
**Investigating the relationship between visual working memory and visual
awareness: Evidence from TMS and OSM**

By

Daniéll Steinberg

BA-Psych(Hons)

An empirical thesis in accordance with the requirements of the degree

MASTERS OF RESEARCH



MACQUARIE
University

Perception in Action Research Centre (PARC)

Department of Cognitive Science

MACQUARIE UNIVERSITY

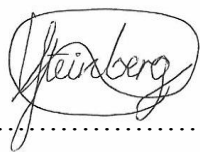
Supervised by Associate Professor Matthew Finkbeiner

Abstract

Human vision seems so fast and effortless that we often don't consider the processes that take place before we have the perceptual experience of "seeing". However, by the time a stimulus first emerges into consciousness it has already been coded at various stages within the visual system. Recent evidence from patients with visual extinction has revealed that the active maintenance of an item in working memory facilitated enhanced awareness of targets that matched a previously viewed memory cue (Soto & Humphreys, 2006). Here, we asked whether the contents of working memory could facilitate efficient visual perception in normal subjects by triggering top-down signals that bias the visual system in favour of a preactivated object representation. Specifically, we hypothesised that target stimuli that matched a previously presented memory cue would be less susceptible to visual masking. In Experiments 1 and 2, we used transcranial magnetic stimulation (TMS) to the occipital pole as a method to degrade visual perception. However, we were unable to adequately mask targets and we instead provide a detailed discussion of the difficulties in localising area V1 using external anatomical landmarks. In Experiment 3, we used object substitution masking (OSM) to reduce awareness of target stimuli. In a typical OSM paradigm, visual masking occurs when a four-dot mask persists on the screen after target offset, whereas target detection is unimpaired by the simultaneous offset of the target and mask (Enns & Di Lollo, 1997). As predicted, we observed a significant main effect of Mask Offset. Detection sensitivity was higher on simultaneous-offset trials, relative to delayed-offset trials. In contrast, the interaction between Memory Match and Mask Offset was not significant. To overcome the limitations of inferential statistics in interpreting null findings, we implemented Bayesian statistics and obtained substantial evidence in favour of the null hypothesis. We conclude that merely holding something in working memory is not sufficient to enhance awareness of degraded visual objects.

Author's Declaration

I declare that that the work in this thesis has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. This project was approved by the Human Research Ethics Committee of Macquarie University (reference numbers = 5201300060 and 5201400585).

SIGNATURE:


DATE: 5th October 2016

Acknowledgments

Thank you to my supervisor, Matthew Finkbeiner, for his help and guidance throughout this year.

I would also like to thank my parents, Cheryse and Arnold, and fiancé, Ben. This is the second thesis that I have put you through and I couldn't have done it without you. May the next one be the last one...

Table of Contents

Abstract.....	i
Author's Declaration.....	ii
Acknowledgments.....	iii
Table of Contents	iv
List of Figures	vii
1.1 Visual Perception.....	1
1.2 Models of Visual Perception.....	2
1.2.1 Feedforward Accounts	2
1.2.2 Limitations of Feedforward Models	5
1.2.3 Reentrant Models	7
1.3 Top-down Effects and Visual Awareness	8
1.3.1 Investigating Top-Down Effects using Neuroimaging Techniques	13
1.3.2 Investigating Top-Down Effects using Neuropsychological Patients.....	14
1.3.3 Top-Down Effects from Working Memory in Healthy Populations.....	16
2. The Present Study	19
2.1 Transcranial Magnetic Stimulation (TMS).....	19
2.1.1 TMS to the Occipital Pole Disrupts Visual Awareness	21
2.2 Aims and Hypotheses	22
3. Experiment 1.....	24
3.1 Methods	24
3.1.1 Design	24
3.1.2 Participants	24
3.1.3 TMS Parameters.....	25
3.1.4 Apparatus.....	26
3.1.5 Stimuli and Procedure	26
3.2 Experiment 1 Results	30
3.2.1 Data Analysis	30
3.2.2 Results.....	30
3.3 Interim discussion for Experiment 1	34
4. Experiment 2.....	37

4.1	Methods	37
4.1.1	Design	38
4.1.2	Participants	39
4.1.3	TMS Parameters.....	39
4.1.4	Apparatus.....	40
4.1.5	Stimuli and Procedure	40
4.2	Experiment 2 Results	42
4.2.1	Data Analysis	42
4.2.2	Results.....	42
4.3	Interim discussion for Experiment 2	46
5.	Experiment 3.....	48
5.1	Masking by Object Substitution.....	48
5.1.2	The mechanisms of OSM	50
5.1.3	OSM and Working Memory.....	52
5.1.4	OSM and Signal Detection Tasks.....	53
5.3	Aims and Hypotheses	55
5.3	Methods	56
5.3.1	Design	56
5.3.2	Participants	56
5.3.3	Apparatus, Stimuli, and Procedure	57
5.4.	Experiment 3 Results	60
5.4.1	Data Analysis	60
5.4.2	Results.....	61
5.4.3	Post Hoc Examination of Non-Significant Results	64
5.5	Interim Discussion for Experiment 3.....	65
5.5.1	Discussion	65
6.	General Discussion	67
6.1	Findings	68
6.2	Limitations and Future Directions.....	72
6.3	Conclusion.....	75
References		77
Appendix A		89

Section 1: Ethics Reference Number 5201300060	89
Section 2: Ethics Reference Number 5201400585	90
Appendix B.....	92
Section 1: Participant Consent Form	92
Section 2: TMS Screener (Keel et al., 2000).....	98

List of Figures

Figure 1. Marr’s object-centred model	4
Figure 2. Bar’s top-down facilitation model.....	11
Figure 3. A schematic diagram of a capacitor discharge magnetic stimulator	19
Figure 4. Visual trial structure for Experiment 1	27
Figure 5. Scatterplot of the correlation between recall and Memory Match	30
Figure 6. Mean accuracy values by Memory Match and SOA	31
Figure 7. Mean accuracy by memory cue present or absent.....	34
Figure 8. Visual trial structure for Experiment 2	39
Figure 9. Scatterplot of the correlation between recall and Memory Match	42
Figure 10. Mean accuracy values by Memory Match and SOA	43
Figure 11. Visual display sequence of OSM paradigm	47
Figure 12. Visual trial structure for Experiment 3.....	56
Figure 13. Scatterplot of the correlation between recall and Memory Match	59
Figure 14. Values of d' separated by Mask Offset	60

Investigating the relationship between visual working memory and visual awareness:

Evidence from TMS and OSM

1.1 Visual Perception

Of all the sensory processes achieved within the nervous system, visual perception is one of the most extraordinary feats of the human brain. This is because no other sense dominates our cognition or behaviour with quite the same authority; after all, they do say that seeing is believing. We rarely question the plausibility of the perceptual world that our visual system constructs for us, even though what we are actually perceiving is our brain's "best guess" interpretation of fairly ambiguous visual input. In fact, although everyday vision appears to be instantaneous, by the time a stimulus first emerges into consciousness it has already been processed across several levels within the visual system.

The ways in which the visual system converts the flat retinal images supplied by our eyes into a conscious percept remains one of the greatest mysteries currently perplexing vision scientists. Historically, visual processing has been described with respect to feedforward models, with processing becoming increasingly more complex and specific as information is projected towards higher-order visual cortex (Hubel & Wiesel, 1968a). Visual awareness is said to occur only once information has been recoded into a global representation at the highest level of processing (Marr, 1982). In contrast, contemporary vision scientists now recognise that feedforward models form only part of the complex puzzle that is visual processing. Specifically, in addition to an ascending, unidirectional sweep of activity, reentrant processes have been identified as a necessary prerequisite of visual consciousness (Di Lollo, Enns & Rensink, 2000; Lamme, 2001; Bar, 2007).

