'imagerie fonctionnelle par résonance magnétique (IRMf).

L'Étude #1 a démontré que les items vivants amènent un effet d'AITF plus important. Ce résultat est en accord avec l'hypothèse selon laquelle les items appartenant à la catégorie "vivants" sont traités de façon spéciale par le système sémantique. Une interprétation de cet effet est que les items de la catégorie "vivants" sont traités de façon plus profonde, peut-être à cause de leur importance au point de vue émotionnel. L'Étude #2 a démontré un effet d'AITF plus important pour les items émotionnels négatifs que pour les items émotionnels positifs ou neutres. Nous avons interprété cet effet comme étant le résultat d'un traitement plus profond car les items émotionnels négatifs constituent des possibilités de menace à la survie des humains. L'Étude #3 a révélé un effet d'AITF subliminal significatif. Sur le plan comportemental, les résultats renforcent l'hypothèse voulant que les stimuli perçus de façon inconsciente sont également traités de façon profonde. Les résultats obtenus à l'aide de l'IRMf ont démontré que des aires corticales (cortex occipitotemporal bilatéral, gyrus temporal antéro-supérieur) impliquées au niveau de la mémoire sémantique jouent un rôle dans l'AITF subliminal. Les résultats de ces trois articles renforcent au niveau théorique les perspectives « activationnelles » de la mémoire implicite.

Mots-clefs: subliminal, forme, amorçage conceptuel, domaine sémantique, saillance émotionnelle, IRMf.

Summary

Implicit memory is revealed by indirect (i.e., priming) tests which do not necessitate effortful retrieval. In priming, an increase in processing efficiency is measured for a previously encountered stimulus or concept. In cross-form identity priming (CFIP), stimulus form is varied from study to test. CFIP reflects conceptual implicit memory because only the conceptual identity denoted by the stimulus is repeated between prime and target.

Motivated by an evolutionary perspective, we used a CFIP paradigm (picture-to-word priming) to investigate whether variables known to impact on explicit and semantic memory would also impact on the strength of implicit memory. Based on findings of category-specific semantic memory impairments recorded among brain-damaged patients, in Study #1, we examined whether items from the domain of living things would show greater CFIP than nonliving items. A separate line of research has shown that long-term memory is enhanced for emotionally salient events or stimuli. In light of this data, we investigated, in Study #2, whether emotional salience would impact on the magnitude of CFIP. Finally, in Study #3, we investigated the neural underpinnings of subliminal CFIP using fMRI.

Study #1 revealed that items belonging to the “living” category led to greater CFIP. This finding is in line with the assumption that the semantic system is particularly tuned to the identification and processing of “living” things. One interpretation of

this effect is that the living items were more deeply processed, possibly because of their increased emotional salience. Study #2 revealed greater CFIP for emotionally negative versus emotionally neutral or positive stimuli. We posit that this difference may be related to spontaneously deeper processing for negative items because they are more likely to conjure real-world items or situations which could be dangerous to the observer. Study #3 found significant subliminal CFIP in a paradigm which eliminates the risk of contamination by explicit memory. Behavioral results bolster claims that unconsciously perceived stimuli can be deeply processed. fMRI results reveal that areas known to be involved in semantic processing (bilateral occipitotemporal and the left anterior superior temporal cortex) play a role in subliminal CFIP. Theoretically, our CFIP results support activational accounts of priming.

Keywords: subliminal, cross-form, conceptual, priming, semantic domain, emotional salience, fMRI

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List of Abbreviations

AC-PC	Anterior commissure – posterior commissure
ANEW	Affective Norms for English Words
ANOVA	Analysis of variance
BA	Brodmann area
BOLD	Blood-oxygen-level-dependent
CFIP	Cross-form identity priming
CS	Conditioned stimulus
DSH	Domain-specific hypothesis
EPI	Echo-planar imaging
ERP	Event-related potential
FMRI	Functional magnetic resonance imaging
FOV	Field of view
FWHM	Full width half maximum
HRF	Hemodynamic response function
IAPS	International affective picture system
MIN	Minute
MM	Millimeter
MR	Magnetic resonance
MRI	Magnetic resonance imaging
MS	Millisecond
OUCH	Organized unitary content hypothesis
PC	Personal computer
PET	Positron emission tomography
PW	Picture-Word
ROI	Region of interest
RS	Repetition suppression
RT	Response time
SD	Standard deviation
SFT	Sensory-functional theory
SOA	Stimulus onset asynchrony
SPM	Statistical parametric map
SVC	Small volume correction
TE	Echo time
TR	Scan repeat time
UCS	Unconditioned stimulus
WIP	Word-image pair
WP	Word-Picture

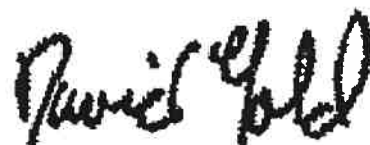
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A handwritten signature in black ink that reads "David Gold". The signature is written in a cursive, slightly slanted style.

Chapter 1: General Introduction

“It is reasonable to assume ... that priming represents a ubiquitous occurrence in everyday life” (Tulving and Schacter, 1990)

Introduction

Over the past five decades or so, various lines of research have converged to reveal that memory is not a unitary phenomenon (Schacter, 1992a; Schacter et al., 1993). Whereas the function of memory is undoubtedly one of enabling organisms to more efficiently navigate their environment by, among other things, learning from mistakes, not all forms of memory do so in the same way. One clear division is between implicit (or nondeclarative) memory and explicit (or declarative) memory (Graf and Schacter, 1985; Squire, 1982; Squire, 1994; Tulving and Donaldson, 1972). In tests of explicit memory, direct reference is made to a learning episode and a conscious effort to recall (or to recognize) an event or stimulus is required. In contrast, implicit memory is revealed by indirect tests which do not necessitate the conscious or effortful recollection of a previous experience (Graf et al., 1984; Schacter, 1995).

The phenomenon of priming is often used to study implicit memory. Priming can be defined as an increase in processing efficiency for a previously encountered stimulus or concept (Bower, 1996; Cofer, 1967; Cramer, 1966; Gabrieli, 1998; Schacter, 1992a; Shimamura, 1986; Tulving and Schacter, 1990). Typically, a studied stimulus, the “prime” is repeatedly presented, and becomes the “target” when a response is required. Within the priming literature, a distinction has been made

between repetition (or “identity”) and semantic (or “associative”) priming (Neely, 1991). The difference between these two forms of priming lies in the relationship between the prime and the target. In semantic priming, a relationship such as category membership, conceptual relatedness, or semantic association exists between the prime and the target. For example, when the word “cat” primes the word “dog”, the two words are semantically related because both are animals, both are pets, and further, they tend to occur together (Fischler, 1977). Early on, Meyer and Schvaneveldt (1971) demonstrated that when two such semantically related words are presented together in a double lexical decision paradigm (the task being to decide whether both words are real), they are responded to more rapidly than when the words are unrelated (e.g., “nurse” and “butter”). Semantic priming research has underpinned network theories of semantic knowledge, and support the notion that related concepts are linked in an associative semantic network (Chang, 1986; Collins and Loftus, 1975).

In repetition priming, instead of priming taking place between two related concepts, the prime and target are identical. In the case of perceptual priming, the structural characteristics of the stimuli are not changed between study and test (Gabrieli et al., 1994). An example of a paradigm that evaluates this form of priming is the “tachistoscopic identification” task. In this task, after having been exposed to words in the study phase, subjects are instructed to identify very briefly presented words in the test phase. Priming is revealed to the extent that words encountered in the study phase are more easily identified in the test phase (Jacoby and Dallas, 1981; Jacoby, 1983). The priming demonstrated by such tasks is deemed to be perceptual because

study manipulations that affect explicit memory retrieval, such as depth-of-processing, have little or no effect on priming, and because study-test manipulations of the structural characteristics of the stimuli (such as changes in font) tend to reduce priming but have no effect on explicit retrieval (e.g., Blaxton, 1989; Graf and Ryan, 1990).

Tachistoscopic presentation has also been used to measure subliminal priming. The motivation for this branch of research is the fact that in most investigations, primes are presented explicitly, making it difficult to rule out the behavioral effects of explicit memory since subjects may spontaneously use explicit remembering of studied items in the supposedly implicit test phase. This situation, commonly referred to as contamination, has been discussed elsewhere (Bar and Biederman, 1998; Beaugard et al., 1997; Beaugard et al., 1999; Merikle and Reingold, 1991). Research has shown that subliminal priming may be used to circumvent possible contamination by rendering primes unconsciously perceivable. In subliminal priming, primes are presented below the level of conscious awareness, although their influence can nevertheless be measured later on (Evetts and Humphreys, 1981; Forster and Davis, 1984; Schacter, 1992a). Bar and Biederman (1998), for example, recently demonstrated that subliminal exposure to pictured objects leads to subsequent facilitation in the processing of those objects in a tachistoscopic identification paradigm. Subliminal priming, therefore, shows that even when a stimulus is not consciously perceived, it can still have an effect on subsequent processing of the same stimulus. One question which has arisen, however, regards the extent to which unconsciously perceived stimuli are nevertheless deeply processed. One of the

earliest studies suggesting that relatively deep processing can occur was performed by Marcel (1983), who showed that subliminal exposure to a word can speed the processing of a semantically related word. This issue is discussed in more detail in Study #3.

Although we have seen that repetition priming is often perceptually based, this needs not always be the case. Indeed, repetition priming can also be conceptual in nature. Such conceptual repetition priming may occur when the structural characteristics of stimuli are transformed between study and test. In cross-form priming, for example, a word is studied and then repeated in a new font, or a picture may be studied and a word may be presented at test. While removing the perceptual component often compromises the strength of the priming effect (e.g., Roediger et al., 1989), significant priming can nevertheless be demonstrated. In this case, because the only repetition between the prime and the target is one of identity (i.e., the concept denoted by the stimulus), a processing advantage at test must reflect enhanced conceptual processing efficiency (Hirshman et al., 1990). Indeed, some repetition priming paradigms are considered to reflect relatively pure forms of conceptual implicit memory (Dell'Acqua and Grainger, 1999; Moscovitch, 1992; Roediger and McDermott, 1993; Vaidya et al., 1997).

To capitalize on the conceptual processing advantage which is garnered by this repetition, most studies which have examined cross-form priming have used relatively conceptual tests such as speeded category membership or lexical decision, as opposed to perceptual tests such as tachistoscopic identification. These sorts of

tests are often used because response times (RTs) are hypothesized to be proportional to the cognitive load expended on the task (e.g., Rubenstein et al., 1971). In Vriezen et al. (1995), for example, category membership decisions to pictures were speeded by having previously made the same decisions to word forms of the very same concepts. Henceforth, priming between two differing forms of the same concept will be referred to as cross-form identity priming (CFIP).

In the current body of work, we have made exclusive use of CFIP in order to distill conceptual priming down to its essential. Rather than using some form of conditioning or relying on pre-existing relationships between concepts stored in semantic memory (as in semantic priming), we were interested in evaluating how variables endogenous to the to-be-remembered stimuli themselves would impact on the magnitude of CFIP. The motivation for this research question is discussed in detail below. First, however, a brief review of theoretical accounts of repetition priming is warranted. Because we were also interested in exploring the neural substrate of CFIP, a brief overview of the neural substrate subserving priming is presented.

Models of priming

Much research and theorizing has been undertaken in order to account for the cognitive nature of priming, and a brief review of theories pertinent to repetition priming is presented in the next section. Because the present work is concerned with

repetition priming, a detailed discussion of semantic priming is beyond its purview (for an in-depth review see Neely, 1991). What follows is a brief survey of theoretical models proposed to account for implicit memory phenomena.

There are a variety of models which have been presented to account for repetition priming. One of the earliest, the multiple memory systems view, posits that the sum of memory phenomena can be divided across a number of dissociable systems (Nadel, 1994; Schacter, 1992a; Schacter, 1992b; Squire, 1992; Squire, 1994; Tulving and Schacter, 1990). In Tulving and Schacter's (1990) influential view, four types of memory systems exist: one procedural, one semantic, one priming, and one episodic. Procedural memory is said to refer to the changes in skill performance that come with practice. It is thought to underlie the skills that are acquired when, for example, learning a new sport. Semantic memory refers to all the general knowledge that is shared by a culture (i.e., the knowledge that Elvis *is* dead). Episodic memory is comprised of all the personal memories that one has of experiences that they themselves have lived through. Tulving and Schacter (1990) account for repetition priming by proposing the existence of a pre-semantic "perceptual representation system" (PRS) which operates independently of episodic memory. Priming in this perspective is considered to exclusively engage perceptual processing (Schacter, 1992b). This view came largely from findings showing that changes in the structural properties of the stimuli between study and test diminish the magnitude of repetition priming, whereas such changes have little effect on classic tests of semantic priming which themselves are typically sensitive to "level of processing" manipulations (Craik and Lockhart, 1972; Graf et al., 1985; Jacoby and Dallas, 1981; Jacoby and

Hayman, 1987; Masson, 1986; Roediger and Blaxton, 1987; Tulving and Schacter, 1990). The fact, however, that priming can be found in the absence of repetition of perceptual information has prompted the elaboration of varying interpretations.

The modular memory approach assumes that the mechanisms that underlie cognition (and memory) are divided into input modules and central systems (Fodor, 1983; Fodor, 1985; Moscovitch, 1992; Nadel, 1994). In this system, modules are highly information-type specific (e.g., an auditory input module) and are impervious to penetration by higher-order cognitive processes, whereas central systems can combine information from various modules and lead to conscious perception. The modal model accounts for repetition priming by proposing that both input modules and central (semantic) systems share the property of maintenance of information, and that identical (and related) stimuli are more efficiently processed upon repeated presentation.

Activational views, which have arisen from theoretical work on the nature of the storage of semantic information, contend that the presentation of a prime activates a lexical or conceptual node in a semantic network and that this activation is maintained long enough to facilitate subsequent processing of the same (or a related) concept (Chang, 1986; Collins and Loftus, 1975; Collins and Quillian, 1969; Mandler, 1980; McClelland and Rumelhart, 1981; McNamara, 1992a; McNamara, 1992b; Morton, 1969). The activational perspective is discussed in more detail in the Discussion section.

Finally, the position that all memory phenomena (even implicit memory phenomena) are episodic in nature has also been proposed to account for repetition priming. In this view, it is argued that a memory trace is perpetuated after exposure to information and this memory trace is exploited when the target is presented (Jacoby, 1983; Ratcliff and McKoon, 1988; Roediger and Blaxton, 1987).

