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Effects of Long-Term Memory on Visual Attention and Access to Visual Consciousness

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For Laura, Elisa, and the little one on the way.

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Zusammenfassung

Zahlreiche aktuelle Studien weisen darauf hin, dass Erinnerungen aus dem Langzeitgedächtnis Einfluss auf die frühe perzeptuelle Verarbeitung ausüben. Diese Schlussfolgerung wird von Kritikern die Wahrnehmung als grundsätzlich unabhängig von Kognition betrachten, in Zweifel gezogen. In dieser Dissertation zeige ich anhand einer Reihe von Beispielen wie das Langzeitgedächtnis die perzeptuelle Verarbeitung beeinflussen kann, sowohl anhand einer Aufgabe zur visuellen Aufmerksamkeit, mittels derer ich verdeutliche, inwiefern episodische Erinnerungen perzeptuelle Distrakoreffekte reduzieren können, als auch mit Hilfe einer Aufgabe zur bewussten visuellen Wahrnehmung, bei der sich das semantische Wissen von Personen auf deren Fähigkeit auswirkt, Objekte bewusst wahrzunehmen. Die Versuchspersonen in Experiment 1 hatten die Aufgabe, zuvor gelernte Worte entweder ins Gedächtnis zu rufen oder die Erinnerung an die Worte zu unterdrücken. Anschließend mussten sie unter Zeitdruck neue, bisher nicht präsentierte Worte semantisch einordnen, wobei die Zielworte von den zuvor abgerufenen oder unterdrückten Worten flankiert waren. Da die flankierenden Worte für die semantische Entscheidungsaufgabe irrelevant waren und die Versuchspersonen instruiert worden waren, diese zu ignorieren, kann ein Einfluss auf die Entscheidungsaufgabe als Hinweis auf einen perzeptuellen Distraktoreffekt gewertet werden. Die Ergebnisse von Experiment 1 zeigen, dass Distraktoreffekte für zuvor unterdrückte Gedächtnisinhalte im Vergleich zur abgerufenen Gedächtnisinhalten deutlich reduziert waren, was darauf hinweist, dass episodische Gedächtnisinhalte die Wahrnehmung beeinflussen. Auf dieser Erkenntnis aufbauend zeige ich in Experiment 2, wie diese suppressionsinduzierte Reduktion der Verarbeitung von Distraktorreizen durch individuelle Differenzen maskiert werden kann. Schließlich wurden den Versuchspersonen in Experiment 3 in einer „Attentional-Blink"-Aufgabe unbekannte Objekte als zweites von zwei aufeinander folgenden Zielobjekten dargeboten. Die Ergebnisse weisen darauf hin, dass die Versuchspersonen Objekte, die mit einer neu gelernten semantischen Information assoziiert waren, besser erkennen konnten als Objekte, die mit minimaler Information assoziiert waren. Dieser Effekt ging mit einer Modulation der ereigniskorrelierten Potenziale 100ms nach Erscheinen des Reizes einher. Zusammengenommen reihen sich diese Experimente in eine wachsende Zahl an Studien ein, die Rückschluss darauf geben, dass Inhalte aus dem Langzeitgedächtnis Wahrnehmungsprozesse beeinflussen können und leisten damit einen weiteren Beitrag zur Erkenntnis, dass die Wahrnehmung gegenüber höheren Kognitionen nicht unabhängig ist.

Schlüsselworte:

Episodisches Gedächtnis, Semantisches Gedächtnis, Wahrnehmung, Bewusstsein, Ereigniskorreliertes Potenzial

Abstract

Numerous studies are emerging which suggest that long-term memories can influence early perceptual processing. Notwithstanding, these finding have come under fire from critics who view perceptual processing as independent of cognition. In this dissertation I demonstrate novel instances of long-term memory effects on perceptual processing, both in the context of an attentional task where I look at the extent to which episodic memory can reduce perceptual distraction and in a conscious detection task where I assess the effect of semantic knowledge on peoples ability to consciously detect briefly presented objects. In experiment one, participants retrieved or suppressed previously memorised words. Following this task, participants made speeded semantic judgments on novel target words that were flanked by the words that had previously undergone suppression or retrieval. Because the flanking words were irrelevant to the semantic judgment and were supposed to be ignored, any influence of their presence on semantic judgment speed can be taken as a marker of perceptual distraction. Results showed that the tendency for flankers to distract from target processing was markedly reduced if those flankers had undergone suppression. In experiment two, I expanded upon this finding by showing how this suppression-induced reduction in distractor processing can be masked by individual differences. Finally, in experiment three, I presented pictures of novel objects to participants as the second of two targets in an attentional blink paradigm. Results showed that participants were able to perceive objects associated with newly acquired semantic knowledge better than objects associated with minimal knowledge, a finding that was associated with a modulation of event-related brain potentials 100 msec after stimulus onset. Taken together, these experiments contribute to the growing body of evidence showing that information from long-term memory can influence perceptual processing.

Keywords:

Episodic Memory, Semantic Memory, Perception, Consciousness, Event-Related Potential

Chapter 1: Introduction and Aims

1. Overview

The question of how the mind is organised is a long standing one and has received much attention since the development of cognitive science as a discipline. A number of theoretical approaches have been proposed to explain the architecture of cognition, taking into account findings from neuroscience, cognitive development, evolutionary psychology and artificial intelligence, which have resulted in the development of constructs such as modularity, informational encapsulation, and serial versus parallel processing. Perhaps one of the most interesting questions regarding the organisation of the mind is the extent to which certain cognitive processes from different domains can be divided into separable systems which operate independently from one another. An area where this issue is perhaps most disputed is our conceptualisation of the relationship between perception and cognition. The debate regarding this relationship is based around a number of questions concerning the manner in which information may be exchanged between early perception and later cognition. A prominent position in this debate is the idea that perception is theory-neutral, that is, perception is informationally encapsulated from cognition, rendering it impervious to its influence. This idea was vehemently put forward by Fodor in his modularity of mind thesis (1983) who argued that perception takes place within a domain specific, informationally encapsulated "module" where perceptual processes operate independently, and thus, are cut off from the influences of cognitive states. Fodor viewed such an encapsulation of perception as essential for efficient and truthful observation of the world. A number of theoretically similar accounts have been proposed since, supporting a modular approach to perception (Carruthers 2006; Cosmides & Tooby, 1994; Firestone & Scholl, 2016; Pinker, 1997; Pylyshyn, 1999; Sperber, 1994).

In direct contrast to this approach is the hypothesis that perception is theory-laden in that, rather than being modular in its architecture or theory-neutral, perception is part of a more general cognitive system and can utilise other aspects of cognition to operate in a more efficient manner. Such an architecture would allow cognitive states such as beliefs, emotions and meaning to exert an influence on processes which are traditionally thought to be purely perceptual in nature (Clark, 2013; Goldstone, Leeuw, & Landy, 2015; Vetter & Newen, 2014; Lupyan, 2015). From this perspective, perception and cognition are part of a continuous processing hierarchy, where perception sits at the lower levels and cognition operates at higher levels. A prolific amount of research in recent years claims to provide examples of cognitive effects on perception (e.g. Anderson, Siegel, Bliss-Moreau, & Barrett, 2011; Kim & Yi, 2013; Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Luypan & Ward, 2014). Cognitive effects on perception can also be viewed as a specific instance of "top-down" influence over sensory processing. The term "top-down" refers to information flow of sensory processing within the perceptual system that is directed by higher cognitive processes such as memory, attention, emotion or language. More recently, Firestone and Scholl (2016) have been highly critical of these purported demonstrations of higher-level cognitive states penetrating lower level perception. They claim that the vast majority of these studies may be subject to various "pitfalls" which can account for the observed effects without recourse to explanations relying on cognitive penetration of perception. One of these pitfalls which can explain many of the observed findings is that what may appear to be an effect on early perception is actually mediated by attentional mechanisms, and is thus not a particularly interesting finding in regards to the organisation of the mind. The role of attention in altering the input to perception and processing that takes place at a post-perceptual stage has been well-established (see Luck & Ford, 1998, for an overview), meaning that any influence of cognition over perception that is mediated by attention has little to say in regards to the perception-cognition relationship. Given that - according to Firestone and Scholl (2016) - the vast majority or in fact all of the studies purportedly showing cognitive effects on perception can be accounted for by these alternative explanations, perception should be viewed as being cut off from and beyond the influence of cognition, in line with modular theories of perception (e.g. Fodor, 1983).

In this thesis, I dispute the conclusion that perception has a clear-cut boundary with the rest of cognition. In particular, I focus on Firestone and Scholl's claim that any cognitive effect on perception that is mediated by attentional processes cannot be considered an instance of higher-level cognition guiding the output of perception. Given the wealth of instances of cognition influencing perception in the literature, I propose that in order to explain the complexity of perceptual experience, a number of interacting processes are involved in producing the final perceptual output such as early perception in the sense of strictly one-to-one sensory transformation, top-down cognitive modulation, and attentional control. I will particularly focus on the role memory plays in this context, how mnemonic processes and systems may intervene in perception, either directly or mediated by attention, thereby shaping its final outcomes. The idea that different processes and varying levels of informational complexity play a role in perception is implied in recent accounts of perception as an instance of predictive coding, whereby the brain is constantly generating predictions regarding the interpretation of incoming sensory signals (Clark 2013). Predictive coding has recently been applied to a wide range of areas in cognition such as memory (Gagnepain & Henson, 2010), language (Lewis & Bastiaansen, 2015) and social interactions (Manera, Schouten, Verfaillie, & Becchio, 2013), and is a powerful theoretical construct for explaining information processing in the brain as a general principle (Clark, 2013). A predictive perspective on perception entails the notion that memory plays a key role in the interpretation and contextualisation of incoming sensory signals, and the aim of this thesis is to contribute to this general perspective by looking at the way in which memory may interact with attentional processes in order to facilitate perceptual processing. The perspective put forward in this thesis supports the position that the boundary between perception and cognition is blurry rather than clear cut.

In this chapter, I will lay out the key components of the cognitive system that come into play, as per the current theoretical understanding within the field. I will start out by describing the basic components involved in perception. I will present two different theoretical views that construe perception as either theory-neutral or theory-laden, to then explore the role of attention as a perceptual filter within each of these opposing views. Attention may be incorporated into both theory-neutral and theory-laden views of perception as a perceptual filter, but it is important to note that there are conceptual differences in how this filtering function is construed within each framework. Understanding these differences is key to evaluating recent evidence on theory-neutral vs. theory-laden views of perception and positioning oneself within the context of this debate. I will then describe some examples of cognitive influences on attention and perception. The subsequent section provides the basis for understanding and interpreting the specific effects of memory over perception. I will go over the basic components of memory in terms of memory systems and processes to then discuss memory effects on perception that have been reported in the literature thus far. Before diving into the empirical part of the thesis, this section will be followed by some theoretical and methodological considerations, specifically regarding the role of individual differences in observing memory effects on perception. In chapter two, I will provide empirical evidence to support this idea by exploring the interaction between memory, attention and perception from different angles and at different levels through three separate experiments. In experiment one I explore the influence of episodic memory suppression on mediating attentional processing. In experiment two I demonstrate how individual differences in mnemonic and overall processing capacity may affect the visibility of such modulatory processes, and in experiment three, I will consider the direct effect of semantic memory over conscious perception. The general discussion will evaluate the presented findings and contextualise them within the predictive coding framework. Against the backdrop of predictive coding theories and alongside other recent research, this thesis contributes to understanding the intermingled relationship between memory, attention and perception.

2. Theoretical background

2.1 The role of bottom-up, top-down and attentional processes in perception

Perception consists of the interpretation of incoming sensory signals into meaningful stimuli in our environment. It involves the binding of basic stimulus properties such as orientation, luminance, colour and motion into high-level representations that are identified and interpreted to allow us to react and respond appropriately to environmental contingencies. On a physiological level, physical information from our environment such as light, sound, taste, touch, and smell is read by sensory receptors and transformed into neural signals which are processed in their respective sensory cortices. Under some circumstances, perception may result in a conscious experience where the object being perceived reaches a level of subjective awareness in the perceiver and becomes associated with specific qualitative experiences. Research into the processes underlying perception and our ability to consciously perceive aspects of our environment has been extensive in cognitive science and a number of different interpretations regarding the processes involved and the information required for perception to take place have been proposed. Here I select and elaborate upon three perspectives on perception which underlie some of the most important questions being framed in modern day research: perception as a theory-neutral process (bottom-up), perception as theory-laden (top-down), and the role of attentional processes in shaping perception. A discussion of these aspects of perception will set the stage for the different research questions addressed in this thesis.

2.1.1 Perception as a theory-neutral Process

Theory-neutral views of perception advocate the idea that our perceptions are a representation of the stimulus being viewed which is wholly based on the available physical input emanating from the stimulus, whilst higher-level cognitive states such as beliefs, emotions and experiences have no influence on the resulting representation (Fodor, 1983; Pylyshyn, 1999). To illustrate this view, different individuals who have had markedly different experiences with the same object and may have differing levels of knowledge pertaining to that object should still perceive that object in the same manner when in the same viewing conditions, as stated by Fodor (1984) "… given the same stimulations, two organisms with the same sensory/perceptual psychology will quite generally observe the same things, and hence arrive at the same observational beliefs, however much their theoretical commitments may differ." (pp. 24, line 42 – pp. 25, line 3). The demand for theory-neutrality in observation was a central motivating factor for modular conceptualisations of the organisation of the mind, where perception is posited to take place within an informationally encapsulated processing module which is immune to the effects of higher order cognitive states.

Early cognitive models of perception were influenced by the work of James Gibson (1972) who argues that the input to the visual system is informationally rich and complex, and therefore, there is no need to transform sensory input or supplement it with additional information. Gibson further theorised that abstract properties of objects are directly perceivable in what he referred to as the "affordances" (1979) that an object possesses. Affordances are the properties of an object that are meaningful to the observer and can be perceived from the patterns of sensory stimulation alone without recourse to previous experience: for example, the affordance of "graspability" offered by a cup is directly perceivable. The availability of affordances from sensory data alone entails the notion that additional theory is unnecessary for perception to occur. Gibson's idea of object affordances fits well with modular approaches to perception. A modular system is limited to the use of bottom-up informational input in order to effectively perceive, and thus, it is a requisite that incoming sensory information be adequately complex and rich in order for a module to output response permitting perceptual representations.

The view that perception is a theory-neutral process is implicit in many early cognitive models of visual perception (e.g. Marr, 1982). Specifically, this is implied by the shared characteristic that information processing during perception should be viewed as a bottom-up process. This notion has additional implications. Bottom-up models of cognition hold the assumption that information processing proceeds in sequential steps along different levels of complexity, with the output from one level of processing serving as the input to the next level. The complexity of the information analysed increases with each processing stage; early stages involve the analysis of rudimentary perceptual properties which in later stages become assembled into holistic object representations that can be recognised by the perceiving agent.

Marr's (1982) multilevel theory of vision describes vision as a hierarchical process which operates in a bottom-up fashion. Early levels of the hierarchy process basic components of the object, and subsequent levels are responsible for the processing of increasingly complex information until object recognition is achieved at the highest levels. The bottom-up nature of Marr's model limits the direction of information flow within the system in that the results of lower processing levels provide the input to higher levels. Specifically, Marr's model contains three levels of object representation where the nature of the information that is processed increases in its level of abstraction along the hierarchy. The model specifies the stages along which our visual system is able to extract a three-dimensional representation of our environment from the input image received by the retina in the form of a two-dimensional array. While viewing a scene or an object, the first level in the model is referred to as the 2D, or primal sketch, here, a two-dimensional rough sketch is created based on elementary features such as edges, regions and local geometric structures. The next level of object representation in the model is the 2.5D sketch, where the representation of textures such as depth and orientation occurs. Both the 2D and 2.5D sketches specify the representation in a viewer-centred coordinate system. In the final level of representation, referred to as the 3D model, the scene is represented as continuous and three-dimensional. The final 3D model is used in the recognition process where it is compared to a catalogue of stored representations and associated with an appropriate description. This comparison of the model with stored representations highlights the late-acting role of memory and previous experiences in the object recognition process. The exclusion of feedback from higher levels to lower levels in Marr's model necessarily rules out the possibility that more complex cognitive states may influence early stages of visual processing. In summary, the defining characteristic of theory-neutral views is that perception operates independently from the rest of cognition, and thus cognitive states such as language and memory have no influence over the perceptual process.

2.1.2 Perception as a theory-laden Process

In contrast with theory-neutral models of perception, theory-laden views extend perceptual theory to include the influence of cognitive processing. An early example of such an alternative perspective on perception can be seen in the work of Helmholtz (1867), with his theory of unconscious inferences. Helmholtz drew conclusions regarding the nature of perception based on optical illusions, where the perceiver has the conscious experience of aspects of their environment that are not present in physical reality. According to Helmholtz, the occurrence of optical illusions suggests that additional processing based upon information that is not present in our environment takes place during perception; sensory signals that meet the retina which are then processed by the nervous system cannot lead to the occurrence of optical illusions without additional information being combined with those signals. Helmholtz suggested that we embellish bottom-up sensory data with additional information in order to draw conclusions about our external environment. Perception in the real world involves the interpretation of physically ambiguous cues. For example, objects in our environment that project a small image onto the retina may represent things that are either small in size, or larger objects at a distance. Thus, an understanding of incoming signals representing aspects such as size and distance needs to be assessed by making an unconscious inference. According to Helmholtz's theory, perception is only indirectly related to objects in the environment in that it goes beyond the processing of sensory data alone. The information used to draw inferences comes from previous experience embedded in long-term memory. Statistical regularities in our world can be analysed by the cognitive system in order to develop hypotheses regarding the nature and significance of the objects being processed. One such example of a statistical regularity in the world is the fact that faces are consistently convex. This knowledge is so strongly embedded in our visual processing system that it leads to the "hollow face" illusion (see figure 1), where the back of a mask which is concave is perceived as convex. The fact that the hollow face illusion persists despite our own conceptual understanding that the mask is in fact hollow demonstrates the unconscious nature of these perceptual inferences. Attempts to rationally convince ourselves that the illusion is not real fail to alter our conscious experience of the effect. Helmholtz's theory on unconscious inference making during perception played an influential role in shaping a prominent model of perception, which comes from Gregory (1970) and put the influence of top-down cognitive processing at the forefront of perceptual theory. According to Gregory (1970), perception is a constructive process in which the brain actively generates hypotheses regarding the nature of incoming signals, shaping perceptual information in order to understand our environment. Hypotheses are generated based upon our past experiences and our understanding of the world, an idea reflected in modern theories of perception such as predictive coding (Clark, 2013).

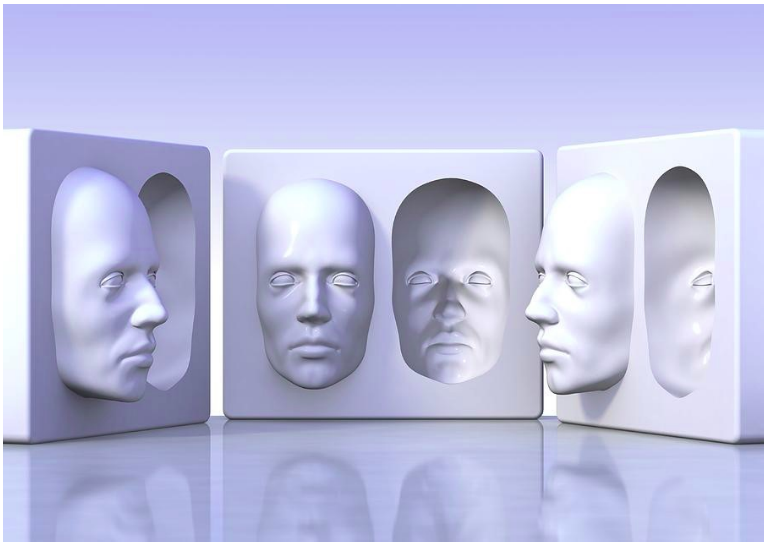


Figure 1: The hollow face illusion.

The idea of unconscious inference received renewed attention in the work of cognitive psychologists Bruner and Goodman, with their publication “Value and need as organising factors in perception” (1947). Bruner and Goodman made the case that sensory stimulation is ambiguously organised, and the resulting percept experienced by an organism reflects the outcome of a compromise between what is “presented” by the predictable functioning of the nervous system and what is “selected” by cognition. This idea of selecting sensory information based upon cognition implies that perception inherently entails a process of hypothesis generation in the interpretation of sensory signals. Given limited sensory input, we formulate hypotheses about what the stimulus may be based on our knowledge and expectations and which we then either accept or reject and subsequently reformulate. According to Bruner, motivations, beliefs, and experiences play a central role and can interfere with our perception of the physical world even at the most basic levels of visual analysis, as Bruner stated *“perception is not merely a neutral registration of what is out there but is, rather, activity affected by other concurrent processes of thought (and) memory (...)” (1992, p. 780).* Bruner and Goodman (1947) tested this hypothesis empirically by assessing the effects of wealth on the perception of coin sizes. They reasoned that the perception of stimuli of high social value would be especially susceptible to higher level cognitive effects, and that the greater an individual’s need for the socially valued object, the more the perception of that object would be susceptible to higher levels factors. The results of their study confirmed their hypothesis.

They showed that children from poorer backgrounds perceive coins as being larger than children from wealthier backgrounds do. Furthermore, this effect did not occur for objects without motivational value, in this case, cardboard disks. Bruner and Goodman's study (1947) launched the "New Look" movement in cognitive science and in the following decade, a large volume of studies was published demonstrating examples of situations where a perceiver's beliefs influence their perception. For example, it was found that hunger can lead people to overrate the brightness of images of food (Gilchrist & Nesberg, 1952), increasing familiarity decreases the recognition threshold for words (Solomon & Postman, 1952), and when participants are asked to adjust the colour of a background until it matches the colour of a centrally presented outline of an object on an orange sheet of paper they adjust the background colour to be more red for typically red objects (such as a strawberry) than for non-typically red objects (e.g. a mushroom), despite the fact that the colour of the central cut-out is the same in both cases (Delk & Fillenbaum, 1965). These studies appear to demonstrate instances of socio-economic status, motivation, and semantics influencing the contents of perception and are just a few examples of the explosion of research into cognitive effects on perception at the time. Based on these findings, perception was viewed as an inference making process where previous experience is used to categorise stimuli in our environment, thus blurring the boundary between perception and cognition. These early demonstrations of theory-laden perception paved the way for more recent theories which give a central role to cognition and past experience in shaping perception. Such outlines include Lupyan's label-feedback hypothesis (2012), Bar's neurocognitive model of the role of object knowledge during perception (Bar et al., 2006), and the predictive coding framework (Clark, 2013, Friston, 2010). I will outline each of these in more detail in upcoming sections of this thesis.

2.1.3 Attention as a Perceptual Filter

In this section, I explore the role of another process that is intimately linked with perception: attention. Attention can be seen as a process that is complementary to perception as conceived by either theory-neutral and theory-laden views, rather than a third contrasting framework for viewing perception. However, there may be important, conceptual differences in how attention operates within each view.