With the rise of reentrant models there has also been developing interest in top-down effects on visual perception. The term “top-down” refers to feedback effects that are driven not by the properties of the stimuli themselves, but by higher-order cognitive processes (Desimone & Duncan, 1995). The present research, for example, addressed whether the contents of working memory can facilitate efficient visual perception by triggering top-down signals that bias the visual system in favour of a preactivated object representation. Here, visual awareness is defined as the perceptual experience of “seeing” or being conscious of those items that fall within the visual field (Tong, 2003).

1.2 Models of Visual Perception

1.2.1 Feedforward Accounts

Feedforward accounts of visual perception claim that neural activity within the visual system travels in one direction along ascending pathways towards higher cortical areas. Visual input enters the eye via the retina and passes the lateral geniculate nucleus (LGN, Kennedy & Bullier, 1985) on the way to areas V1 and V2 (Felleman & Van Essen, 1991). Activation spreads from these early visual areas to V4, V5/MT, and inferotemporal cortex (Tanaka, 1996). A much-cited computational account based on this feedforward scheme is that proposed by David Marr in his book *Vision* (1982). Marr assumed that visual processing occurred along a series of hierarchically organised descriptions, beginning with the extraction of low-level features and concluding with the construction of a global object representation (see Figure 1). Marr believed that the building of this three-dimensional (3D) representation occurred over three consecutive stages. The first stage was comprised of building a two-dimensional (2D) primal sketch that contained information about lines and edges; the second stage involved a $2\frac{1}{2}$ D sketch, which described orientation, depth, and the distance of visible

surfaces; and the last stage involved the construction of a global 3D model. Marr suggested that this third stage of processing provided the visual system with all the necessary information to generate a fully formed percept that was available to conscious experience (Marr, 1982). Although Marr did acknowledge the potential for top-down processes to influence visual awareness, and, in some cases to be “necessary” for perception to occur (pp. 100-101), his theory focused on bottom-up visual processing, with top-down influences being of secondary importance (Mather, 2015).

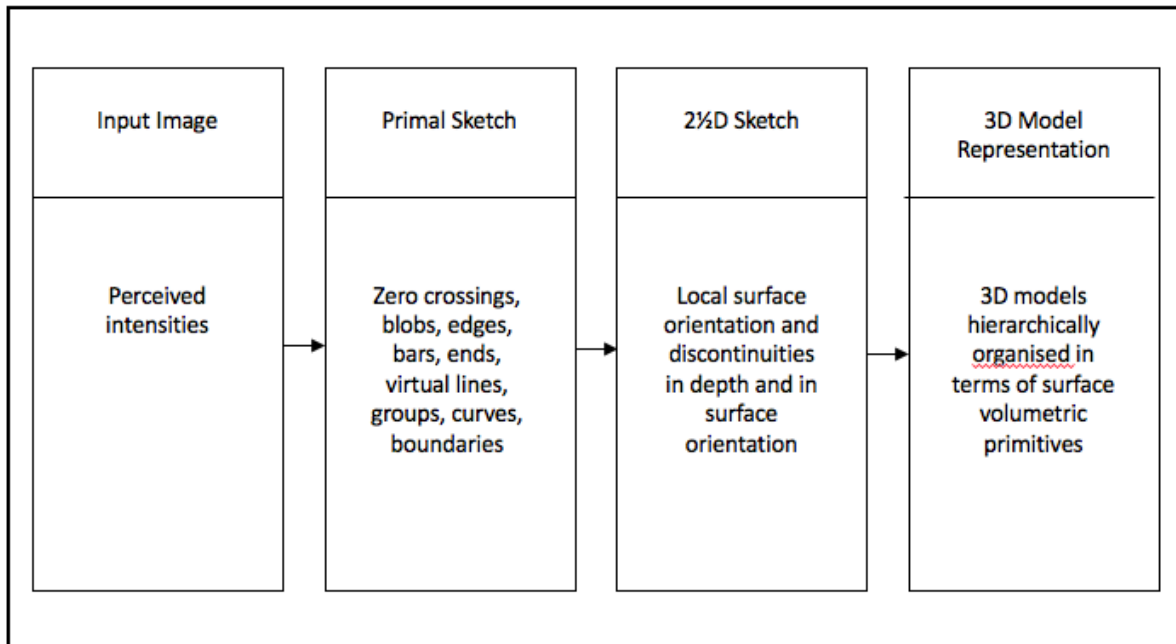


Figure 1. An illustration of Marr's original account of view-invariant object recognition.

According to the model, the building of the 3D object representation required for recognition occurs over three consecutive stages. The first stage involves building a 2D primal sketch that contains information about lines and edges; the second stage involves a 2½D sketch describing local surface features; and the last stage involves the formation of a global view-invariant 3D model. Modified from "Vision: A computational investigation into the human representation and processing of visual information," by D. Marr, 1982. Copyright [1982] by Freeman and Company.

1.2.2 Limitations of Feedforward Models

One of the major limitations of feedforward models is that they are unable to account for the wealth of data demonstrating a dense network of descending projections that feedback from higher-order to lower-level areas within visual cortex (Van Essen & Maunsell, 1983; Felleman & Van Essen, 1991; Bullier, 2001; Hupé, James, Girard, Payne & Bullier, 2001; Sporns & Zwi, 2004). For example, early investigations of the macaque visual system (which is often used as a model for the human visual system, Hinds et al., 2008) revealed a dense network of feedback projections from area V5 to V1 (Woolsey, 1981; Maunsell & Van Essen, 1983). Similar results were reported by Shipp and Zeki (1989a; 1989b), who traced ascending and descending neural pathways between V1 and V5. These researchers showed that descending projections did not simply complete a feedback loop (i.e., from the source neuron to a higher neuron and back), but were widely distributed throughout various cortical layers.

The finding that descending projections are widely distributed throughout macaque visual cortex has led neuroscientists to infer that feedback pathways are also present in the human visual system. This inference has been strengthened by research within human subjects that showed that feedback signals play a major role in conscious awareness. For example, Silvanto, Lavie and Walsh (2005) administered pulses of transcranial magnetic stimulation over V1 and V5 at various durations relative to stimulus offset during a motion-detection task. They observed that magnetic stimulation administered to V1 at both 40–60 ms and 80–100 ms after stimulus offset disrupted the detection of a moving target, whereas the critical period of disruption for V5 occurred later between 60–80 ms. Silvanto and colleagues concluded that this pattern of results reflected the early feedforward sweep of visual information from V1 to V5 at 40–60 ms and the later back projection of activity from V5 to V1 at 80–100 ms post target onset.

In addition to the evidence above, which highlights the existence of feedback fibres within the visual system, another convincing limitation of feedforward accounts is the problem that is caused by unidirectional communication in the context of receptive field properties. To illustrate, consider Hubel and Wiesel's (1962; 1968a; 1968b) investigations of receptive field properties in the feline striate and extrastriate cortex. They demonstrated that the orientation tuning of a simple cell in V1 could emerge from the converging inputs from neurons in LGN. Simple cells with a common optimal tuning could themselves then provide the input that determined the tuning of complex cells. In the same way, the properties of hypercomplex cells could be produced from the convergence of inputs from complex cells. Hubel and Wiesel found that the size and tuning of a cell's receptive field became progressively larger and more specific as they travelled higher up within the visual system (Hubel & Wiesel, 1968). A serial scheme of this nature, however, poses a major problem for the visual system. This is because a neuron located in an orientation column in V1 can process low-level features of a stimulus, including spatial location, but cannot encode global details about the overall configuration of the object. In contrast, a neuron located higher up in the system can encode information about global stimulus configuration, but cannot indicate the precise spatial location of the external stimulus due to its large receptive field.