Functional Neuroanatomy

Varying forms of memory are often assumed to be subserved by (at least partially) dissociable brain structures (for a detailed account see Zola-Morgan and Squire, 1993). Because amnesic patients tend to show largely preserved priming and gravely impaired explicit memory, it is assumed that priming relies on neural structures outside of the medial temporal lobe and diencephalon (since ablation of these structures provokes anterograde amnesia) (Scoville and Milner, 1957; but see Beaugard et al., 1998; Jernigan and Ostergaard, 1993; Ostergaard, 1999; Ostergaard and Jernigan, 1993 for arguments against this conclusion). Both neuropsychological and neuroimaging evidence points to occipitotemporal cortex as playing an important role in perceptual priming (Buckner et al., 1998; Cabeza and Nyberg, 2000; Fleischman et al., 1995; Gabrieli et al., 1994; Graf and Ryan, 1990; Schacter, 1992b). More often than not, a decrease in regional cerebral blood flow or blood-oxygen-level-dependent (BOLD) signal response is recorded in relation to increased efficiency in the processing of primed items. On a neuronal level, this increased efficiency is termed “repetition suppression” (RS) and suggests that decreased

resources are necessary to process previously processed items (Ungerleider, 1995; Wiggs and Martin, 1998). Evidence further suggests that brain areas subserving conceptual priming include temporal and frontal associations areas (Demb et al., 1995; Dhond et al., 2001; Fleischman et al., 1995; Gabrieli et al., 1994; Gabrieli et al., 1996; Martin and Chao, 2001; Wagner et al., 2000; Yasuno et al., 2000). Further detail regarding the neural substrate of priming is presented in Study #3.

Evolutionary Perspective

The next section will discuss priming from an evolutionary standpoint. Evolutionary psychology is an approach to psychology which attempts to understand the human mind (and brain) in the context of evolutionary pressures. In this perspective “the mind is a set of information-processing machines that were designed by natural selection” (Cosmides and Tooby, 1997). In the evolutionary psychological perspective, we speculate that the capacity for repetition priming may have been primordially important to human survival across millennia of evolution. The author fully acknowledges that it is impossible to directly test any hypothesis with respect to evolution since any behavior expressed by modern humans must have been selected for or else it would not exist. Indeed, the evolutionary perspective can be accused of being circular in this regard. Nevertheless, this perspective was used as a starting point to generate specific hypotheses with respect to variables which may affect the strength of CFIP. A brief review of the background context of the evolutionary perspective is presented in the following paragraphs.

Darwin's (1859) (and Spencer's) theory of evolution makes four basic claims: first, living entities within a species must compete for limited resources in order to survive; second, natural variations will occur across members of that species; third, those entities which are better able to compete will survive; and finally, those entities which survive will pass on to their progeny the very trait which helped them to survive. How can repetition priming be seen to play a role in this process? To put it simply, by improving behavior and the chances of reproductive success. Let me illustrate here by example: we begin with perceptual priming. In perceptual priming, previous exposure to an object facilitates subsequent perception of that object. Let us imagine that the object in question is a well-camouflaged Gaboon viper. Picture an early Homo sapien walking through the equatorial African rain forest. He fails to notice an aptly camouflaged Gaboon viper (hidden amongst the fallen leaves) until his almost steps on it. The snake begins to hiss and the rain forest wanderer; appropriately scared (Gaboon vipers are extremely venomous; time to death ~15 minutes), immediately makes off to rejoin the others back at the compound. Research in perceptual priming suggests that the next time the wanderer is off in the rain forest, the camouflaged snake will be more easily perceived, and the wanderer will drastically reduce his chances of being attacked.

This example clearly illustrates how perceptual priming (of a well camouflaged snake) might lead to reduced chance of death (by snake bite), and ultimately to improved reproductive success. In other words, perceptual priming can be seen as a fundamental mechanism of learning and by extension, of survival. This analysis

bears a striking similarity to LeDoux's (1996, 2000) conception of fear conditioning (Figure 1). According to Ledoux, emotional memory (i.e., fear conditioning) is implicit because no conscious reference to a learning episode is necessary in order to trigger a learned response. Ledoux makes the case that such unconscious effects of previous experience on current behavior are mediated by the amygdala and its neural connections. Further, because the amygdala has been shown to play a crucial role in fear conditioning across a wide variety of organisms, Ledoux considers such a system to be of immense survival value and suggests that this ability was selected for and preserved across evolution. The scope of the current postulate, however, is greater than Ledoux's conception because all repetition priming phenomena are included (not just fear conditioning). Fear conditioning, in this perspective, is simply one easily measured example of the unconscious effect of past experience on future behavior.

In conceptual repetition priming, previous exposure to any concept in one form leads to improved processing of the same concept, even in a varying form. To illustrate by returning to the above example, perhaps the equatorial wanderer would have more easily perceived the snake the first time around if he had recently had a conversation about snakes in general, or the Gaboon viper in particular (even if he did not explicitly remember the conversation). In such a case, a verbally processed concept would lead to an increased efficiency of processing the very object denoted by that concept.

According to Ledoux (1996), the amygdaloid fear system is hypothesized to work independently of the cortex and is thought to be evolutionarily very old. It is

reasonable to assume, however, that as the brain developed across mammalian evolution, the principles of this form of learning were incorporated into the ever-developing cortex. Because the functional purpose of all memory is maintenance of information, the capacity for perceptual, and ultimately conceptual, repetition priming is most likely the result of such incorporation. Indeed, there is speculation that the underlying molecular mechanisms of all forms of learning are similar (Abel and Lattal, 2001; Izquierdo and McGaugh, 2000; McEachern and Shaw, 1999). Further, there is some evidence that while repetition priming is mediated by posterior cortical areas (in the occipitotemporal lobes), conceptual priming also involves more anterior areas which are generally considered to have developed more recently in human evolution (Deacon, 1990).

While the current position is that the fundamental function of all forms of memory is to aid in the survival of the species, it is impossible to directly examine whether the capacity for priming in general, or CFIP in particular, are the result of this process. The only method at our disposal in order to address this fascinating question is that of inference. The model proposed by Cosmides and Tooby (1997) clearly illustrates this principle (Figure 2). According to Cosmides and Tooby (1997), we must first understand the adaptive problem. In this case, the adaptive problem is one of quickly and efficiently processing meaningful external stimuli. Next, we must investigate the way in which the mind solves these problems. These questions are considered in terms of variables which potentiate CFIP which is investigated in Studies #1 and #2. Finally, we must examine the neural substrate of these cognitive processes. This final question is investigated in Study #3.

This thesis has endeavored to examine certain variables which can be seen to impact, from an evolutionary perspective, on repetition priming. Two variables which can be seen as having survival value are also known to interact with the long-term storage of information (both explicit recall and semantic knowledge): the ability to better remember emotionally salient events (relative to emotionally neutral ones), and the purported existence of a specialized system for the semantic representation of living versus nonliving things. In this thesis we first examined whether living and nonliving things would prime in equal magnitudes. There have been many documented cases of category-specific semantic impairment, with the domain of living things being more frequently impaired (Bunn et al., 1998; Caramazza et al., 1982; Caramazza and Shelton, 1998; Laiacona and Capitani, 2001; Montanes et al., 1996; Moss and Tyler, 2000; Tranel et al., 1997; Warrington and McCarthy, 1983; Warrington and Shallice, 1984). A number of perspectives have been proposed to account for these findings, although one in particular is based on an evolutionary perspective. Caramazza and Shelton (1998) have suggested that, evolutionarily speaking, the semantic system first evolved for the rapid classification of living things, and that the rest of the semantic system was built around this base. If this is true, then living things hold a vital place in the processing of external stimuli. We saw this premise as a logical place to begin our research, and thus the first question which we sought to answer was whether living and nonliving concepts would yield equal amounts of CFIP. We reasoned that in our study, differences in the magnitude of priming for living and nonliving concepts would reflect their differing status (and prominence) in semantic memory. In line with Caramazza and Shelton (1998), we predicted that greater priming would

be found for living things because, across evolution, living things were fundamentally important to the survival of the human organism and the capacity for priming is a direct result of the evolutionary process. Study #1, **Category Differences in Cross-form Priming**, which employed a relatively pure CFIP paradigm, was conducted to test this hypothesis.

Subsequently, we wondered whether a role for emotional salience (and by consequence, arousal) may be found in the strength of implicit memory. We therefore sought to evaluate whether the variable of emotional salience (operationally defined as emotional valence) would increase the magnitude of identity priming. Many studies have shown that emotional salience has an impact on explicit memory (Blake et al., 2001; Bradley et al., 1992; Brown and Kulik, 1977; Cahill and McGaugh, 1995; Christianson and Faellman, 1991; Christianson and Loftus, 1987; Christianson and Safer, 1996; Dewhurst and Parry, 2000; Doerksen and Shimamura, 2001; Finkenauer et al., 1998; Hamann et al., 1999; Maratos et al., 2000). Some of this research has pointed to a greater potentiation of memory by negative items or events, relative to positive or neutral items or events. Akin to this line of research, in Study #2, **Negative Valence Potentiates Repetition Priming**, we hypothesized that negatively valenced images (presented together with their respective words) would lead to increased priming.

Finally, we were interested in learning more about brain areas which might be involved in CFIP. A further goal of this research was to use our findings of subliminal CFIP to inform theoretical accounts of repetition priming, and hence of

implicit memory. In Study #3, **Neural Substrate of Subliminal Cross-Form Priming**, we sought to better understand the neurological underpinnings of CFIP. Here we were motivated by the perspective that both phylogenetically older and newer areas of the cerebral cortex which are known to subserve semantic processing would participate in CFIP.

Chapter 2: Articles

Study #1: Semantic Category Differences in Cross-Form Priming

in press at the Journal of the International Neuropsychological Society

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Abstract

Findings of category-specific impairments have suggested that human semantic memory may be organized around a living/nonliving dichotomy. In order to assess implicit memory performance for living and nonliving concepts, one group of neurologically intact individuals participated in a cross-form conceptual priming paradigm. In block 1, pictures primed words while in block 2 words were used to prime pictures. Across all phases of the experiment, subjects decided whether items represented something which was living or nonliving, and response times were recorded. Results revealed greater priming for living concepts across both blocks. Greater priming for living concepts may have occurred because of increased or prolonged conceptual activation of these concepts. Results are discussed in the context of theoretical accounts of the category-specific impairments observed in brain-damaged populations.

Keywords:

Priming, category-specificity, living, nonliving

Introduction

The finding that some patients with focal brain lesions exhibit semantic deficits which are limited to one particular semantic category lends support to the possibility that semantic knowledge is stored in functionally dissociable brain systems (Caramazza & Shelton, 1998; Forde & Humphreys, 1999; McKenna & Warrington, 1978; Moss & Tyler, 2000; Shelton et al., 1998; Warrington & McCarthy, 1983). More often than not, category-specific semantic deficits affect the general domain of living things.

Theoretical accounts of category-specific semantic deficits fall into two broad classes: those which posit the existence of (independent) multiple semantic stores and those that do not. Unitary semantics theories argue that category effects are “artifactual” in that they reflect the influence of extraneous variables such as concept familiarity, usage frequency, or stimulus complexity¹, but do not reflect any functional or anatomical division within the semantic system. Multiple semantics perspectives posit that there may be separate stores of information, with at least partially dissociable underlying brain systems responsible for the representation of various categories of knowledge.

1 Complexity refers to the visual attributes of a picture. For example, the silhouette of a car would be far less complex than a regular picture of a car – which would contain much more visual information and visual objects (i.e., antenna, door handles, windows etc ...).

The multiple semantics theory which has received the most attention to date considers that semantic knowledge is divided across a sensory/functional division (the sensory/functional theory – or SFT; Warrington & McCarthy, 1983; Warrington & Shallice, 1984; see also Hart and Gordon, 1992). Warrington and colleagues (1983, 1984) have suggested that a “sensory” or “visual” semantic system stores information about an object’s structure (its form – its color etc...), whereas a “functional” system stores information about an object’s function (what it’s for – what it does etc...). According to Warrington and Shallice (1984), living concepts may be selectively impaired because information about living things relies more heavily on visual information stored in the sensory system. They further propose that it is particularly this system which is most often damaged in cases of category-specific semantic impairment. The SFT has, however, been critiqued by Caramazza and Shelton (1998) on logical and experimental grounds which demonstrate that the sensory/functional distinction does not apply uniformly across categories of knowledge in patients with category-specific impairments.

One defense of the unitary semantics position is the proposal that an interaction between the variables of structural similarity and semantic proximity leads to apparent category-specific impairments. The claim is that living things resemble each other more closely (that is – they share many highly inter-correlated features) than nonliving things – both on a structural (sensory) and a semantic level (Humphreys et al., 1988). In this view, difficulty in naming living items occurs because living items are relatively harder to disambiguate from each other (Dixon et al., 1999; Forde & Humphreys, 1999). Whereas Dixon and colleagues (1999) have

supported this position using abstract computer generated forms, Caramazza and Shelton (1998) have pointed out that this situation should lead to naming impairments for tools (which tend to resemble each other) as often as it does for animals or fruits and vegetables, which is not the case. McRae and Cree (2002) contend that a given concept may be associated with a pattern of activation among a set of features which themselves could be segregated in semantic space. The Organized Unitary Content Hypothesis (OUCH) proposed by Caramazza et al. (1990) stipulates that because properties that define living objects are highly inter-correlated, these properties are “clumped” together (i.e., semantic space is “lumpy”), with the densest regions occupied by properties corresponding to living things. In all of these conceptions, brain damage is more likely to lead to a deficit for living things because their properties are more highly inter-correlated and stored together.

To elucidate whether artifactual variables account for apparent category-specific semantic impairments, researchers have tested brain-damaged patients on semantic memory tests (usually picture naming) while holding constant such variables as stimulus frequency and complexity, which can affect how easily a picture can be named (Bunn et al., 1998; Caramazza & Shelton, 1998; Forde & Humphreys, 1999; Funnell & Sheridan 1992; Kurbat & Farah, 1998). Although the results of such studies are not unequivocal, the existence in some brain-damaged patients of category-specific deficits even under conditions of strict stimulus control tends to support the view that living and nonliving concepts are treated differentially within the semantic system. Importantly, this line of research has underscored the importance of strict variable control in investigations of category-specificity.

Further support for an anatomical basis of category-specificity has been found in functional brain imaging studies conducted among normal subjects (Martin et al., 1996; Moore & Price, 1999; Perani et al., 1995). Data has been accumulated using techniques including event-related potentials (ERP), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). An early picture matching PET study by Perani et al. (1995), for example, found that animal recognition was associated with bilateral inferior temporal cortex activation while nonliving objects differentially activated the left dorsolateral frontal cortex. Reinforcement of the notion of dissociable brain areas underlying semantic knowledge for living and nonliving items was taken to the level of the individual neuron by Kreiman et al. (2000) who implanted intracranial depth electrodes into the brains of epileptic patients. Their investigation revealed that a percentage of individual neurons in the medial temporal lobe responded selectively and exclusively to individual categories (i.e., faces, houses, animals) of pictured objects.