Incoming sensory information consists of a multitude of objects that may be perceived, whilst the computational resources available to our cognitive system are limited

(Broadbent, 1958). Thus, there is a fundamental need for the cognitive system to filter out sensory information in a way that promotes sufficient analysis of the particular subset of stimuli that are contextually relevant for momentary, adaptive responding. This process of filtering out irrelevant sensory signals and mobilising the analysis of contextually relevant stimuli is driven by attention.

Focusing attention on specific stimulus characteristics such as colour or location is beneficial for responding to the environment in an adaptive way. Posner (1980) demonstrated that participants' speed and accuracy in responding to a stimulus is improved whenever that stimulus is presented at an attended location. Furthermore, attention can enhance the signal of attended stimuli, thus increasing perceptual sensitivity for attended objects (Lu & Dosher, 1998), and can filter out distracting non-target information (Shiu & Pashler, 1995). On a neural level, the influence of attention on the visual processing stream is pervasive, modulating multiple neuronal populations that underlie sensory processing. At an early stage, attentional modulations have been demonstrated in subcortical areas such as the lateral geniculate nucleus (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990), and cortical activity during attentional tasks can differ depending on the availability of attentional resources (Rees, Frith, & Lavie, 1997). In the primary visual cortex, attention to select line orientations has been shown to modulate neuronal populations that code for that particular orientation (Liu, Larsson, & Carrasco, 2007), and attention to motion and colour has been shown to modulate activity in areas MT and V4 (Saenz, Buracas, & Boynton, 2002). Thus, attention can be viewed as a multilevel selection process, influencing different stages of the visual processing stream depending on the nature of the attended stimulus.

Attention interacts with bottom-up and top-down processes during perception by adjusting the dominance of each in response to contextual changes and task demands. Thus, the deployment of attention over perceptual processes can be driven by either bottom-up and top-down incentives. One of the most studied and effective factors that drives bottom-up deployment of visual attention is the relative saliency of objects in our environment. Saliency refers to the conspicuity of a stimulus; for example, in an otherwise black and white painting, a person wearing a red jacket will stand out to a greater extent than other stimuli in the painting because of its unique colour feature. Koch and Ullman (1985) proposed that attentional focus is driven by a pre-attentive "saliency map", which is a two-dimensional map of objects in our environment wherein the relative saliency level of each object is encoded. A saliency map is represented in the firing of neuronal populations: competition takes place between different map locations leading to a winning location which corresponds to where the most salient stimulus in the environment is present. After this winning location has been processed, it is then inhibited, allowing attention to focus on the next most salient object. On the other hand, cognitive states such as knowledge, experience and emotion may also drive the allocation of attention in a top-down way. The contextual cuing paradigm (Chun & Jiang, 1998) provides an illustration of one such top-down experience-based contribution to attentional allocation. In this study, the authors found that previous experience may guide attention. The repeated exposure to the same arrangement of target and distractor items will result in more efficient search times for the target item, with search times progressively decreasing as a function of array repetition in comparison to novel arrays. Contextual cuing reflects a form of implicit learning of the visual array, which results in the extraction of knowledge regarding the contextual co-occurrence of the target and distractors. This extracted knowledge can then be employed on subsequent trials in order to guide attention. At this point it is important to clarify our interpretation of the use of the term "top-down" in order to avoid any confusion. The attentional modulation of perception in itself can be viewed as a top-down process because attention is regarded as a cognitive mechanism. However, the deployment of attention can be manipulated by other cognitive factors such as memory, language and emotion. Whenever attention is directed by such cognitive factors, we can conceptualise this as the "top-down" modulation of attention by cognition. Specifically, in such a circumstance we have an instance of a cognitive process directing top-down attention.

The key question regarding the nature of attention in weighing evidence for theory-neutral vs. theory-laden models of perception is whether it operates by simply changing the sensory input to perception, or whether attention can alter the perceptual process itself, and thus the appearance of a stimulus. In regards to this question, Firestone and Scholl (2016) have argued that the former is the case, with attention implementing its effect over perception by changing the sensory input. Analogous to simply turning off the lights or closing our eyes, attention exerts its influence by selectively focusing on specific features of an object, for example, attending to colour rather than shape, or to whole objects in the sensory environment, such as by focusing on a car rather than a face. They further suggest that any apparent cognitive effect on perception is in fact mediated by attention, such that cognition directs the focus of selective attention to implement peripheral changes in sensory input, rather than influencing what we see directly. Thus, following this line of argument, cognitive effects on perception do not provide any evidence against theory-neutral perspectives on perception. From their view, influence of attention over perception is well-established, and therefore any top-down effect on perception which originates from cognitive factors such as memory or language that is mediated by attention should be seen as a relatively trivial phenomenon as it is subserved by well-studied mechanisms. In chapter three, I will argue that the conceptualisation of the relationship between perception and attention made by Firestone and Scholl (2016) is inaccurate, and that particularly when viewed in terms of the predictive coding framework, which will be outlined in greater detail below, a clear separation between the two becomes untenable.

2.2 Examples of cognitive influences on attention and perception

As I will argue later in this thesis, the dissociation between attention and perception is not always clear. However, there are clear instances of separable effects of cognition influencing processes that are more attentional - for example, when a cognitive factor directs limited processing resources towards a stimulus and away from another - and those that are more perceptual in nature, for instance, when cognition alters the subjective experience of a stimulus. Here I outline some of these effects.

2.2.1 Influences on attention.

Demonstrations of cognitive factors influencing attention are pervasive in the literature and their occurrence is relatively uncontroversial. A well-established example can be seen in the role that task goals play in the deployment of attention. Task goals can be defined as a tool which people use to execute volitional behaviour (Dijksterhuis & Aarts, 2010). For example, in the context of a psychological study, a participant's task goal may be to attend to the left of the computer screen. Hopfinger, Buonocore and Mangun (2000) demonstrated that such spatial anticipatory goals activate a widespread network of cortical areas reflecting voluntary attentional control in frontal, parietal and temporal regions. Activation in these areas was furthermore associated with the biasing of activity in visual areas contralateral to the position of the target stimulus, indicating that anticipation modulated activity wherever spatial attention was directed. Depending on the task description, task goals may also be based on a number of different stimulus features beyond spatial dimensions, such as motion (Treue & Trujillo, 1999), colour (Sun, Chubb, Wright, & Sperling, 2016), orientation (Lui & Hou, 2011) temporal onset (Correa, Sanabria, Spence, Tudela, & Lupiáñez, 2006) and whole objects (Baldauf & Desimone, 2014).

Emotion is another factor which has pervasive effects on the deployment of attention. In regards to bottom-up processing, stimuli in our environment which are laden with emotional content can capture our attention in an involuntary way. Angry faces are detected more quickly than neutral and happy faces (Tipples, Atkinson, & Young, 2002; Rellecke, Palazova, Sommer & Schacht, 2011), and emotional stimuli in general attract our attention to a greater extent than non-emotional stimuli (Fox et al., 2000). On a neural level, these bottom-up effects are partially independent from frontoparietal regions that underlie non-emotional exogenous attentional deployment (Vuilleumier & Driver, 2007). The adaptive importance that emotions have on bottom-up processing is intuitively obvious; however, emotions may affect top-down attentional processing when emotion-related goals guide the deployment of attention. In real life, much of the way in which we process our environment is guided by a monitoring of potential rewards and threats. Such an anticipatory approach to environmental processing has clear adaptive advantages from an evolutionary perspective. Motivational factors can play a role in guiding the extent to which bottom-up processing is prioritised. For example, whilst angry faces may attract our attention exogenously during visual search, this effect can be reduced if face stimuli are in opposition to task goals, for example, if the task goal of the participant is to search for happy faces (Hahn & Gronlund, 2007). Thus, attentional capture by emotional faces is partly dependent on peoples' emotion-related goals. Associating basic low-level non-emotional features such as colour with reward contingencies can alter the priming of pop-out effects – where reaction times to pop-out stimuli in visual search are faster for repeated arrays (Kristjansson, Sigurjonsdottir, & Driver, 2010) – again suggesting that cognition, specifically motivational factors, can influence the top-down deployment of attention.

2.2.2 Influences on perception.

In the perceptual domain, there are an increasing number of demonstrations of cognitive factors resulting in a change in subjective perception. Perhaps one of the most striking demonstrations can be seen in the effect that verbal labels have on perceptual processing. Lupyan and Thompson-Schill (2012) found that priming an image in an orientation discrimination task with the presentation of its verbal label facilitated task performance in comparison to priming the image with an equally informative sound. For example, the auditory presentation of the label "cat" lowers reaction times and improves response accuracy when indicating which part of a following display contains an upright cat, more so than the auditory presentation of a "meow" sound. Because it can be argued that such an effect on orientation judgements is due to facilitated processing at a later decision-making stage rather than an early perceptual stage, Lupyan and Ward (2013) investigated the effect of labels on participants' ability to consciously perceive objects. Using a continuous flash suppression paradigm, they presented objects in interocular competition with a noise pattern, which suppresses visual awareness of the competing object. They found that priming objects with their labels increased both reaction times and sensitivity (d'), in detecting the objects, indicating that labels can change perception by improving visual awareness of objects. Lupyan's label-feedback hypothesis (2012) proposes that when objects are presented, specific perceptual features that are diagnostic of the object's identity trigger the activation of the object's label, which then feeds back to boost the processing of those features. Such a feedback mechanism highlights the online and top-down nature of these linguistic effects on perception.

Our subjective emotional state has also been shown to modulate perceptual awareness where for example, inducing a negative mood in participants will increase their ability to detect briefly presented stimuli (Kuhbandner et al., 2009), and the affective state of the observer interacts with the emotional valence of the stimulus in dominating conscious perception during binocular rivalry (Anderson, Siegel & Barrett, 2011). Motivational factors can also modulate conscious perception of stimuli. For example, hunger causes participants to consciously perceive briefly presented food related words more accurately than food-unrelated words (Radel & Clément-Guillotin, 2012), and learned predictiveness for monetary outcomes reduces the exposure duration required to consciously recognise faces (O'Brien & Raymond, 2012).

Bar and colleagues (2006) proposed a neural mechanism by which cognition may exert a top-down influence over perception. Using a forward and backward masking procedure where they compared recognised to unrecognised object trials, they showed that object recognition was associated with activity in the orbitofrontal cortex 50 ms before object recognition-related activity occurred in the fusiform gyrus and occipital cortex – neural regions which have been shown to be responsible for object recognition (Grill-Spector, Kourtzi, & Kanwisher, 2001). Furthermore, Bar and colleagues (2006) found that orbitofrontal activity was modulated by the presence of low spatial frequency information in the object images. They suggest that the orbitofrontal cortex is responsible for generating hypotheses regarding the identity of the presented object based upon previous experience by "sensitising" potential candidate object representations in temporal regions (see figure 2).

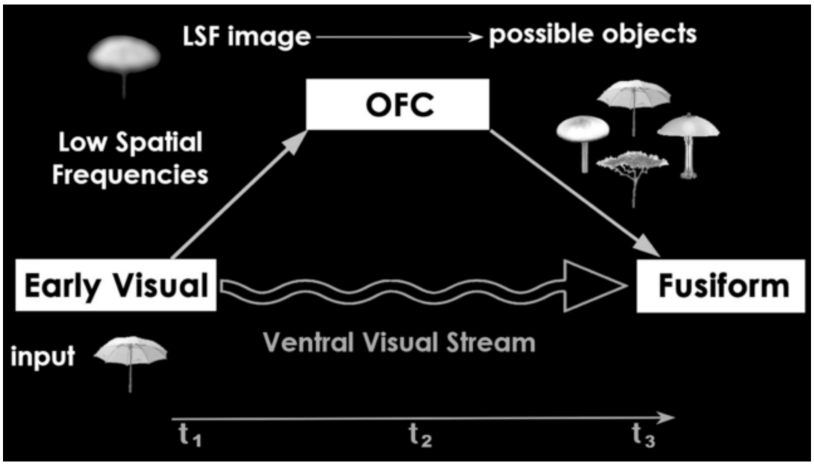


Figure 2. Schematic illustration of the model proposed by Bar et al. (2006). Low spatial frequency information is rapidly projected to the orbital frontal cortex which generates hypotheses regarding the identity of the stimulus based upon previous knowledge.

To summarise, so far, I have outlined some of the different theoretical approaches that have been put forward in explaining perception. Perception has been hypothesised as a theory-neutral process involving the bottom-up processing of information across increasing levels of complexity, whereby the viewer forms their perception based upon incoming sensory signals alone. This position is reflected in various theories of perception, such as Gibson's theory of affordances (1972) and Marr's multilevel theory of vision (1982). The view that top-down cognitive factors play a causal role in the modulation of perception has also been presented, an idea that can be found as early as Helmholtz's (1867) theory of unconscious inferences, in Gregory's (1970) theory regarding the role of top-down cognitive processes in perception, and in the "New Look" movement in the 1940s. The idea that attention can be seen as a process that serves an intermediary role between theory-neutral and theory-laden views of perception has been introduced, suggesting that attention influences the balance of bottom-up and top-down contributions to perception. Finally, I have touched upon the widespread disagreement regarding the extent to which cognitive factors may play a role in shaping perception, despite the range of experimental findings which support the view that cognition appears to play a role in shaping both attention and perception, and I have outlined some examples of such.

In this thesis, I investigate the influence of cognition over both perception and attention. The cognitive process that I will focus on will be long-term memory processing, specifically semantic and episodic memory, and their influences over attentional processing and conscious perception. A central argument in this thesis is that mnemonic processing can influence perceptual processing, and that this influence may be a direct one over perception itself, or, may be mediated by attention, and that any mediation of cognitive influences over perception by attention still quality as valid instances of cognition shaping perception. In the following sections I will give a brief overview of the key elements of human memory, and I will place particular emphasis on the types of memory and mnemonic processes that will be investigated in chapter two.

2.3 Memory systems and processes

2.3.1 Memory Systems

The influence of long-term memory over perceptual and attentional processing is interesting because memories define who we are; they guide our everyday interactions with the environment, and they form our self-identities. Our ability to encode, store and later retrieve specific goal relevant memories has been the subject of psychological investigation for over half a century. Recently, an increasing body of evidence suggests that memory processes may exert an influence over the perception of stimuli in our environment. A key focus of this thesis is on the way in which both explicit conceptual and episodic memory processing can influence perception and attention. Rather than being viewed as a single entity, memory is differentiated and may manifest itself in varying ways depending on task demands, resulting in differing effects on performance in cognitive tasks and contrasting subjective experiences. In order to address the question of how people's memories might modulate perception and attention it is important to understand the structures and processes that together constitute memory. Although different models of memory exist, this section will provide an overview of the structures and processes that are most relevant in the context of this thesis.

The structure and organisation of memory is by no means clear cut, and different views can be found regarding which framework to use to describe memory. For example, memory can be viewed as a collection of distinct sub-systems, where each is responsible for the storage and processing of different types of mnemonic information. At the broadest level of distinction, theoretical models differentiate between long-term memory, where information is stored over prolonged periods of time and short-term memory which subserves the maintenance of information in memory for short periods of up to a few seconds (Atkinson & Shiffrin, 1971). In this thesis I will focus on long-term memory.

Two commonly studied aspects of long-term memory are implicit and explicit memory. Implicit memory acts unintentionally, for example, in faster response times to a stimulus such as a face or a word that has been previously presented, a phenomenon known as repetition priming (Bruce & Young, 1986; Boehm & Sommer, 2012). Explicit memory, conversely, involves conscious awareness of the stimulus being remembered, such as during recognition tests, where participants are required to retrieve the study episode of a previously presented stimulus (Yonelinas, 2002). Schacter and Tulving (1994) proposed that explicit and implicit memory represent entirely different memory systems. They drew the distinction between declarative memory, which supports the explicit recollection of memories, and non-declarative memory, which is reflected in a variety of implicit types of memory and is expressed in performance differences such as priming and habit formation. Alternatively, apparent differences that define the boundary between memory systems may reflect differential engagement of distinct processing modes or levels of processing. For example, explicit and implicit memory may in fact reflect the type of processing that operates over a single memory trace, in this case, conceptual versus perceptual processing, where the explicit manifestation of memory during recall is dependent upon the conceptual or "deep" processing of the stimulus during study (Blaxton, 1989, Roediger & McDermott, 1993). Despite the various different views regarding the organisation of memory, it is clear that memory processing can occur in a conscious and purposeful way (explicit memory), or in a more automatic way outside of awareness (implicit memory). In this thesis I will focus on explicit memory.

Most theories agree that explicit memory consists of two dissociable types, these being episodic memory, which reflects the conscious recollection of specific events and involves the retrieval of temporal and contextual elements associated with the event, and semantic memory, which refers to the knowledge we have regarding the world (Tulving, 1983). Episodic memory is a personal record of the past in that it consists of autobiographical events – events that occur with a connection to the self – which are associated with a specific time and place and can be consciously recalled. Tulving (1983) described episodic memory retrieval as a type of mental time travel. For example, remembering what you had for dinner last night requires the retrieval of an episodic memory trace which contains information regarding the meal that was eaten and is associated with temporal information, in this case yesterday evening, and contextual information, such as where you had the meal. Episodic memory has been shown to rely heavily on the medial temporal lobes, in particular the hippocampus, as well as prefrontal regions (Wheeler, Stuss, & Tulving, 1997). Semantic memory differs from episodic memory in that it lacks any specific temporal or contextual information regarding its source of acquisition, but rather consists of the storage of conceptual knowledge about the world such as facts, ideas and concepts. For example, the knowledge that Paris is the capital of France is represented in semantic memory as generally one has no recollection of the context in which this information was acquired. Contrary to episodic memory, semantic memory has been shown to be represented in a widely distributed manner across the neocortex, with semantic concepts that relate to more specific sensory experiences being represented in the respective unimodal association areas that are responsible for that sensory modality, for example, fruit names will activate orbitofrontal regions that are associated with taste and smell (Goldberg, Perfetti, & Schneider, 1996). In contrast, more abstract conceptual information is represented in heteromodal association areas such as the anterior temporal cortex (Hoffman, Binny, Lambon Ralph, 2015; Mesulam, 1998). Nadel and Moscovitch (1997) proposed that semantic knowledge develops when multiple episodic memory traces index the same type of information, thus leading to an abstract representation that is no longer connected to a specific context. A single episodic memory trace consists of a distributed informational representation throughout the neocortex which is bound together via the hippocampus. As the trace is reactivated across different contexts, it becomes associated with multiple other hippocampal traces, eventually leading to the neocortical informational representation to be abstracted as a "gist" which becomes semantic knowledge and as such can be accessed independently of episodic retrieval.

In summary, memory can be subdivided into distinct types according to a variety of features such as the duration of the memory trace (long-term memory), the conscious awareness of the memory (explicit or declarative memory), the relation of the memory to the self (episodic memory) and the conceptual content of the memory (semantic memory). In this thesis I will be focusing on episodic and semantic memory and their influence over perceptual and attentional processing. In the following section I will discuss different memory processes and their effects on perception.

2.3.2 Memory processes

It is important to note that instead of distinguishing between structural aspects of memory, memory can also be categorised into distinct processes. For example, in order to assess the relative contribution of the two types of memory during recognition decisions, Tulving (1985) developed the remember/know procedure, a paradigm which is based upon the assumption that episodic memory involves the retrieval of a discrete event, whilst semantic memory access involves the subjective feeling that an item has been processed in the past without knowing exactly under which circumstances. Alternatively, it has been suggested that responses in the remember/know procedure may represent different processes that underlie memory retrieval. According to the dual-process account (Yonelinas, 2002), recognition decisions can involve both recollection and familiarity processes. Recollection involves a controlled and effortful conscious retrieval of contextual details surrounding an event, whereas familiarity is a fast-acting automatic process that results in the subjective feeling that an item has been encountered before but lacks any contextual details. This point highlights the role of retrieval processes in memory. Indeed, memory should not be considered as a veridical storage of past events but rather, as a constructive process which links together different pieces of information to create a simulation of past events (Schacter, Norman, & Koutstaal, 1998). In fact, retrieval itself can be seen as a two-sided process as it inherently involves the simultaneous re-encoding of the trace with the newly associated retrieval context. Thus, while simultaneously strengthening the trace (Karpicke & Roediger 2008), retrieval alters the contents that are retrieved (Bridge & Paller, 2012).

Another process that can shape the contents of memory can be seen in our ability to control retrieval itself, by resolving interference between competing memories. Upon presentation of a cue to signal the retrieval of a specific memory to be retrieved, other memories that are related to the cue and that share characteristics with the target memory through contextual or semantic similarity, will compete with each other for selection. In order to overcome this competition between memories, executive control may be recruited which suppresses the trace of the competing memories and allows for successful selection of the target. This process of suppressing the memory has long lasting consequences for later recall, in that participants will show a lower level of recall for suppressed items (Anderson, Bjork & Bjork, 1994). Control over memory retrieval can also be observed whenever we attempt to avoid the retrieval of unwanted memories (Anderson & Green, 2001). Often in daily life, we would rather avoid the retrieval of certain memories, for example, something as rudimentary as the thought of a pressing email which distracts us from our current task, or something more severe such as the memory of a traumatic event. Anderson and Green (2001) demonstrated that people are able to consciously modulate the retrieval of such memories. They developed a paradigm known as the Think/No-Think paradigm which uses a similar procedure to the

Go/No-Go paradigm, except that instead of requiring participants to retrieve and suppress motor responses, participants are asked to selectively retrieve and suppress episodic memories. In their study, Anderson and Green (2001) presented participants with a series of cue-target word pairs, for example, "Ordeal – Roach" and asked them to memorise each pair to the best of their ability so that they could produce the associated target word when presented with the cue. After having learned these cue-target word pairs to a criterion, participants performed the Think/No-Think phase. During this phase, cues from one third of the word pairs are presented alone on the screen and participants are asked to retrieve the associated target word ("Think" words), whereas another third of the cue words are presented on the screen without their associated target and here, rather than being required to retrieve the associated target word, participants are required to prevent the target word from entering consciousness, and to actively suppress it if it does ("No-Think" words). The remaining third of the word pairs are not presented during this phase and serve as a baseline to compare the effects of selective retrieval and suppression ("Baseline" words). Following the Think/No-Think phase participants are asked to recall Think, No-Think and Baseline items. Predictably, results from Anderson and Green's (2001) study revealed that Think items showed a higher level of recall than Baseline items, highlighting the beneficial effects of repeated retrieval on later recall. However, in contrast, items from the No-Think condition showed a lower level of recall than baseline items suggesting that efforts to control mnemonic contents result in those memories becoming less accessible later on. To explain this finding, the authors proposed that during attempts to avoid retrieval of certain memories, executive control comes into play which suppresses the activation level of the memory trace, therefore rendering it less accessible later on. In support of this idea, Anderson and colleagues (2004) showed that prefrontal brain regions that are also involved in the suppression of pre-potent motor responses are activated whenever participants attempt to avoid the retrieval of unwanted memories, and that this prefrontal activity was correlated with a down-regulation of activity in the hippocampus, an area which mediates the binding of episodic memories.