If conscious vision were truly achieved by a unidirectional sweep of activity, then what we might actually see in a visual scene are free-floating, low-grain shapes that are not pinned down to any spatial location. If we wanted to determine the precise spatial position of a specific object, then we would need to access information from higher-order neurons and would most likely lose access to information about the item's overall shape. To overcome this issue, Di Lollo, Enns and Rensink (2000) suggest that feedforward accounts of visual perception require revision in the form of an information exchange between various levels

within the visual system. Specifically, they propose that reentrant processes provide the necessary bridge between hierarchical levels.

1.2.3 Reentrant Models

Evidence supporting the existence of feedback pathways from higher to lower cortical regions has prompted the revision of feedforward models to recognise the role of reentrant processes in conscious perception. Reentrant models describe a framework in which visual input is directed through a feedback loop that involves both ascending and descending pathways (Bar, 2003; Di Lollo, 2014). Specifically, incoming visual input from the retina is propagated from early visual cortex towards higher visual regions via ascending pathways. Along this feedforward sweep of neural transmission, the representational code of the stimulus increases in complexity and specificity as the cell properties become progressively more refined; specifically, receptive field size increases and neuronal tuning becomes selective for more complex features of objects as we move higher up within the visual hierarchy (Hubel & Wiesel, 1968). This ascending wave of processing provides the visual system with sufficient information to generate “perceptual hypotheses” regarding the likely nature of the incoming sensory stimulation (Trapp & Bar, 2015).

However, because the initial representation may be incomplete, ill-defined, or may even have given rise to the generation of various perceptual alternatives, the visual system requires verification of the original sensory input (Bar, 2007). Perceptual ambiguity of this kind can be resolved via descending pathways by comparing higher-order hypotheses with the initial pattern of neural activity within early visual areas. If a match (or correlation) is found between descending codes and low-level activity, then this provides the visual system with confirmation that the generated perceptual hypothesis is a plausible interpretation of the

incoming sensory stimulation. If no match occurs, the visual system discards its initial hypothesis about the identity of the stimulus and generates a new tentative representation (Di Lollo, Enns & Rensink, 2002). Processing then continues as if for an entirely new stimulus until verification can be achieved and a unified percept can emerge into consciousness. In this way, feedforward and reentrant models of visual perception are not mutually exclusive ideas, but, rather, are complementary approaches to visual perception.

1.3 Top-down Effects and Visual Awareness

The discussion of reentrant models above demonstrates the bidirectional flow of information within the visual system, such that visual perception is facilitated by both bottom-up and top-down processes. With the rise of reentrant accounts of visual processing there has also been a developing interest in the role of top-down effects on visual perception. The term “top-down” refers to those higher-order cognitive processes that facilitate the perception of low-level stimulus features via descending feedback signals (Desimone & Duncan, 1995). An illustration of a recent model of top-down facilitation can be seen in Figure 2. This model claims that a coarse representation of incoming visual input is rapidly projected from early visual cortex to a region in the frontal cortices known as the orbitofrontal cortex (OFC, Bar, 2007). This coarse representation is comprised of low spatial frequency (LSF) information, which provides the visual system with information about the overall configuration of items that fall within the visual field. In using information from this global level analysis of sensory input, the visual system generates a minimal set of perceptual inferences regarding the likely identity of the incoming stimuli. At the same time, visual input from early visual areas is propagated along the relatively slower ventral visual stream towards inferotemporal (IT) cortex. Perceptual inferences are then fed back from OFC to IT and are integrated with the

initial pattern of low-level visual activity to facilitate object recognition. In this way, Bar and colleagues claim that the brain is proactively involved in generating “predictions” regarding the nature of incoming sensory input, with these predictions prompting the widespread dissemination of feedback signals throughout visual cortex (Bar, 2007).

Recent extensions of the top-down facilitation model propose that in addition to the generation of perceptual hypotheses, the rapid propagation of low-level visual input to OFC allows for the production of *global context signals* (Trapp & Bar, 2015). Global context signals function to further constrain the space of perceptual hypotheses that are generated in response to visual input and can also be used to “preactivate” object representations that are consistent with (or expected to appear within) a specific context frame (Bar & Aminoff, 2003; Aminoff, Gronau & Bar, 2007). A kitchen setting, for example, typically contains objects like fridges, sinks, and toasters. Viewing a kitchen scene, in combination with prior knowledge about the scene’s typical content, rapidly activates or sensitises the representations of contextually related objects (e.g., fridge, dishwasher, kettle etc.). This means that when a contextually-related item appears within the visual scene (e.g., a kettle), a match between low-level visual input and perceptual hypotheses can be achieved more efficiently.

Another way to extend the top-down facilitation account is to compare the model’s assumptions against similar approaches that exist within the broader field of vision science. In many ways, the top-down facilitation model relies on a similar set of concepts to predictive coding accounts, which claim that all sensory systems learn statistical regularities from the natural world and use this information to form predictions about upcoming events (Summerfield & Egner, 2009; Huang & Rao, 2011). For instance, predictive coding accounts conceptualise neural activity within early visual cortex as reflecting the congruence between top-down predictions and incoming input, rather than being driven entirely by the low-level

properties of the stimulus itself (Rauss, Shwartz & Pourtois, 2011). In this way, both the top-down facilitation model and predictive coding theories outline a process in which the visual system is actively searching for a match between internally generated predictions (or perceptual hypotheses) and external sensory stimulation (Rauss & Pourtois, 2013).

Furthermore, both of these approaches aim to describe how the visual system maintains efficiency in conscious vision. As previously mentioned, Bar and colleagues claim that global context signals serve to streamline the process of perceptual verification by constraining the generation of perceptual hypotheses to a specific context frame. In a similar way, predictive coding accounts assume that the visual system achieves efficient coding of perceptual input through learned contingencies regarding the predictability of the visual world, which can then be used to make subsequent predictions about upcoming sensory input (Rauss et al., 2011).

These extended accounts of top-down facilitation raise certain theoretical and methodological questions that are yet to be addressed. For instance, it is claimed that global context signals are generated *in response* to incoming visual input; however, is it possible that contextually-based feedback might also be triggered *before* visual input even arrives?

Evidence for this idea comes from a functional magnetic resonance imaging (fMRI) investigation that used neural classifiers to show that simply imagining visual objects is sufficient to trigger top-down mechanisms (Stokes, Thompson, Cusack & Duncan, 2009).

Furthermore, Soto and Humphreys (2006) have demonstrated that the active maintenance of a representation in working memory significantly enhanced awareness for matching targets in patients with visual extinction. These results suggest that global context signals in OFC might be triggered by the active maintenance of items held in mind. If so, it might be possible to set up perceptual hypotheses (or templates) based on the contents of visual working memory prior to the arrival of visual input. Any visual input that enters the visual system after this working memory template has been generated will therefore be compared to a preactivated

representation of the item held in mind. A match between low-level visual input and higher-order perceptual templates can therefore occur more efficiently, and, potentially, without the need for distributed reentrant processes.