Although functional neuroimaging studies have tended to support the multiple semantics perspective, disagreement between just which areas are involved in the processing of living versus nonliving things have left questions about the nature of this division unresolved (Chao et al., 1999; Kreiman et al., 2000; Mummery et al., 1998; Perani et al., 1999). Furthermore, some studies have suggested that apparent category-specific activations may actually be reflecting the influence of artifactual variables (e.g., Gerlach et al., 2000; Moore & Price, 1999). Similarly, others have interpreted findings of category-specific activations as reflecting the distribution of

feature processing modules which are selectively activated by members of particular categories (e.g., Ishai et al., 2000). Finally, a number of studies have failed to find category-specific effects (e.g., Devlin et al., 2002).

To account for neuropsychological and functional brain imaging data which has upheld the possibility of dissociable brain regions involved in category-specific effects, Caramazza and Shelton (1998) have proposed a multiple semantics “Domain-specific” hypothesis (DSH). They propose the existence of at least partially “dedicated neuronal circuits for processing animals and plant life” and suggest that this system may have developed because living things were primordially important to human survival to the extent that they represent sources of comestible or lethal food, medicinal compounds, or dangerous threats. They further proposed that because of this special status, living things may be more emotionally salient than nonliving things. In accordance with the common finding of superior (explicit) memory performance for emotionally salient stimuli (Cahill & McGaugh, 1995; Christianson & Faelleman 1991; Christianson & Safer, 1996; Colombel, 2001; Danion et al., 1995; Dewhurst & Parry 2000; Doerksen & Shimamura, 2001; Kitayama, 1996; Labar & Phelps, 1998; Palomba et al., 1997; Phelps et al., 1997), the notion that living things may promote improved implicit memory receives initial plausibility.

In light of the above review, we were interested in determining the strength of conceptual repetition priming for living and nonliving items. In conceptual priming the concept denoted by a studied stimulus is repeated at test, and this repetition yields more efficient conceptual processing of the studied concept (Blaxton, 1989; Brown &

Mitchell, 1994; Carlesimo, 1994; Graf & Ryan, 1990; Schacter, 1987; Schacter & Buckner, 1998; Sperber et al., 1979). Activational theories of priming interpret such results as indicating that exposure to a stimulus provokes activation of that concept in the semantic network, leading to more efficient processing upon subsequent presentations (Bower 1986, 1996; Collins and Loftus, 1975, Morton, 1969; Paivio, 1986). According to Paivio's (1986) "dual code hypothesis", for example, concepts are stored in two parallel systems in the brain: one (visual) system contains "imagens," which are pictorial representations of objects, whereas the other (verbal) system contains "logogens". Both logogens and imagens are individual conceptual representations of objects (i.e., conceptual nodes). In Paivio's system, activation of a logogen spreads to its respective imagen and vice versa (Paivio & Begg, 1981).

In the current study, we used a cross-form conceptual repetition priming paradigm to compare the magnitude of priming for living and nonliving concepts. This was chosen as a way to eliminate carry-over of perceptual information from study list to the test list (Vanderwart, 1984). Specifically, a picture-to-word (and word-to-picture) priming paradigm was used. In line with Paivio's dual code hypothesis, conceptual priming was predicted using this paradigm. Specifically, it was hypothesized that (1) the semantic activation of a concept would yield reduced response times on a subsequent task that required a conceptual appraisal of the same concept (even when the two presentations of the concept were in different forms i.e., pictures or words); and that (2) greater priming would be found for items belonging to the category of living things. This second hypothesis was motivated by the DSH and its contention of increased emotional salience for living things. It was reasoned that this increased

emotional salience would lead to greater study-phase semantic activation of living as opposed to nonliving concepts.

Methods

Generally, studies which have examined cross-form priming have found significant priming effects, although the effects are typically smaller than those usually found in within-form priming (Thompson-Schill & Gabrieli, 1999; Weldon et al., 1995). Nevertheless, we were interested in determining whether living and nonliving concepts would show equal priming in a relatively pure conceptual implicit memory paradigm. An attempt was made to match living and nonliving items as closely as possible for variables such as frequency (a measure of how often one comes into contact with a particular concept in every day life), word length, and pictorial complexity (which tends to be higher for living versus nonliving things) which have all been assumed to play a role in category effects in previous studies (see Kurbat & Farah, 1998).

Subjects

Thirty-two normal right-handed francophone subjects (17 females; average age = 23.3, range = 20-40, sd = 4.8; 15 males; average age = 24.8, range = 18-35, sd = 4.6) with neither neurological nor psychiatric history voluntarily participated in this study.

French was the dominant language used by all participants. Each subject signed a consent form and received five dollars for their participation.

Materials

All stimuli were presented on an Apple Macintosh computer running the Psychlab software (Bub & Gum, 1988). The stimulus items were either pictures taken from the Snodgrass and Vanderwart (1980) set or their French lexical counterparts (see Table 1). Each stimulus item denoted a concept which belonged either to the category of living things (animals, or fruits and vegetables) or nonliving things (clothing, household objects, tools, or vehicles).

[Insert Table 1 about here]

Procedure

One experiment was conducted to test for the cross-form priming of living and nonliving concepts. Block PW tested for picture-to-word priming, while block WP tested for word-to-picture priming. The order of blocks was counterbalanced across subjects. The study phases of both blocks consisted of the presentation of living and nonliving primes, while the test phases contained four groups of stimuli; living and nonliving targets (repeated from study), and living and nonliving distractors (new unstudied items). Thus, for example, subjects may have seen the picture prime of a dog in the study phase and responded to the target word “dog” in the test phase. The order of stimulus presentation was always (pseudo) randomized with the condition

that no more than 3 items from the same category (living/nonliving) appeared on successive trials. There was no overlap between items used in the two blocks.

During the study and the test phases of both blocks, subjects were instructed to decide if the stimulus denoted something which was natural or man-made. The experimenter provided an example such as “the word or picture could be of an orange, which would be naturally occurring, or a table, which would be man-made”. Subjects revealed their choices by pressing on one of two keys on the keyboard, using their index and adjacent middle finger of their right hand for responding. Keys used were counterbalanced as to category; that is, the left-hand key was used as often as the right-hand key to represent living things. The computer recorded response times (RTs), i.e., the latency to key-press following the onset of each stimulus. The presentation parameters for each stimulus in both the study and testing phases were as follows: a fixation point was presented for 500 ms followed by a blank screen for 500 ms which in turn was followed by the presentation of the experimental stimulus itself. Each experimental stimulus disappeared when the subject pressed a key. On average, study pictures remained on the screen for 660 ms, and study words remained on the screen for 682 ms. The disappearance of the stimulus was followed by a 500 ms pause after which the fixation point was again presented. Thus, the average inter-stimulus interval was 1500 ms. Study items were presented in blocks, and each study block was directly followed by a test phase. No mention was made as to the eventual repetition of studied items. Informal post-experimental interviewing revealed that most subjects believed that the purpose of the test was to see how quickly they could classify words as compared to pictures.

Sixteen picture primes were presented in the study phase of block PW (see Table 2). Half of these pictures denoted objects which belonged to the category of living things, and half denoted objects which belonged to the category of nonliving things. Study phase nonliving pictures had significantly higher familiarity ratings than study phase living pictures ($t(7) p < 0.05$). Study phase living and nonliving pictures did not differ with respect to stimulus complexity. During the test phase, 32 words were presented. Test phase target and distractor words did not differ significantly from each other in terms of length. According to the “Brulex” French word norms, test phase words had a mean usage frequency rating of 306.5, which is considered to be medium (Content et al., 1990). Usage frequencies did not differ significantly between living and nonliving words or between distractor and target words within each category.

During the study phase of block WP, 16 words were presented (see Table 2). Half of these words denoted objects which belonged to the category of living things, and the other half denoted objects belonging to the category of nonliving things. Study living and nonliving words did not differ significantly with respect to frequency or number of letters. During the test phase, 32 pictures were presented. Whereas living concepts were significantly less familiar than nonliving concepts, ($t(15) p < 0.05$), complexity did not vary significantly. Importantly, target and distractor items were matched for both familiarity and complexity and did not differ significantly on these measures.

Across both blocks, the important variable of age of acquisition² did not vary between living and nonliving items.

[Insert Table 2 about here]

Data analysis

The data were analyzed as follows. Responses to the first item in the test phase were eliminated in order for the subjects to acclimate to the task. For each subject, the average RTs to each of the four stimulus types were computed for test phase items. Errors were eliminated from the analysis, as were any RTs which were more than 3 standard deviations from the mean of each subject's overall average RT. Removed data were left void; i.e., the data were not replaced.

Pre-experimental control

Twelve normal right-handed francophone subjects (7 male, mean age = 25.1, range 18 to 41, sd = 7.8) participated in a pilot study designed to establish that no baseline differences in RTs were found when no priming had taken place. The instructions given to these volunteers were identical to those given to the research subjects who participated in the experiment. Since these subjects were not exposed to the primes (i.e., they did not participate in the study phases), the averages of their RTs were used

² Age of acquisition data taken from Alario & Ferrand (1999).

to create groups of stimulus lists for the experiment. Student's T-tests revealed that no significant differences in RTs for sets of stimuli to be used as targets and distractors in the experimental task were found (all t-tests: $t(7) p \geq 0.86$).

Results

A three factor (prime status, category, block) mixed ANOVA performed on all test-phase RTs was carried out (see Figure 1). The analysis confirmed an overall main effect of priming ($F_{1, 31} = 32, p < 0.0001$), reflecting the fact that subjects responded more quickly to targets (613 ms sd = 90.6) than to distractors (638 ms sd = 102). A main effect was also found for block ($F_{1, 31} = 7.1, p = 0.012$), reflecting the fact that subjects responded more quickly to test pictures (613 ms sd = 103) than to test words (638 ms sd = 90). The analysis also revealed that RTs were faster to living (613 ms sd = 89) than nonliving items (638 ms sd = 103) ($F_{1, 31} = 10.6, p < 0.005$) across both blocks (block PW: living = 630 ms, nonliving = 647 ms; block WP: living = 596 ms nonliving = 630 ms). Finally, an interaction was observed between category and prime status ($F_{1, 31} = 15.25, p = 0.0005$). Decomposition of this effect revealed that significant priming occurred for living things ($F_{1, 31} = 61.8, p < 0.0001$), whereas there was no significant difference between RTs to nonliving target and distractor items. Indeed, averaged across both blocks, the priming percentage³ was much

³ The formula is $((\text{distractor RTs} - \text{target RTs})/\text{distractor RTs}) * 100$.

greater for living items (6.1%) as compared to nonliving items (1.3%). Importantly, this pattern was repeated in both blocks. A three-way interaction was not observed.

To further confirm these results, an analysis was run on average RTs to each stimulus across all subjects. Although the power of this test is significantly less than that of the “by subject” ANOVA (because each “group” now contains only 8 items) the three main effects were replicated. Specifically, this ANOVA revealed that subjects responded faster to pictures than to words ($F_{1, 7} = 5.83, p < 0.05$), to living versus nonliving items ($F_{1, 7} = 7.95, p = 0.026$), and to targets relative to distractors ($F_{1, 8} = 59.2, p < 0.0001$). The interaction observed between category and prime status failed to reach significance on this test.

Finally, an analysis of errors made in the categorization task failed to reveal any significant differences between living and nonliving items. Nor were there many errors committed (average of 0.6 errors per subject across both blocks). In contrast, more errors were recorded when subjects responded to pictures (average of 0.38 errors per subject) than when subjects responded to words (0.21 errors per subject).

[Insert Figure1 about here]

Discussion

This study compared cross-form priming for living and nonliving concepts in a group of young, normal subjects. Block PW demonstrated that overall priming took place when pictures primed words, while block WP revealed similar effects when words primed pictures. Analysis across both blocks revealed greater priming for living concepts as compared to nonliving concepts. The critical finding of this study is that the magnitude of conceptual priming differed significantly as a function of semantic category: greater priming for living as compared to nonliving concepts was found regardless of whether pictures primed words or words primed pictures.

The current implicit memory paradigm might be criticized for its inherent potential for contamination by explicit memory strategies. There are reasons to believe, however, that the results reported here reflect implicit memory retrieval devoid of such contamination. Although the subjects undoubtedly noticed that the paradigm included the repetition of items, they were naïve as to the real purpose of the study. Indeed, given that the subjects were asked to respond as quickly as possible to all stimuli, it would seem unreasonable to assume that they would purposely and explicitly recall a previously encountered concept in order to respond to the stimulus with which they were faced (Vriezen et al., 1995). Also, previous studies have found an advantage for the recall of pictures over words in explicit memory tasks but not for implicit memory tasks (Paivio & Csapo, 1973; Stenberg et al., 1995; but see Vaidya & Gabrieli, 2000). Because we did not find improved memory when pictures primed

words relative to when words primed pictures, it is unlikely that explicit memory played a role in our results.

Before interpreting the results, it is important to be confident that they reflect the operation of implicit memory and not the influence of extraneous variables which could have influenced RTs including the frequency and complexity of target stimuli. In both blocks, test phase target items did not differ from distractor items in terms of familiarity or complexity. In block PW there was no difference between the number of letters of target versus distractor living words. Distractor nonliving words, however, were an average of half a letter shorter than target nonliving words. This minimal difference, however, could not reasonably be expected to negate any priming which might have otherwise been evident if the target and distractor nonliving word lists were more closely matched for word length. Further, even when no such difference existed in the target items in block WP, much greater priming was still found for living as compared to nonliving items. Finally, it is important to note that the stimuli used in the current paradigm were first run on subjects who were not primed. Thus, any baseline differences in RTs to these items (which could result from these variables) were eliminated in the process of preparing the test phase stimulus groups. Clearly then, the variables of familiarity, complexity, frequency, and word length alone can not account for the significant priming evidenced for living concepts or the lack of priming observed among nonliving items.

A number of variables in this experiment would have led to the prediction of greater priming among nonliving concepts. First, it has been observed that slower RTs in

semantic priming paradigms usually lead to greater observed priming (Neely, 1991⁴). In the current study, results from both blocks revealed that subjects responded more quickly to living items. This was even true in block WP in which nonliving test phase items had higher familiarity ratings. As such, these quicker RTs could have been expected to lead to a reduction in measured priming. A second factor which could have led to the prediction of greater priming for living things is a direct conclusion of featural theories of semantic category effects. That is, if living things are more highly inter-correlated than nonliving things, and in line with the notion of semantic spreading of activation, it could be argued that activation of study phase living concepts would spread to supposedly distractor living items in the test phase more so than for nonliving things (which supposedly share less features in common), thereby reducing observed priming for living things (Collins & Loftus, 1975; Dixon et al., 1999; McRae & Cree, 2002). Regardless of these considerations, however, greater priming was found for living concepts.