2.3.3 Memory effects on perception

A number of studies to date suggest that both episodic and semantic information from long-term memory can have an effect on perceptual processes. Anderson, Siegel, Bliss-Moreau and Barrett (2011) investigated the effect of socially relevant information on the conscious perception of novel faces. In their study, novel faces that had been previously associated with negative gossip were found to dominate perception more whenever placed along with faces that had been previously associated with positive or neutral gossip in a binocular rivalry paradigm. Similarly, Abdel Rahman (2011) found that associating well-known faces with newly acquired negative or positive information modulated ERP components as early as 180ms in the EPN time range – a component that has been suggested to reflect increased attention to emotionally laden stimuli. These two studies indicate that biographical (that is, episodic) information can affect perceptual processing. Regarding semantic knowledge, Abdel Rahman and Sommer (2008) found that associating rare objects with a functional description modulates ERP components in the P1 time range 100ms after stimulus presentation, whenever the objects are presented for recognition (see figure 3). In a second experiment, the authors degraded a subset of the objects in order to make them less identifiable and found that semantic modulations in the P1 component were larger for objects that were perceptually degraded. They further found that semantic effects emerged behaviourally with increased error rates in recognition performance for visually degraded objects. These results show that semantic memory can shape the contents of perception by modulating the earliest processing stages.

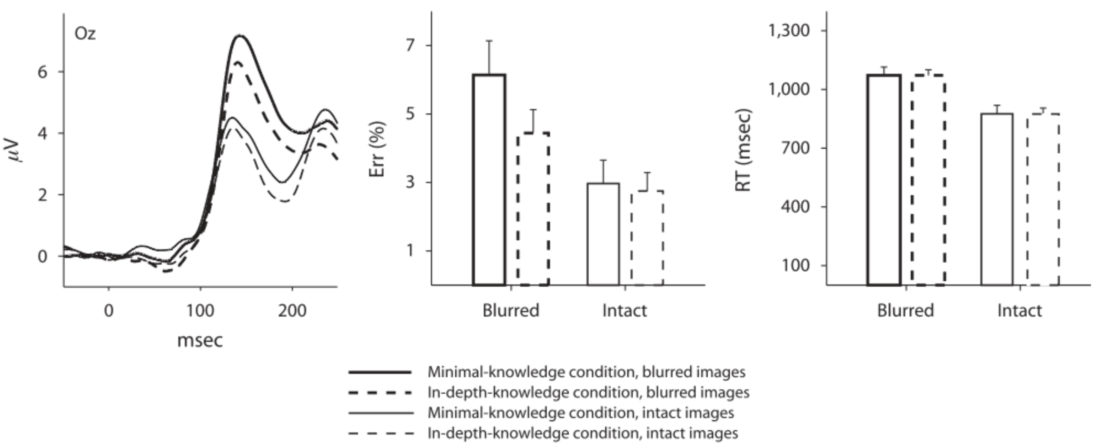


Figure 3: Results from Abdel Rahman and Sommer (2008). Showing the contrast between minimal-knowledge and in-depth-knowledge conditions with ERP differences emerging 100ms after stimulus presentation.

Two studies to date have addressed the relationship between memory suppression and perceptual processing. Kim and Yi (2013) asked participants to repeatedly retrieve or suppress a series of object line drawings that had been previously associated to word cues. Following this retrieval and suppression phase, participants were presented with the objects under conditions of difficult perceptual identification – objects were briefly presented on either the left or the right of the screen and were followed by a backward mask, and participants were required to identify the objects. The authors found that participants were less able to identify objects that had undergone suppression in comparison to a baseline condition. In a second experiment, objects were embedded in visual noise and participants were required to reduce the noise level via a button press until the object was identifiable. The results of this second experiment reflected those of the first in that participants needed to reduce the noise level to a greater extent for suppressed items in order to identify the object. These results suggest that memories can have drastic effects on basic perceptual processing and that intentional modulation of memory traces via suppression can modulate these effects. The results of Kim and Yi (2013) were expanded upon by Gagnepain, Henson, and Anderson (2014), who, using a similar paradigm, showed that attempts to suppress episodic memories reduced activity in neocortical areas that are involved in object perception. The consequences of suppression-induced reductions in memory accessibility for attentional processing, however, remain unexplored. Thus, an additional focus of this thesis will be on investigating this question.

2.4 Theoretical and methodological considerations

2.4.1 Individual differences in cognitive performance

People vary widely in their ability to perform. This is the case both across different individuals, where performance on cognitive tasks can vary according to factors such as age, personality, or political leaning, and within individuals, where factors as simple as the time of day or the amount of time that has passed since their last meal, can alter cognitive performance. Given that individual differences in task performance as so pervasive, an additional aim of this thesis will be to explore the possibility that individual differences may occur when investigating the effects on mnemonic information over attentional and perceptual processes.

One of the domains where people show marked differences in performance is in working memory capacity (WMC). WMC is reflected in peoples' ability to maintain information over limited periods of time, whilst simultaneously manipulating, integrating and rejecting parts of it in the service of a specific short-term goal (Jarrold & Towse, 2006). The concept of WMC was initially developed by Baddeley and Hitch (1974), who shifted theoretical approaches of short-term memory away from a storage view to a functional view where short term memory plays a role in the storage and retrieval of information from long-term memory and in setting the work place for carrying out cognitive operations which are involved in a wide variety of different tasks. In this sense, WMC can be seen as the "workbench of cognition" (Klatzky, 1980). For example, calculating a mathematical problem often involves maintaining the output of a series of sub-calculations in mind whilst carrying out additional operations, and the output from the initial operations will then need to be retrieved and combined with the output of latter operations in order to reach the final result. WMC itself can vary highly between individuals, and this inter-individual variation is in turn predictive of cognitive performance across a wide range of cognitive domains.

Given the assumed involvement of WMC across a range of cognitive processes, researchers began to speculate that individual variation in WMC may be responsible for task performance variation across different individuals and populations. For example, it has been shown that WMC variation is highly correlated with differences in academic aptitude (Turner & Engle, 1989), in learning vocabulary (Daneman & Green, 1986) and in the acquisition of new computer programming languages (Kyllonen & Stephens, 1990). WMC has also been shown to correlate highly with measures of fluid intelligence (Unsworth & Engle, 2005).

In addition to showing quantitative differences in how successful people may be in carrying out tasks in a wide variety of domains, individual difference in WMC may also lead to qualitative differences in how people execute certain cognitive processes. For example, according to the "Dual Mechanisms of Control" framework (Braver, 2012), WMC differences may determine the style of cognitive control that participants engage in whenever performing cognitively demanding tasks. According to this framework, high WMC individuals have more resources available and are thus able to engage in a proactive mode of interference control, where the task goal of avoiding the processing of interfering information can be maintained over the long term, resulting in faster and more efficient stimulus processing. The sustained maintenance of task goals is a resource-consuming process and is therefore more difficult for low WMC individuals to engage in. Thus, low WMC individuals are more likely to engage in a reactive mode of interference control, where task goals are activated on a moment-to-moment basis in order to override interference from distracting information. The transient activation of task goals is a resource-efficient processing style. Thus, differences in WMC may determine whether a certain cognitive process will occur or not, resulting in people carrying out a task in a fundamentally different way. From this perspective, individual variation in working memory contributes to proactive control capacity (PCC), that is, people's ability to implement proactive control, a concept closely linked to but more comprehensive than WMC in describing a certain processing style.

Given that differences in PCC can lead to both quantitative and qualitative differences in task performance, PCC differences are of theoretical interest when assessing novel cognitive processes for two reasons. First, differences in PCC may lead to differences in peoples' ability to engage in the process under investigation, and secondly, PCC differences can result in methodological issues for measuring the cognitive construct of interest. For example, if PCC variation induces qualitative differences in participants' ability to carry out cognitive operations that are crucial for the observation of the effect of interest. Given the range of effects on task performance that individual differences can have, an additional aim of this thesis will be to assess the role of PCC differences on the influence of mnemonic information over attentional processing. The possibility of the presence of individual differences in cognitive effects on attention and perception would be consequential. Failures to demonstrate cognitive effects on perception may in fact be explained as due to individual differences in processing style. For example, if as proposed by Firestone and Scholl (2016), a vast amount of cognitive effects on perception can be explained by the mediation of attention, then differences in attentional processing style may predict the likelihood of observing such effects.

In summary, individual differences in cognition are pervasive. A key construct that may explain many of these effects is people´s ability to engage in proactive control, which involves the sustained maintenance of task goals and is highly resource dependent. An additional question addressed in this thesis will be the relationship between PCC and cognitive effects over perception, specifically when mediated by attention. In the following section I will discuss the theory of predictive coding and its consequences for our understanding of the architecture of the cognitive system and our conceptualisation of the relationship between cognition and perception.

2.4.2. The predictive coding framework

The predictive coding framework has been mentioned in previous parts of this introduction. Here I provide an overview of the theory with a specific focus on perceptual processing and its relevance for research into the cognitive penetration of perception. Predictive coding is a theoretical perspective that has been gaining attention in recent years and offers a powerful approach which can explain cognitive processing across diverse domains.

Predictive coding places an emphasis on the brain's ability to use past experiences in predicting the type and nature of incoming signals. From this perceptive, neural systems are able to take advantage of statistical regularities in the environment by incorporating these consistencies into the perceptual process (Rao & Ballard, 1999). Predictive coding theories propose that information taken from life-long experience is used by the brain to continuously generate internal predictions about future events, allowing for more efficient stimulus processing (de-Wit, Machilsen, & Putzeys, 2010) and action-oriented responding (Engel, Fries & Singer, 2001). Information from long-term experience can be seen as a prior which biases the processing of incoming sensory information (Friston, 2010). For example, a common prior used in object perception is orientation – we are accustomed to seeing objects such as cars and tables in their appropriate, upright orientation, and the regularity with which we encounter upright objects means that 'upright orientation' is a useful prior to use in perception. Priors are thought to be implemented in a top-down manner with regions higher up in the visual hierarchy exchanging information with lower regions, where the predictions are matched with incoming sensory information. In the case that incoming information does not match the information predicted in the prior, a mismatch occurs, and an error signal is created at these lower levels. This error information is then propagated back upstream via feed forward connections to further refine the prediction, resulting in a reduction of the amount of error (Friston, 2010; Murray, Kersten, Olshausen, Schrater, & Woods, 2002). In the case that incoming sensory signals match the prediction, recognition is facilitated, and will be accompanied by reduced activation in lower visual processing regions. This reduced activation can be interpreted in terms of the prior accounting for some of the input, and thus, reducing the need to reconstruct incoming signals. The use of predictive information in interpreting sensory input permits efficient processing and frees up cognitive resources to be allocated to the processing of novel stimuli. The predictive coding framework emphasises the role of feedback in the generation of object percepts (Panichello, Cheung, & Bar, 2013). The role of feedback to posterior regions as postulated by predictive coding accounts is supported by the anatomical organisation of the cerebral cortex, which can be seen as a functional hierarchy of different levels, with each level coding for different stimulus features and increasing levels of complexity (Friston, 2005). Extensive reciprocal, feedforward, and feedback connections also exist between different cortical regions. Such anatomical arrangements facilitate the transfer of information both up and down the cortical hierarchy (Friston, 2005). The role of predictions in perception has been demonstrated in a wide range of phenomena. In binocular rivalry, where disparate images that are presented separately to each eye compete for selection, stimuli that have been presented more frequently in the recent past will dominate rivalry; here the probability of stimulus presentation is estimated based on previous experience and thus, participants build up expectations for frequent stimuli, which guide perception (Chopin & Mamassian, 2012). Similarly, in the context of the continuous flash illusion, where the continuous presentation of dynamic noise suppresses awareness of words presented in the opposite eye, the presentation of a semantically related prime word will cause a following target word to break suppression more often than when preceded by an unrelated word (Costello, Jiang, Baartman, McGlennen, & He, 2009). The role of statistical regularities in guiding perception can be further demonstrated with contextual effects where objects are recognised more quickly whenever they are presented along with the typical environmental context in which they would normally be encountered (Biederman, 1972; Davenport & Pottern, 2004). Expectations can also develop rapidly upon object presentation. Low spatial frequency stimulus information is extracted more rapidly than high spatial frequency information, which can then be used to elicit predictions regarding the basic level category to which the object may pertain (Bar et al., 2006). On a neural level, a variety of studies using EEG and MEG recordings have demonstrated prediction-related neural feedback from higher order cortical regions to lower levels (Summerfield et al., 2006; Gamond et al., 2011). In studies looking at the role of contextual information in facilitating object recognition, Kveraga and colleagues (2011) demonstrated the role of a distributed neural network in mediating contextual information including the parahippocampal cortex and medial prefrontal cortex. MEG studies have shown that objects with strong contextual associations elicit activity in the contextual network as early as 170ms after object presentation (Kveraga et al. 2011; Panichello et al., 2013). Activity in this network has also been shown to modulate responses in the lateral occipital cortex – a part of the ventral processing stream implicated in object perception (Grill-Spector, Kourtzi, & Kanwisher, 2001). The rapid generation of expectations upon object presentation also involves feedback from prefrontal areas. Bar and colleagues (2006) have shown that the presentation of objects lacking in high-frequency information elicits activity in the orbitofrontal cortex before eliciting activity in inferior temporal areas, and that the activity in both areas is functionally coupled. Together, these studies illustrate the fact that predictive feedback is a common mode of brain processing, occurring in different contexts and for different stimulus types.

Predictive coding provides a fitting context wherein cognitive effects on perception and attention can be theoretically placed. Predictive coding itself can be viewed as an extreme form of cognitive penetration of perception in that it posits that every level in a processing hierarchy, even those involved in the most rudimentary feature processing, may be influenced by signals received from higher levels, leaving little room for theory-neutral observation to take place. Thus, according to predictive coding, the brain always has some presuppositions regarding the way in which sensory signals should be processed (Vetter & Newen, 2014). In a system that formulates hypotheses based upon contextual information and long-term memory which influence every stage of processing, cognition and perception are inherently intertwined. In the following section, I will briefly summarise what has been discussed up until now and then give an overview of the specific objectives that are addressed in chapter two.

3. Organisation and aims of the experimental series

Throughout this chapter I have discussed some of the key theoretical constructs that will be important for chapter two. The controversy in the field regarding the relationship between cognition and perception has been introduced and I have described some of the key theories and proponents of each point of view. I have introduced the concept of attention as an interface between cognition and perception, functioning as a mediating factor between the two. Furthermore, the emphasis placed on memory in generating hypotheses which are used to interpret sensory signals via predictions has been discussed. In particular, I described the different systems and processes that compose memory. While discussing memory I have placed particular emphasis on semantic and episodic types and on the role of memory suppression in modulating mnemonic content. From this overview of the field it is clear that there is no consensus regarding the relationship between cognition and perception, with convincing experimental evidence and lines of argumentation having been presented on both sides of the debate. The potential for attention to serve a mediating role when cognition influences perception is particularly controversial with some authors claiming that any effects of cognition upon perception that are mediated by attention cannot be seen as true demonstrations of cognitive penetration of perception (Firestone & Scholl, 2016). Despite the large body of research into the relationship between cognition and perception, there are many open points and interesting areas of exploration still to be conducted. In chapter two I will investigate the influence of different types of information from long-term memory on different aspects of perceptual processing. I will look at different manifestations of this phenomenon both when the influence is mediated by attention (experiment one and experiment two) and when it influences the conscious processing of stimuli in our environment (experiment three). Regarding different memory processes, although the question of how a process such as memory suppression may influence perception has been investigated (Gagnepain, Henson and Anderson, 2014; Kim & Yi, 2013) the role that memory suppression may have in shaping attentional processes remains unstudied. I will address this question by looking at the influence of episodic memory suppression on attention in experiment one and two. I previously discussed how individual differences in PCC can influence task performance and that individual differences in cognitive performance more generally can lead to widely different results in experimental paradigms (Daneman & Green, 1986; Turner & Engle, 1989; Kyllonen & Stephens, 1990), however, despite the prolific amount of research into these effects there is a lack of research regarding the role that individual differences in task performance may have in the demonstration of top-down effects over perception. Thus, another goal of this thesis will be to explore the idea that any potential effect that memory suppression may have over attention may be modulated by individual differences in cognitive processing style, as measured by PCC. Finally, an area of investigation which has received little attention in the area of top-down effects over perception is the relationship between semantic memory and conscious perception. Whilst the role of lexical labels (Lupyan & Ward, 2013), emotional valence (Sklar et al. 2012) and socially relevant information (Anderson, Siegel and Barrett, 2011) in shaping conscious perception has been studied, relatively few studies have investigated the role that semantic information may play (Costello et al., 2009), therefore a third aim of this thesis will be to consider the direct effect of semantic memory over conscious perception.

In experiment one, I will look at the influence of episodic memory on attentional processing. In this experiment, I will manipulate episodic memories strength using the Think/No-Think paradigm (Anderson & Green, 2001), which provides us with three conditions of varying episodic memory strength, and additionally allows us to assess the effects of memory suppression on attentional processes. Additionally, the flanker paradigm will be used, a procedure where participants are required to respond to target items which are flanked on either side by distractor stimuli. The flanking distractor stimuli can be either congruent or incongruent with the target stimulus and participants tend to be slower to respond to target stimuli then they are flanked by incongruent distractors, a phenomenon known as the flanker congruency effect. Because participants are required to focus their attention on central target items only, the flanker procedure can be used to measure the extent to which distractors capture participants attention. In order to evaluate the effect of memory suppression on subsequent attentional capture, I will present stimuli from Think, No-Think and Baseline conditions as flanking stimuli in a modified version of the flanker paradigm. Thus, experiment one will focus on the influence of episodic memories on attentional capture.

In experiment two, I will address the question of whether individual differences in PCC can influence the presence of - or our ability to measure - cognitive effects over attention. It is plausible that any effect of long-term memories on attention may be masked by individual differences in peoples' PCC. As previously outlined, people can process distracting information in either a proactive or reactive style, and the type of processing style employed is highly relevant for the manner in which distractors in attentional paradigms are processed. Thus, it remains plausible that differences in PCC can determine whether flanker congruency effects will occur or not. An absence of flanker congruency effects would mask the ability to observe any influence of memory suppression on attentional capture, as some individuals would not process distractors across memory conditions to an efficient extent to allow differences between memory conditions to manifest. In experiment two, I will investigate this possibility by measuring participants' PCC, and assessing the relationship between PCC and memory suppression effects on attentional capture.

In experiment three, I will assess the influence of mnemonic information on perception more directly by employing a task where attention is otherwise engaged during perceptual processing. Here, I will use the attentional blink paradigm where, under conditions of rapid serial visual presentation, participants are unable to detect the presence of a second target stimulus (T2) when its presentation falls within a certain time window following the processing of a first to be reported target (T1) (Raymond, Shapiro, & Arnell, 1992). In experiment three, this procedure is employed to assess the effect of semantic memory on the conscious detection of object stimuli. Objects are presented as the second of two target stimuli whose presence participants are required to detect. Furthermore, the amount of semantic information that participants acquire about each object will be manipulated. Additionally, EEG activity will be recorded while participants perform this task in order to assess the time course of semantic influences on conscious perception. Thus, experiment three will look at the extent to which semantic memory can influence people's conscious perceptual experience and the measuring of ERPs can provide key evidence regarding the stage in which this influence takes place.

Taken together, with the experiments put forth in chapter two, I hope to contribute to the current debate regarding the influence of cognitive factors over perception by showing how both episodic and semantic memory can influence perceptual and attentional processing, and how individual differences in cognitive style can modulate these effects. I hope that this work will contribute both empirically and conceptually to the understanding of the relationship between memory, attention and perception.

Chapter 2: Experimental Series

Experiment 1: Controlling Mnemonic Distraction Reduces Attentional Capture

Human experiences can be divided into those arising from events in our external environment, and those occurring internally such as thoughts, emotions and memories. Our external environment contains an abundance of informationally rich items, each of which may be associated with diverse meanings and significances across individuals, depending on our past interactions with those items. A crucial aspect of human cognition is the ability to appropriately focus our attention on goal relevant parts of our external environment for further analysis permitting the selection of appropriate actions, whilst avoiding the processing of potentially distracting stimuli that may be detrimental to performance.

An analogue to perceptual selection from our external environment applied to our internal states can be seen in attempts to control the contents of conscious awareness, when avoiding the retrieval of unwanted memories. Often memories come to mind that we would rather not think about, perhaps because they elicit unpleasant feelings associated with the event in question, making it necessary to mentally "push" the unwanted memory out of consciousness. This process has been studied using the Think/No-Think paradigm outlined in chapter one (Anderson & Green, 2001), where repeated suppression of learned words leads to a reduced recall of those words later on when subsequently tested (see figure 4). Reduced recall for these "No-Think" items in response to the original cue word could be due to a number of different mechanisms. One possibility is that whenever participants attempt to avoid thinking about No-Think items when presented with the cue word, they distract themselves from the target by substituting it with a new thought, for example, by thinking of "House" instead of "Roach" when presented with the cue word "Ordeal". Such a strategy may alter the relative associative strength of the connection between the cue and the target, causing the newly associated word "House" to interfere with the retrieval of "Roach" during the final test. Alternatively, repeated suppression may reduce access to No-Think items by directly targeting the memory trace itself via an inhibitory mechanism, reducing its activation and therefore its accessibility during retrieval in the final test phase. In order to test between these competing explanations, Anderson and Green (2001) tested participants' memory for No-Think words with an altered testing procedure, where instead of providing the original cue word to retrieve the associated target, participants were given a novel word that was semantically related to the target, referred to as an "independent probe" (Anderson & Spellman, 1995; Anderson, 2003) and demonstrated that a similar pattern of forgetting for No-Think items also occurs when tested under these conditions. The independent probe technique circumvents the association between the original cue word and the target word and thus forgetting under these conditions implicates a role for inhibitory mechanisms in reducing the mnemonic accessibility of No-Think items.

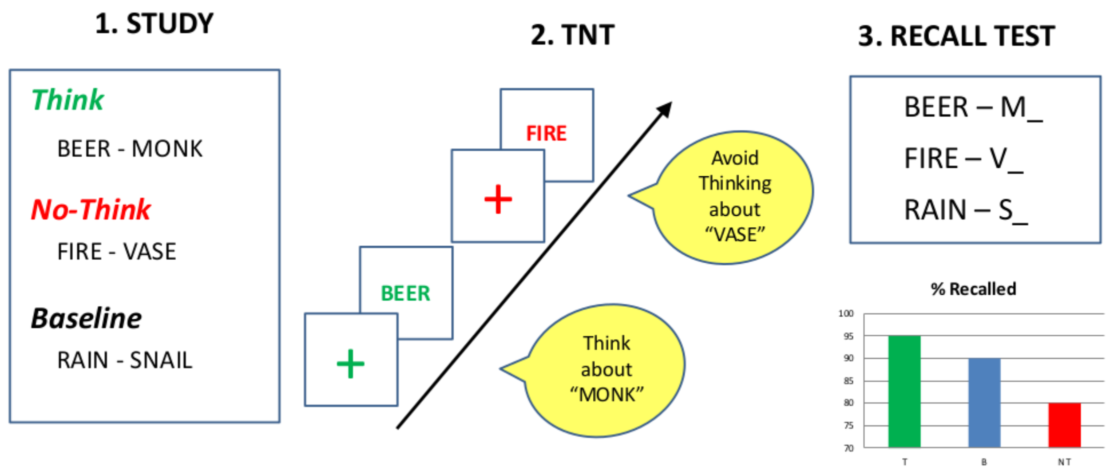


Figure 4: Schematic illustration of the Think/No-Think paradigm.