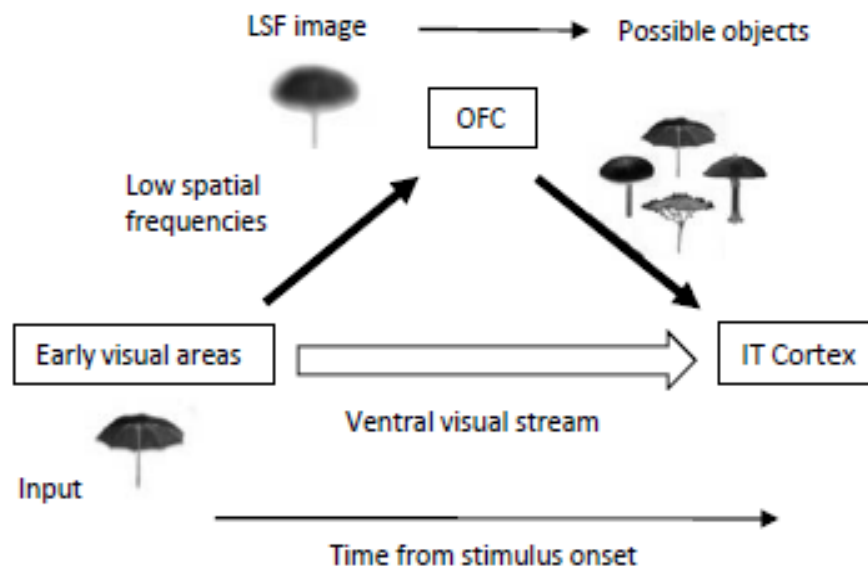


Figure 2. An illustration of the top-down facilitation model proposed by Bar and colleagues. LSF information is rapidly projected from early visual cortex to OFC, which is sufficient for the generation of perceptual inferences. At the same time, low-level visual information is propagated from early visual cortex to IT cortex along the slower ventral visual stream. Perceptual inferences generated by OFC are projected along descending pathways to IT, where they are integrated with incoming visual input. Modified from “The proactive brain: Using analogies and associations to generate predictions,” by M. Bar, 2007, *TRENDS in cognitive Sciences*, 11(7), 282. Copyright [2007] by Elsevier LTD.

1.3.1 Investigating Top-Down Effects using Neuroimaging Techniques

Top-down effects on visual perception have been investigated using neuroimaging techniques, with researchers placing a specific focus on addressing **where** in visual cortex feedback signals originate and **when** they are triggered in relation to visual input? A tool with adequate spatial resolution to locate the primary area involved in generating top-down feedback is fMRI. For instance, based on evidence suggesting that OFC generates predictions about upcoming events (Carlsson et al., 2000), in combination with anatomical data showing strong connections between OFC and IT cortex (Cavada et al., 2001), Bar et al. (2001) identified OFC and IT cortex as the regions of interest during an object recognition task. Whilst in the scanner, participants responded to briefly presented items by pressing one of four buttons that indicated their level of knowledge about the target stimulus (i.e., press “1” if you had no knowledge of the item; “2” if you noticed the presentation of the image, but nothing else; “3” if you could identify the general shape of image; and “4” if you successfully recognised the image). Differential activity in blood oxygen level dependent (BOLD) signals was observed for recognised trials compared to unrecognised trials in object recognition areas of IT cortex; which is not surprising given the surplus of evidence pinpointing these areas as being pertinent to object recognition (Kanwisher, McDermott & Chun, 1997; Malach, et al., 1995). The more interesting result, however, was the finding that OFC showed exponentially increasing activation according to recognition success (i.e., a transition from ratings of 1 to 4). This finding provided the first convincing demonstration of OFC involvement in top-down facilitation of conscious vision.

Whilst fMRI provided Bar and colleagues with the appropriate spatial resolution to comment on **where** top-down facilitation was triggered, this technique does not have adequate temporal resolution to observe the sequential progression of object recognition in visual cortex. However, if the OFC is in fact involved in top-down facilitation of visual

perception, then activity in this region should be observed *earlier* than in object recognition areas of IT cortex. This is because top-down facilitation of bottom-up perception implies that predictions generated in higher-order areas would have to be triggered *before* the process of visual perception is complete. This prediction was addressed in a subsequent investigation that employed a combination of imaging techniques to bolster temporal resolution; specifically, Bar et al. (2006) utilised magnetoencephalography (MEG) and fMRI in combination with the same object-recognition task. Results revealed that neural activation in OFC occurred 50 ms earlier than activation of the object recognition areas of IT cortex. This was important as it demonstrated that a region typically considered to be “higher-order” within the visual hierarchy could be activated before lower-level visual areas. Moreover, a time-frequency, trial-by-trial covariance analysis of the MEG data showed synchronised activity between occipital visual cortex and OFC at a relatively early stage of visual processing (i.e., approximately 80 ms after stimulus onset) and a strong synchronised coupling of OFC and temporal regions at a relatively later stage (i.e., around 130 ms after the target appeared on the screen). These findings were interpreted to reflect the early propagation of information along ascending projections from occipital visual cortex to OFC, with visual object recognition being achieved only after IT cortex received descending feedback from the frontal cortices.

1.3.2 Investigating Top-Down Effects using Neuropsychological Patients

A complementary but different approach to neuroimaging studies in the investigation of top-down effects is the use of neuropsychological populations. By directly studying the cognitive effects of brain damage, cognitive neuropsychologists can make inferences about normal models of cognitive functioning. For instance, when it comes to visual awareness, the

most appropriate neuropsychological population for investigation is that of patients with visuospatial neglect or extinction. This is because patients with visual extinction show reduced awareness for stimuli presented on the side of space that is opposite (or contralateral) to the brain lesion when competing stimuli are presented to the same (or ipsilateral) side of space (Karnath, 1988). Importantly, there is evidence to suggest that contralesional stimuli are processed to some degree, even if these items do not gain access to conscious awareness (Riddoch, Humphreys, Edwards, Baker & Wilson, 2003). For example, Soto and Humphreys (2006) examined whether top-down mechanisms engaged during a working memory task could enhance awareness in patients with visual extinction due to parietal lesions. At the start of each trial, patients were asked to hold in mind a memory cue by forming a mental image of it. Briefly presented target items were then displayed on the left, right, or both sides of the screen and patients were required to report the colour and shape of the targets. On approximately half of the trials, one of the target items was a direct match to the memory cue. A memory probe was included on 20 percent of trials to ensure that the patient actively engaged working memory throughout the experiment.

Clear extinction was observed on trials in which the memory cue did not match the target, as there was poor report of the contralesional target. In contrast, there was a significant reduction in extinction on trials in which the contralesional target item matched the memory cue, with a significant increase in the proportion of correctly identified targets. The same results were not observed in subsequent experiments that presented subjects with a verbal memory cue or simply required them to view a prime shape without committing it to memory. Together, these results suggest that active maintenance of a memory cue in working memory facilitated enhanced visual awareness for subsequent targets that were a direct match to the maintained representation. With respect to normal models of cognitive functioning, these findings imply that visual items that match the contents of working memory are given

privileged access to conscious awareness. Soto and Humphreys argue that this is because the active maintenance of an item in working memory facilitates the generation of top-down signals that bias the visual system in favour of a preactivated representation. Visual awareness is therefore achieved more efficiently, as the visual system is already “primed” or in some way expecting the arrival of these objects.