Greater priming among living concepts may be interpreted within Warrington and Shallice's (1984) SFT. In this perspective, living things are identified and processed in terms of their visual attributes much more than are nonliving things. Because research has shown category-specific activations in the fusiform gyrus to even word forms of living objects, it is possible that the linkage between visual and verbal representations of living things may be stronger than those for nonliving things (e.g., Chao et al., 1999; Perani et al., 1999). Thus, because pictures were used to prime

⁴ Note that Neely (1991) does not discuss repetition priming such as that carried-out here.

words and vice versa, increased priming for living things could be expected. Further, to the extent that the paradigm employed in the current study makes exclusive use of the visual modality, it may be argued that greater implicit memory for living things benefited from this increased reliance on visual properties. In block PW in particular, the SFT would predict that activation of studied living items would have been greater in a visual semantic system, whereas nonliving items would have led to relative activation within a functional semantic system. Because test phase items were visual (i.e., words), perhaps this sensory/functional activational difference could have led to greater priming.

The processes which underlie the type of conceptual priming tested here presumably involve the activation of a concept node (or logogen) in semantic memory (Bower 1986, 1996; Collins and Loftus, 1975, Morton, 1969; Paivio, 1986). In this perspective, a concept is activated, either by a picture or by a word, during the study phase. The activation of the concept lingers into the test phase, and re-appraisal of the same concept in the test phase is easier and more rapid compared to new, unstudied items, resulting in faster RTs. An interpretation of the current results within this perspective, especially given the fact that the variables discussed above could have been expected to attenuate priming for living concepts, is that more priming for living items occurred as a function of either: 1) greater study phase activation for living than nonliving stimuli; and/or 2) improved retention of activation of living as opposed to nonliving concepts.

The question is, therefore, why greater activation may have taken place for living versus nonliving things? In discussing the DSH, Caramazza and Shelton (1998) suggest that when an object is encountered, rapid processing is carried out in order to determine whether the object is living or nonliving. Because one of the hypothesized differences between living and nonliving things - according to the DSH - involves an increased emotional component for living things (fighting/fleeing/feeding), they submit that a specialized system probably involving areas of the limbic system is responsible for this process.

Although Caramazza and Shelton (1998) do not specify which structures of the limbic system may play a role in this early analysis and classification process, it is reasonable to hypothesize that the amygdala is involved. Various lines of evidence indicate that the amygdala can respond automatically, rapidly, and without the co-occurrence of conscious awareness to emotionally salient stimuli (Ledoux, 1996; Morris et al., 1996).

While no study has directly evaluated the hypothesis that living things have a greater emotional significance overall, at least one line of research supports this position. A number of functional neuroimaging studies have found that the selective processing of living items (both pictures and words) potentiates activation in early processing areas of the ventral object processing stream, including the primary visual cortex, the lingual, fusiform, medial occipital, and inferior occipital gyri (Chao et al., 1999; Goodale & Milner, 1992; Martin et al., 1996; Okada et al., 2000; Perani et al., 1999, 1995). Aside from suggesting dissociable brain areas for the processing of living and

nonliving concepts, however, an interpretation of these results is lacking (Caramazza and Shelton, 1998). It is not known why early visual areas would be more active for living versus nonliving stimuli.

One explanation, however, may come from parallel research investigating the processing of emotional stimuli. A common finding, in such investigations, is increased activation in the occipital lobe to emotionally salient stimuli (Junghofer et al., 2001; Lang et al., 1998; Rama et al., 2001; Schneider et al., 1994; Tabert et al., 2001; Taylor et al., 2000). Lang et al. (1998), for example, have found increased occipital lobe activation in the area of the fusiform and occipital gyri when subjects viewed either emotionally negative or positive as opposed to emotionally neutral images. A putative explanation of these results is that increased attention potentiates early visual processing (Lane et al., 1999; Lang et al., 1997). It is further hypothesized that the amygdala plays a role in this process. If this is true, and if the increased activation recorded in visual areas to pictures of living versus nonliving concepts functions along similar lines, then the notion that living items are more emotionally salient than nonliving items receives some empirical support. An implication of the amygdala in this process is supported by a study by Simpson and colleagues (Simpson et al., 2000) who found increased activation in the right fusiform gyrus to negatively valenced pictures together with an increase in activation of limbic areas, including the amygdala. If the ability to recognize living things has a Darwinian survival value, then it is reasonable to expect that the processing of living entities may similarly benefit from increased attention.

While this position makes intuitive sense in the case where study phase items are pictorial representations of living things, the relationship is less clear when the items presented at study are words. In accordance with Paivio's (1986) dual code hypothesis, however, it is possible that lexical representations of living things may activate their (abstract) pictorial representations. In this view, the hypothesized increased emotional salience of living things may have given rise to potentiated attention, which in turn led to greater conceptual activation. Within this perspective, therefore, it is possible that greater priming for living things took place because living items were more emotionally salient. Because this study did not directly manipulate the variable of emotional salience with respect to living and nonliving things, it is difficult to draw specific conclusions on this point. It would be interesting indeed to directly address this hypothesis in future research.

Finally, it is somewhat troublesome that the priming observed for nonliving items failed to reach significance. Priming in the current paradigm is very subtle and difficult to measure. The fact that, on average, subjects responded 20 milliseconds faster to target than to distractor nonliving items when words primed pictures, however, is somewhat comforting. It suggests that while the magnitude of priming was insufficient to be revealed by a three way ANOVA, the effect may have been present at a low level.

As discussed in the Introduction, explanations of category-specific semantic deficits fall under two main divisions: theories which posit the existence of multiple semantics, and unitary semantics theories. The current finding of differential

conceptual priming for living versus nonliving concepts among neurologically intact subjects is in line with a wealth of research conducted among brain-damaged patients which has found category-specific semantic memory loss across a living/nonliving distinction. As such, the current results provide converging evidence for differences in the representation of living and nonliving concepts. A parsimonious account of the current results lies within the idea of greater (or longer lasting) study phase activation for living items. These results are compatible with the view that these two categories of objects are differentially processed within somewhat dissociable semantic systems.

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Table 1: Items used in both blocks

<u>Block PW</u>			<u>Block WP</u>		
Study Picture	Test Word	Status	Study Word	Test Picture	Status
Butterfly	Papillon	Target	chèvre	Goat	Target
Monkey	Singe	Target	mouton	Sheep	Target
Horse	Cheval	Target	alligator	Alligator	Target
Chicken	Poule	Target	chameau	Camel	Target
Peanut	Arachide	Target	fraises	Strawberry	Target
Grapes	Raisins	Target	tomate	Tomato	Target
Celery	Celery	Target	banane	Banana	Target
Cherry	Cerise	Target	ananas	Pineapple	Target
Motorcycle	motocyclette	Target	tournevis	Screwdriver	Target
Pen	Stylo	Target	ciseaux	Scissors	Target
Saw	Scie	Target	bicyclette	Bicycle	Target
Fork	Fourchette	Target	chemise	Shirt	Target
Train	Train	Target	voilier	Sailboat	Target
Airplane	Avion	Target	peigne	Comb	Target
Hat	Chapeau	Target	pantalon	Pants	Target
Dress	Robe	Target	ceinture	Belt	Target
	Oiseau	Distractor		Snail	Distractor
	Lapin	Distractor		Penguin	Distractor
	Poisson	Distractor		Zebra	Distractor
	Souris	Distractor		Tiger	Distractor
	Mangue	Distractor		Mushroom	Distractor
	Abricot	Distractor		Apple	Distractor
	Betterave	Distractor		Carrot	Distractor
	Haricot	Distractor		Pear	Distractor
	Veston	Distractor		Truck	Distractor
	Balai	Distractor		Coat	Distractor
	Autobus	Distractor		Shoe	Distractor
	Tablier	Distractor		Broom	Distractor
	Crayon	Distractor		Sock	Distractor
	Casque	Distractor		Knife	Distractor
	Gant	Distractor		Bow	Distractor
	Chaise	Distractor		Car	Distractor

Table 2: Stimulus characteristics. Mean (and standard deviations) for familiarity and complexity ratings according to the Snodgrass & Vanderwart (1980) norms. Frequency ratings are according to Brulex French word norms (Content, Mousty & Radeau, 1990).

Block PW: Study phase picture data

Group	Familiarity	Complexity
Living	2.89 (.74)	3.45 (.97)
Nonliving	3.69 (.67)	3.14 (.68)

Block PW: Test phase word data

Group	Frequency	Number of Letters
Primed Living	287 (79.8)	6.38 (1.2)
Distractor Living	288 (67.6)	6.63 (1.2)
Primed Nonliving	325.5 (77.8)	6.38 (2.97)
Distractor Nonliving	326 (30.6)	5.88 (0.99)

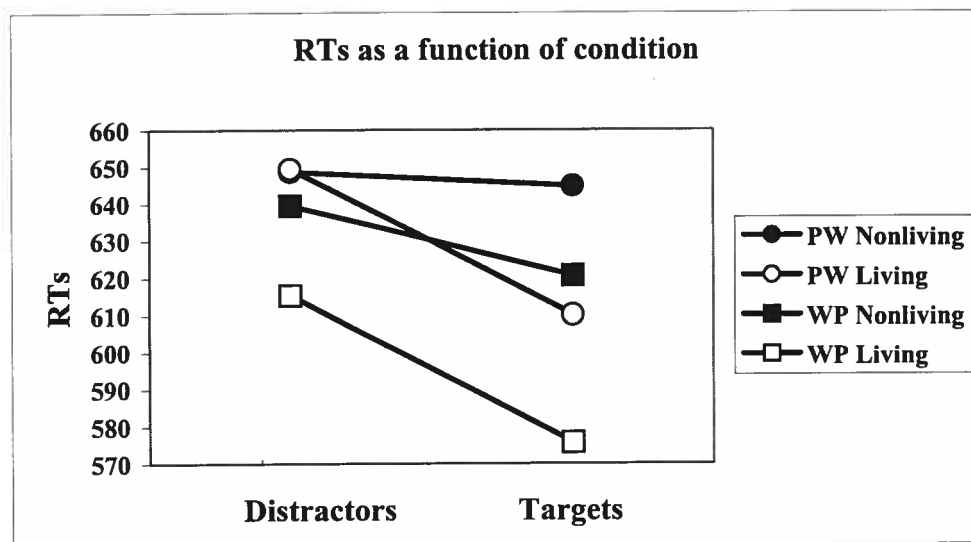
Block WP: Study phase word data

Group	Frequency	Number of Letters
Living	258.4 (53)	6.6 (1)
Nonliving	295.5 (59)	7.7 (1.3)

Block WP: Test phase picture data

Group	Familiarity	Complexity
Primed Living	2.6	3.2
Distractor Living	2.7	3.1
Primed Nonliving	4.0	2.7
Distractor Nonliving	4.0	2.7

Figure 1: For both blocks, RTs (measured in ms) were faster to living items, RTs were quicker to targets than to distractors items, subjects responded more quickly to pictures than to words, and significant priming was observed for living items whereas nonliving items showed negligible priming.



Study #2: Negative Valence Potentiates Repetition Priming

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Abstract

This study investigated whether the strength of implicit memory would vary as a function of emotional valence. Thirty-three participants were presented with pictures which were preceded by subliminally presented words which denoted the objects imaged in the pictures. Pictures and words were either emotionally positive, negative, or neutral. Directly following study sessions, a lexical decision test was administered to record response times to primed (repeated from the studied list) versus distractor (unstudied) words. Results revealed that negative items led to significantly more priming than positive or neutral items which failed to elicit significant priming. Results suggest that negative - but not positive - emotional valence potentiates repetition priming.

Keywords

Emotions, Subliminal, Priming, Valence

Introduction

Research has demonstrated an explicit memory advantage for emotionally salient as opposed to emotionally neutral stimuli across a wide range of tasks (e.g., Cahill & McGaugh, 1995; Danion, Kauffmann-Muller, Grange, & Zimmerman, 1995; Doerksen & Shimamura, 2001; Palomba, Angrilli, & Mini, 1997). Some evidence suggests that negative items are better remembered than their positive counterparts (Dewhurst & Parry, 2000; Kitayama, 1996; Phelps, LaBar, & Spencer, 1997).

Less research has been conducted to examine the impact of emotional salience on implicit memory. Whereas tests of explicit memory call for effortful conscious recall (or recognition) of studied material, implicit memory tasks make no reference to studied material; implicit memory is revealed by increased efficiency in the processing of previously encountered information (Blaxton, 1992; Graf & Schacter, 1985; Squire, 1992).

Three paradigms have been employed to explore the question of emotional implicit memory. The first resembles Pavlovian classical conditioning (Morris, Oehman, & Dolan, 1998; Pavlov, 1927). Parra, Esteves, Flykt, and Oehman (1997), for example, paired a mild electric shock (UCS) with the picture of an angry face (CS). Changes in subjects' skin conductance revealed the effects of the UCS when the CS only was presented.

A second paradigm which has sought to investigate emotional implicit memory is the mere exposure effect. In this paradigm, a previously neutral item garners a certain emotional status relative to other neutral items merely as a function of repetition. In a typical paradigm, a meaningless ideogram is flashed so briefly as to be below the level of conscious awareness. Emotional implicit memory is revealed to the extent that subjects develop a preference for that particular ideogram as opposed to other (almost identical) ideograms upon subsequent supraliminal presentations (Morris et al., 1998; Whittlesea & Price, 2001; Zajonc, 2001).

A third method for evaluating implicit emotional memory is that of mood-congruent learning (e.g., Bower, 1981). This method is exemplified in a study by Bradley, Mogg, and Millar (1996), in which clinically depressed subjects showed increased priming of subliminally presented depression-relevant words on a lexical decision test. Mood-congruent memory takes advantage of the inherent valence of studied stimuli but only so far as it interacts with mood state.

To evaluate whether implicit memory may be strengthened by the endogenous emotional nature of studied items, Matthews, Pitcaithly, and Mann (1995), compared semantic priming for positive (ex: “attractive” primes “desirable”), negative, and emotionally neutral adjectives in a semantically primed lexical decision paradigm among normal subjects and found greater priming for negative as opposed to positive and neutral words.

To our knowledge, no published studies have examined the effect of emotional valence among concrete objects on cross-form identity priming. The current experiment was conducted in order to examine whether this form of priming is modulated by the emotional valence of presented items. The paradigm employed picture-to-word priming with test phase words presented in a lexical decision task.