Impaired recall for No-Think items has been replicated extensively (Anderson et al., 2004; Bergström, Fockert, & Richardson-Klavehn, 2009; Hanslmayr, Leipold, Pastötter, & Bäuml, 2009; Hertel & Calcaterra, 2005; Joormann, Hertel, Brozovich, & Gotlib, 2005; Paz-Alonso, Bunge, Anderson, & Ghetti, 2013), with different material types, such as emotionally valenced stimuli (Depue, Banich, & Curran, 2006), and autobiographical memories (Noreen & MacLeod, 2013), and across different testing conditions such as recognition (Waldhauser, Lindgren, & Johansson, 2012), free association (Hertel, Large, Stück, & Levy, 2012), and perceptual identification (Kim & Yi, 2013).

In the current study, I asked whether attentional control, when directed to internal episodic memories in order to avoid their intrusion in consciousness, may have consequences for the extent to which items related to those memories may capture our attention whenever they are presented in our external environment. When dealing with the memory of an unpleasant experience, it is likely that we may encounter reminders of that experience in our environment, e.g., the face of someone who has been complicit in the unpleasant event. After having repeatedly suppressed the event, it would be maladaptive for the reminder to attract our attention and thereby elicit memories related to the event, causing us to relive the traumatic experience that we would rather forget. If memory suppression has adaptive consequences for the manner in which we process stimuli in our environment and if the face's content in memory has been adequately suppressed, then it should be processed to a similar degree as other unfamiliar faces, or even attract our attention to a lesser degree, therefore reducing the likelihood of eliciting thoughts related to the traumatic experience. The aim of this article is to investigate this possibility.

A wide body of evidence has demonstrated that the relationship between memory and perception is a reciprocal one (Clark, 2013) and that different kinds of cognitive information may influence the extent to which stimuli in our environment are attended to, such as emotional content (Barratt & Bundesen, 2012), associated value (Anderson, Laurent, & Yantis, 2011) and goal relevance (Corbetta, Patel, & Shulman, 2008), yet the influence of episodic memory status on visual distractor processing remains unstudied. Given that diverse types of memory contents have been shown to affect perceptual processing, e.g. short-term memory representations (Olkkonen & Allred, 2014), semantic knowledge (Abdel Rahman & Sommer, 2008) and episodic memory (Jacoby, 1983), it remains possible that episodic memory contents may interact with perceptual selection processes and affect the extent to which items in our environment may capture our attention. The existing literature on the relationship between long-term memory and the guidance of attention to stimuli in our environment is limited. Moores, Laiti and Chelazzi (2003) demonstrated that pre-exisiting associations in semantic memory can bias visual search. They showed that whenever a distractor that is semantically related to a target is presented in a visual search array, participants show higher subsequent levels of recall for the distractor, are slower and less accurate in indicating the absence of the target in comparison to a control object, and eye movements show that the first saccades after stimulus onset are directed towards semantically related distractors more often than to control items. Their findings indicate that items that are semantically associated to targets may grab attention and thus access perceptual stages of processing more often than semantically unrelated items, suggesting a role of semantics in early attentional selection processes. Using eye-tracking to investigate the influence of episodic memory on the allocation of visual attention, Chanon and Hopfinger (2008) showed that objects in scenes are fixated sooner and show a longer fixation duration whenever they have been studied in a previous encoding block in comparison to novel items. In a similar study, Summerfield, Lepsien, Gitelman, Mesulam and Nobre (2006) found that in a target detection task where participants are required to respond to the onset of a target in pictures of naturalistic scenes, participants were faster to detected the onset of the target if its location in the scene had been previously studied, in comparison to a condition where participants had previously studied the scene without the target's location, showing that episodic memory can guide attention in a similar manner to valid spatial cues. These two studies indicate that episodic memory for objects and for the spatial position of objects in scenes can guide the allocation of visual attention. Summerfield and colleagues (2006) further showed that whenever participants detected targets that were embedded in scenes where the location had been previously studied, hippocampal activity increased along with activity in a parietal-frontal network which has been shown to be involved in the spatial orienting of attention during vision (Corbetta & Schulman, 2002). Patai, Doallo and Nobre (2012) expanded on this finding by showing that target locations that were validly cued from memory modulated EEG activity as early as 200ms after stimulus onset in an attenuated N2PC, a component which has been proposed to reflect the top-down signal biasing to enhance feature selection (Kuo, Rao, Lepsien, & Nobre, 2009). The finding that episodic and semantic memory may play a role in guiding visual attention suggests that the modulation of memory status via mnemonic suppression may also have consequences for attentional processing.

To investigate the effects of memory suppression on the distractive power of stimuli presented in our visual environment, episodic memory strength was manipulated using the Think/No-Think paradigm (Anderson & Green, 2001; Levy & Anderson, 2012), by placing response words from Think, No-Think and Baseline conditions as task-irrelevant distractors in a subsequent semantic flanker task. The flanker task is a paradigm that investigates people's ability to filter out distracting stimuli and to suppress responses that are contextually inappropriate. In the original conceptualisation of the flanker task, known as the Erikson flanker task, (Erikson & Erikson, 1974) participants are presented with letters in the centre of a screen which are associated with either a left or a right response (e.g. the letters H and K are associated with a right response and S and C are associated with a left response) and participants are required to give a speeded manual left or right response depending on the presented letter. The target letter may be flanked on either side by additional letters that may require the same response, (congruent) or the opposite response (incongruent). Reaction times are typically slower on incongruent trials where the target and the flanker stimuli are mapped to opposite responses, reflecting the additional time required for the cognitive system to suppress the incorrect response. In the current study, a semantic version of the flanker task will be used, where participants are required to respond to the animacy of the target, which was flanked above and below by words which could be of the same animacy or opposite. Hertel and Hayes (2015) employed a similar procedure providing indirect evidence that episodic memory status may influence perceptual processing. In their study, they presented the cues from the cue-target word pairs as the distractor stimuli in a flanker paradigm after participants carried out repeated suppression and retrieval attempts on the target words that were associated with those cues. The authors showed that words used as cues to target words that have undergone direct suppression distract attention to a greater extent than do cues to baseline response words that have not been directly suppressed, whenever they are presented as distractors in the flanker task. However, this is only the case when the target associated with the cue has undergone directed suppression, whereas whenever participants are required to substitute the target with a diversionary thought, No-Think cues distract attention to a similar extent as baseline cues. The authors reasoned that direct suppression of response words leads participants to increase the amount of attention allocated to the cue word, which causes those cues to be processed to a greater extent, possibly therefore increasing the strength of their representation in episodic memory. However, in their study, episodic memory was not directly manipulated.

If, as reasoned, the extent to which items in our external environment may distract our attention depends in part on participants' recent mnemonic experience with the contents of those items, then the distractive power of flanking stimuli should differ across item conditions. Furthermore, if suppression attempts result in an overall reduced accessibility for the representation of those memories, then distractors from the No-Think condition should interfere with the evaluation of the target stimulus to a lesser extent than items that haven't undergone suppression. Additionally, whilst the majority of studies investigating the effects of memory suppression in the Think/No-Think procedure employ an explicit memory test, in the present design, words from No-Think, Baseline and Think conditions are task irrelevant, and therefore any influence of No-Think words on target processing would provide a more ecologically valid, indirect measure of suppression.

Method

The current experiment aimed to investigate whether memory suppression in the Think/No-Think paradigm would result in a reduction of the distractive power of words that have undergone suppression. To this end, words from Think, No-Think, and Baseline conditions were presented as flanking stimuli in a task where participants are required to make speeded animacy judgments on centrally presented target words. Flanking words from the three critical conditions were presented as either congruent or incongruent with the animacy of the target word. I predicted that repeated mnemonic suppression of No-Think items would result in a reduction of the congruency effect whenever No-Think items are presented as distractors during the final flanker task. I further reasoned that the observation of a reduction in flanker interference for No-Think items would emerge under conditions where flankers are highly distracting. To this end, two adjustments were made to the standard flanker procedure based upon previous literature. First, the saliency of the flanking words was increased by presenting the central target word in grey. As all stimuli are presented on a black background with the flanking words presented in white, the clarity, and therefore the discriminability of the central target word should be reduced. Schlaghecken and Eimer (2002) demonstrated that manipulating the saliency of a prime word using a similar approach leads to a reduction of prime influence. Likewise, Zeischka, Coomans, Deroost, Vandenbossche, and Soetens (2011) found that manipulating the brightness of flanking stimuli by presenting them in grey led to a reduction in congruency effects. Following the same logic, decreasing the saliency of central target words should increase the impact of the flanking words, therefore rendering them more difficult to filter out. Secondly, the spatial position of the flanker target pair was manipulated by presenting it at random in either the upper or lower portions of the monitor. Wendt, Kluwe and Vietze (2008) demonstrated that flanker processing selectivity can be adjusted for distinct stimulus locations in the visual field. They showed that the effect of trial proportion compatibility manipulations is limited to the spatial location of the manipulated flanker trial. This finding indicates that participants can make location specific adjustments in order to reduce processing selectivity for interfering stimuli occurring in particular regions of the visual field, (see Crump, Gong, & Milliken, 2006, for a similar finding). Following this, trials were presented unpredictably at different stimulus locations in order to reduce participants' ability to selectively filter out flanker words at specific locations, thereby increasing the extent to which they interfere.

Participants

Thirty-six students (nine male, age range: 18 - 32 Mean (M): 20.97 years, Standard deviation (SD): 2.82 years) from the University of Granada took part in the experiment for course credit. All had normal or corrected-to-normal vision and none had previously participated in an experiment using the Think/No-Think paradigm. Ethics approval was given for the experiment and all participants signed a consent form.

Materials

Seventy-two words of five to seven letters in length were selected, half of which were animate (e.g. 'snail') and half inanimate (e.g. 'cork'). Half of these were used as the response words for Think, No-Think and Baseline pairs, and half were assigned as targets for the final flanker task. A further 36 words were created in order to be paired with each response word. An additional 10 cue--response word pairs were created to be used as filler and practice items. All forward and backward associations between all cue and response words, between all target words, and between all cue words were minimised and any overly related word pairs were replaced, per assessment of four independent evaluators. The allocation of word pairs to Think, No-Think and Baseline conditions during the Think/No-Think phase was counterbalanced across participants, as was the allocation of flanker targets, Think, No-Think and Baseline items to congruent and incongruent conditions in the final flanker phase.

Procedure

Think/No-Think Paradigm.

Learning phase. The experiment began with an initial study phase where participants were presented with the 36 cue-response word pairs for memorisation. Word pairs were presented in random order for five seconds each. Primacy and recency effects were controlled for by presenting filler items at the beginning and end of the learning session. Participants were instructed to learn the word pairs in order to be able to subsequently recall the response word out loud when presented with the cue word. Immediately following, participants were presented with each of the cue words on the screen for six seconds. During the first three seconds the cue word appeared alone and during the final three seconds the corresponding target word was re-presented for additional study. Participants were required to recall and say out loud the associated response word before it appeared on the screen. If participants were unable to reach a recall criterion of 50% or more, this procedure was repeated, if after three attempts a participant was still unable to reach the criterion, the participant was dropped from the experiment. Once a participant reached the criterion they were sequentially presented with each of the cue words on their own for four seconds each and asked to again recall out loud the response word.

Think/No-Think phase. Participants were presented with instructions for the Think/No-Think task. Direct suppression was emphasised and participants were asked to avoid substituting the response words with other thoughts. Participants then engaged in six practice trials before commencing with the experimental items. Critical Think/No-Think trials were divided into six separate blocks, with each block consisting of 24 Think trials and 24 No-Think trials, making a total of 12 presentations of each think item and 12 presentations of each No-Think item. Think trials consisted in the presentation of a green fixation cross for 100ms followed by the cue word in green for 3500ms, this was then followed by a blank screen for 750ms. No-Think trials were the same as think trials with the exception that the preceding fixation cross and cue words were presented in red. Each block began and ended with two filler trials. Between blocks participants were administered a letter search task in an unknown language for one minute which served as a distractor in order to eliminate rehearsal of no think items between blocks.

Flanker test phase. Following the Think/No-Think phase, participants were presented with the instructions for the flanker task. Participants were advised that they would be presented with words upon which they were to make an animacy judgment, indicating whether the word was living or non-living, and that these could be flanked above and below by a different word which was to be ignored. A flanker trial consisted of the presentation of a fixation cross for 500ms, followed by the presentation of the target word along with the flanking word which could be from Think, No-Think or Baseline conditions. Flanker and target words remained on the screen until a response was made. Target items were presented in grey, with the flanking words remaining in white on a black background. Additionally, the spatial position of the target/flanker group was manipulated by presenting it at random in either the upper quarter or the lower quarter of the computer monitor. Participants were asked to respond both as fast and as accurately as possible. Participants first carried out two practice trials before beginning the experimental trials. All trials were presented in a random order (see figure 5).

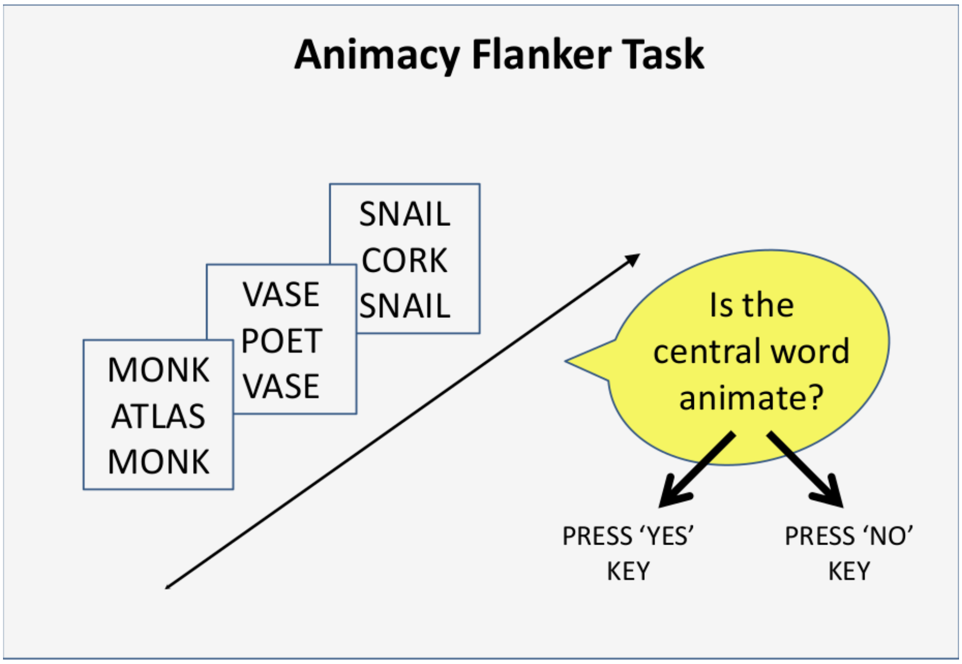


Figure 5: Schematic illustration of the final test.

Data Analysis

Data filtering. Mean reaction times and accuracy rates for the flanker task were analysed. Reaction time data was first filtered by excluding items that were unsuccessfully recalled in the assessment phase of the learning procedure, and erroneous trials were removed. Remaining correct responses were first normalised using a transformation approach as recommended by Cousineau and Chartier (2010). Response times were then filtered using a median absolute deviation procedure as recommended by Leys and colleagues (Leys, Ley, Klein, Bernard, & Licata, 2013). An exclusion criterion of 3.5 standard deviations above or below the median was used. This procedure resulted in the removal of 5% of trials.

Linear Mixed Models. Filtered data were subjected to linear mixed model analyses (LMMs) using the lmer function of the lme4 package for R, version 1.17 (Bates, Maechler, Bolker, & Walker, 2016). Linear mixed models extend upon the generalized linear model by allowing the inclusion of random effects along with fixed effects. Item type (Think/No-Think, Baseline), and congruency (Congruent, Incongruent) were included as fixed factors, and participants and items as crossed random-effect units. Because the Think and No-Think conditions index different cognitive constructs (memory retrieval and inhibition) rather than different levels of a continuous variable, mean reaction times and error rates from these conditions were analysed separately, sharing a common baseline condition (see Anderson, Reinholz, Kuhl, & Mayr, 2011; Depue et al., 2013; Hanslmayr et al. 2009; Levy & Anderson, 2012, for examples of a similar approach). Linear mixed models (LMMs) offer a flexible alternative to repeated measures analyses of variance (ANOVAs) by incorporating random variations by subject and item into the model. To define random structures, the maximum random structure was initially fitted (see Barr, Levy, Scheepers, & Tily, 2013), including random intercepts by participant and item, item type and congruency, and their interaction terms, for each model. Counterbalance (with six levels) was included as a fixed factor, but as a control variable, it was not included in the random portion of the model (see Barr et al., 2013). Convergence problems were solved by simplifying the model by, i) removing the correlation terms for random effects, ii) removing random intercepts, and iii) removing the random slopes that accounted for the least amount of variance in the partially converged model, until convergence was reached. After determining the maximum random structure justified by the data (Barr et al., 2013), significance of the fixed effects was tested using the anova function of the lmer package (in combination with lmerTest version 2.0). Effect sizes were calculated using the pamer.fnc function of the "LMERConvenienceFunction" package, version 2.5, yielding explained deviance values (*dv*), a generalization of the R^2 statistic. All reported analyses use an alpha level of .05%.

Results

Reaction times

No-Think items. Main effects of item type, $F(1) = 0.12$, $p > .05$, $dv < .01$, and congruency, $F(1) = 2.52$, $p > 05$, $dv = .02$, were non-significant, but there was a significant interaction between both, $F(1) = 3.99$, $p = 0.047$, $dv = .03$. This interaction was due to a significant congruency effect for Baseline items, $F(1) = 6.27$, $p = 0.02$, $dv = .09$, but not for No-Think items, $F(1) = .07$, $p > .05$, $dv < .01$. See Figure six for descriptive values. This result confirmed the hypothesis that memory suppression may reduce the extent to which items distract our attention whenever they are presented in our visual environment. Repeated suppression of learned word associates resulted in an elimination of interference effects whenever the suppressed words were presented as distractors during target processing (see figure 6).

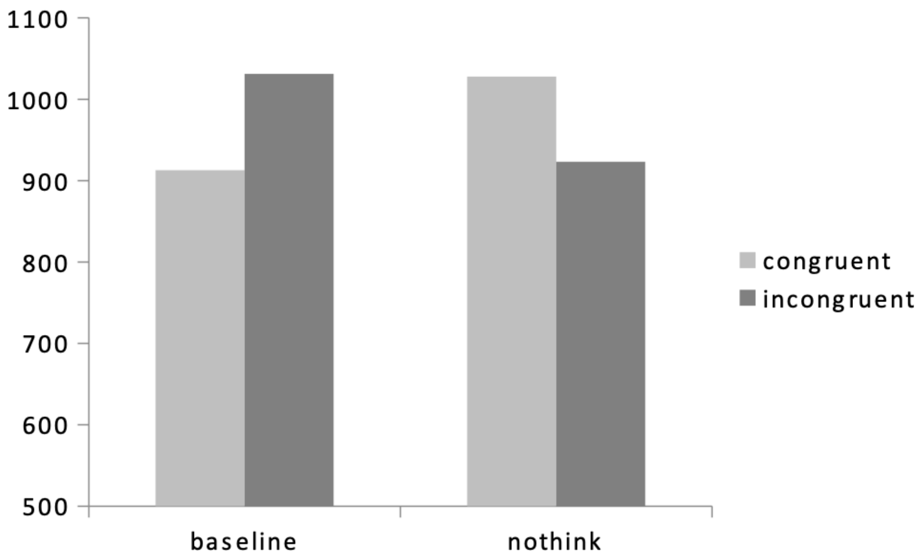


Figure 6. Mean reaction times and standard errors for congruent and incongruent items divided by item type (Baseline, No-Think).

Think items. There was a significant effect of congruency, F (1) = 10.0, p = .003, *dv*= .07, and a marginal effect of condition, $F(1) = 3.35$, $p = .08$, *dv* = .02. The interaction between both variables was not significant, $F(1) = 0.04$, $p > .05$, *dv* < .01.

Accuracy

Main effects of congruency and condition as well as their interactions did not reach significance for No-Think items or Think-items (*ps* >.1, Fs <= 1).

Discussion

The results of experiment one yield novel insights into the consequences of direct suppression of memory retrieval. Memory suppression interacted with congruency effects – a classic hallmark of perceptual distraction – attenuating distractor influence and allowing more efficient target processing. These results provide evidence for the non-independence of episodic memory and attention and demonstrate the role of mnemonic processes in influencing the extent to which distracting stimuli presented in our external world may be attended to.

These results also show that the negative effects of suppression are not limited to recall by causing people to forget suppressed items, but rather, can be generalised to the distractive power of perceptual cues to those memories. This effect may be beneficial in certain situations. Suppression in daily life is presumably motivated by the goal to avoid thinking about particular unpleasant memories, which in extreme cases may induce a vivid re-experience of the associated unpleasant event (Whalley, Farmer & Brewin, 2007). For such a strategy to be optimal, environmental cues to those memories should become less salient, avoiding the retrieval of unpleasant experiences. The findings from experiment one indicate that mnemonic suppression effectively reduces the processing of environmental triggers that may otherwise elicit those unwanted memories.

The findings from experiment one can be explained in light of biased competition models of visual processing (Desimone & Duncan, 1995), where the selection of stimuli in our environment depends on the competition between different cortical representations of those stimuli for further processing. Both targets and distractors are represented in patterns of neural activity in neocortical areas. In a cognitive system of limited processing capacity, target and distractor representations compete with each other on a cortical level for selection. Therefore, in order to resolve this competition, top-down biasing inputs may elevate and maintain the neural activity associated with the desired target. As previously discussed in the general introduction, Gagnepain, Henson and Anderson, (2014) provided fMRI evidence which suggests that cognitive control over memory reduces activity in the same neocortical regions that are involved in perceiving objects, such as the fusiform gyrus. In their study, participants performed a modified version of the Think/No-Think paradigm where they first encoded a series of word-object pairs, and then performed repeated suppression and retrieval attempts on the object pictures upon presentation of their associated word cues. After this standard Think/No-Think phase, the object pictures from each of the three conditions were presented along with new items in a perceptual identification task; objects were scrambled, rendering them unrecognisable, and were gradually unscrambled until participants were able to recognise the embedded object. Reaction times for participants to be able to recognise the embedded object were slower for objects that had undergone suppression in comparison to baseline objects, indicating that repeated suppression reduced the amount of perceptual priming between the study and perceptual identification phases. Memory suppression was associated with a reduction in neural activity in the fusiform cortex, an area which has previously been linked to the conscious awareness of visual objects during perception (Bar et al., 2001) and crucially, the same areas that showed a reduced activation during suppression also exhibited reduced neural priming during the perceptual identification task. The suppression-induced reductions in neocortical activity associated with the perception of suppressed objects found by Gagnepain and colleagues (2014) may contribute to explaining how memory suppression reduced distractor interference in the current study. If distractor and target representations compete on a neural level for selection, then the suppression of No-Think stimuli may dampen the potency of the neural signals corresponding to those items whenever they are presented as distractors during the final flanker task, causing target related activity to be relatively higher, thus permitting the efficient selection of target representations. However, such a theory remains speculative until further neural evidence is provided.