1.3.3 Top-Down Effects from Working Memory in Healthy Populations

Whilst it is true that cognitive neuropsychologists aim to make inferences about normal processing through the investigation of the cognitive effects of brain damage, the flow of knowledge also travels in the opposite direction. To provide corroborating evidence to theories of cognition developed through the lens of patient data, it is necessary to demonstrate the workings of these models in a normally functioning population. Indeed, there is substantial evidence to suggest that top-down feedback from object representations in working memory can bias visual processing in healthy participants in favour of items that match preactivated object representations. For example, Soto, Heinke, Humphreys and Blanco (2005) flashed a memory item at fixation for three brief presentations of 35 ms each. Participants were then presented with a search array containing between two or eight objects that each contained a line inside of it. The lines were all vertical, except for one tilted line (i.e., the target). The target line could appear inside the memory item (i.e., valid trial), in a novel item when the memory item was presented in the search array (i.e., invalid trial), or in a novel item when the memory item was not presented in the search array (i.e., neutral trial). The task was to indicate as quickly as possible whether the target line was tilted towards the left or right. Memory for the initial memory item was then probed by asking participants to indicate whether a subsequent object was identical to the memory item or not.

Results revealed that participants were significantly faster to identify the orientation of the target on valid trials, relative to neutral trials; they were also significantly slower on invalid trials, relative to neutral trials. This effect has since been replicated several times (Soto, Humphreys & Heinke, 2006; Han & Kim, 2009; Kumar, Soto & Humphreys, 2013; Pan, Lin, Zhao & Soto, 2013). This finding suggests that the active maintenance of an item in working memory can elicit a bias to deploy attention, even in instances in which this is detrimental to successful task performance. Furthermore, the fact that the same results were not demonstrated when participants were not required to actively maintain an item in mind eliminated the possibility that these effects were driven by bottom-up perceptual priming from a previously viewed stimulus.

Importantly, the research above provides evidence supporting enhanced *attentional selection* of shapes that match items held in mind; however, it is unable to test the hypothesis that items held in working memory have privileged access to conscious *awareness*. This is because the design used to test healthy participants did not incorporate any form of visual masking, such that all target and distractor items were fully available to conscious perception. In contrast, the study investigating patients with visual extinction clearly tapped into mechanisms of awareness, which may or may not have been the same mechanisms as those in the attentional selection experiments. Current literature is therefore limited to the demonstration of enhanced awareness in **patients** with visual extinction and facilitated attentional selection in **neurotypical** participants. If attention and awareness do in fact rely on the same mechanism, then it needs to be shown that items held in mind specifically enhances awareness in healthy participants. If this result cannot be demonstrated, then perhaps the contents of working memory affect attentional selection and awareness differently.

In order to make comments about enhanced visual awareness and not attentional selection, it is necessary to first degrade awareness to a point where subtle improvements in performance can be noted. In this way, visual awareness can be treated as if it is a “ceiling effect” in visual processing, with some method of visual masking required in order to draw performance away from the upper limit that is conscious vision. In the present study, we aimed to test the idea that working memory could enhance visual awareness in neurotypical participants using a method of visual masking that afforded us precise control over the time point at which visual processing was disrupted. Namely, we utilised the application of transcranial magnetic stimulation (TMS) to the occipital pole (Lamme, 2001).

2. The Present Study

2.1 Transcranial Magnetic Stimulation (TMS)

TMS provides researchers with a non-invasive and relatively painless method of stimulating the brain. In contrast to neuro-imaging tools, which only *measure* neural activity, TMS has the capacity to *modulate* human brain activity (Walsh & Pascual-Leone, 2003). This provides cognitive neuroscientists with the ability to investigate brain-behaviour relationships without being restricted to anaesthetised surgical patients (Barker, 2002). Specifically, the application of TMS under the right conditions can induce “virtual lesions” by artificially producing a synchronised burst of discharge in a large population of neurones (Pascual-Leone & Walsh, 2003). This causes a rapid series of impulses that are then suppressed by a long lasting period of GABAergic inhibition (Siebner, Hartwigsen, Kassuba & Rothwell, 2009). This burst of synchronised excitation followed by persistent silencing of neural activity temporarily disrupts functioning within the stimulated brain region and serves to transiently mimic the effects of a focal cortical lesion (Pascual-Leone & Walsh, 2003). If this disruption of activity serves to impair behaviour, then this suggests that the stimulated region plays a *causal* role in that particular behaviour (Saad & Silvanto, 2013).

A schematic diagram of a standard magnetic stimulator can be seen in Figure 3. During magnetic stimulation, a biphasic current flows through looped wire coils to generate a short-rise magnetic pulse. The magnetic pulse passes through the skull with little attenuation and induces a secondary electric current in superficial cortical tissue (Barker, 1991). This secondary current causes a cascade of biochemical reactions that depolarise the neuronal membrane, thereby provoking action potentials that propagate via nerve conduction pathways (Rossini et al., 2015). When a circular coil is positioned on the skull, the maximum current induced in the brain is located in an annulus directly underneath the coil.

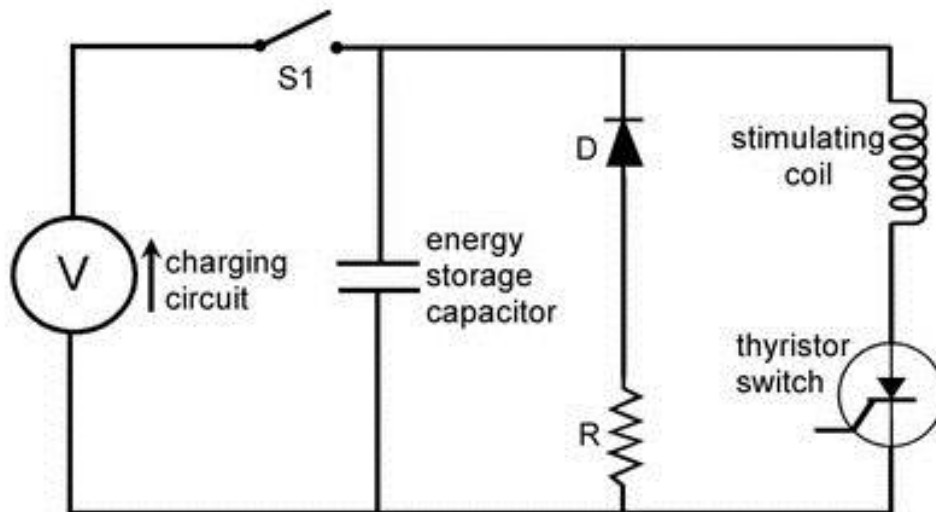


Figure 3. A schematic diagram of a capacitor discharge magnetic stimulator. When switch S1 is closed, the energy storage capacitor is charged up to a high voltage by the power supply. To activate the stimulator, S1 is opened and the thyristor switch is closed. Current then flows from the capacitor through the stimulating coil, which induces a magnetic field. The Diode (D) and resistor (R) can be used to regulate the rate of decay of the magnetic field. Circular stimulating coils induce maximal current in the tissue directly under the coil, with minimal stimulation from the centre of the loop. Reprinted from “An introduction to the basic principles of magnetic nerve stimulation,” by A. T. Barker, 1991, *Journal of Clinical Neurophysiology*, 8(1), 30. Copyright [1991] by American Electroencephalographic Society.