According to Paivio's dual coding theory, individual conceptual representations (concepts) are stored in two parallel semantic systems: one (visual) system contains "imagens" which are pictorial representations of objects, and another (verbal) system contains "logogens" which are lexical representations of objects (Paivio, 1978; Paivio & Begg, 1981). In Paivio's system, priming can be seen as the result of a transitive activation of logogens or of imagens. Because activation spreads from an imagen to logogen and vice versa, cross-form priming is expected to occur.

In the study phase of the current experiment, presented images were preceded by subliminally presented words. Each subliminally presented word depicted the object denoted by the subsequent image. Words were presented in order to increase the likelihood that an encountered image would activate a specific lexical entry; that is to enhance the mapping of an imagen to a specific logogen.

In line with evidence that negative items are better remembered than their positive counterparts and with Matthews et al.'s (1995), finding of greater priming for negative words, it was predicted that negative images would lead to increased priming relative to both neutral and positive images.

Methods

Subjects

12 male and 21 female volunteers, aged 18 to 35 years old (mean = 22.6, SD = 3.2) participated in this study. Subjects were recruited from local university and college campuses. All subjects signed informed consent forms and were paid a nominal fee for their participation. Upon questioning conducted prior to the start of the study, none of the subjects reported any history of neurological or psychiatric problems. All subjects were native English speakers.

Materials

The study phases included the presentation of images taken from the International Affective Picture System (IAPS) stimulus database (Lang, Bradley, & Cuthbert, 1997). IAPS images have been rated for valence (pleasantness). From the IAPS, a total of 12 negative images (mean valence rating = 2.6, SD = 0.76), 12 positive images (mean valence rating = 7.5, SD = 0.62), and 24 neutral images (mean valence rating = 5.2, SD = 0.5) were presented during the study phases of the experiment.

Words were taken from the Affective Norms for English Words (ANEW) corpus prepared by the Center for the Study of Emotion and Attention at the University of Florida (Bradley & Lang, 1999). This corpus is a collection of words which have similarly been rated for valence. From the corpus, a total of 12 negative, 12 positive,

and 24 neutral words were chosen to match the images presented during the study phases of the experiment. An equal number of words, matched for valence and length, served as distractors during the test phases. Words were matched group by group by t-tests (for all comparisons $p \geq 0.73$)

Test phase primed (repeated from the study phase) and unprimed words were matched for valence, frequency, and number of letters using t-tests (all $p \geq 0.92$). More importantly, these items were matched based on lexical decision RTs produced by a pre-experimental group of 31 subjects (matched for age, education, and gender with the experimental group). Groupings of words used in the current experiment were created based on these results. Average frequency for positive, negative, and neutral words was 29 per million according to the Kucera & Francis (1967) norms. T-tests revealed that whereas positive items and neutral items did not differ from each other in terms of frequency, negative items were slightly less frequent (frequency = 15.6) than both neutral items (frequency = 35; $p < 0.05$) and positive items (frequency = 33; $p < 0.05$). Note that frequencies between 10 and 75 per million are considered to be of medium frequency (Burgess & Livesay, 1998). Thus, notwithstanding this statistical difference, phenomenologically, all test words were of medium frequency. The average number of letters for all words was 6.1 (SD = 1.9). The three groups of words did not differ significantly from each other with respect to number of letters. Test phase nonwords were created by replacing one or two letters from a separate list of real words.

Procedure

In order to minimize memory load, the implicit memory experiment was divided into 4 sessions, each session consisting of a study phase directly followed by an associated test phase. A given test phase followed its respective study phase by a delay of approximately one minute. In the study phases, images were directly preceded by subliminally presented words. The subliminal effect was achieved by presenting the word in yellow text on a white background (thereby reducing the contrast of the stimulus). Pilot testing (among the 31 pilot subjects) was used to determine presentation parameters. When words were presented in black text on white background or when the yellow text was presented for longer than 77 ms, they were clearly visible. When words were presented in yellow text at 60 ms, these pilot subjects were unable to verbally report the words. The presentation parameters were therefore set as follows (see Figure 1): A word was presented for 60 ms. The word was immediately followed by the presentation of a row of yellow number signs on a black background for 17 ms. Following this masking stimulus, the screen was blank (i.e., black) for 500 ms. Next, an image which repeated the concept denoted by the preceding word was presented for 595 ms. A 2000 ms pause occurred before the presentation of the next word.

The emotional valence of each word-image pair (WIP) was congruent (ex: negative word “corpse” paired with the image of a dead body). A total of 12 WIPs were presented in each study phase. Therefore, a total of 36 WIPs were presented to each subject. Half of the WIPs were affectively neutral (ex: stool) while the other half

were either negative (ex: corpse) or positive (ex: flower), depending on the session. A given session either included negative and neutral WIPs or positive and neutral WIPs, but negative and positive WIPs were never presented in the same session. The order of sessions was counterbalanced across subjects and the order of WIP presentation was randomized for each subject.

In each test phase, a lexical decision task was administered. In this test, stimuli (words and nonwords in equal proportions) were presented one at a time in black font on a white background. Word or nonword stimuli were presented for 3000 ms – or until the subject made a response. Upon the presentation of each stimulus, the subject had to decide if the presented stimulus constituted a real word in the English language or not. Subjects revealed their decisions by pressing one of two keys on the computer keyboard using their index or adjacent middle finger for responding. Response side was counterbalanced across subjects (i.e., an equal number of subjects used their index finger to indicate words and nonwords). Half of the presented words repeated the items that had been presented at study (targets) and half were new, previously unencountered words (distractors).

All stimuli were presented on a laptop computer and the computer recorded each subject's RTs.

(Figure1 about here)

Results

In line with pilot testing results, many subjects reported having seen the masking stimulus (number signs). Only one subject, however, suspected that words were being subliminally presented. This subject's data was not used for study analyses. Indeed, the remaining subjects were surprised to learn that words had been presented.

All errors were removed from the analysis (note that a comparison of errors per stimulus type did not show any differences and that generally speaking, very few errors – less than 3% were committed). Median RTs for each subject to each group of word targets were calculated, and a 2 (target vs. distractor) X 3 (neutral vs. positive vs. negative) analysis of variance (ANOVA) was carried out on the data (see Table 1). Results revealed a main effect of condition ($F(1,32) = 22.41$; $p < 0.0001$). A Tukey test was used to determine that subjects responded more quickly to positive (617 ms) than to neutral (647 ms) or negative words (666 ms). A main effect was also found for priming ($F(1,32) = 4.93$; $p = 0.0335$) reflecting faster RTs to targets (638.7 ms) than to distractor (648 ms) words. Importantly, this effect interacted with condition ($F(2,64) = 4.18$; $p = 0.0196$). Significant priming (29 ms, RTs were 4.3% faster to targets than to distractors) was found for emotionally negative items ($F(1,32) = 9.83$; $p = 0.0037$), whereas emotionally positive and neutral items failed to elicit priming.

(Table 1 about here)

Discussion

This study has used a novel research approach to demonstrate that implicit memory is stronger for negatively valenced than for neutral or positively valenced stimuli. The present finding of enhanced implicit memory for stimuli carrying a negative emotional charge is in line with previous research discussed in the Introduction. This valence-dependent effect did not rely on mood-state, no preference judgment was accrued by subjects, and no classical conditioning took place. Rather, it was shown that previous passive processing of negatively valenced stimuli led to enhanced implicit memory of those stimuli later on.

What might account for these results? One possibility is that the negative stimuli in the current experiment were more effective at eliciting emotional responses. Because many of the negative WIPs implicated the human body (mutilations) or fearful creatures (like snakes), it may be that the emotions of disgust or fear were more effectively elicited by these stimuli as compared to the positive stimuli. In this case, the studied negative stimuli may have left a stronger impression on the subjects than the relatively benign neutral or positive stimuli.

We were surprised to find that neutral and positive stimuli did not provoke significant priming. It should be noted, however, that the type of priming used in our experiment may be quite subtle and difficult to measure (Greenwald, Draine, & Abrams, 1996). Previous research in our lab (Beauregard, Chertkow, Gold, & Karama, 1997;

Beauregard, Benhamou, Laurent, & Chertkow, 1999) and in others (e.g., Whittlesea et al., 2001) has found that a number of repetitions of the to-be-remembered items may be helpful in this form of priming. In the current study, each study item was presented only once. This was done in order to avoid a ceiling effect in the priming performance of our subjects which we felt would be necessary given that we were attempting to examine subtle differences in the magnitude of priming as a function of emotional valence. In the face of these limitations, the finding of significant priming for negative items supports the notion that negative stimuli are better remembered, even on tests of implicit memory.

In conclusion, the results of this study suggest that negative stimuli lead to enhanced implicit memory performance. These data fit with the findings of improved explicit memory for negatively valenced stimuli. These converging lines of evidence suggest that there is something special about negative stimuli as they interact with memory. Possibilities include the greater ease on the part of negative stimuli to elicit emotional responses. These data are also consistent with the idea that differential neural structures process negative stimuli, although that question is best suited to brain imaging studies.

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Figure 1: An example of stimulus presentation during the study phase of the implicit memory experiment. Presentation times are represented in milliseconds (ms).

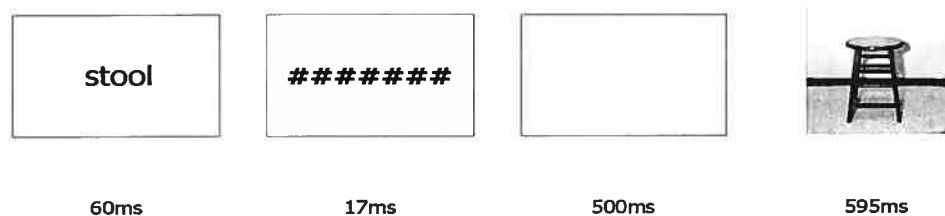


Table 1: RTs (standard deviation) to test phase items

	Neutral	Positive	Negative
Primes	647.7 (103)	617.1 (98)	651.1 (94)
Distractors	647 (97)	617.3 (86)	680.3 (119)

Study #3: Neural Substrate of Subliminal Cross-form Priming

Submitted to Journal of Neuroscience

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Abstract

No previous brain imaging studies of priming have used a cross-form subliminal paradigm. This study employed such a paradigm with the objective of studying the neural substrate of conceptual priming in the absence of repetition of perceptual information from study to test and in the absence of the possibility of contamination by explicit memory. Using functional magnetic resonance imaging, 10 male subjects were scanned while they were subliminally exposed to pictures which were immediately followed by primed or unprimed target words. Results revealed that priming among nonliving targets was accompanied by a decrease in activity in bilateral occipitotemporal areas as well as the left anterior superior temporal gyrus. Results are discussed in the context of the kind of processes which may underlie this type of priming and of the repetition suppression which occurred in areas known to be implicated in semantic processing.

Key words: conceptual priming, cross-form priming, repetition suppression, subliminal, magnetic resonance imaging, semantic memory

Introduction

Priming is a form of implicit memory in which the processing of a stimulus is rendered more efficient as a result of previous exposure to that stimulus (Schacter, 1987). Priming has been related to decreased regional cerebral blood flow, commonly referred to as repetition suppression (RS) (Desimone, 1996; Lebreton et al., 2001; Squire et al., 1992). In conceptual priming, it is probable that brain areas underlying semantic processing are involved because semantic processing of the test items is often required (Chertkow et al., 1992; Riddoch and Humphreys, 1987).

Semantic memory has been linked to a network of brain areas which proceeds anteriorly (and ventrally), from the occipital through to the temporal and frontal lobes (Martin and Chao, 2001; Vandenberghe et al., 1996). Indeed, many areas of this network have been associated with priming. In the occipitotemporal lobes, the lingual, fusiform, and cuneus gyri (Brodmann area – BA - 18, 19, and 37) have been linked to picture naming (Murtha et al., 1999), and both perceptual and conceptual priming (Koutstaal et al., 2001; Lebreton et al., 2001; Yasuno et al., 2000). Further, Badgaiyan et al. (2001) have hypothesized that BA 19 partially mediates within-modality priming. In the lateral temporal lobes, Mummery et al. (1999) found RS in BA 38 using semantic priming and hypothesized that activity in this area was related to the identification of a concept denoted by a word. Finally, the left inferior frontal lobe, hypothesized to be involved in phonology and semantic retrieval (Murtha et al., 1999), has shown RS in studies of conceptual priming (e.g., Gabrieli et al., 1996).

In most studies, because primes are consciously perceivable, activity ostensibly related to implicit memory may be contaminated by explicit memory. Subliminal priming, however, can be used to circumvent this problem (Beauregard et al., 1998, 1999). In a study by Dehaene et al. (2001), subliminal priming-related RS was observed in left fusiform gyrus (BA 37). Although words were presented in differing case, font change may not be a strong enough manipulation to conclude that RS in the fusiform reflects abstract non-lexical semantic activation. A stronger way to circumvent the repetition of perceptual information is with the use of cross-form priming in which primes and targets are of differing form altogether (e.g., pictures and words).

The present functional magnetic resonance imaging (fMRI) study was conducted to determine the neural substrate of subliminal cross-form conceptual priming. We were motivated by the prediction that brain areas implicated in semantic memory play a role in conceptual priming. Specifically, we hypothesized that priming would lead to RS in areas of the occipitotemporal cortex known to be implicated in the semantic processing of pictures, because in our study, priming depends on such processing. We also predicted that RS would be observed in BA 38 of the lateral temporal lobe because information gleaned from the processing of pictures would facilitate the processing of words at test. Finally, based on results from previous studies of conceptual priming, we predicted that the left inferior prefrontal cortex would show priming-related blood-oxygen-level-dependent (BOLD) signal changes.

Materials and Methods

Subjects

Ten male French-speaking subjects (right-handed Caucasian university students; age range: 19-28, mean = 24, S.D. = 2.3) participated in this study. No subject had a history of either psychiatric or neurological disorder. These subjects all gave written informed consent and the ethics committee of Centre hospitalier de l'Université De Montréal (CHUM), Hôpital Notre-Dame, approved the study. All subjects were paid an honorarium for their participation.

Materials

Virtual reality style goggles connected to a MR compatible video system (Resonance Technology, Inc., Van Nuys, CA, USA) were used to present the stimuli to subjects within the environment of the fMRI scanner. These goggles were connected to a PC which presented all stimuli and collected response times (RTs).

Simple line drawings of common objects (compiled by Alario and Ferrand, 1999) were presented in gray on a white background. Following each drawing, French words were presented in black text on a white background (for stimuli used, see Appendix A).

Procedure

BOLD signal changes were measured while subjects responded to target words preceded either by subliminally presented distractor or prime drawings. Prime-target pairs referred to the same concept; for example, a drawing of a helicopter preceded the French equivalent of the English word “helicopter”. Distractor-target pairs referred to different concepts; for example, a drawing of a book preceded the French equivalent of the English word “cat”. One hundred and twelve targets were presented, half of which were primed, and half of which were unprimed. Half of the targets represented living things, and half represented non-living things. Thus, in all there were 28 primed living targets, 28 unprimed living targets, 28 primed nonliving targets, and 28 unprimed nonliving targets.