In conclusion, the present experiment demonstrates the influence of memory suppression in reducing the distractive power of items presented in our visual environment. These findings suggest that the relationship between memory and perception is a reciprocal one, with the contents of memory influencing how stimuli in our environment may be processed, and that cognitive control strategies such as memory suppression can mediate this dynamic relation, adaptively filtering the contents of perception by modulating episodic memory. This study contributes to a growing body of evidence indicating the role of long-term memory in attention and reveals the adaptive consequence of memory suppression in processing stimuli in our external environment.

Experiment 2: Individual Differences in Proactive Control Capacity mask Suppression-Induced Reductions in Attentional Capture

Experiment one investigated the relationship between episodic memory and attention. The experiment demonstrated that modulations of episodic memory strength via repeated suppression attempts can reduce the extent to which environmental cues related to those memories may attract our attention. In that experiment, participants performed repeated retrieval and suppression attempts on a set of previously memorised response words, using the Think/No-Think procedure. Immediately following this Think/No-Think phase, they carried out speeded animacy judgments on a set of novel target words which were flanked by task-irrelevant words from Think, No-Think and Baseline conditions, and the congruency of the target-flanker relation was manipulated to measure attentional capture. The results revealed a suppression-induced reduction in target-flanker congruency effects that was selective to items that had previously undergone suppression, suggesting that perceptual distraction depends in part on the consequences of internal, mnemonic processes.

The objective of the current study was to expand upon the findings of experiment one by investigating the extent to which this observed suppression induced reduction in flanker interference may be dependent on individual differences in participants' susceptibility to distraction. This experiment addresses a methodological issue that may arise whenever a procedure used to investigate novel phenomena is dependent on secondary processes that may vary across individuals. People's performance on cognitive tasks may vary markedly according to inter-individual differences (Henrich, Heine & Norenzayan, 2010). More importantly for the present topic, our ability to focus on goal relevant aspects of our environment whilst simultaneously filtering out potentially distracting information from further processing is a skill that can vary widely across individuals. Differences in attentional capacity can be observed along a number of different dimensions; across the developmental lifespan attentional abilities improve over childhood reaching their peak in adulthood (Astle & Scerif, 2009) and subsequently declining in old age (Banich, 2009), cognitive factors such as language use have been shown to improve people's capacity to filter out distracting information (Barac & Bialystok, 2012), and alcohol consumption has been shown to reduce performance in attentional tasks (Roberts Miller, Weafer, & Fillmore, 2014). Given that performance differences in attentional tasks can be predicted according to a number of different factors, in this experiment I predict that between-participant differences will be present for performance during the semantic flanker task employed in experiment one. Furthermore, if flanker congruency effects differ depending on between-participant differences in overall susceptibility to interference, I additionally postulate that differences across participants in the extent to which the flanking stimuli succeed in distracting attention from the target will predict the elimination of the congruency effects for No-Think items observed in experiment one, that is; the ability to observe a suppression-induced reduction in flanker interference will be highly dependent on the extent to which the flanking stimuli succeed in distracting attention from the target.

As previously discussed in the introduction, according to the dual-mechanisms framework, participant related differences in distractibility can be explained in terms of reactive and proactive processing (Braver, 2012). As they engage in goal-directed task performance, participants may recur to two different control modes. In the reactive control mode, control is recruited 'reactively' on a moment-to-moment basis through temporary activation of task goals whenever conflict is detected. In this case, interference is managed after it occurs, for example, by suppressing the interfering information. Proactive control, on the other hand, reduces interference pre-emptively through sustained maintenance of task goals in working memory, and anticipatory monitoring (see also, Braver, Paxton, Locke & Barch, 2009). Thus, successful maintenance of a proactive control mode makes the recurrence to inference suppression less likely. For example, when performing an arrow flanker task in which participants are required to indicate the direction in which a central arrow is pointing, on an incongruent trial where the central target is flanked by arrows pointing in the opposite direction, conflicting responses between the target and the distractor may be simultaneously primed. During a mixed block of trials where incongruent trials occur randomly with congruent trials, when in the reactive mode of control, distractors are initially processed along with the target, allowing interference to occur and requiring the cognitive system to suppress the irrelevant response arising from the distractor – interference resolution between the two responses only occurs in response to the detection of the presence of interference, and thus cognitive control is only required periodically, whenever an incongruent trial occurs. In the reactive mode, the task goal is reactivated only in cases where control is needed, in a stimulus driven matter. Conversely, in the proactive mode, participants may be maintaining task goals through an entire block regardless of the proportion of congruent and incongruent trials. This task goal could tell the cognitive system to avoid processing whatever stimuli appear in the distractor location, regardless of whether the response they map onto is congruent or incongruent with the response required for the target. The proactive mode can be conceptualised as a form of early selection, where targets are selected and distracting information is filtered before conflict takes place. Thus, interference between targets and flankers has no opportunity to occur, as flankers are filtered from further processing at an early stage. Reliance on reactive control (as opposed to proactive control, which generally tends to be associated with better task outcomes) and consequentially, the experience of inference, are likely under conditions of restricted resource capacity, either due to individual differences in WMC or due to increased inference load at the design-level (Braver, 2012). This is due to the fact that proactive control is highly resource-consuming, in that it requires the dedication of working memory resources to engage in anticipatory monitoring, while the transient activation of task goals in the reactive mode is resource effective, leaving WMC available for ongoing information processing. Evidence for the differential involvement of working memory resources in the two modes of cognitive control is reflected in Prefrontal Cortex (PFC) involvement, a region associated with the active maintenance of task goals (Paxton, Barch, Racine & Braver, 2007). Burgess and Braver (2010) recorded fMRI activity in participants as they performed the recent probes task, a paradigm used to measure proactive interference in working memory. Of key interest in the recent probes task are recent negative trials, where memory for a target stimulus set is probed with an item that is also part of a previously memorised target set. Participants performed the task under conditions of both high interference expectancy, where recent negative probes occurred frequently, therefore encouraging participants to adopt a proactive mode of control due to the high probability of experiencing interference, and low interference expectancy, where recent negative probes occurred sporadically, thus encouraging participants to adopt a reactive strategy, engaging control only when required. FMRI results showed that in the low expectancy condition, activation in the PFC occurred after the onset of the probe and was limited to recent negative trials, reflecting the transient activation of task goals subserved by the PFC in response to the detection of proactive interference. In contrast, for the high expectancy condition, PFC activation began during the delay period before the probe onset, and occurred on all trials, suggesting that task goals were maintained throughout the block of trials. Furthermore, Burgess and Braver (2010) assessed the relationship between participants' fluid intelligence – an index that is highly correlated with WMC – and proactive control, and found that participants with higher fluid intelligence showed PFC activations that reflected proactive control more so than low fluid intelligence participants, whose brain activation patterns reflected the reactive mode of control to a greater extent. Behaviourally, WMC related differences in task performance can be observed in a number of different cognitively demanding paradigms. Distributional analysis, which can be used in order to examine the behaviour of both fast and slow responses in the Simon task, a paradigm where the spatial location of a target stimulus may be congruent or incongruent with the directional response that the target stimulus maps onto, reveal that low WMC individuals show a larger reduction in interference effects in the slowest portion of reaction times (Gulbinaite & Johnson, 2013) – a behavioural marker of the reactive recruitment of cognitive control (Ridderinkhof, 2002). Similarly, individuals with low WMC experience greater interference from visual distractors in both the Flanker task (Redick & Engle, 2006), and the Stroop paradigm (Kane & Engle, 2003; Meier & Kane, 2013). Kane and Engle (2003) further highlighted the relationship between goal maintenance and WMC. They demonstrated that whenever the proportion of congruent trials was high, participants with low WMC committed more errors than the high WMC capacity group, suggesting that without the experience of incongruent trials to frequently remind participants of their task goals, participants with low WMC are more likely to lose access to the task goal of ignoring the distracting information, whereas those with high WMC are more capable at maintaining it over a longer period. Braver (2012) suggests that the availability of two distinct modes of control reflects a cost/benefits trade off. Whilst the maintenance of task goals in working memory is highly resource demanding, it provides a robust strategy to selectively focus attention and ignore distracting information, whereas in the reactive mode, the transient reactivation of task goals frees up resources which can then be dedicated to other attentional demands. However, the stimulus-driven and late acting nature of this form of control leaves it vulnerable to disruption via attentional capture effects, increasing the probability of error during goal reactivation.

Taking into account possible differences in people’s distractibility, it can be predicted that the presence of any effects of suppression on the extent to which flanker words are processed will be observable only for those individuals who demonstrate a high level of susceptibility to distractor processing. Therefore, the current study takes individual differences in participants’ proactive control capacity (PCC) into consideration. In light of the studies outlined above, individuals with low PCC will likely show higher levels of interference during the semantic flanker task than participants with high PCC, due low PCC participants’ tendency to rely on a reactive mode of processing. Furthermore, the presence of differing levels of susceptibility to interference in the flanker task between the two groups should have consequences for the observation of the suppression-induced reduction in flanker interference effects observed in experiment one. The observation of the effect is highly dependent on participants showing some susceptibility to interference from the flanking stimuli to begin with. If participants are maintaining a task goal throughout the flanker task which leads them to filter out any stimuli that appear as a distractor at an early stage of processing, then the difference in activation levels for Baseline and No-Think items will not have any opportunity to be observed; both Baseline and No-Think items may be filtered from processing at a similar stage, thus preventing them from exerting their differing levels of interference over target selection. Therefore, it can be predicted that participants with low PCC only will demonstrate an impairment in distractor processing for No-Think items. In contrast, participants with high PCC, due to their increased ability to filter out distracting information, are unlikely to show any initial level of distractor susceptibility and thus episodic memory related differences in congruency effects will be masked for this group.

Method

Participants

Forty-eight students (nine male, age range: 18- 35, mean: 22.45 years, SD: 3.68 years) from the University of Granada took part in the experiment for course credit. All had normal or corrected-to-normal vision, and none had previously participated in an experiment using the Think/No-Think paradigm. Ethics approval was given for the experiment and all participants signed a consent form. Participants were categorised into two groups according to their Proactive Control Capacities (High vs. Low PCC, see the sub-section on Proactive Control below for details).

Materials, Procedure and Data analysis

The materials and procedure were the same as used in experiment one, with the exception of the final flanker phase. Target words and flanker words were both presented in white on a black background and appeared at the centre of the screen only.

Operation span (O-Span) task Following completion of the flanker task participants complete an automated version of the operation span task (automated O-Span) as developed by Unsworth, Heitz, Schrock and Engle (2005). The automated O-Span task is based on the operation span task devised by Turner and Engle (1989) where participants are required to memorise a series of words which are presented interspersed with mathematical operations, and then to subsequently recall the to-be-remembered words in serial order. The addition of mathematical operations interspersed between each word serve as a distracting activity. The automated version of the operation span task differs from the original in that letters are used as the to-be-remembered material, and the experiment can be completed with minimal intervention on the part of the experimenter as it is almost completely computer driven, and produces a score upon completion. Participants first completed three practice phases. In the first practice phase, participants viewed single letters on the screen which remained for 800 ms. Participants were then presented with a 4 x 3 letter matrix and were asked to recall the letters in the correct order of presentation, using the mouse to point and click on the appropriate letter. Recall was self-paced, and participants were given feedback on each trial. Next, participants practiced the mathematical operations, where an equation was presented on the screen, which participants were required to complete as fast as possible and to then click the screen to move on to the next screen, where a digit was presented and participants were required to click a true or false box depending on their answer. In the final practice phase, participants completed both the letter and equation tasks together. Here, participants were required to complete a mathematical operation which was followed by a letter item for memorisation. If participants were slower than their average speed plus 2.5 SD, the trial was counted as an error. After the practice session, participants completed the test trials which were identical to phase three of the practice session. In the test session, participants completed three trials of each set size, with set sizes ranging from three to seven. The order of presentation for each set size was randomised across participants. Upon completion of the Automated O-Span, participants' final scores were written down by the experimenter. The task took approximately 25 minutes to complete. The automated O-Span task has been shown to correlate highly with the original operation span task, and other traditional working memory measures (Unsworth et al., 2005).

Proactive Control Capacity. Two variables were taken into account in order to categorise participants into two separate groups based on the proactive control capacity: O-Span scores and global reaction times in the flanker task (Monitoring scores). Slow reaction times on interference paradigms index reliance on reactive rather than proactive control (Ridderinkhof, 2002), and generally speaking, global reaction times in flanker-type interference tasks can be used to quantify individual differences in conflict monitoring (see, e.g., Hilchey & Klein, 2011), a means of proactive control, with faster reaction times reflecting enhanced monitoring skill. O-Span and Monitoring scores were standardised and submitted to a Principal Component Analysis (PCA) to obtain a single Proactive Control score (this analysis also allows one to confirm the empirical correlation between both measures). A single component with an eigenvalue above 1.00 was extracted which accounted for 62.74% of overall variance (factor loadings were .79, for O-span scores, and -.79, for Monitoring scores, respectively). The 48 participants were ranked based on their Proactive Control Capacity (PCC) scores and subjected to a median split, resulting in two groups: lowPCC (n = 24) and highPCC (n = 24).

Data Filtering and Analysis. Reaction time data was subjected to the same transformation and filtering approaches as described in experiment one. Data filtering resulted in the removal of 4.9% of the trials. Reaction times and accuracy data were then entered into separate LMMs with item type (Think & Baseline for Think items, No-Think & Baseline for No-Think items), congruency (congruent, incongruent) and Proactive Control Capacity (High, Low) as fixed effects. Random structures included an additional random slope for PCC. They were determined using the same procedure as detailed above and are reported for each model.

Results

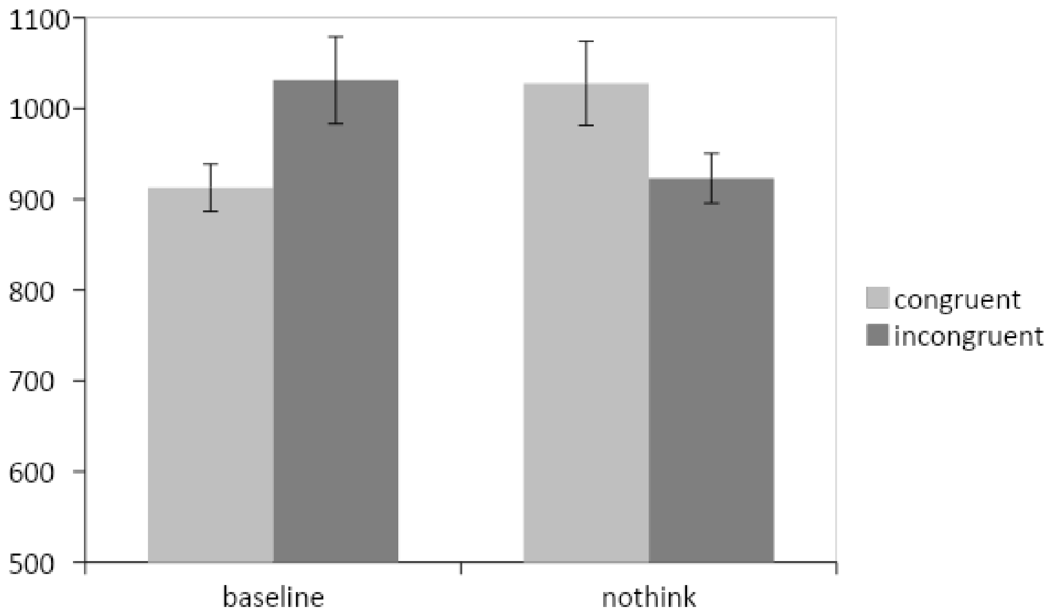
Reaction times

Reaction times were submitted to a linear mixed model analysis with random intercepts by subject and item, random slopes by subject for PCC and congruency, and random slopes by item for condition and congruency (see description above for fixed effects).

No-Think items. Analyses revealed a significant effect of PCC, $F(1) = 7.85$, $p = .01$, dv= .05, a significant two-way interaction between item type and congruency, $F(1) = 5.73$, $p = 0.02$, dv = .04, and a significant three-way interaction between PCC, item type, and congruency, $F(1) = 9.71$, $p = .002$, dv=.06. The main effects of item type, $F(1) = 0.09$, $p > .05$, dv< .01, and congruency, $F(1) = 0.03$, $p > .05$, dv< .01, were not significant, and neither were their two-way interactions with PCC (PCC x congruency, $F(1) = 1.52$, $p > .05$, dv<.01, PCC x condition, $F(1) = 0.01$, $p > .05$, dv< .01). The three-way interaction was due to the fact that the interaction of item type with congruency was significant for participants with low PCC, $F(1)$

= 13.4, p <.001, dv=.17, but not for those with high PCC, $F(1) = 1.02$, $p > .05$, dv=.01. For low PCC participants, the effect of congruency, with longer response latencies for incongruent than congruent items, was significant in the Baseline, $F(1)=4.18$, $p = 0.047$, dv= .11, but not in the No-Think condition, $F(1) = 2.40$, $p = 0.13$, dv= .07. Other main effects and interactions were non-significant for participants with low (all Fs ≤ .2.33, ps> .05, dv≤ .03) or high PCC (Fs ≤ 1.96, ps> .05, dv≤ .03). See figure 7 for descriptive values.

a) Low Proactive Control Capacity



b) High Proactive Control Capacity

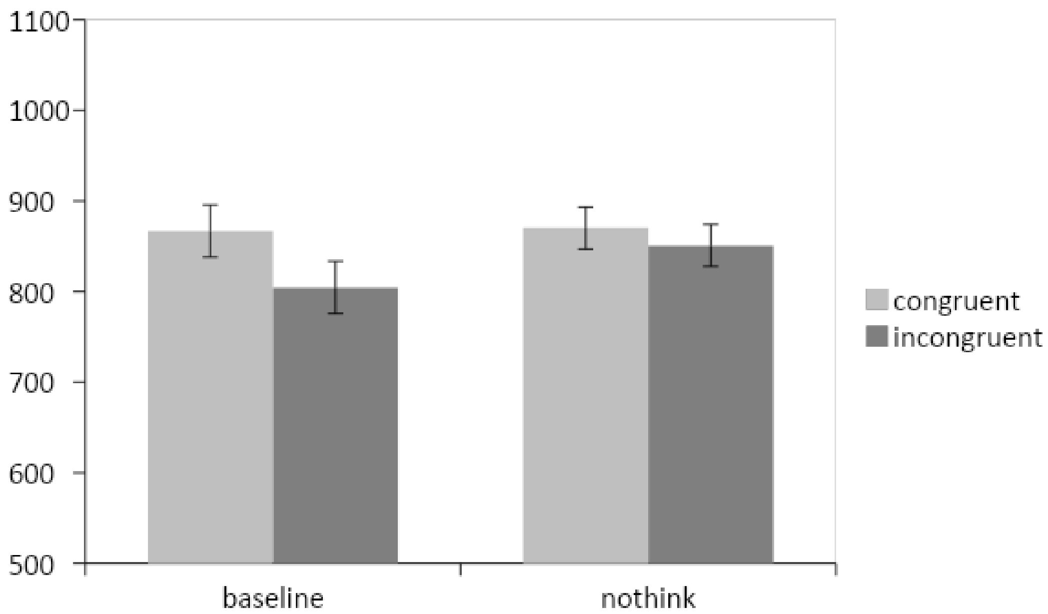


Figure 7. Mean reaction times for congruent and incongruent items divided by item type for participants with a) high PCC and b) low PCC.

Think items. For think items, there was a main effect of PCC, $F(1) = 8.73$, $p = .005$, $dv = .06$, as well as significant interactions between PCC and congruency, $F(1)=13.35$, $p <$

.001, *dv*= .09, and condition and congruency, *F* (1) =5.19, *p* =.02, *dv*= .04. Other main effects and interactions were non-significant, *F*(1) =1.47, *p* >.05, dv≤.01.The interaction between PCC and congruency was due to a reversed congruency effect in individuals with high PCC (congruent: M = 904.41, SE = 22.1, incongruent: M = 823.19, SE = 17.34), *F*(1) =5.89, *p* =.02, dv=.08, combined with a non-significant effect for those with low PCC, (congruent: M = 945.12, SE = 21.72, incongruent: M = 1007.2, SE = 30.7), *F*(1) =2.13, *p* >.05, dv= .03. Following up on the two-way interaction between condition and congruency, no significant congruency effects were observed for baseline or think items, Fs ≤ 1.58, *p* > .05, dv<.01, although congruency effects showed a different direction within each item type (for baseline items, congruent: M = 888,29, SE = 19,58, incongruent: M = 917,3, SE = 26,95; for think items, congruent: M = 957,81, SE = 23,73, incongruent: M = 915,86, SE = 24,96).

Accuracy

Effects for PCC, congruency, condition, as well as their interactions were not significant for either No-Think items nor Think items (ps>.05, Fs <= 2).

Discussion

The results of this experiment demonstrate a reduction in flanker interference effects for No-Think items that is limited to individuals with low proactive control capacity (low PCC). Such a finding is in line with a wide body of studies indicating that low PCC individuals are more susceptible to interference effects from distracting stimuli than high PCC participants. The results suggest that participants with a large capacity for cognitive control are capable of filtering out the influence of the flanking words at an early stage of processing. If this is the case, then the effect of flanker words over target processing should be minimal, and any suppression induced differences in flanker saliency will be masked from observation in group with high PCC.

An alternative explanation for the PCC-related differences in the modulation of the congruency effect across Baseline and No-Think items is that it reflects differences in the suppression strategies used to prevent No-Think items from entering consciousness during the No-Think trials. Specifically, the distinction between reactive and proactive control styles could also be applied to the type of cognitive strategy used to suppress unwanted memories. In the case of the Think/No-Think paradigm, a proactive mode would involve a sustained ability to refrain from retrieval of the No-Think item, thus preventing it from entering consciousness, via the maintenance of task goals in working memory. With such a strategy, the suppression of No-Think items is unnecessary because those items would not elicit any initial entry into consciousness, thus rendering targeted inhibition of the intruding memory unnecessary. As previously discussed in the introduction of experiment two, the maintenance of task goals is a resource-costly process, requiring a large proportion of working memory resources. It is therefore conceivable that participants with low PCC do not have sufficient resources in order to maintain the task goal of avoiding the retrieval of No-Think items over an entire trial, and will therefore experience more intrusions of the unwanted item into conscious awareness. If this is the case for the low PCC group, then the targeted suppression of the intruding item would be necessary to push it out of awareness. Such an approach to memory suppression mirrors the reactive control mode used by participants with a lower PCC to overcome interference resolution during attentional tasks.