2.1.1 TMS to the Occipital Pole Disrupts Visual Awareness

Evidence from various behavioural tasks suggests that TMS applied to the occipital pole between 80–120 ms after stimulus onset masks objects from visual awareness in letter-discrimination tasks (Corthout, Uttls, Walsh, Hallet & Cowey, 1999), number-identification tasks (Miller, Fendrich, Eliassen, Demirel & Gazzaniga, 1996), and detection tasks that relied on contrast threshold measurements (Kammer, Puls, Strasburg, Hill & Wichmann, 2005). This finding was first demonstrated in the seminal investigation by Amassian et al. (1989). Participants were required to identify a briefly presented target item, which was comprised of a string of three letters displayed using a tachistoscope for approximately 2 ms each. Magnetic stimulation was delivered by a round magnetic coil positioned approximately 2 cm above the inion of the occipital bone to target area V1. Stimulation was applied at various stimulus-onset asynchronies (SOAs) between zero to 200 ms after stimulus onset. This method revealed a U-shaped function of visual suppression, with subjects generally reporting the three letters correctly at SOAs below 60 ms and above 120 ms. In contrast, the proportion of correctly reported letters dropped dramatically when TMS was applied around 100 ms after stimulus onset. A similar finding was reported by Boyer, Harison and Ro (2005). In this experiment, subjects were required to report the orientation or colour of target items that were displayed for 14 ms. Subjects were unable to see the target on trials where TMS was applied at 86, 100, and 114 ms after stimulus onset. A recent review of the reliability of the TMS visual masking procedure as a function of the time at which magnetic stimuli are applied provides further evidence that this effect has been well replicated within the visual awareness literature (de Graaf, Koivisto, Jacobs & Sack, 2014).

Together, the results outlined above provide further support for the involvement of early visual cortex in conscious visual perception. Specifically, a *causal* brain-behaviour relationship can be implied between early visual cortex and visual awareness from the finding

that disruption of neural activity at area V1 significantly degraded participants' ability to see briefly presented target stimuli. This highlights one of the fundamental limitations of Bar's top-down facilitation model: it cannot account for extensive anatomical and psychophysical data demonstrating the involvement of primary visual cortex in achieving visual awareness (Woolsey, 1981; Van Essen & Maunsell, 1983; Shipp & Zeki, 1989a; 1989b; Bacon & Egeth, 1994; Kim & Cave, 1999). An alternative account of conscious perception states that awareness is achieved once reentrant signals from extrastriate regions descend back to primary visual cortex, rather than to IT cortex (Lamme & Roelfsema, 2000; Pascual-Leone & Walsh, 2001; Bullier, 2001; Lamme, 2006; de Graaf, Koivisto, Jacobs & Sack, 2014). Given that signals from incoming visual input have been shown to arrive at V1 as early as 30–40 ms after stimulus onset (Lamme & Roelfsema, 2000), a plausible account based on reentrant models of perception is that TMS delivered to the occipital pole between 80–120 ms after stimulus onset blocks reentrant feedback from entering area V1 (Lamme, 2001). This method therefore provides an ideal tool to investigate the role of top-down effects on the very early stages of visual processing due to the temporal precision with which magnetic stimuli can be administered. By administering magnetic stimuli at various durations relative to stimulus onset, this paradigm affords the ability to investigate whether a causal relationship exists between visual awareness and information from top-down signals.

2.2 Aims and Hypotheses

The aim of the present study was to test for the possibility that the contents of working memory can facilitate enhanced awareness by biasing the visual system in favour of items that match preactivated object representations. In order to achieve this aim, we used a working memory task in combination with TMS to the occipital pole. Based on the design of Soto and

Humphreys (2006), participants were shown an initial memory cue that they were required to hold in mind. They were then presented with four target-classification trials in which they were shown a single target per trial. Visual awareness was operationalised as the ability to correctly classify the target shape according to two alternatives displayed on either side of the screen. On each of the classification trials, TMS was administered to the occipital pole at an SOA of 100 ms or 200 ms. Memory for the initial cue was then probed by asking participants to indicate its identity from four alternatives.

Our first hypothesis was that TMS administered to the occipital pole would mask visual perception at 100 ms after stimulus onset, but would have no effect on visual processing at an SOA of 200 ms. This is because at an SOA of 100 ms TMS is assumed to block reentrant feedback to V1, whereas the process of visual awareness should already have been completed by 200 ms after stimulus onset (Lamme, 2001). Our second hypothesis was based on the research by Soto and Humphreys (2006). We suspected that top-down signals from working memory would bias the visual system in favour of a preactivated representation of the item held in mind. If the generation of this preactivated representation meant that the process of perceptual verification could occur more efficiently, such that the visual system might require less activation to reach a “threshold” of awareness, then items that match the contents of working memory should be less susceptible to masking by TMS. In contrast, targets that do not match the memory cue might require more processing time, such that they would be vulnerable to visual masking by TMS at an SOA of 100 ms. This hypothesis would be demonstrated by a significant interaction between the factors of Memory Match and SOA. Specifically, we predicted to see greater accuracy on match trials relative to no-match trials for an SOA of 100 ms, but we predicted that the difference between match and no-match trials would not be significant at an SOA of 200 ms.

3. Experiment 1

3.1 Methods

3.1.1 Design

Experiment 1 used a 2 x 2 fully-crossed factorial design. The factors were Memory Match (match vs. no-match) and SOA (100 ms vs. 200 ms). Participants completed five practice blocks (not included in the analysis) and 80 experimental blocks over the course of a 90-minute testing session. Each block included one memory probe and four TMS classification trials.

3.1.2 Participants

A total of 16 Macquarie University undergraduate students aged between 18 and 51 years ($M = 24.81$ years, females = 11) were recruited to participate in Experiment 1 for course credit or financial reimbursement. This number is consistent with previous studies that have found significant masking effects using TMS to the occipital pole (Corthout, Uttls, Walsh, Hallet & Cowey, 1999; Miller, Fendrich, Eliassen, Demirel & Gazzaniga, 1996; Kammer, Puls, Strasburg, Hill & Wichmann, 2005). All participants reported to be strongly right-handed, with normal or corrected-to-normal vision, and provided their written informed consent (see Appendix B section 1). The study was approved by the Macquarie University Human Research Ethics Committee (reference numbers = 5201300060 and 5201400585, see Appendix A sections 1 and 2) and procedures were in accordance with the Declaration of Helsinki. All participants were provided with extensive information regarding the nature of TMS and completed the TMS Adult Safety Screen Questionnaire (Keel, Smith &

Wassermann, 2001) to ensure that there was no contraindication for TMS (see Appendix B section 2).

3.1.3 TMS Parameters

A round TMS coil was fixed in position using a clamp and tripod. To establish the appropriate intensity of magnetic stimulation we first established participant's individual motor thresholds. An individual's motor threshold was defined as the minimal intensity of left motor cortex stimulation required to elicit a visible muscle twitch in the right hand (Rossini et al., 2015). Accordingly, magnetic stimuli were given at the optimal site of the left motor cortex for eliciting contractions of the right fingers. The coil was positioned in line with the parasagittal plain, with the handle pointing posteriorly. The intensity of TMS was initially set at 50 percent of maximum stimulator output for all participants. This value was adjusted until the minimal value required to observe a visible twitch response was determined. Participants' individual motor thresholds ranged from 38 to 65 percent of maximum output intensity, with a mean value of 51.38 percent.