The sequence of events representing one trial in the experiment was as follows: a masking stimulus was presented for 100 ms, a line drawing was presented for 34 ms, the screen went blank for 17 ms, the mask appeared again for 100 ms, the screen again went blank for 200 ms, a target word appeared for 1600 ms, and a fixation point appeared in the middle of the screen for either 2.8, 3.0, 3.2, 3.4, or 3.6 s (see Figure 1). This procedure was based on work conducted by Dell'Acqua and Grainger (1999). Thus, the primes (i.e., drawings) were presented subliminally. Upon the presentation of targets, the subject was required to make a two-choice response. The question to which the subject responded was: “Does this word represent something which is man-made or naturally occurring?” Subjects were instructed to respond as

quickly as possible. To do so, they used the first two digits of their right hands and finger laterality (left-right) was counterbalanced across subjects.

[Insert Figure 1 about here]

Image acquisition and analyses

Echoplanar images (EPI) were acquired on a 1.5 Tesla system (Magnetom Vision, Siemens Electric, Erlangen, Germany). Twenty-eight slices (5 mm thick) were acquired every 2.65 sec in an inclined axial plane, aligned with the AC-PC axis. These T2 weighted functional images were acquired using an event-related EPI pulse sequence (TE = 44 msec, Flip = 90°, FOV = 215 mm, Matrix = 64 x 64). The functional image run consisted of 247 sequential whole-brain acquisitions and lasted for 12.5 min. Prior to each run, 3 images were acquired and discarded in order to allow longitudinal magnetization to reach equilibrium. Following the functional run, high-resolution anatomical data were acquired via a T1-weighted three-dimensional volume acquisition obtained using a gradient echo pulse sequence (TR = 9.7 ms, TE = 4 ms, Flip = 12° FOV = 250 mm, Matrix = 256 x 256).

Data were analyzed using Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology, London, UK). Images for all subjects were realigned to correct for artifacts due to small head movements. The images for all subjects were then spatially normalized (voxel size: 3 mm x 3 mm x 3

mm) into an MRI stereotaxic space (Talairach and Tournoux, 1988) using this masked mean image. Images were then convolved in space with a three-dimensional isotropic gaussian kernel (12 mm FWHM) to improve the signal-to-noise ratio and to accommodate for residual variations in functional neuroanatomy that usually persist between subjects after spatial normalization. Normalized data were then selectively averaged in relation to condition within and across subjects.

For the event-related statistical analysis, a hemodynamic response function (hrf) with time derivative was used to model the activation patterns. Effects at each and every voxel were estimated using the general linear model. An averaged event-related statistical parametric map of the t statistic (SPM t), subsequently transformed to the unit normal distribution (SPM Z) was computed for each trial type. A “fixed-effects model” was implemented to contrast the brain activity associated with responses to primed and unprimed target words.

To delineate the brain regions associated with priming, the brain activity associated with responses to unprimed words was directly compared with the brain activity associated with responses to primed words. A small volume correction was performed in brain regions (ROIs) defined a priori. The search volume corresponding to the ROIs was defined a priori based on a meta-analysis of brain activity recorded in relation to tasks which tap semantic memory and conceptual priming (see Introduction). This meta-analysis yielded focal points and penumbras of activation in the fusiform gyrus (BA 19/37), the lingual gyrus (BA 19), the cuneus (BA 17/18), the anterior superior temporal gyrus (BA 22/38), and the left inferior

prefrontal cortex (BA 45, 46, 47). This information was applied to the MR reference image (MNI template) using the small volume correction (SVC) and sphere volume function in SPM99. For this search, a corrected probability threshold for multiple comparisons of $p < 0.05$ was used. Only clusters showing a spatial extent of at least 5 contiguous voxels were kept for image analysis.

Results

Behavioral

As expected, subjects were unable to consciously perceive the primes in the current study. Indeed, following the experimental session, all subjects were surprised to learn that the line drawings had been presented at all. Thus, the desired subliminal effect was achieved with complete success.

A two factor ANOVA (priming, semantic category) was carried out on the data. Results revealed a main effect of priming ($F_{1,9} = 15.4$, $p < 0.005$), indicating that a significant priming effect (2.5% overall; percentage priming = $(RT \text{ Distractor} - RT \text{ prime} / RT \text{ Distractor}) \times 100$) was present (RTs primed = 782 ms, RTs unprimed = 802 ms). An interaction was also observed between priming and semantic category ($F_{1,9} = 6.1$, $p < 0.05$), with significant priming occurring for nonliving things (5.4%) (RTs primed = 765 ms, RTs unprimed = 809 ms). No priming effect was noted for living things (see Figure 2).

[Insert Figure 2 about here]

Neuroimaging

Unprimed Targets – Primed Targets

Voxels which were less active in the primed condition relative to the unprimed condition are shown in Table 1. This subtraction revealed that areas of the bilateral inferior occipital lobe (BA 17, 18/19) and an area in the left superior temporal lobe (BA 22/38) were less active when subjects responded to primed versus unprimed target words (see Figure 3).

[Insert Table 1 about here]

[Insert Figure 3 about here]

Living targets – Nonliving Targets

Although there was no significant difference in RTs to living and nonliving items, a subtraction of these two conditions was nevertheless performed due to the long-standing debate as to the possibly dissociable neural substrates of these semantic categories (Bunn et al., 1998; Caramazza, 2000; Caramazza and Shelton, 1998; McRae and Cree, 2002; Warrington and Shallice, 1984). Greater activity was

recorded in right middle frontal gyrus (BA 6/9) in response to living versus nonliving targets. No other voxels reached significance.

Discussion

Behaviorally, this study confirmed the findings that unconsciously perceived primes can have a conceptual effect on the processing of subsequently presented targets. In terms of the underlying brain activity associated with this priming, occipitotemporal areas which have shown RS in other priming studies also displayed RS in our paradigm. Fusiform gyrus, however, did not show priming-related modulation in BOLD signal response. Finally, as predicted, an area implicated in higher-order semantic processing, the anterior superior temporal gyrus, was also implicated in the current conceptually driven priming paradigm.

There is some debate as to the extent to which semantic processing is carried out on subliminally presented stimuli (Damian, 2001; Dehaene et al., 2001; Marcel, 1983). In a study by Dehaene et al. (2001), the subliminal presentation of numerical primes (Arabic numerals or English equivalents) decreased RTs to a subsequent “large or small” binary decision task (above or below 5). The interpretation proposed for this “response congruity” effect was that primes were being so deeply processed that subjects were unconsciously applying the task instructions to them. The authors suggested that when the responses to the prime and to the target were incongruent, a slowing of RT occurred either because the subjects inhibited the original response or

because the subject had to switch motor programming for the response output to the target. A subsequent experiment by Damian (2001) has, however, called this assumption into question. In these experiments, when the primes were not part of the response set (i.e., were not responded to explicitly at some point in the experiment), the effect disappeared. Damian (2001) submitted that rather than semantic categorization of the primes being responsible for the effect, automatic processing may have played a role. In this perspective, because the primes in Dehaene et al. (2001) and in Damian (2001) were repeatedly paired with a given response, the process became automatic and a stimulus-response relationship rather than deep processing of the primes resulted in the effect. In contrast, our results, and those of Dell'Acqua and Grainger (1999) support the contention that subliminally presented primes are processed in a meaningful way. A casual examination of Figure 2 suggests that the priming effect observed here may have reflected an interference effect (i.e., negative priming) of living primes on RTs to nonliving targets. In other words, when our subjects unconsciously perceived a stimulus denoting a living entity, the stimulus may have been categorized as such, and it is possible that an appropriate response was prepared, ultimately leading to a need to “switch gears” in order to respond to the incongruent target. When the prime and the target were both nonliving, a small facilitatory effect was probably also present. As such, the priming observed in this study may be attributable to semantic activation of the primes leading to increased processing efficiency when prime and target were identical, or to the interference effect that could have occurred when they were from opposing semantic categories, or both. Future research will be needed to further explore this question.

The present finding of decreased activity in left BA 19 in relation to cross-form subliminal priming supports the hypothesis of Badgaiyan et al. (2001) that this area is at least partially responsible for the mediation of within-modality priming. Left extrastriate involvement in priming is consistent with previous studies using a variety of methodologies (e.g., Badgaiyan et al., 2001; Buckner et al., 1995). Whereas Badgaiyan et al. (2001) demonstrated priming-related changes in activity in BA 19, even when the surface form of stimuli was varied from study to test, our results further reveal that this area remains involved even when primes are unconsciously perceived. Further, this activity survives a stronger change in form than that used by Badgaiyan et al. (2001); namely, picture-to-word priming. In contrast, the right occipital involvement measured in our paradigm is likely to reflect the nonverbal (pictorial) nature of the priming stimuli. This result extends the contention by Lebreton et al. (2001) that right occipital cortex represents a format-specific system that processes the form of figurative drawings by suggesting that the right occipital lobe (cuneus) may represent an interface between object form and semantic knowledge relative to form. Findings of right cuneus involvement in the semantic processing of pictures supports this notion (Kosslyn et al., 1994, 1995; Martin et al., 1996; Murtha et al., 1999).

The lack of priming-related changes in BOLD signal in left fusiform cortex is intriguing because many other studies have found priming-related changes in this area. There is some debate, however, as to whether this area may subserve the lexical activation provoked by either visually or auditorally presented pictures or words

(Grill-Spector, 2001; Koutstaal et al., 2001). Because our pictures were presented subliminally, it is possible that this lexical-level activation did not take place. Further, previous investigations which have found BOLD signal changes in this area have used explicit perception of studied stimuli. Future research will undoubtedly continue to delineate the role that left fusiform cortex plays in priming.

RS recorded in the superior temporal gyrus may reflect a facilitation of semantic retrieval of item specific information. This view follows from Damasio et al.'s (1996) idea that the anterior temporal lobes are involved in this process. Ours is not the first conceptually driven brain imaging study to find priming-related changes in this area. RS has been found, for instance, in the superior temporal lobe (BA 22/40) in word-stem completion priming study (Yasuno et al., 2000). Further anteriorly, the temporal polar region (BA 38) has been implicated in a brain imaging investigation of semantic priming (Mummery et al., 1999). Lesions of the temporal lobes have been shown to promote difficulties in object naming and in defining objects (Hart and Gordon, 1990; Martin and Chao, 2001; Tranel et al., 1997; Warrington, 1975). Because the priming employed in the current paradigm repeated the identity of the targets, our results concur with the notion that the anterior superior temporal gyrus is critically involved in the selection and short-term maintenance of item specific semantic information.

The left inferior frontal cortex was hypothesized to show priming-related BOLD signal changes in the current study. The fact that no changes were observed was a surprise which is somewhat difficult to interpret. This area is hypothesized to be

involved in the phonological aspect of semantic activation. In this perspective, because the task was one of classification and because the primes were drawings that were presented subliminally, it is unlikely that phonological processing would have been elicited by the task. Left inferior prefrontal cortex is also hypothesized to be crucially involved in semantic retrieval. The results presented here do not support this position.

Finally, the fact that this study yielded priming for nonliving things but not for living things is somewhat troubling. After all, theories regarding an apparent living-nonliving distinction in semantic memory may have predicted the opposite effect. For example, Caramazza and Shelton (1998) have suggested that living things hold a special place in semantic memory and experimental evidence suggests that living things in particular are evaluated very rapidly by the brain, perhaps because throughout evolution they were more important to survival (LeDoux, 1996). We interpret this effect, however, in the perspective that the priming observed in this paradigm included both interference and facilitation. If it is true that living things are more semantically salient than nonliving things, then it is possible that the interfering effect of living things on responses to nonliving targets would be greater than in the opposite scenario. Further, it is possible that RTs to living items were less susceptible to priming due to a ceiling effect on RTs. Future research will be needed to clarify these issues.

In conclusion, our results support the notion that even unconsciously perceives stimuli can yield conceptually bound effects on behavior. This study also shows that

this process can lead to changes in cortical activity measurable with fMRI. Whereas occipital areas were involved in these changes, the fact that fusiform gyrus was not activated in our study suggests that previous paradigms which have generated BOLD signal changes in this region may have relied on either explicit lexical activation or on the repetition of perceptual information. Finally, the implication of the left anterior temporal cortex in cross-form conceptual priming is in line with the idea that this region is involved in the short-term maintenance of semantic information.

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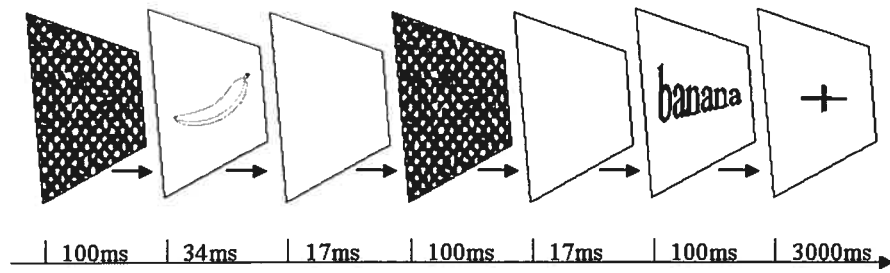
Table 1. Significant loci of decreased activity

Region	Brodmann area	Talairach coordinates			Z - statistic	Corrected p value
		X	Y	Z		
Nonliving Neutral – Nonliving Primed condition						
R. Cuneus	17/18	21	-63	14	3.50	p = 0.019
L. Lingual	19	-6	-65	-9	3.45	p = 0.022
L. Anterior superior temporal	22/38	-59	6	-5	3.20	p = 0.046
Living Target – Nonliving Target condition						
R. Middle frontal gyrus	6/8	51	14	44	3.64	p = 0.01

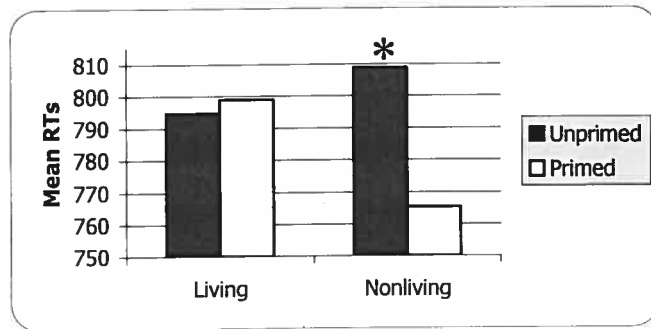
Stereotaxic coordinates are derived from the human atlas of Talairach and Tournoux (1988) and refer to medial - lateral position (x) relative to medline (positive = right), anterior - posterior position (y) relative to the anterior commissure (positive = anterior), and superior - inferior position (z) relative to the commissural line (positive = superior). Designation of Brodmann areas are also based on this atlas. L, left; R, right.