This division of suppression strategies into reactive and proactive modes parallels a proposal by Depue (2012) who outlines two different approaches to cognitive control over memory retrieval; a direct inhibition mechanism, which is similar to a reactive mode, whereby the specific representation of episodic memory traces are inhibited in response to their automatic retrieval, and a reactivation inhibition mechanism which is similar to a proactive control mechanism, whereby cognitive control operates over the memory retrieval process itself, preventing the unwanted memory from coming to mind. Evidence to suggest that individuals with high PCC are more capable of selectively disengaging retrieval can be seen in EEG studies of recognition tests combined with an exclusion task where only a subset of learned items are designated as to be recognised targets, and another subset of learned items are designated as non-targets (Elward, & Wilding, 2010; Elward, Evans, & Wilding, 2013). Here, participants with higher working memory capacity (WMC), a factor closely related to PCC, show a larger difference between targets and non-targets in the magnitude of ERP correlates of episodic retrieval (the parietal old-new effect) during a subsequent recognition test than those with a relatively lower capacity for proactive control. This finding can be understood as an indicator that individuals with a lower PCC experience a similar degree of episodic retrieval for both targets and non-targets, whereas high-PCC individuals are more capable of prioritising recollection of targets over non-targets. Additional evidence for the dual-mechanism view of memory suppression can found in the retrieval practice paradigm

(Anderson, Bjork & Bjork, 1994), a situation where inhibitory control over memory is required during retrieval to resolve the competition between memory traces (Anderson & Spellman, 1995). Mall & Morey, (2013) have shown that only individuals with low WMC show a forgetting effect that is diagnostic of inhibitory control, leading to the suggestion that these individuals utilise inhibitory control to avoid the retrieval of competing memory traces, whereas those with high WMC engage in a more controlled and focused memory search for target items and thus experience less competition at retrieval. This result is additionally important as it indicates that as a result of individual differences in working memory and proactive control capacity, different control strategies may emerge in similar situations that require the inhibitory control over memories.

Such a difference in suppression strategy between high vs low PCC groups during No-Think trials has consequences for the extent to which No-Think items interfere during the flanker task for both groups. The use of a reactive strategy by the low PCC group means that in their attempts to avoid thinking about the No-Think response words, participants are unable to truncate the retrieval process and instead inadvertently retrieve the response word. In order to then purge the response word from consciousness, inhibitory control is recruited which targets the episodic representation of No-Think items. A consequence of inhibiting No-Think items is that these items have less of an influence on central target word processing later on in the subsequent flanker task, predicting, as was found in the current experiment, a difference in congruency effects across Baseline and No-Think items for the Low PCC group. In contrast, if participants with high PCC engage in a proactive control strategy during No-Think trials, they have more control over the initial retrieval process itself, enabling them to avoid any initial retrieval of the unwanted No-Think items. Thereby, the No-Think items enter consciousness to a lesser extent, with the consequence that inhibition of those items is not required, and therefore, No-Think and Baseline items should influence central target word processing in the final flanker task to a similar extent, also predicting the lack of difference in congruency effects between Baseline and No-Think items for high-PCC participants found in the current study.

Whilst an explanation in terms of a difference in the type of strategy used during suppression trials does predict the same between-group differences in congruency effects across Baseline and No-Think items, the pattern of results also suggests that differences in cognitive strategies are present between groups during the final flanker task. Participants with lower PCC show a standard congruency effect for baseline items, where they are slower to respond on incongruent trials compared to congruent trials. For the high-PCC group, however, this effect is eliminated, with participants actually responding faster on incongruent trials than on congruent trials, though this difference was non-significant. A reduction or elimination of congruency effect can be interpreted as an indication that participants are engaging in a proactive control mode (Logan & Zbrodoff, 1982), and therefore the between-group difference in the size and direction of the congruency effect for baseline items indicates that differences in the mode of control are present during the flanker task. Furthermore, a selection of studies suggests that participants with a high WMC may in fact inhibit distracting information to a greater extent than those with low WMC participants do. Hasher, Lustig, and Zacks (2007) see variations in WMC as a reflection of inhibitory control capacities, where improvements in WMC are due to an increased efficiency at actively suppressing interfering information. By this account, if high WMC individuals possess superior inhibitory mechanisms then they may also be more efficient at suppressing unwanted memories and thus, one may predict that they will show a larger difference in congruency effects between Baseline and No-Think items.

In addition, the results for the low PCC group of the present experiment provide a partial replication of the finding from experiment one, namely, a reduction in flanker congruency effects whenever distractor items have previously undergone mnemonic suppression. This replication can give us confidence in the robustness of the observation from experiment one. Together with the results from experiment one, this finding provides novel insights into the consequences of direct suppression of memory retrieval. In both experiments, memory suppression interacted with congruency effects – a classic hallmark of perceptual distraction – attenuating distractor influence and allowing more efficient target processing.

In the present experiment, the suppression-induced reduction in flanker inference was limited to the low-PCC group, which I suggest is due to their overall increased susceptibility to the interfering effects of distracting stimuli, whereas experiment one demonstrated this effect across the entire participant sample. The reason for the discrepancy in this result across the entire sample between experiment one and the current study likely lies in minor variations in design related parameters between the two studies. In experiment one, specific procedural adjustments to the standard flanker task were made by randomly presenting each trial in either the upper or lower portions of the monitor – an adjustment aimed at decreasing the spatial predictability of the location of the target/flanker cohort, thus rendering it more difficult for participants to selectively filter out stimuli appearing at specific locations of the screen – and furthermore, target and flanker items were presented in grey and white respectively on a black background. This difference in font colour aimed to make flanking stimuli relatively more salient than their corresponding targets. It is possible that these procedural differences in experiment one augmented the interfering effect of the flanking stimuli for the entire sample, thus reducing their ability to sustain a proactive control style and leading them to adopt a more reactive mode of control when carrying out the task. The assumption of increased interference in experiment one is validated by the observation of overall increased response latencies relative to the current study, indexing a shift towards reactive control and, conversely, a reduction of proactive control recruitment. Reaction times for the entire sample in experiment one resemble reaction times for the low PCC group in the current study.

As noted above, in this study, the perceptual consequences of previous mnemonic suppression were only detectable under certain conditions, namely, when participants were more likely to engage in a reactive control mode and thus experience distractor interference, either due to individual capacity limitations or due to increased cognitive load due to design manipulations. This suggests that individual differences and situational demands can modulate the dynamic relation between memory and perception. Nevertheless, by showing that attentional processes can, in principle, be susceptible to the effects of memory suppression, our findings speak to the fundamentally interactive and dynamic nature of memory and attention.

Finally, it is important to highlight the power limitations in the design of experiment one and the current experiment. For both experiments, the amount of trials available for analysis for each individual participant by condition is low due to the limitation in the amount of stimuli that participants are able to adequately memorise, resulting in a relatively low signal-to-noise ratio when compared to common reaction time studies. The repetition of stimuli in the final flanker task was purposefully avoided to evade any possible effects of stimulus re-exposure, however, in further experiments, it would be recommendable to test out the repetition of flanking stimuli in a block-wise fashion, thereby increasing the signal-to-noise ratio.

In conclusion, the current experiment expands upon the findings from experiment one, by showing that the demonstration of a suppression-induced reduction in flanker interference effects is highly dependent on the type of control strategy that participants utilise when carrying out the task. The effect in question may only be observed whenever participants process the flanking stimuli to an adequate extent that allows flanker interference to take place, such as when engaging in a late acting reactive control mode of control. On the other hand, participants who rely on a strategy that filters out distracting stimuli at an early stage of selection such as in the proactive mode of control, may show no indication of a suppression induced reduction in flanker congruency effects. For these participants, flanking stimuli do not sufficiently interfere with target processing and therefore, suppression-induced differences in flanker interference are masked. Furthermore, the results of the current study expand upon the results of experiment one by providing a partial replication of the effect, with low-PCC participants showing a reduction in flanker interference effects whenever flanking stimuli have been subjected to memory suppression in the Think/No-Think paradigm. This partial replication adds confidence to the main findings of experiment one.

Experiment 3: Semantic Knowledge Promotes Conscious Awareness of Visual Objects

Successful conscious detection of stimuli in our environment may vary according to purely sensory properties of the stimulus, such as salience or luminosity, as well as non-sensory aspects arising from the observer's internal states such as motivations, beliefs and expectations (Collins & Olson, 2014; Gilbert & Li, 2013). The idea that factors such as previous experience, emotional content, verbal categories, or semantic information may play a role in shaping our perceptual experience of the world is supported by various findings. For example, afterimages for objects with intrinsic colour are stronger than those for arbitrarily coloured objects (Lupyan, 2015), and memory for intrinsic colour categories can modulate colour experience (Hansen et al., 2006; Mitterer, Horschig, Müsseler, & Majid, 2009; Witzel, Valkova, Hansen, & Gegenfurter, 2011). Semantic knowledge facilitates the recognition of objects across changes in viewpoint (Collins & Curby, 2013), and associating socially relevant negative information with faces leads participants to judge the faces and their emotional expressions as more negative (Abdel Rahman, 2011; Rabovsky, Stein, & Abdel Rahman, 2016; Suess, Rabovsky, & Abdel Rahman, 2015). Furthermore, verbal categories have been shown to modulate the detection and discrimination of visual features such as colour and shape (Regier & Kay, 2009; Thierry, Athanasopoulos, Wiggett, Dering, & Kuipers, 2009) as well as entire objects (Maier, Glage, Hohlfeld, & Abdel Rahman, 2014). This experiment asks to what extent semantic knowledge may influence our ability to consciously detect an object, independently of object features and familiarity.

The possibility that semantic information may be involved in shaping the contents of conscious perception coheres with predictive coding theories of visual perception (Rao & Ballard, 1999; Friston, 2005; Clark, 2013). While modular theories take perception to be encapsulated from cognitive factors (Pylyshyn, 1999; Firestone & Scholl, 2016), predictive coding emphasises the brain's ability to use past experiences to predict the type and nature of incoming signals. From this perspective, neural systems are able to take advantage of statistical regularities in the visual environment by incorporating these consistencies into the perceptual process. Such information may come from many sources, including life-long experiences, implicit memory, or conceptual knowledge. Predictive coding theories state this information is used by the brain to continuously generate internal predictions about future events, allowing for more efficient stimulus processing (de-Wit, Machilzen, & Putzeys, 2010).

Evidence to suggest that semantic information may play a role in conscious detection comes from a number of recent studies. Two priming studies employed the continuous flash suppression (CFS) paradigm (Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Tsuchiya & Koch, 2005). In this paradigm, stimuli presented to one eye undergo suppression due to the simultaneous presentation of a pattern mask of high contrast to the other eye. Costello and colleagues (2009) demonstrated that target words that were undergoing suppression, and thus could not be consciously detected, could break free from suppression earlier when they were preceded by the presentation of a semantically related prime word. Similarly, Lupyan and Ward (2013) showed that hearing an object's name improved the subsequent detection of objects during CFS. Emotional valence has also been shown to affect suppression times, with negatively valenced utterances showing shorter suppression times than neutral utterances (Sklar et al., 2012), and faces associated with negative social information dominating for longer during binocular rivalry than neutral faces (Anderson, Siegel, & Barrett, 2011; but see Rabovsky et al. (2016) for null effects during CFS). These studies suggest that conceptual information can alter the time course and extent to which associated stimuli enter into conscious awareness. However, previous studies provide little indication regarding which stage of processing semantic information acts upon. When only behavioural measures are employed, e.g., detection times during CFS, effects that appear to reflect facilitated perception may instead index an influence on later semantic stimulus evaluation and decision making. Furthermore, while the studies discussed above reported semantic effects on CFS, a considerable number of studies have failed to provide clear evidence for such influences (see Gayet, van der Stigchel, & Paffen, 2014, for review). Thus, while semantic influences on CFS are controversial and difficult to obtain, other paradigms such as the attentional blink (AB; see below) are well-suited to investigate semantic effects because they may interfere with access to consciousness at a later stage after extensive unconscious processing.

In the third experiment of this thesis, electroencephalographic (EEG) activity was recorded to elucidate the time course of semantic influences over conscious perception and to relate behavioural measures of stimulus detection to preceding modulations of perceptual stages, indexed by early event-related brain potential (ERP) effects. ERP recordings provide an ideal tool to elucidate the time course of cognitive processes. A number of ERP studies have demonstrated that cognitive factors can influence perception at the earliest stages. Categorical perception effects have been shown to reliably modulate the mismatch negativity, an ERP marker taken to be an index of pre-attentive processing, occurring between 150 and 250ms

(Boutonnet, Dering, Viñas-Guasch, & Thierry, 2012; Mo, Xu, Kay, & Tan, 2011; Thierry et al. 2009). Thierry and colleagues (2009) further demonstrated influences of verbal categories on the P1, an early ERP component peaking between 100 and 150ms post stimulus onset that is thought to reflect basic visual perception, e.g., the perception of individual stimulus features (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002), indicating that high level information can affect an early stage of stimulus processing. Similarly, using a priming procedure, Boutonnet and Luypan (2015) showed that the P1 component for objects is modulated when they are preceded by the auditory presentation of the object's name. As previously described in chapter one, Abdel Rahman and Sommer (2008) using a learning paradigm, selectively manipulated the amount of semantic information associated with initially unfamiliar objects which were later presented for naming, recognition evaluation and semantic classification tasks. They found that in addition to a later modulation of the N400 ERP component which is related to semantic processing (Kutas & Federmeier, 2011), objects that were associated with semantic information elicited P1 components of reduced amplitude. Rabovsky, Sommer and Abdel Rahman (2012) found a similar P1 effect when performing the same task on object names. Together, these findings suggest that semantic information can modulate early perception. More specifically, semantic information may induce such modulation by modifying the perceptual representations of the novel objects formed during training, resulting in more efficient bottom-up propagation of information. Alternatively, given that studies have shown that feedback from frontal cortices to early visual modules can occur soon after stimulus onset (Lamme & Roelfsema, 2000), semantic information may exert an influence over extrastriate areas in the form of feedback, resulting in a modulation of the P1 component. The P1 modulation in the studies by Rabovsky and colleagues (2012) and Abdel Rahman and Sommer (2008) was however, not accompanied by a corresponding change in reaction times, making the functional role of semantic effects in stimulus processing unclear. It is possible that the P1 effects in these studies did have a functional role in perception which did not come to bear on behaviour because the tasks were very easy at a perceptual level. Thus, the functional role of the semantic influence on P1 amplitudes might only become behaviourally relevant in situations of increased perceptual difficulty.

To directly address the role of semantic information in conscious detection, experiment three utilised a similar learning procedure to that used by Abdel Rahman and Sommer (2008), where participants are familiarised with a series of initially unfamiliar object pictures, and the amount of semantic information provided for each object was manipulated. Subsequent to this learning procedure, object pictures with in-depth functional versus minimal associated semantic information were presented under conditions of difficult conscious detection in the attentional blink paradigm. In the attentional blink paradigm, as previously outlined in chapter one, target stimuli are presented to participants for detection during a time window when attention is occupied with the processing of a preceding target. Object pictures were briefly presented as the second of the two targets, and participants were required to detect the presence of an object within the presentation stream, a task that does not require semantic analysis of the stimulus.

EEG studies of the attentional blink show that in addition to the early P1/N1 complex, blinked trials (i.e. trials with missed T2) show a preserved N400, an ERP component associated with semantic processing (Kutas & Federmeier, 2011). This finding indicates that unreported targets undergo extensive processing, at least to the level of semantic analysis, without participants' awareness. Because unreported targets undergo a high level of stimulus processing, the attentional blink paradigm provides an ideal context to test the hypothesis regarding the influence of semantic information on conscious detection. In contrast to the N400, the P300, a component which has been suggested to reflect the consolidation of information into working memory, is reduced for unreported T2 trials (Sergent, Baillet, & Dehaene, 2005), suggesting that the attentional demands of T1 processing in working memory encoding, episodic processing and response selection reduce the amount of resources that are available for the processing of T2, resulting in a reduction in conscious detection of T2.

In summary, the aim of experiment three is to add to the findings of experiments one and two by assessing the impact of a different aspect of memory - that is semantic memory - on perceptual processes related to conscious perception. Furthermore, in addition to the use of behavioural methods, EEG activity will be recorded in order to obtain information on the time course of any potential cognitive influence over perception. I predict that if semantic information plays a role in the conscious detection of visual stimuli under difficult conditions in the attentional blink task, then objects associated with more functional-semantic information should be detected to an overall greater extent than objects associated with minimal information. Additionally, in line with previous studies using similar materials and learning procedures (Abdel Rahman & Sommer, 2008; Rabovsky et al., 2012), I expect semantic information to induce modulations of the P1 and N400 ERP components.

Method

Participants

A sample of 32 right-handed participants (17 female), from the Humboldt University of Berlin took part in the experiment in return for a monetary compensation or course credit. All participants were native speakers of German with normal or corrected-to-normal visual acuity. The sample had a mean age of 27 years (range = 20 - 34 years). This research was approved by the Ethics Committee at the Department of Psychology, Humboldt-Universität zu Berlin. Participants provided written informed consent prior to participation.

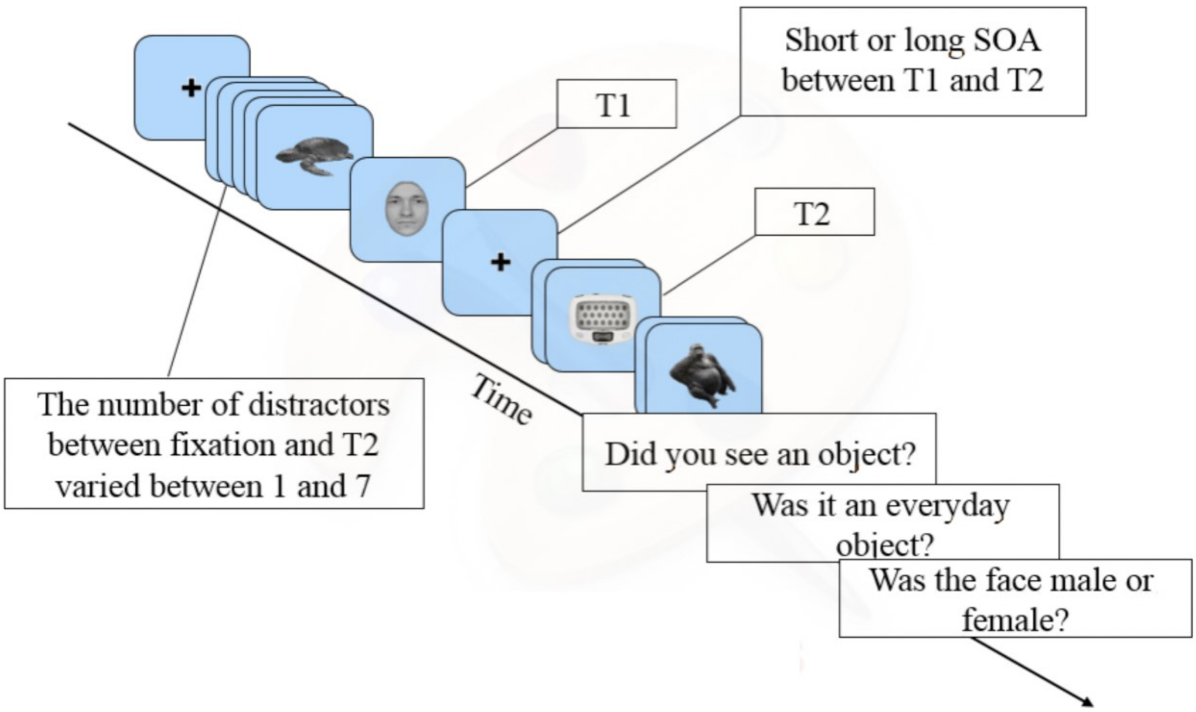
Materials

Stimuli for T2 targets consisted of grayscale BMP pictures (207 x 207 pixels) of 25 well-known and 40 rare objects, previously used by Abdel Rahman & Sommer (2008) and Rabovsky et al. (2012). Of the 40 rare objects, half were real objects and half were fictitious. Five of the well-known objects were used for practice trials. For all objects, a sentence was recorded stating the object's name (for example, "This is a sofa."). For the rare objects, pseudo words were used as names that did not reveal any meaningful information regarding functional properties. (e.g., "This is a squonker"). Additional sentences were recorded for the rare objects which explained their functional use (for example, "This is a machine for breeding chicken eggs."). Rare objects were randomly divided into two subsets to be allocated to the two semantic conditions. The assignment of objects to semantic conditions was counterbalanced across subjects so that bottom-up influences of differences in contrast, luminance, complexity etc. could be excluded. For T1 targets 164 grayscale photographs of neutral faces were selected, half of which were female, and all were edited for homogeneity of features outside of the face. Masking stimuli consisted of 127 grayscale animal pictures. All stimuli were presented in the centre of the screen on a light blue background (RGB value: 169,217,255).

Procedure

Learning Phase. In the learning phase participants were familiarised with the objects along with the information associated with each condition. Well-known and rare objects were presented in random order in the centre of the monitor screen (DELL 1908FPb, 19 inches, 1280x1024, 75 Hz). Simultaneously, an auditory sentence was presented. For half of the rare objects, the sentence contained information about the name of the object (minimal knowledge condition), and for the remaining half, the sentence consisted of functional information regarding the use of the object (functional knowledge condition). Well-known objects were presented along with their name across all participants. All objects were presented for 4000ms with a 500ms inter stimulus interval during which a fixation cross appeared on the screen and a briefly presented blank screen was used to separate sequential stimuli. Each object was presented three times.

Test Phase. Each trial consisted of the following series of events: A central fixation cross was presented for 500ms, followed by a series of one to seven masks with the number varying randomly on each trial. T1 was then presented, followed by a single mask. During the SOA between T1 and T2, a fixation cross remained on the screen. T2 was then presented and was followed by two masks. Masks, T1 and T2 were each displayed for 27ms and were separated by blank screens lasting 41ms. The SOA between T1 and T2 was either short (258ms) or long (688ms). T1 consisted of a male or female face, and masking stimuli were created from a selection of animal pictures. On T2 present trials, rare and well-known objects were presented, and on T2 absent trials, participants were presented with a blank screen. Following the presentation of the stimuli, participants were required to answer a series of questions regarding their experiences for T1 and T2. Participants were first asked whether they have seen an object using a perceptual awareness scale (Sandberg & Overgaard, 2015). They pressed one of four keys: (a) if they did not see any object, (b) if they had the impression of there being an object present, (c) if they were able to perceive parts of but not the full object, and (d) if they perceived a full object. Participants were encouraged to use the full range of response options throughout the experiment. On trials where participants indicated some level of object awareness (responses b, c or d), a second question was presented on the screen asking, "Was the object an everyday object?" to which participants gave a binary manual yes or no response. Finally, participants were asked to classify the face presented as the T1 stimulus as male or female with a manual response. For all questions, a schematic representation of the different response options was presented on the screen below the question. Figure 8 provides a visual illustration of the trial scheme. All questions were presented on the screen until a response was given. On two thirds of the trials T2 was present and the remaining third were comprised of T2 absent trials. 75 percent of all trials, i.e., both T2 present and absent trials, were presented in the critical blink condition at the short SOA. Within a single block, all rare and well-known objects were presented once, requiring participants to complete four blocks in order to rotate all items across the two SOA conditions (due to the 75/25 ratio of short/long SOA). Participants carried out eight blocks with a short break after each block. Before beginning the experiment,



there were 20 practice trials, and in the experiment proper, participants completed 720 trials, 240 of which were T2 absent trials and 480 were T2 present trials, 360 with short and 120 with long SOA. For each of the two rare object conditions, and for the well-known condition, 120 and 40 trials were presented at the short and long SOAs respectively. Thus, each object was presented twice at the long SOA and six times at the short SOA.

Figure 8: Sample of the stimulus sequence presented during the attentional blink phase. After a learning procedure where participants studied novel object images which were associated with either functional information or a meaningless name, participants performed the attentional blink task. The second of the two targets (T2), when present, was either a functional knowledge object, a minimal knowledge object or a well-known object.