TMS intensity for the experiment proper was set at 110 percent of an individual's motor threshold. This procedure was used to ensure optimal visual suppression whilst still maintaining comfort for the participants. The mean intensity of TMS used during the main experiment was 56.19 percent of maximum output, with a range of 41 to 72 percent. This equated to a mean of 1.9 Tesla, which is in line with the recommended intensity required to achieve visual suppression by occipital lobe TMS (Kammer et al., 2005). Magnetic stimuli were initially given at the occipital pole approximately 2 cm above theinion of the occipital bone. This location has been identified as the optimal site for visual masking by V1 stimulation (Amassian et al., 1989; Kammer, 2007; Boyer et al., 2005). The coil was then

systematically moved from this starting point both horizontally and vertically within a predefined grid in order to find the ideal pulse location for each participant. The main axis of the coil was oriented parallel to the sagittal plane and the handle positioned upright to induce current flow along the inferior-superior axis. This orientation was chosen based on work by Amassian et al. (1994), which found that a parasagittal coil orientation was the most effective in suppressing visual information. During each block participants received 12 TMS pulses (a train of 3 pulses per trial, with 4 TMS trials per block). Throughout the entire testing session participants received 1020 magnetic stimulations, which is in accordance with safety and ethical guidelines for the use of TMS (Rossi, Hallet, Rossini & Pascual-Leone, 2008).

3.1.4 Apparatus

Participants sat upright at a rigid table in front of a 62 cm x 35 cm LED monitor positioned 35 cm from the front edge of the desk. Throughout the task, the participant's head was restrained within a chinrest. Participants responded on a keyboard directly in front of them by pressing either "A" or "L" to classify the target shape and "1", "2", "3", or "4" to indicate the shape of the memory cue.

3.1.5 Stimuli and Procedure

The visibility of target stimuli was titrated in each participant using a stochastic staircase procedure to manipulate the opacity of the stimulus by varying the alpha channel in rgba colour space. The higher the alpha value, the more opaque the stimulus is and, hence, the more visible a stimulus is to the participant. During the staircase procedure, participants were asked to classify the shape of a target item presented at central fixation for a duration of 14 ms. Target stimuli were selected randomly from four greyscale shapes (i.e., diamond, circle,

triangle, or pentagon) extending 0.75 degrees of visual angle from a viewing distance of 38 cm. The visibility of all stimuli used in the main experiment was set at the obtained alpha level from the staircase procedure that yielded a classification accuracy of approximately 65 percent for each participant. This included the memory cue, target stimuli, and memory probe items. Alpha values ranged from 39 to 168, with a mean value of 73.43.

The visual trial structure for Experiment 1 can be seen in Figure 4. Each trial was self-initiated by pressing the space bar. Based on the design of Soto and Humphreys (2006), participants were presented with an initial shape (i.e., the memory cue) for 1000 ms that they were required to hold in mind. They were then required to classify the shape of four subsequent target items that were presented one at a time for 8.3 ms at central fixation. On one out of every four target-classification trials the target shape was a direct match to the memory cue. TMS was applied during the four target-classification trials only. A train of three magnetic pulses was administered at two SOAs, with the middle pulse set to arrive at either 100 ms or 200 ms after stimulus onset. The pulses occurred at a rate of 5 Hz and were separated by 20 ms. This meant that for the first SOA magnetic stimuli were delivered at 80, 100, and 120 ms in order to target the entire temporal window during which TMS stimulation of V1 has been shown to mask visual perception (Lamme, 2001). At the second SOA (i.e., control condition), TMS was delivered at 180, 200, and 220 ms. At this later SOA, the process of perceptual verification should already have been completed and TMS was not expected to suppress visual awareness. After each target had been presented, two shape words (selected from “*DIAMOND*”, *CIRCLE*”, *TRIANGLE*”, or “*PENTAGON*”) were presented, with one on the left and one on the right side of the screen as part of a two-alternative forced-choice response procedure. Participants pressed either “A” or “L” to classify the shape, with “A” representing the word presented on the left side of the screen and “L” representing the word on the right. The shape word representing the target item (i.e., correct response option)

appeared equally on the left and right side of the screen in random order. Following the four target-classification trials, the participant's memory for the initial memory cue was then probed by asking participants to press either "1", "2", "3", or "4" on the keyboard, with these numbers corresponding to a shape displayed on the screen.

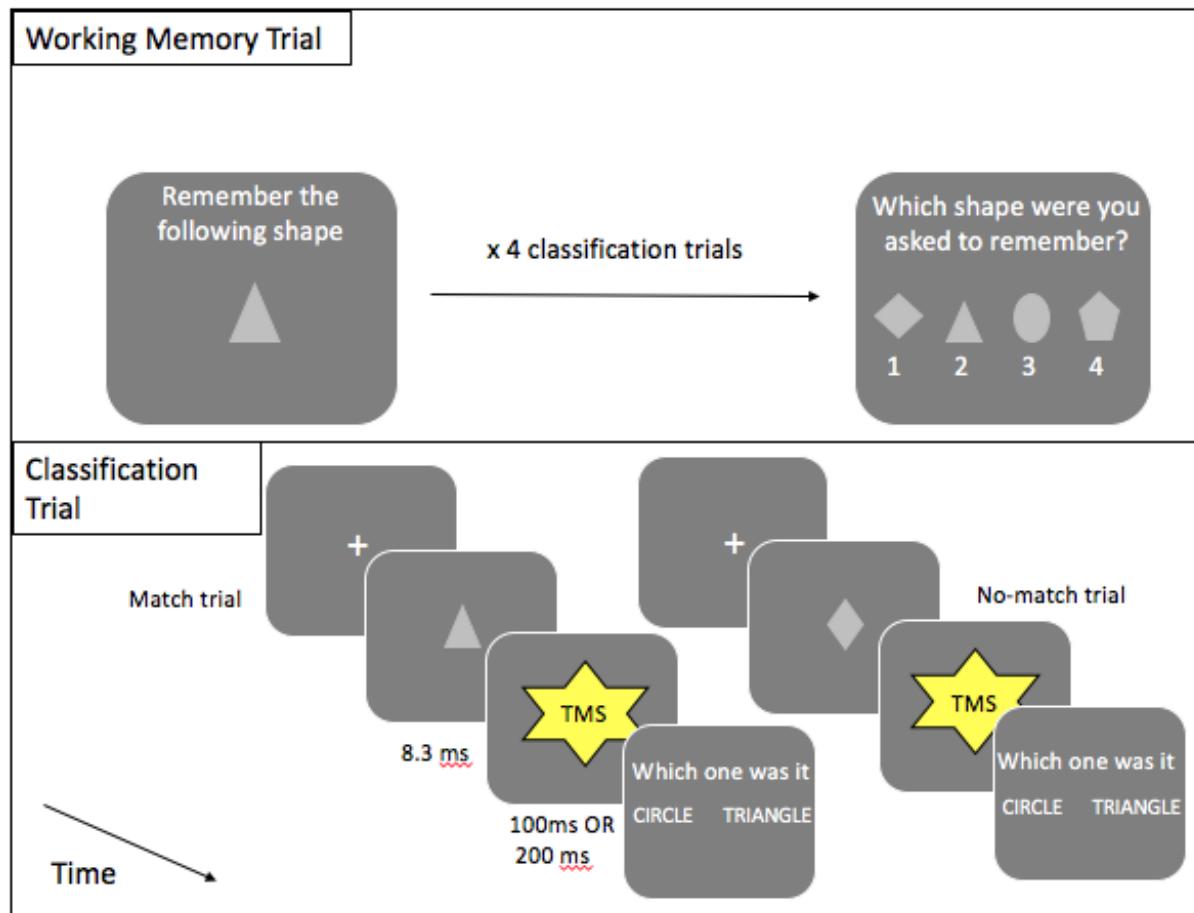


Figure 4. Trial structure in Experiment 1. Participants were presented with a memory cue that they would be required to recall at the end of the run (top panel). They were then presented with four target-classification trials in which they had to indicate the shape of a briefly presented target by pressing either “A” or “L” according to two response options that appeared on either side of the screen (i.e., “DIAMOND”, CIRCLE”, TRIANGLE”, or “PENTAGON”). On one out of every four trials the target shape was identical to the memory cue (left trial sequence of bottom panel). TMS was applied on the classification trials at an SOA of either 100 ms or 200 ms. Memory for the initial shape was then probed by asking participants to select the memory cue from four response options.