Figures

Figure 1: Graphical representation of behavioral paradigm

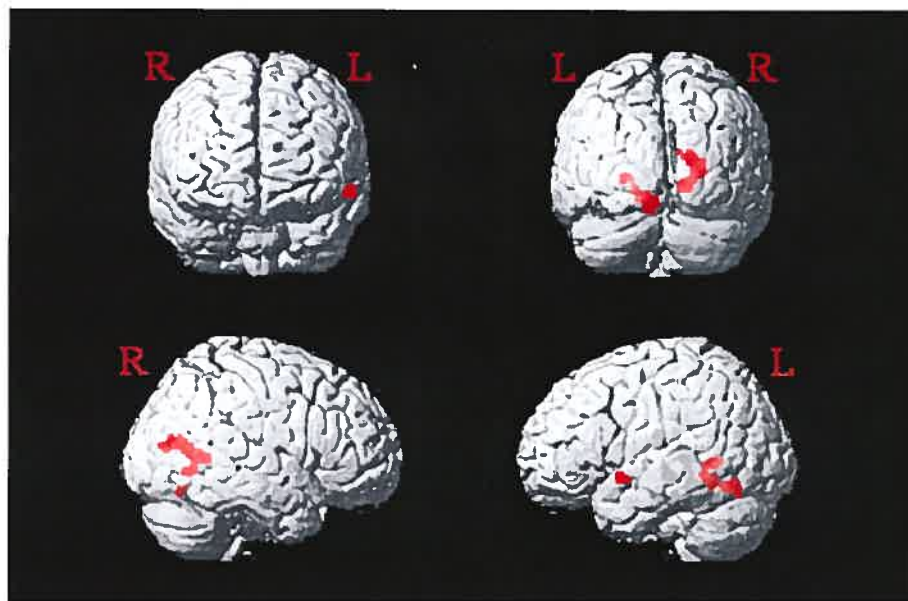


Schematic representation of images as they appeared to subjects in the cross-form subliminal paradigm.

Figure 2: Mean RTs to targets

Graphical representation of behavioral data. RTs are given in ms. There is no significant difference in RTs to primed and unprimed living targets. * Indicates that a significant difference in RTs was recorded for primed versus unprimed nonliving targets ($p < 0.005$).

Figure 3: Priming-dependent BOLD signal changes on rendered cortex



Whole-brain statistical activation maps showing distinct foci of cortical activations (red voxels) in the neutral – primed subtraction. Activation foci are superimposed on a rendered template brain. L, left; R, right.

Appendix A: items used in the current experiment

Category	Status	Images	Words
living	distractor	accordion	abeille
living	distractor	anchor	agneau
living	distractor	anvil	âne
living	distractor	ashtray	baleine
living	distractor	axe	bison
living	distractor	bench	carotte
living	distractor	bicycle	chameau
living	distractor	book	chat
living	distractor	bottle	chenille
living	distractor	bowl	chèvre
living	distractor	broom	cochon
living	distractor	brush	crabe
living	distractor	bus	fourmi
living	distractor	car	fraise
living	distractor	chimney	grenouille
living	distractor	clothespin	hibou
living	distractor	couch	lama
living	distractor	door	lézard
living	distractor	dresser	lion
living	distractor	drum	morse
living	distractor	dustpan	oignon
living	distractor	fence	phoque
living	distractor	fire hydrant	poisson
living	distractor	frying pan	poule
living	distractor	funnel	rat
living	distractor	garbage can	renard
living	distractor	iron	sauterelle
living	distractor	ladder	tomate
living	prime	eagle	aigle
living	prime	pineapple	ananas
living	prime	spider	araignée
living	prime	ostrich	autruche
living	prime	banana	banane
living	prime	cactus	cactus
living	prime	mushroom	champignon
living	prime	dolphin	dauphin
living	prime	squirrel	écureuil
living	prime	elephant	éléphant
living	prime	flower	fleur
living	prime	giraffe	girafe
living	prime	kangaroo	kangourou

living	prime	rabbit	lapin
living	prime	wolf	loup
living	prime	sheep	mouton
living	prime	bear	ours
living	prime	palm tree	palmier
living	prime	panda	panda
living	prime	parrot	perroquet
living	prime	penguin	pingouin
living	prime	pear	poire
living	prime	shark	requin
living	prime	rhinoceros	rhinocéros
living	prime	tiger	tigre
living	prime	turtle	tortue
living	prime	cow	vache
living	prime	zebra	zèbre
nonliving	distractor	alligator	église
nonliving	distractor	ant	boîte
nonliving	distractor	apple	train
nonliving	distractor	artichoke	tasse
nonliving	distractor	bee	crayon
nonliving	distractor	beetle	règle
nonliving	distractor	bird	chaussette
nonliving	distractor	buffalo	casque
nonliving	distractor	butterfly	violon
nonliving	distractor	camel	poêle
nonliving	distractor	carrot	bague
nonliving	distractor	cat	poubelle
nonliving	distractor	chicken	moto
nonliving	distractor	corn	horloge
nonliving	distractor	deer	montre
nonliving	distractor	dog	fouet
nonliving	distractor	donkey	brosse
nonliving	distractor	duck	jupe
nonliving	distractor	fish	valise
nonliving	distractor	flamingo	collier
nonliving	distractor	fly	cadenas
nonliving	distractor	fox	chariot
nonliving	distractor	frog	canapé
nonliving	distractor	hippopotamus	bouton
nonliving	distractor	horse	tonneau
nonliving	distractor	hyena	poupée
nonliving	distractor	koala	éventail
nonliving	distractor	lamb	penderie
nonliving	prime	boot	botte
nonliving	prime	screwdriver	tournevis
nonliving	prime	knife	couteau

nonliving	prime	hammer	marteau
nonliving	prime	truck	camion
nonliving	prime	lamp	lampe
nonliving	prime	saw	scie
nonliving	prime	desk	bureau
nonliving	prime	guitar	guitare
nonliving	prime	tractor	tracteur
nonliving	prime	bell	cloche
nonliving	prime	tie	cravate
nonliving	prime	helicopter	hélicoptère
nonliving	prime	airplane	avion
nonliving	prime	screw	vis
nonliving	prime	chair	chaise
nonliving	prime	ball	ballon
nonliving	prime	watering	arrosoir
nonliving	prime	basket	panier
nonliving	prime	telephone	téléphone
nonliving	prime	piano	piano
nonliving	prime	rake	râteau
nonliving	prime	fork	fourchette
nonliving	prime	light bulb	ampoule
nonliving	prime	candle	bougie
nonliving	prime	comb	peigne
nonliving	prime	glove	gant
nonliving	prime	pyramid	pyramide

Chapter 3: General Discussion

Discussion

The main objective of the research carried out in this thesis was to evaluate the hypothesis that the variables of emotional salience and semantic category would interact with repetition priming. While studies have examined the effect of variables including mood-relevance (Bradley et al., 1996; Challis and Krane, 1988; Danion et al., 1995), global lexical imageability (abstract versus concrete concepts) (Jin, 1990), age of acquisition (Barry et al., 2001), and frequency of occurrence (Forster and Davis, 1984) on repetition priming, only a handful of studies have investigated the effects of more meaningful variables endogenous to the to-be-remembered stimuli. To our knowledge, no studies have been undertaken with the goal of establishing how semantic category and emotional salience, two highly meaningful variables known to influence other forms of memory, interact with priming. The studies contained within this thesis were conducted in order to rectify this oversight, and to garner increasingly detailed information with respect to the neural and cognitive architecture that underlies subliminal cross-form priming. Specifically, two studies tested specific hypotheses with respect to these variables: Study #1 tested whether living or nonliving concepts would yield greater CFIP; and Study #2 tested whether items with higher emotional salience would lead to greater CFIP. Finally, Study #3 established that areas of the cerebral cortex which are known to participate in semantic memory also participate in subliminal CFIP.

This Discussion will have three parts. In the first, conclusions relative to the central questions raised in each of the three studies will be discussed within the evolutionary perspective. Next, the results reported will be discussed in the context of theoretical models of implicit memory. Finally, conclusions will be drawn with respect to the importance of the data regarding both the evolutionary perspective and the conventional cognitive accounts of implicit memory.

Living-Nonliving

The hypothesis that the strength of implicit memory may be modulated in relation to characteristics endogenous to the to-be-remembered stimuli was confirmed in Study #1 **“Semantic category effects in cross-form priming”**. The central finding of this article is that greater CFIP was obtained for living versus nonliving things. This result is in line with the assumption that the semantic system is particularly tuned to the identification and processing of living things as proposed by Caramazza and Shelton (1998) and LeDoux (1996). Across the span of evolution, living things have most probably played a much more important role in everyday life than nonliving things. We agree with Caramazza and Shelton (1998) that this fact may have led to the organization of brains which are particularly tuned to the perception and categorization of living things. If living things are more salient, and if the capacity for priming is a response to evolutionary pressures, then it follows that priming should be more robust for living versus nonliving things, and this is exactly what was found.

In the discussion of the article, a number of hypotheses were generated to account for the enhanced strength of priming observed among living things, including an interpretation within the sensory-functional dichotomy originally proposed by Warrington and colleagues (Warrington and McCarthy, 1983; Warrington and Shallice, 1984), and the supposition that increased study-phase processing and semantic activation may have occurred for living things because they may be more emotionally meaningful than nonliving things (Caramazza and Shelton, 1998). This emotional salience hypothesis was one factor which motivated the research undertaken in the second study.

Emotional valence and Arousal

The goal of Study #2, “**Negative valence potentiates repetition priming**” was to test the hypothesis that greater emotional salience leads to greater CFIP. One of the assumptions underlying this thesis is that all forms of memory exist for the same purpose; namely, to allow the organism to learn from experience. There is ample evidence that stimuli or events of increased emotional salience lead to greater long-term memory than relatively neutral stimuli. For example, early research found that emotionally salient stimuli led to increased long-term memory formation; a so-called “reminiscence effect” (Revelle and Loftus, 1992). Although many researchers have found both short-term detriment and long-term benefits of arousal on memory, a

number have also found that arousal may benefit both types of learning (Revelle and Loftus, 1992).

The question which must be asked in the current evolutionary perspective is why emotionally salient events would lead to improved memory. It seems reasonable to answer this question by pointing out that events or stimuli of great emotional salience more often than not represent real world situations which could potentially impact on survival. For example, many of the more highly salient and arousing (negative) stimuli in our study depicted dangerous animals or situations of bodily mutilations, stimuli/events which could be seen to be imperiling to survival itself. In Study #2 we predicted that, in line with findings obtained in studies of explicit memory, improved CFIP would be recorded in relation to emotionally salient (negative and more arousing) versus emotionally neutral stimuli. The results of the study confirmed this hypothesis. Indeed, our finding that negative but not positive emotional valence potentiated priming is in line with the reasoning behind Caramazza and Shelton's (1998) hypothesis. In that conception, the very reason why items belonging to the category of living things are more emotionally salient is based on Darwinian survival. In order to survive, animals must avoid death, and, as such, safety is of paramount importance. Safety can be defined as the avoidance of danger. Danger is closely associated with negativity, and thus our negative stimuli may have had a greater effect on our subjects than neutral or even positive stimuli. When faced with something dangerous (i.e., a ferocious animal), the human must prepare (think fight or flight), and the increased attention paid to stimuli representing threats might aid in memory formation, both explicit and implicit (Revelle and Loftus, 1992).

What then is the mechanism by which emotionally salient stimuli improve implicit memory in particular? One hypothesis which has been proposed seems to fit with the current priming data. In Study #2, we discussed the notion that emotionally salient (and arousing) stimuli may garner increased attention and processing; a “natural selective attention” (Lang et al., 1990). Revelle and colleagues (Humphreys and Revelle, 1984; Revelle, 1989; Revelle and Loftus, 1990) have introduced the "tick rate hypothesis" to account for this effect. In an analogy to the CPUs of computers, this hypothesis posits that arousal increases the rate at which the environment is sampled. A stimulus which is more often sampled will lead to deeper processing, to greater semantic activation, and, hence, to enhanced CFIP. Indeed, these authors have proposed that a high level of arousal facilitates the detection and strengthens the retention of information. A similar way to conceive of this effect is in the context of the levels of processing framework originally proposed by Craik and Lockhart (1972). With respect to the current results, this theory would dictate that the more salient and arousing stimuli in our study would garner more attention and therefore be spontaneously processed at a deeper level.

Neuronal Underpinnings

Because we were interested in learning about the neural underpinnings of CFIP, in Study #3 “**Neural Substrate of Subliminal Cross-form Priming**” we used a subliminal paradigm in the hopes of finding changes in the BOLD response which

relate exclusively to the increase in processing efficiency for conceptually primed items. Behaviorally, results suggest that the subliminal presentation of pictures can lead to semantic activation of concepts denoted by those pictures and that these concepts are subsequently processed more efficiently when they are repeated in their lexical form. Importantly, the effects of this conceptual activation were measured even though there was no repetition of perceptual information between study and test items. Equally important was the fact that this activation occurred in the absence of any possibility of explicit recall of the studied items.

This study tested the hypothesis that cortical areas which subserve semantic processing of external stimuli are involved in subliminal CFIP. More specifically, we wondered whether brain areas which are closely related to perceptual processing, or those which participate in higher-level semantic processing, might be involved in this form of priming. The results of the study indicated that perceptual processing areas of the occipitotemporal cortex, which participate early on in the stream of object processing, showed RS. An area further anterior, in the anterior lateral superior temporal lobe, however, also showed this effect. Because these results suggest that areas within a semantic network involving phylogenically recent neocortical areas play a role in CFIP, the notion that priming is a mechanism which has been incorporated into ever-increasingly complex associative cortex is supported.

Models of Implicit Memory

The results of this thesis support the notion that emotional salience and items from the category of living as opposed to nonliving things both increase the strength of repetition priming. It is important, however, to situate these results in the context of contemporary models of priming. The following discussion not only attempts to situate our results in contemporary theories but, also, evaluates these theories in light of our data.

Priming, in the memory systems perspective, is deemed to exist solely in the service of the identification of objects. As such, it resembles procedural memory (if perception is seen as a skill - Tulving and Schacter, 1990; see also Gabrieli et al.'s (1994) structural-perceptual memory system). According to Tulving and Schacter (1990), priming effects are mediated by the PRS. The PRS (itself divided into a visual word form, a structural description, and an auditory word form system) is believed to be a hyper-specific memory system that stores information only about an object or a word's form but not about its meaning (Schacter, 1992b). This conception is able to account for perceptual priming, as may occur, for example, in tachistoscopic identification paradigms. It does so by assuming that once an object or a word's form is processed, subsequent processing of the same structural form becomes more efficient. It should be noted, however, that the theory does not say *how* this occurs. While the systems view, however, is capable of explaining perceptual repetition priming, it has great difficulty in accounting for CFIP. By this

view, to the extent that identity priming is a form of implicit memory, it must implicate either the PRS or some analogous system. The presentation of a word may indeed activate a “word form” system, and the presentation of a picture may activate a “structural description” system, but where the systems view fails is in drawing a link between the two. Indeed, because such sub-systems are deemed to be hyper-specific and independent, it is not clear how the systems view is capable of explaining the CFIP observed in our studies.