Post-experimental Questionnaire. Participants were subsequently presented with a list of pictures of all rare objects and were asked to write down any information that they could remember from the learning phase for each object.

EEG Recording

Continuous EEG was recorded throughout the experimental session with Ag/AgCl electrodes at 64 sites positioned according to the extended 10-20 system (Pivik et al., 1993) at a 500 Hz sampling rate, using a bandpass (0.032-70 Hz) filter. During recording, all electrodes were referenced to the left mastoid, and electrode impedance levels were kept below 5 kΩ. Horizontal and vertical electrooculograms (EOGs) were recorded from the external canthi and from above and below the midpoint of the right eye. Offline, the EEG was re-referenced to the average voltage of all electrodes, and a low-pass filter of 30 Hz was applied. Eye-blink and horizontal and vertical EOG activity was removed using a Gratton and Coles correction (Gratton, Coles & Donchin, 1983). Remaining artifacts were eliminated using an automatic rejection procedure where amplitudes exceeding +/- 100uV or changing by more than 75uV between successive samples were eliminated. Baseline activity was corrected to a 100ms time period before the onset of T2, and trials were segmented into time windows 200ms before and 800ms after T2 onset. Trials on which participants responded incorrectly to T1 were excluded from the analysis. Time windows for the P1 (100 - 150ms) and N400 components (300 - 500ms) were based on previous studies demonstrating semantic effects on low-level visual perception and later stages of meaning access (Abdel Rahman & Sommer, 200; Rabovsky et al., 2012). Regions of interest were selected based on those clusters of electrodes where effects were maximal (see below).

Data Analysis

In analysing participants' ability to perceive T2 across conditions, T1 error trials were first excluded, and an index of overall object detection was obtained by calculating mean responses within each condition. This detection score ranges from one to four, with one indicating no object perception and four indicating complete object perception. To assess the influence of semantic information and SOA on conscious detection linear mixed models were constructed using the lmer function from the lme4 R package, version 1.1-12 (Bates, Maechler, Martin, & Walker, 2016). For behavioural performance and ERPs, semantic condition (minimal vs. functional knowledge) and SOA (short, long) were included as fixed factors, and participant as a random unit. Well-known objects were not included in this analysis since they cannot be assigned to different conditions and therefore visual differences cannot be excluded. For ERP effects, electrode was additionally included as a random unit, nested within participants (Aarts, Verhage, Veenvliet, Dolan, & van der Sluis, 2014). Due to convergence problems for the maximal random effects structures, a data-driven model comparison using restricted maximum likelihood estimation (REML) approach was used (Zuur, Ieno, Walker, Saveliev, & Smith 2009; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2015) to identify the optimal random structure that accounted for the most variance, as indicated by AIC and log-likelihood values. The final model included a random slope for SOA by subject, and by electrode nested within subject, respectively. Subsequently, fixed effects were tested using Maximum Likelihood estimation. Models were tested using the ANOVA function from the lmerTest R package, version 2.0-30 (Kuznetsova, Christensen, & Brockhoff, 2014). Explained deviance (*dv*) was calculated using the *pamer.fnc* function from the LMERCovenienceFunctions R package (Tremblay & Ransijn, 2015) Post-hoc comparisons were Bonferroni corrected and calculated using the testInteractions function from the R package phia, version 0.2–1 (De Rosario-Martínez, 2015). Post-experimental questionnaires were scored by two independent evaluators. For the minimal knowledge condition, participant recall for an object was scored as correct if it matched the name that was previously learned. For objects from the functional knowledge condition, participants recall was scored as correct if the gist of the description matched the description that was previously learned for that object. Recall was scored as correct or incorrect.

Results

Post-experimental Questionnaires

Participants varied widely in their ability to recall the functional information associated with objects at the beginning of the experiment (mean: 74%, sd: 20%, range: 20% to 100%). Recall for object labels was generally lower than that for functional information (mean: 17%, sd: 16%, range: 0% to 70%). To ensure that the manipulation was effective, two participants who showed recall levels for functional information lower than two standard deviations below the mean were removed.

T1 Detection

Mean performance on T1 classification was 93%, (range 76% – 98%).

Semantic Knowledge effects

Performance. Trials where participants incorrectly classified T1 were removed from any further analysis. Participants were able to detect objects to a greater extent at the long SOA (m = 3.21) than at the short SOA (m = 2.84), $F(1, 29) = 151.03$, $p < .001$, $dv = .79$. More importantly, participants also slightly differed in their overall detection of T2 objects across semantic conditions (functional knowledge, m = 2.64; minimal knowledge, m = 2.61), reflected in a significant main effect of semantic condition $F(1, 58) = 4.15$, $p < .05$, $dv = .27$ (Figure 9A). This difference in mean detection between semantic conditions, whilst statistically significant, is small and should be interpreted accordingly. The interaction between the factors semantic condition and SOA was non-significant, $F(1, 58) = .11$, $p = .75$, $dv = .01$.

ERPs. Of primary interest regarding the effects of semantic information on early stages of visual processing, analysis of the P1 time window (ROI: O1, Oz, O2, PO3, POz, PO4) revealed no significant main effects of semantic condition, $F(1, 508) = .004$, $p = .96$, $dv < .01$ or SOA $F(1, 29) = 2.34$, $p = .14$, $dv = .02$. The effect of semantic condition at the different SOAs showed opposing effects with a positive modulation (i.e., larger amplitudes for the functional knowledge as compared to the minimal knowledge condition) at the short SOA and a negative going modulation (i.e. smaller amplitudes for the functional knowledge condition) at the long SOA (Figure 9B and 10); this pattern was confirmed by a significant interaction between semantic condition and SOA $F(1, 508) = 13.81$, $p < .001$, $dv = .09$. Follow-up comparisons showed that these effects were significant at both the short, $\chi 2 = 6.68$, $p < .02$, and the long, $\chi 2 = 7.14$, $p < .02$, SOA.[1]

[1] An alternative way of looking at these findings is that it is not the presence of functional knowledge that is modulating responses to the P1, but rather the lack of a name for those objects. In order to rule out this possibility, we analysed P1 amplitudes within the minimal knowledge and functional knowledge conditions according to participants' subsequent memory for the information that was associated with each object. To this end, we conducted two separate one-way ANOVAs with participant recall (yes/no) as independent variable, and P1 amplitude as dependent variable. If it is the association with semantic knowledge that drives

For the N400 component (ROI: O1, Oz, O2, PO3, POz, PO4), there was a significant main effect of SOA $F(1, 29) = 13.22$ $p = .001$, $dv = .21$, whilst the main effect of semantic condition was non-significant $F(1, 29) = 1.51$ $p = .23$. $dv = .02$. SOA interacted with semantic condition $F(1, 479) = 20.71$, $p < .001$. $dv = .32$. Follow-up contrasts revealed a significant effect of semantic condition at the long SOA with smaller amplitudes for the functional knowledge condition, $\chi2 = 7.23$, $p < .02$. whereas at the short SOA the effect of semantic condition was non-significant, $\chi2 = 0.14$, $p = 1$.

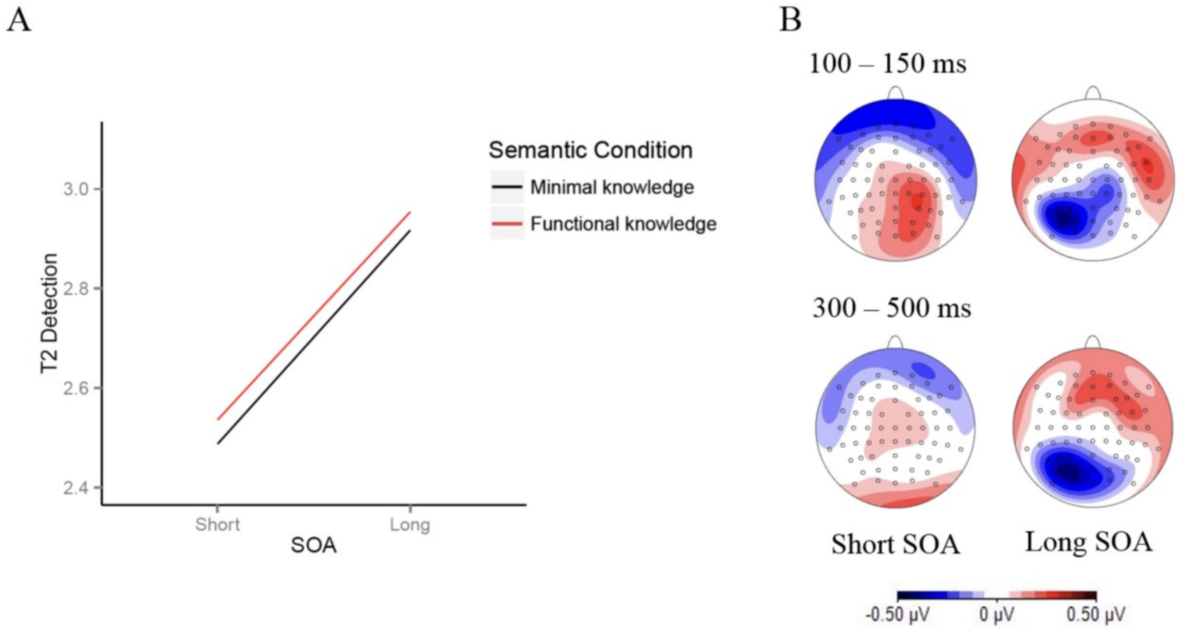


Figure 9: Results from the attentional blink task. (*A*) Participants consciously perceived more of the objects which were associated with semantic knowledge in comparison to those from the minimal knowledge condition. (*B*) Scalp topographies of event-related potential difference

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the P1 effect, then significant differences in the magnitude of the P1 between remembered and forgotten descriptions should be present within the functional knowledge condition only, whereas no differences in P1 amplitude should be observed according to participants' memory for object labels. In line with our theoretical framework, we found a modulatory effect of memory for functional knowledge, $F(1, 26) = 4.26$, $p < .05$ (.049), but no significant modulatory effect of memory for object labels, $F(1, 27) = 0.19$, $p = .23$.

waves between knowledge conditions (functional minus minimal knowledge) for the P1 and N400 components, separated for long and short SOAs.

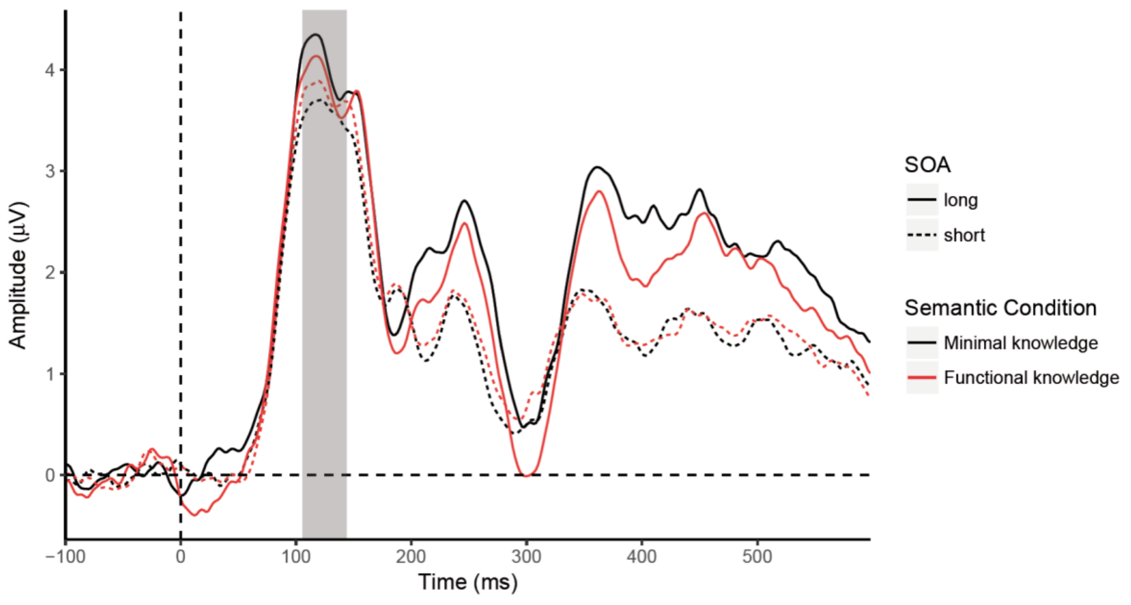

Figure 10: Waveforms from the pooled region of interest where the P1 component was maximal (Linear derivation of electrodes O1, Oz, O2, PO3, POz, PO4), with the time frame of sequential significant point-by-point correlation coefficients highlighted.

Correlation analysis between ERP amplitude differences and T2 detection

To assess the relation between the P1 modulation and behavioural measures of conscious access, the mean amplitude difference of the P1 component was correlated with the difference in detection between knowledge conditions (functional minus minimal knowledge) separately for each SOA. This analysis resulted a non-significant correlation at the short SOA (r = -.05, p = 0.79) and a marginally significant correlation at the long SOA (r = -.31, p = 0.095). In order to further explore the relationship between the semantic modulation of the P1 component and the behavioural measure of conscious detection I collapsed across both SOA's to calculate the overall effect of semantic information on both the P1 and behaviour, revealing a significant negative correlation (r = -.46, p = .01) (Figure 11). Thus, stronger knowledge effects on P1 amplitudes as reported in previous studies (Abdel Rahman & Sommer, 2008; Rabovsky et al., 2012) were associated with stronger knowledge induced facilitation of detection performance. To further explore this relation and its time course point-by-point correlations between amplitude differences and the behavioural effect size over consecutive sampling points, every 2ms from 0ms to 200ms were calculated. A series of sampling points was considered significant when a minimum of 15 significant, uninterrupted correlations appeared consecutively (Guthrie & Buchwald, 1991). The P1 modulation began to correlate significantly with behaviour at 106ms continuing uninterrupted until 144ms, a time window which encompasses 20 sampling points in a row, corresponding to 38ms (see Figure 11).

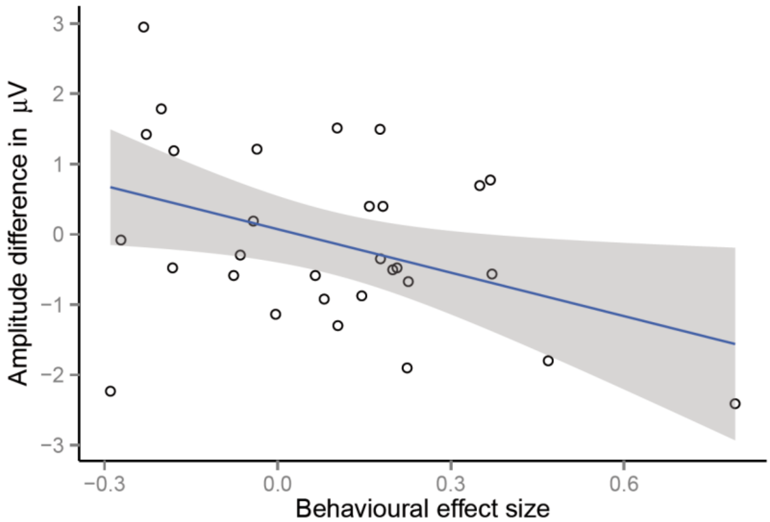

Figure 11: Scatterplot showing amplitude differences in the P1 component between functional knowledge and minimal knowledge conditions on the y-axis, with corresponding detection differences between functional knowledge and minimal knowledge conditions on the x-axis for each participant.

Familiarity Effects

In analysing the effects of familiarity on object detection rates and ERP effects, well-known objects, which contain both semantic information and extensive previous perceptual exposure were contrasted with minimal knowledge objects which are void of any previous perceptual exposure.

Performance. For participants' subjective reports of object detection, there was a main effect of object type, $F(1) = 356.13$, $p < .001$, $dv = .46$, and SOA, $F(1) = 117.79$, $p < .001$, *dv*

= .12. Object type also interacted significantly with SOA, $F(1) = 9.19$, $p = .005$. Follow-up contrasts revealed significant familiarity effects at both the long, $\chi2 = 255.56$, $p < .001$, and short SOAs, $\chi2 = 340.9$ $p < .001$ (see Figure 12).

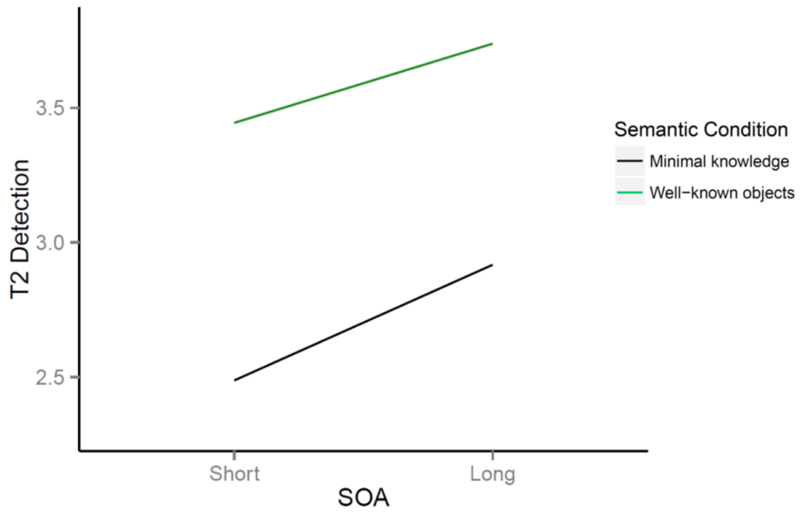

Figure 12: Detection performance for well-known and minimal knowledge objects.

ERPs. Analysis of the P1 component revealed a marginally significant effect of object type, $F(1) = 3.18$, $p = .09$, $dv = .03$, and SOA, $F(1) = 3.09$, $p = .09$, $dv = .03$, as well as a significant interaction between the two factors, $F(1) = 8.80$, $p = .003$, $dv = .08$. Follow-up contrasts revealed a significant familiarity effect at the short SOA only, $\chi2 = 6.24$, $p < .03$ (Long SOA: $\chi2 = 0.89$, $p = .69$) (figures 13A and 13B).

For the N400 component the analysis showed a significant main effect of object type, $F(1) = 6.84$, $p < .01$, $dv = .09$, and a significant main effect of SOA, $F(1) = 15.2$, $p < .001$, $dv = .21$. The interaction between object type and SOA was also significant, $F(1) = 7.88$, $p < .005$, $dv = .1$. Follow-up comparisons revealed a significant N400 at the long SOA, $\chi2 = 10.58$, $p < .002$, whereas at the short SOA, this effect was non-significant, $\chi2 = 3.25$, $p = .14$ (figure 13A and 13B).

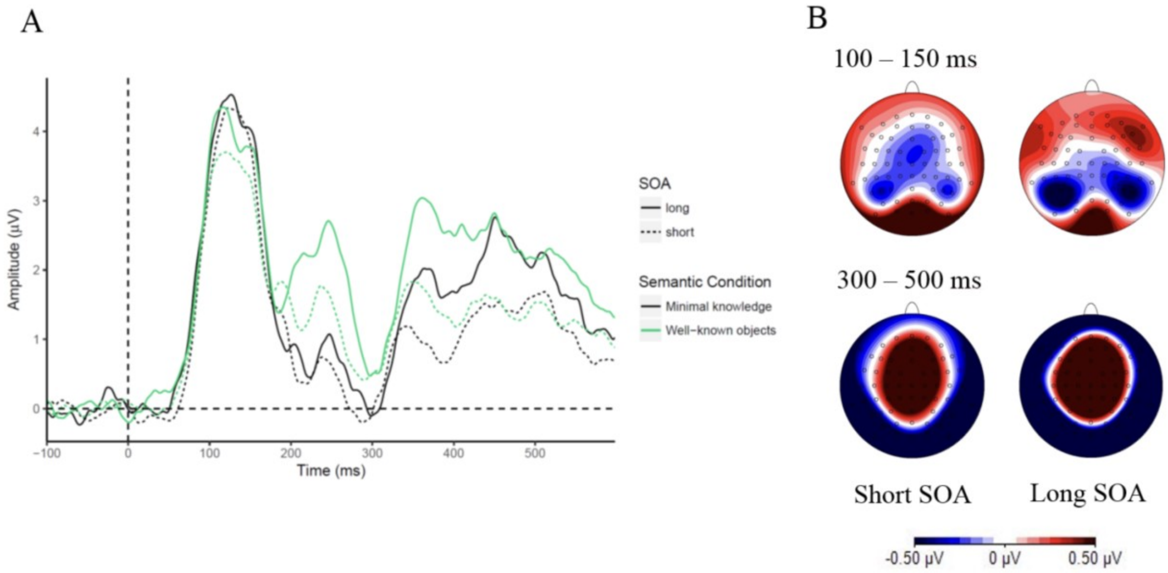

Figure 13: (*A*) Waveforms from the pooled region of interest for the P1 component for well-known objects (Linear derivation of electrodes O1, Oz, O2, PO4, POz, PO4). (*B*) Scalp topographies of event-related potential difference waves between well-known and minimal knowledge objects (well-known minus minimal knowledge), separated for long and short SOAs.

Discussion

The results from experiment three demonstrate that semantic information increases the extent to which objects may be consciously detected. In the attentional blink, at the short SOA, when attention is occupied, or under conditions of less severe perceptual difficulty in the long SOA, semantic information increased the likelihood of visual objects reaching awareness, causing the observer to consciously experience a more complete object percept. This study is the first to demonstrate that semantic modulations of the P1 component can influence the contents of visual awareness. This finding, which was observed across SOAs, was associated with a change in the EEG signal occurring as early as 100ms after object presentation, in the form of a modulation of the P1 component. Previous studies have shown semantically induced P1 modulations for clearly visible objects, but without significant behavioural differences between conditions. Experiment three showed a similar P1 modulation, namely an amplitude reduction, associated with semantic information limited to the long SOA and accompanied by behavioural differences in conscious perception. Crucially, the P1 modulation was correlated with subjective reports of conscious perception, indicating that semantic information – through a modulation of the brain activation generating the P1 – has a functional role in shaping the contents of conscious perception.

An unexpected finding was the interaction between semantic information and SOA on the P1 component, with a reduction at the long SOA, as reported in previous studies (Abdel Rahman & Sommer, 2008; Rabovsky et al. 2012), and an increase at the short SOA. Given that the correlation between conscious detection and the P1 effect was negative, the results from experiment three suggest that it is the reduction in the P1 amplitude that is associated with facilitation of visual analysis and increases in conscious perception. Additionally, objects associated with functional-semantic information elicited an N400 effect at the long SOA only, indicating that it was primarily in this condition that objects were processed at a semantic level. This is interesting in light of prior studies demonstrating preserved N400 amplitudes during the attentional blink (Rolke, Heil, Streb, & Henninghausen, 2001; Vogel, Luck, & Shapiro, 1998). The short SOA represents a condition of increased difficulty as attention is unavailable here, suggesting that semantic information may operate in distinct ways when task difficulty is increased. It seems plausible that the accessibility of semantic information under such conditions may depend on the novelty of this information in the sense that semantic knowledge which is well-established in long-term memory may be unconsciously activated while the activation of newly acquired knowledge may more strongly depend on attention and consciousness. This is an interesting question for future research.