Because it explains in much more detail exactly how each module works, and how the various modules and levels of abstraction interact, the modular memory approach is superior to the multiple memory systems view in accounting for CFIP. Both Nadel (1994) and Moscovitch (1992) define the terms of the component modules that comprise their systems: For Nadel, differing systems handle particular kinds of information, perform different kinds of computations, and store the information for differing lengths of time. For Moscovitch, the main difference between input modules and central systems is that the output from the modules is devoid of meaning, which is assigned at the level of central systems (which receive their input from these modules). Within the central systems, a “semantic record” is created upon the presentation of a meaningful stimulus. According to the model, consciousness, referred to as Working Memory (Baddeley, 1992), may have access to these processes, although this is not necessarily always so, as in cases where the stimulus is perceived unconsciously. When consciousness does take place, semantically encoded information is sent to the frontal lobe working memory system, and subsequently to the medial temporal lobe hippocampal system. The modular approach is able to

account for CFIP to the extent that both modules and central systems have the property of maintenance of information. In this perspective, the semantic record (originally instantiated by the presentation of a stimulus) is reactivated by another stimulus with a similar (or identical) conceptual meaning, and processing efficiency is bolstered.

Whereas the modular approach is able to account for CFIP, a similar though much more explicit explanation comes from the “activational” perspective. In the activational perspective, the perception of a meaningful item directly leads to activation of the item’s stored representation within semantic memory. This approach is thus well suited to explaining CFIP because activity promoted by the first encounter with a concept is maintained long enough to aid in the processing of the same concept the next time around – even when form is varied from study to test.

Morton’s (1969, 1970) logogen model (together with its subsequent revisions) constitutes an activational account of implicit memory (Figure 3). Activational accounts can be opposed to the memory systems approach because in the latter, early perceptual systems are assumed to be devoid of semantic information whereas the former assumes that priming depends on such pre-existing representations. The logogen model, originally proposed to account for word recognition, proposes the existence of informational codes (internal representations) called “logogens” which are stored in a “Logogen System”. A logogen is a combination of semantic, acoustic, and visual information about a given concept. It is not a basic linguistic unit (a morpheme) but rather an internal representation of the concept itself. In the system,

logogens are defined as counting devices. They are considered to have baseline levels of activation whose “count” can be increased by the perception of external stimuli. That is, a logogen may be activated (increasing the count) by a variety of input sources (e.g., written word, spoken word). If the count reaches a certain threshold (or critical) value, that particular logogen is made available for (verbal) responding. Importantly, the count is assumed to fall back to its baseline level quite rapidly with time. According to the model, priming can be understood in the following manner: Upon the presentation of a word, the count of its logogen is increased, which lowers its relative threshold, such that a subsequent presentation may more easily raise the activation above some critical value.

Bower’s (1986, 1996) “reactivation” model extends Morton’s (1969, 1970) logogen model and is superior in the clarity of its account of CFIP. The critical addition that Bower makes is that logogens now also have perceptual analogs which describe canonical versions of objects (imagens). In a “Sensory Analysis System” akin to Biederman’s geon theory (1986, 1987), objects activate a set of geons (simple shape primitives such as cylinders and wedges that discriminate visual objects at a basic level). As also proposed in Paivio’s “dual-coding” approach (Paivio, 1978; Paivio and Begg, 1981), these geons map to imagens (the pictorial equivalent of logogens) which map back to logogens (Figure 4). In this model, a mechanism is in place to fully account for the type of CFIP employed in this thesis: a picture is presented and captured by a low-level Sensory Analysis System → activated geons in turn activate an imagen → activation is transferred to the imagen’s referent logogen thus lowering its threshold → the word is presented → due to residual activation, the

logogen is already near its threshold → conceptual processing of the concept denoted by the word is rendered more efficient.

Importantly to the present thesis, the activational perspective is able to account for subliminal priming. Bower (1996) accounts for subliminal priming by saying that depending on quantity of activation, the logogen may or may not be experienced (perceived) consciously. Thus, in this conception, activation of a logogen is not all-or-none. Rather, varying levels of magnitude of activation are possible. By this account, in subliminal priming, low-level activation is present even when no conscious perception has occurred. A subsequent lexical decision, then, is faster if the word refers to the same logogen (as compared to a less-activated logogen). The activational perspective therefore is very much compatible with findings of subliminal CFIP observed in Study #3. Although the effects of the CFIP manipulation may be small, a sensitive test may nevertheless be able to reveal the effects of an unconsciously perceived stimulus.

In contrast to these models, a number of theorists hold that all forms of memory result from common mechanisms (Masson and Bodner, in press; Mayes et al., 1997; Ratcliff and McKoon, 1988). In this perspective, all memory phenomena are the product of the episodic retention of the learning episode, although such retention need not be available to consciousness.

Motivation for this “retrospective” view comes from the apparent failure on the part of activational perspective to account for certain priming phenomena. For example,

although some research has shown decay of masked priming to occur quite quickly (Forster and Davis, 1984), it has been observed that priming effects can last for days or weeks (e.g., Jacoby and Dallas, 1981; Mitchell and Brown, 1988). As discussed above, activation theories assume that the count level of a logogen (or imagen) returns to baseline relatively quickly following stimulation, certainly within a few minutes. Thus, the activation perspective is at a disadvantage in accounting for very long-term priming. Furthermore, priming has been repeatedly shown for nonwords (Bodner and Masson, 1997; Light et al., 1995; Light et al., 1996; Masson and Isaak, 1999; McKone and Trynes, 1999) which is difficult to explain in the activation perspective since in that perspective logogens must exist before priming can occur. It is possible, however, that priming for nonwords may merely reflect perceptual processing advantages for previously encountered letter strings.

In light of these considerations, Masson and Bodner (in press) propose that a prime event creates a memory processing resource (or memory trace) which is accessed upon the presentation of a target and which ultimately leads to increased processing efficiency. Ratcliff and McKoon's (1988, 1994) "compound-cue" theory is similar to Masson and Bodner (in press) view in the sense that they consider that a priming event sets-up a memory trace which is used to increase processing efficiency when a target is presented. At test, the trace and the target are combined to create a "compound-cue" which is a function of the match between the cue (target) and the memory trace. To account for semantic priming, the theory suggests that instead of activation spreading from a prime to its related target, the pre-existing relationship between the prime and the target will be accessed by the compound-cue. The greater

the relationship between the prime and the target in long-term memory the greater the processing advantage. Accuracy and response time are determined by the “familiarity” of the compound-cue; that is, the extent to which the two items are pre-associated in long-term memory. An interpretation of CFIP within this perspective, therefore, is that the memory trace of a prime is accessed when the target is encountered. If the prime and the target refer to the same concept, then they are infinitely related in long-term (semantic) memory. As such, priming is expected to occur. The results recorded in the current three studies, therefore, support the compound-cue approach.

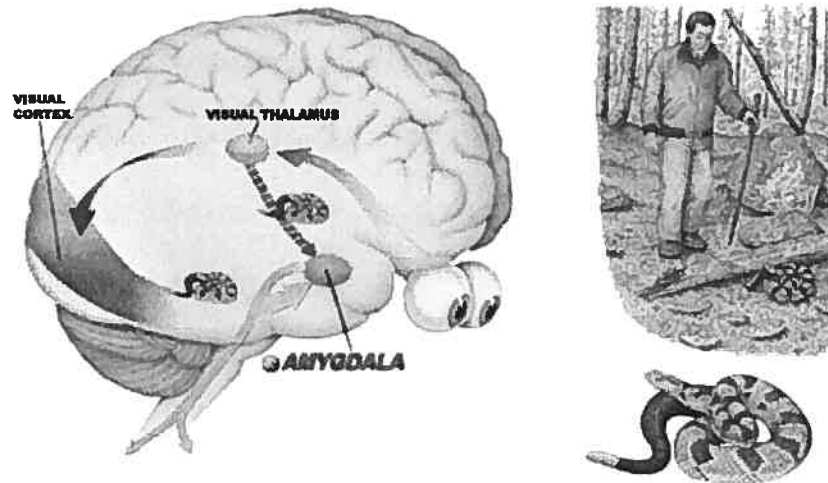
Conclusions

This thesis has accomplished a number of important goals. First, it has helped to establish the CFIP paradigm as a viable tool for the investigation of implicit and semantic memory. While CFIP has been used in the current thesis to investigate semantic category and emotional salience effects on implicit memory, further exploitation of this technique should lead to additional knowledge regarding other research questions in the future. Secondly, we have firmly established that emotional salience and items from the semantic category of living things lead to enhanced CFIP, and by extension, implicit memory. We have seen that the activation perspective is best suited to accounting for these results (together with those of subliminal CFIP obtained in Study #3), and that an evolutionary perspective is able to provide a theoretical context in which to understand them. Finally, Study #3 has shown that

areas which participate in the semantic processing of individual items, both at a relatively early perceptual level and further ahead in the processing stream, participate in the increased conceptual efficiency which the paradigm of subliminal CFIP confers. Ultimately, this thesis has supported the position that priming is a ubiquitous phenomenon which has probably helped humans to come this far in evolution, and which is most certainly at play in our everyday lives.

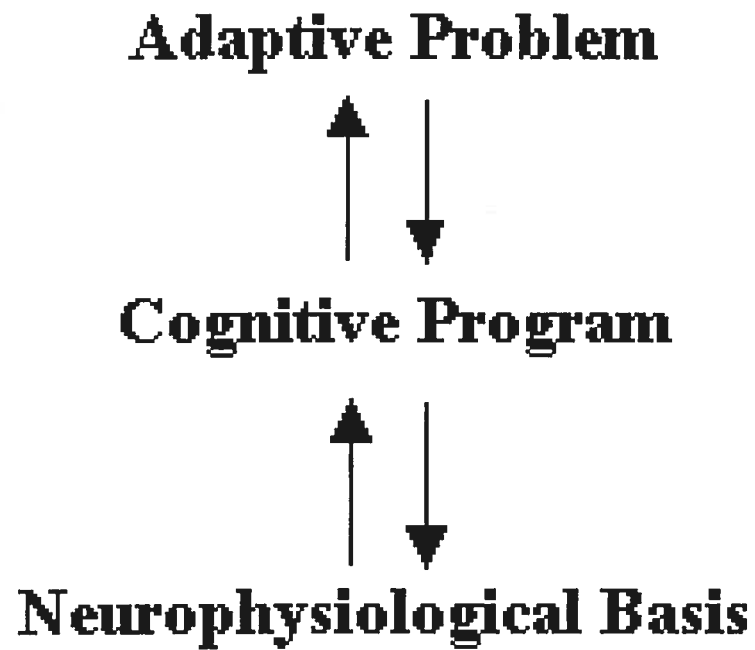
Figures

Figure 1



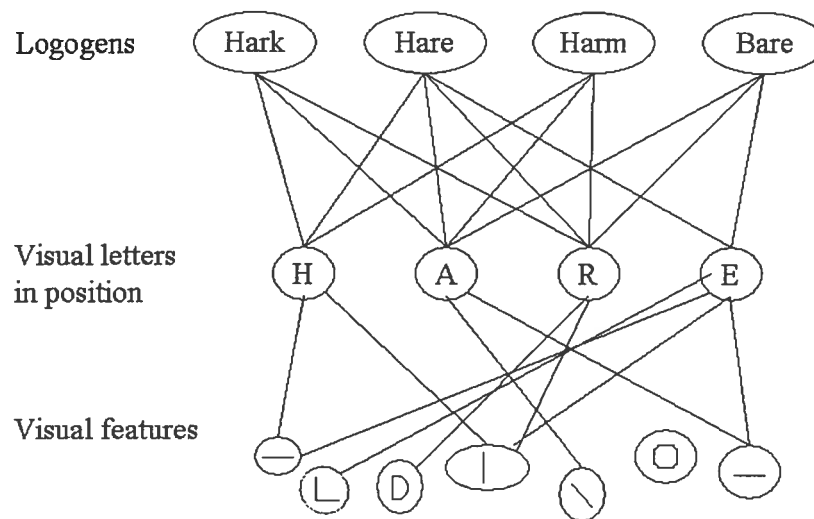
Adapted from LeDoux (1996). This figure graphically illustrates LeDoux's conception of a rapid neuronal system for the classification and response to potentially dangerous animals.

Figure 2



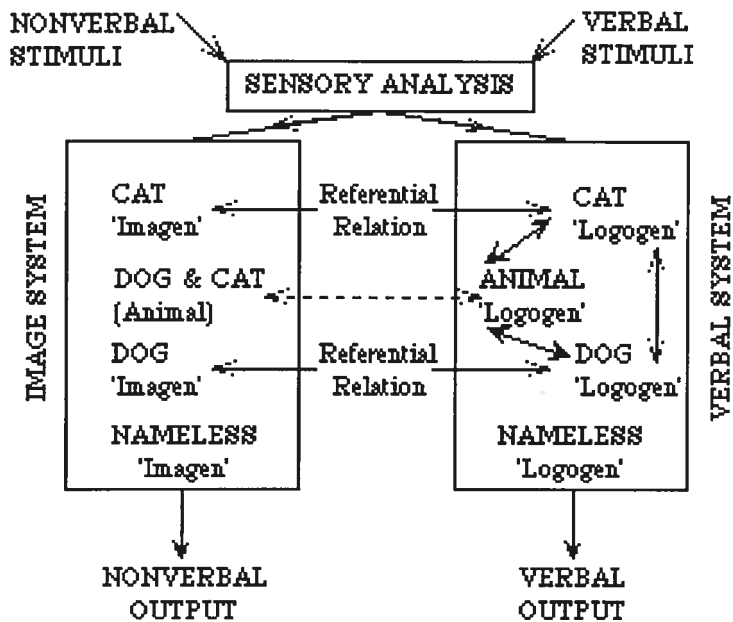
Three complementary levels of explanation in evolutionary psychology. Inferences (represented by the arrows) can be made from one level to another. Based on Cosmides and Tooby (1997).

Figure 3



Based on Bower's (1996) schematic representation of logogens near the logogen "HARE". Visual features map to letters, and these in turn map to logogens.

Figure 4



Based on Bleasdale (1983). The schematic shows how the logogen and imagen systems are hypothesized to interact.

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