Underlying Mechanisms

The influence of semantic information on conscious object detection observed here could reflect a number of different underlying mechanisms. One possibility is that the effect is due to a direct modulation of visual processing at a pre-attentive stage. Semantic information may alter the visual processes that generate the P1, allowing for more efficient perceptual processing of target objects. This kind of facilitation in visual processing may operate via the recruitment of feedback from higher cortical areas involved in the generation of hypotheses regarding the nature of incoming sensory signals (e.g., Bar et al., 2006). Such a mechanism may recruit functional semantic information associated with objects to generate more efficient predictions regarding the nature of the target, thus reducing early perceptual processing demands. This explanation is in line with the recent surge of studies claiming that higher level cognitive factors can influence early perception (e.g., Lupyan, 2015) and with research showing that information may propagate from visual cortices to frontal and parietal areas within 30ms, and frontal areas may become active within 80ms after stimulus presentation, allowing sufficient time for feed-back to extrastriate areas within the P1 time range (Foxe & Simpson, 2002). Modulations in the P1 time range have also been discussed as potential correlates of visual awareness. The ERPs most often reported in relation to conscious perception are an early posterior negativity at around 200ms (visual awareness negativity, or VAN) and a later positivity in the P3 time window (late positivity, or LP), both of which are enhanced for reported stimuli (Koivisto and Revonsuo, 2010). A large body of studies that contrast reported with unreported conditions also show modulations in the P1 time range, e.g. in visual masking (Del Cul, Baillet, & Dehaene, 2007), change blindness (Pourtois, De Pretto, Hauert, & Vuilleumie, 2006) and during bistable perception (Britz, Landis, & Michel, 2009; Kornmeier & Bach, 2006). Koivisto and Revonsuo (2010) interpret these P1 modulations related to seen stimuli as reflecting the preconscious allocation of attention to perception (cf. discussion below). However, a recent study (Davoodi, Moradi, & Yoonessi, 2015) where attention and consciousness were orthogonally manipulated revealed a similar change in the P1 amplitude for seen trials under inattentive conditions whilst modulations in the P3 range occurred for seen trials in the attentive condition only. Wyart, Dehaene and Tallon-Baudy (2012) found a similar early component reflecting consciousness under conditions where attention was otherwise engaged, reporting a correlate of conscious detection 120ms after stimulus onset.

The semantic effects in the present study may also be mediated by attention. Attention driven by functional object-related semantic information may lead to a selective enhancement of relevant visual features associated with object functions. Given that attention has been shown to operate at early time scales, modulating the P1 component, the time course of semantic modulations reported here is also in line with such an “attention to perception” explanation. Indeed, it is well established that P1 modulations may reflect the attentional tuning of early visual processing, with stimuli that are presented at attended locations being associated with larger amplitudes (Mangun, 1995; Di Russo, Martinez, & Hillyard, 2003). This has been interpreted as reflecting an attentional "gain control", or amplification of incoming sensory signals (Hillyard, Vogel, & Luck, 1998). Similar P1 modulations can also be observed when attention is directed to non-spatial features such as colour (Zhang & Luck, 2008). The P1 may therefore reflect more engagement of attentional resources at an early stage of visual processing, preceding the appearance of the object into conscious awareness, but giving sufficient amplification of the signal to be able to cross the threshold into consciousness.

As discussed above, the relation between consciousness and attention is complex, with various studies demonstrating that they may be two distinct processes and therefore attention is not a prerequisite for conscious experience (e.g. Kentridge, Nijboer, & Heywood, 2008; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008). These studies, in combination with the significant correlation between the size of the P1 effect and subjective measures of conscious detection, suggest that rather than exclusively representing preconscious processes, the semantically induced P1 modulation in the current study is functionally linked to conscious perception. Whether conscious detection is mediated via pre-attentive or early attentive processing, the present findings demonstrate that semantic information has an influence on the emergence of a conscious visual percept, and thus is a determining factor for conscious perception.

Conclusion

The present research is the first to demonstrate that semantic modulations of the P1 component may shape the contents of conscious awareness by penetrating early stages of visual perception as reflected in a modulation of EEG activity as early as 100ms after stimulus presentation. Crucially, behavioural and electrophysiological effects are correlated. The results from experiment three provide support for the hypothesis that visual perception is influenced by higher-level cognitive processes. I suggest that the power of semantic information to shape the contents of conscious awareness reflects an adaptive mechanism in the sense that semantic meaning – in a similar way to prior experience - can serve as a basis for generating predictions regarding the nature of incoming sensory signals, thus affording a processing advantage for stimuli that match the contents of these predictions.

Chapter 3: General Discussion

A central theme of this thesis has been the role that cognition plays in perception. I have outlined how perception involves a multitude of processes. These include the bottom-up construction of sensory signals, the top-down influence of cognitive factors such as language, emotion and experience which can guide the interpretation of sensory signals, and the role of attention in selecting and prioritising sensory information. The aims of this thesis have been to contribute to the expanding literature on the relationship between cognition and perception by investigating the role of long-term memory in shaping perception. I asked to what extent explicit memory, specifically episodic and semantic types, can affect perceptual processes, both directly, and when mediated by attention. In addition, the role that individual differences have to play in the demonstration of cognitive effects over perception was investigated. Finally, the time-course of memory related effects over perception was looked at.

Overall, the empirical part of this thesis provides evidence for a theory-laden view of perception. Experiment one and two demonstrated that episodic memory influences perception via attention, whereas experiment three demonstrates an influence of semantic memory over conscious perception. More specifically, experiment one showed that processes that manipulate the content of episodic memory such as suppression play an influential role in the focusing of our attention to aspects of our environment, by modulating the distractive power of sensory signals. Experiment two replicated the results of experiment one and extended upon them by showing that the observation of long-term memory effects over attention is subject to individual differences. More specifically, experiment two showed that the influence of long-term memories on attentional focusing demonstrated in experiment one varies across individuals and is highly dependent on people's general distractibility as indexed by their proactive control capacity. Finally, experiment three is concerned with the role of semantic memory in conscious perception. Specifically, experiment three showed that associating semantic information to novel objects increases participants ability to consciously detect those objects. Furthermore, this effect was associated with ERP modulations during early stages of stimulus processing. Together, these studies demonstrate novel insights into the relationship between cognition, attention and perception and the findings from each experiment will be discussed in turn.

Discussion of experiments one, two and three.

Experiment one manipulated the strength of long-term memory traces by admonishing participants to selectively retrieve and suppress previously learned words, and found that the selective suppression of episodic memories resulted in reduced interference effects whenever previously suppressed words were presented as distractors while making semantic judgments. Reduced interference effects were measured with the flanker effect, i.e. the extent to which participants are slower to carry out semantic judgements on target words whenever they were flanked by incongruent words. A reduced flanker effect for suppressed distractors indicates that repeated episodic suppression has perceptual consequences for the processing of sensory signals in that it leads to an improvement in people's ability to focus perception on target related information. Furthermore, the finding indicates that memory suppression interacts with attentional processing by facilitating the filtering of sensory signals that are related to the suppressed episodic memories. Finally, considering that people are likely to use a suppression strategy to avoid re-experiencing memories that are related to unpleasant life events, the finding from experiment one can be interpreted as reflecting an adaptive consequence of memory suppression. It would be advantageous to avoid the processing of information in our external environment that is related to the suppressed memory in question, as this may prevent the reactivation and subsequent re-experience of events related to the suppressed memory.

Experiment two addressed a methodological issue that arises when measuring memory related effects on attentional processing, namely, the fact that individual differences in attentional processing style may determine the extent to which these effects can occur. Here, it was reasoned that qualitative variations in processing style would result in differences in the extent to which participants demonstrate flanker congruency effects overall, and that these differences would determine whether memory related effects on attentional processing would be observed. Experiment two showed that variations in proactive control capacity between participants determine the presence of the effects observed in experiment one, where individuals with a higher proactive control capacity showed a lack of congruency effects across all memory conditions and thus, differences related to memory suppression were undetectable for this group. This result shows that memory effects on perception, especially when mediated by attention, may be difficult to capture, and suggest that methodological considerations need to be taken into account when investigating memory effects on perception and attention. Parameters relating to the distractive power of the flanker stimuli need to be adjusted in order to create sufficient amounts of interference, giving suppression-related changes in attentional processing the opportunity to emerge. With this in mind, and given that individuals may not always execute tasks in the same way, gathering secondary indices that can dissociate cognitive processing styles such as working memory capacity may be recommendable when investigating effects of cognition on perception. Experiment two additionally provides a partial replication for the effects shown in experiment one, albeit limited to the group with low PCC.

An interesting question that arises from the findings of experiments one and two is whether memory suppression results in reduced congruency effects because suppressed flanker items exert less of a bottom-up influence on sensory processing, in that the ‘potency’ of the sensory signals arising from suppressed flankers may be reduced, and therefore interfere with target processing to a lesser extent (Eriksen & Eriksen, 1974), or, whether suppression leads to a reduction in congruency effects by influencing processing goals that operate ‘on-line’ during trial execution (Paxton et al., 2007). Such an on-line processing strategy could emerge by participants acquiring the habit of avoiding the processing of No-Think items during No-Think trials, which could lead to a general task-goal of avoiding No-Think items in other circumstances. This task-goal account implies that participants would develop a general tendency to avoid the processing of stimuli related to suppressed memories whenever they appear in the external environment, for example, when presented as flanking stimuli during target processing. Such an on-line explanation for the effects of experiments one and two would suggest that individuals who are better at proactive control – a process that requires the maintenance of a task-goal - in general should be better at preventing the processing of flanking stimuli that are related to suppressed memories. This interpretation cannot unfortunately be evaluated in experiment two, where the potential for any difference in the maintenance of a task goal requiring the avoidance of No-Think stimuli in general is confounded by differences in participants’ ability to filter out the flanker stimuli. Future research could investigate this question by further increasing the distractive power of the flanker stimuli to render them more difficult to filter out for high PCC individuals, or by interfering with the maintenance of task goals by requiring participants to maintain information in working memory during flanker trials. If the memory effect on flanker processing demonstrated in experiments one and two is due to the on-line execution of task goals, then such a disruption of task goals should interference with participants’ ability to avoid the processing of flanking stimuli related to No-Think items. An “on-line” strategy involving the maintenance of the task goal of avoiding the processing of any information that is related to suppressed materials could be reflective of a more general mode of processing of the cognitive system, whereby cognition filters out perceptual experience in an ongoing way. As outlined in the introduction, predictive coding theories state that we are continually using motivations, goals and memories to interpret sensory information. The motivation to filter perception in order to prevent certain stimuli in our environment from reaching awareness would be consistent with such theories.

Experiment three looked at a different aspect of memory - that is, semantic information - and its effect on our conscious perception of stimuli in the environment.

Specifically, experiment three compared participants' performance in detecting novel objects which were associated with semantic information when presented as the second of two targets in the attentional blink task with objects that were associated with an uninformative label. The key finding here was that objects associated with semantic information were consciously detected by participants to an overall greater extent than objects associated with an uninformative label. Furthermore, this finding was accompanied by a modulation of the P1 ERP component 100ms after object presentation, which was correlated with participants' subjectively reported conscious experience. The results of this study indicate that semantic knowledge plays a role in conscious perception and that this effect is tightly linked to early stages of perceptual processing. Chapter one introduced the idea of modularity as proposed by Fodor (1984) and his statement that "… given the same stimulations, two organisms with the same sensory/perceptual psychology will quite generally observe the same things, and hence arrive at the same observational beliefs, however much their theoretical commitments may differ." Thus, according to Fodor, whether or not we have semantic knowledge about the objects we perceive should not have any bearing on our conscious perception of them, because if it did, it could lead to different people arriving at contradicting observational beliefs about the world. The findings from experiment three, thus, provide evidence against this claim and instead support the position that the lines between perception and cognition are more blurred than clear cut, in line with a theory-laden view of perception.

Beyond the observation of memory effects on perception per se, Firestone and Scholl (2016) highlighted that an important distinction to make when investigating effects on perception is between "front-end" and "back-end" stages of processing. An effect on front-end processing would correspond to a direct modulation of the visual processing stages underlying object perception, whereas an effect on back-end processing relates to object recognition, involving memory retrieval processes where incoming sensory signals from the object are compared with stored representations in memory, influencing subsequent decision making regarding the object. An effect on back-end processing, on the other hand would be in direct conflict with an explanation which implicates a role of semantic information in modulating perception.

In the present experiment, the fact that the semantic modulation of conscious perception is associated with processing taking place during the P1 time window suggests that the effect of semantic information on consciousness reflects a "front-end" effect on perception. Furthermore, given the correlation between semantic modulations of the P1 component and semantic modulations of conscious perception found in experiment three, and given the association between the P1 component and visual processing in the literature (Hillyard et al. 1998; Di Russo et al. 1999), it is reasonable to infer that experiment three demonstrates a manipulation of front-end processes.

Together, the experiments presented in chapter two suggest that semantic and episodic long-term memory can modulate processes that underlie perception. These modulations can occur as early as 100ms after stimulus processing and individual differences in cognitive processing style can potentially mask the demonstration of such effect. Taken together, the experiments show that memory can have both direct and indirect effects on perception. The following section will discuss these findings in light of predictive coding theories.

Predictive Coding as an Explanatory Framework

In Chapter one, the predictive coding framework was introduced. Predictive coding provides a theoretical framework to place effects of long-term memory on perceptual processing, and the empirical evidence presented in this thesis can be interpreted in light of this framework. As outlined in greater detail in chapter one, predictive coding refers to the process of continually generating models of the world based upon information from long-term memory, which are then used to predict the nature of incoming sensory information. Chapter one introduced the idea that predictive coding can be viewed as an extreme form of cognitive penetration of perception in that predictions are rife and can influence every stage of stimulus processing, resulting in a stimulus being processed in different ways depending on the prediction made. This section will discuss how the findings from chapter two can be explained in terms of predictive coding.

Predictive coding can readily explain the findings from experiments one and two, where it may be operating in multiple ways during the final flanker task. First, predictive coding may guide the processing of target and flanker stimuli in general when participants are performing the flanker task. Avital-Cohen and Tsal (2016) have demonstrated the role of predictions in the allocation of attention to flanker stimuli. Traditionally, flanker interference has been interpreted as a consequence of the unintentional bottom-up processing of flanking stimuli, or of a "spill-over" of attention from the target to the flanker stimuli (Gaspelin, Ruthruff & Jung, 2014; Eriksen & Eriksen, 1974). However, Avital-Cohen and Tsal (2016) demonstrated that flanker congruency effects arise from active top-down processing of the flanker stimuli. In their letter-digit flanker task, targets could either be the letter "S" or the letter "O" and were flanked by distractors that were ambiguous in their interpretation. Specifically, flankers were composed of a character that could either be interpreted as the digit "5" or the letter "S" or a character that could either be interpreted as the digit "0" or the letter "O". Participants were informed before beginning each block of trials that the targets would always be letter stimuli and they should respond by indicating what letter the target was with a keyboard press, however, they were additionally informed that the flanking stimuli would consist of either letters or digits, a manipulation that was carried out across blocks. Their results showed that flanker congruency effects were dependent on participants' expectations regarding the nature of the upcoming flanking stimuli – whenever participants expected letter flankers then congruency effects emerged, but whenever participants expected digit flankers, the congruency effect was reduced, indicating that flankers only interfered with target processing when they were interpreted as being similar in nature to the target stimuli. The influence of expectations regarding the nature of the flanker stimuli can be interpreted in terms of predictions. Whenever participants are primed to expect letter stimuli, then a prediction is used to interpret sensory signals from the flanker stimuli as letters, which causes them to interfere with target processing due to the fact that the task goal is to monitor for and respond to letter stimuli, whereas whenever participants are led to expect digits as flanking stimuli, then a prediction is used to interpret flanking stimuli as digits, preventing them from interfering with target processing because they map onto responses that are not part of the participants task goals. Similarly, in experiment one, in order to process the target stimuli, participants may use predictions which lead them to interpret word stimuli in terms of their semantic content in order to carry out animacy evaluations. Other stimuli which appear on the screen in the position of the flankers that are also associated with semantic content may also then be processed as they are similar to the target materials. As a result, target and flanker stimuli are then both processed and evaluated to a semantic level due to the fact that they both map onto responses that are part of the participants task goal. Secondly, the reduction in flanker interference effects for No-Think items may reflect the use of predictions to avoid the processing of No-Think stimuli in general. An explanation in terms of predictive coding for the reduction in congruency effects for No-Think trials is similar to the previously discussed idea that participants may develop a "task-goal" of avoiding the processing of information related to No-Think items in general. The requirement to repeatedly avoid the processing of No-Think items during the Think/No-Think phase may lead participants to develop this task-goal which may then be implemented during the flanker task through the use of predictions. These predictions would bias the interpretation of incoming sensory signals "away from" an analysis relating them to previously suppressed No-Think items, and therefore prevent the participant from re-experiencing the suppressed information. Although such an interpretation is at present purely speculative.

An explanation in terms of predictive coding readily provides an explanation for the findings of experiment three. Predictions can be formed on the basis of previous knowledge and prior experience. Experiment three directly manipulated the amount of knowledge that participants possess regarding newly learned objects, and it seems plausible that participants may be able to utilise this knowledge when attempting to detect T2 targets. Semantic information could help to form the predictions made regarding the sort of perceptual features that may appear as part of the T2 stimulus, e.g. predictions about the presence of curved edges could be formed based on the knowledge that an egg incubator requires a circular area in which an egg must fit. Objects that match participants' predictions will be facilitated, thus causing those objects to be consciously perceived to a greater extent than objects which lack features that are consistent with the predictions made. Such a use of predictions may also be implemented online upon the presentation of T2 targets. Chapter one discussed an experiment by Bar and colleagues (2006), who demonstrated that low spatial frequency information is analysed rapidly and can provide a basis for the generation of hypotheses regarding the identity of the object presented by limiting the possible candidate objects which the target may be. In a similar way, the rapid extraction of low spatial frequency information for T2 objects may be utilised along with the learned semantic descriptions in order to narrow down the set of possible predictions that can be made in order to perceive T2 targets completely.

The finding of a semantic modulation of the P1 component in experiment three, and its link to participants' conscious perception of T2 objects is difficult to reconcile with previous findings indicating that conscious perception of stimuli is reflected in neural modulations beginning around 200ms after stimulus presentation (Koivisto & Revonsuo, 2010). However, an investigation by Melloni and colleagues into the relationship between stimulus expectations and the timing of ERP correlates of conscious perception offers a potential explanation for this result (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011). Melloni and colleagues (2011) demonstrated that the conscious perception of letter stimuli was associated with a modulation in the P3 time range whenever participants did not have the opportunity to develop expectations about the identity of the target stimulus. However, whenever target expectations were induced, participants showed improved conscious detection of target stimuli – a finding that provides further evidence for the role of predictions in facilitating conscious perception. More importantly, however, expectations shifted the timing of ERPs associated with the conscious perception of targets, with modulations of the N1 and P2 components occurring during conscious target perception. Thus, predictions can shorten the latency of neuronal modulations associated with conscious perception. Similarly, expectations based upon semantic information which are implemented via the use of predictions may be the cause of the early ERP modulations associated with conscious perception reported in experiment three.

The role of predictions in the semantic modulation of the P1 component is also supported by the finding that the correlation between the magnitude of semantic modulations of the P1 component and the magnitude of semantic modulations of conscious perception was negative, which indicates that more negative modulations of the P1 component were accompanied by increased conscious perception. In the study by Melloni and colleagues (2011), expectations regarding target stimuli resulted in amplitude reductions of the N1 and P2 components. Such an amplitude reduction is consistent with predictive coding, as it has been shown that processing of prediction error is associated with increases in neural activity. For example, during auditory processing, unpredicted stimuli evoke larger N1 amplitudes than predicted stimuli (Garrido et al., 2009). Thus, the facilitation of perceptual processing that occurs whenever sensory evidence is compatible with top-down predictions is reflected in reduced neural activity, and the association of P1 amplitude reductions and conscious perception in experiment three are in line with this hypothesis.

Predictive coding and the relation between attention and perception.

In addition to providing a framework for interpreting memory effects on perception, predictive coding theories suggest that a re-evaluation of the distinction between attention and perception is required (Clark, 2013; 2016; Lupyan, 2015). Traditional views of attention view this relationship in terms of the spotlight metaphor - the idea that attention prioritises specific parts of the visual field for further perceptual processing (Müller, Malinowski, Gruber, & Hillyard, 2003). From this perspective, our cognitive system is limited in its ability to process the overwhelming amount of sensory input, and attention operates by changing the input to perception by sampling smaller sections of the environment. However, after attention has prioritised specific parts of the visual field for processing, perceptual processing takes place in a theory-neutral manner. Predictive coding challenges this view. According to predictive coding theories, most of the perceptual work, which has been traditionally thought to be carried out by reconstructing sensory evidence alone, is in fact accounted for by predictions which accentuate the processing of elements in our environment that are consistent with them. Any disjoint between the representation we create of the world in our predictions and the way the world actually is, is represented in the error term. Clark (2016) has argued that the role of attention in perception is in balancing the relative contribution of predictions, and incoming sensory signals. Given a situation of unreliable perceptual input, for example, when viewing a blurry image, attention will prioritise the use of the predictions in guiding perception, whereas in a situation of high reliability regarding the sensory signal, more weight may be placed on sensory information. Thus, attention becomes intimately linked with the modulation of perception itself. Predictions transform the processing of sensory information and their deployment and relative influence are modulated by attention. Such an interpretation of the role of attention over perception conflicts with Firestone and Scholl's (2016) view of attentional changes as reflecting simple shifts in sensory input, and renders their criticism of instances of cognitive penetration of perception as reflecting attentional modulations moot. From a predictive coding perspective, attention is viewed as a mechanism which manages the relative contributions of top-down predictions and bottom-up signals and exerts an influence over every stage of the processing hierarchy. Clark (2013, 2016) specifies that attention can alter the influence that one neural area or specific process has on other neural areas or processes. Such a proliferation of neural tuning across the visual processing hierarchy results in a highly adaptive cognitive architecture which can shift in a flexible manner under the influence of attention. If attention can alter the flow of processing across all stages, then its effect is much deeper than the peripheral conceptualisation put forward by Firestone and Scholl (2016). In fact, from this perspective, the boundary between "peripheral" shifts of attention and pure perception is so difficult to determine that its utility as a construct becomes questionable; attention becomes so intertwined with perception that there is little room left to define where pure perception without the influence of attention occurs. In line with this perspective, a handful of studies suggest that rather than simply changing the sensory input to perception, attention may actually alter the appearance of stimuli, making people perceive them in a phenomenally different way. For example, Carrasco, Ling and Read (2004) showed that stimuli that appeared in a spatially cued location were perceived as having increased stimulus contrast, indicating that attention can intensify the sensory impression of stimuli, and thus alter the phenomenal experience of a percept. Firestone and Scholl's (2016) criticism relies on an interpretation of attention as being a process that is separable from perception, however, from the perspective of predictive coding, attention is intricately entangled with perceptual processing.

Conclusion

This thesis has studied the influence of information from long-term memory on attention and perception. With a focus on the relation between cognition, attention and perception, demonstrations of the pervasiveness of long-term memory influences on perception, both directly and via attentional processing have been demonstrated. The predictive coding framework provides the explanatory power to situate these results and these findings advance empirical research into the relationship between cognition, attention and perception.

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