3.2 Experiment 1 Results

Practice trials were excluded from the analysis. All data were analysed using custom software written in R (www.rproject.org). The significance level for all analyses was set at $\alpha = 0.05$.

3.2.1 Data Analysis

Data were analysed by implementing linear mixed-effects modelling (LMM, Baayen, Davidson, & Bates, 2008; Bates, 2005) using the lmer4 package (<http://lme4.r-forge.r-project.org>, cf. Bates, Maechler, & Bolker, 2011). To evaluate the reliability of each effect of interest we used an incremental model comparison procedure that relied on goodness-of-fit statistics (i.e., AIC, BIC, and Log Likelihood values, Akaike, 1974; Schwarz, 1978). This procedure enabled us to determine whether a model that included the term under inspection, or the same model without this term, fit our data best. In model comparison procedures, the best model fit is the one which minimises AIC and BIC, and maximises Log Likelihood. For each comparison we selected the model that best fit these stipulations. In order to increase generalisability beyond the individuals who participated in this study, we included Participant as a random factor within the model. Any individual differences in our sample were therefore modelled jointly by means of a participant random effect (Baayen et al., 2008). Below we report the results of the Likelihood ratio test. We have also reported the coefficients, standard errors (SEs), and z-scores for terms included in the final model.

3.2.2 Results

Mean accuracy for memory probe trials averaged across all participants was 80.14%, indicating that participants were successfully holding the memory cue in mind during the classification trials. To determine whether there was a correlation between participants' ability to remember the memory cue and their performance on the classification trials, we

calculated the effect of Memory Match by subtracting each participant's mean accuracy on no-match trials from their accuracy on match trials. We then tested for a correlation between this variable and mean recall accuracy and found that the relationship was not significant ($r_{(14)} = -0.22, p = 0.41$, see Figure 5). The lack of a correlation here suggests that participants with greater ability to remember the memory cue were no more likely to classify the memory-match shapes correctly, compared to participants who performed poorly on the memory probe trials. Nevertheless, we found that the main effect of Memory Match was reliable, $\chi^2(1) = 81.28, p < .001$, indicating that classification accuracy was more likely to be correct for memory match targets (79.21%), compared to no-match targets (66.51%), $b = 0.69, SE = 0.11, z = 6.13$ (see Figure 6). The main effect of SOA was also reliable, $\chi^2(1) = 9.75, p < .001, b = -0.19, SE = 0.07, z = -2.72$, however, the direction of this effect was against our initial predictions, with classification accuracy being higher for an SOA of 100 ms (71.67%) than for 200 ms (67.68%). The interaction between Memory Match and SOA was not significant, $\chi^2(1) = 0.02, p = .878$, as the difference in mean accuracy between match and no-match trials averaged across participants did not differ by SOA. Specifically, mean accuracy for match trials was 80.96% at an SOA of 100 ms and 77.44% at an SOA of 200 ms and mean accuracy for no-match trials was 68.56% at an SOA of 100 ms and 64.46% at an SOA of 200 ms.

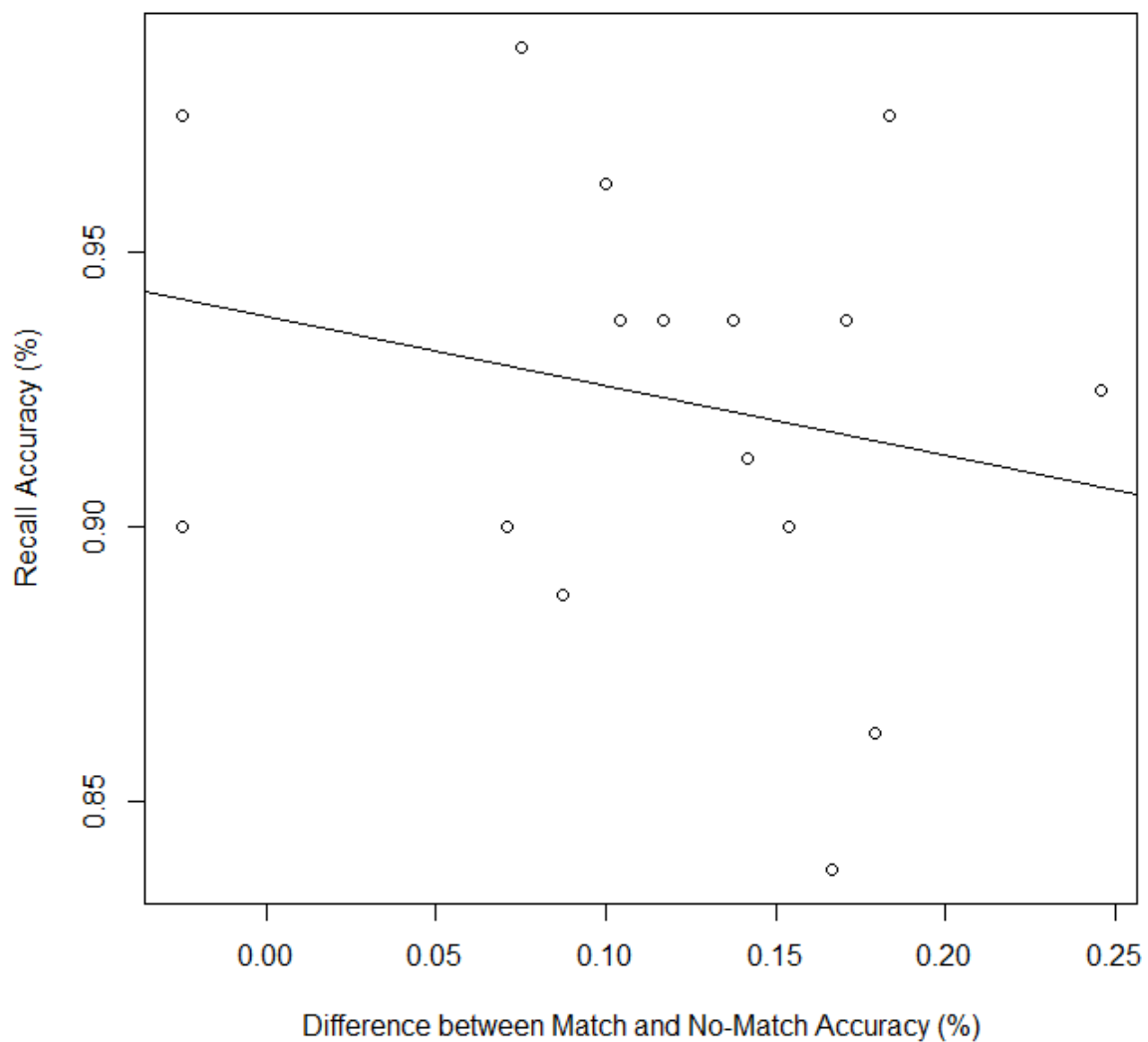


Figure 5. Scatterplot depicting the correlation between memory recall and the effect of Memory Match on classification accuracy. This figure shows that participants' ability to remember the memory cue was not correlated with the effect of Memory Match on their ability to identify the target stimulus. Participants with greater ability to remember the memory cue were no more likely to classify the memory-match shapes correctly, compared to participants who performed poorly on the memory probe trials.

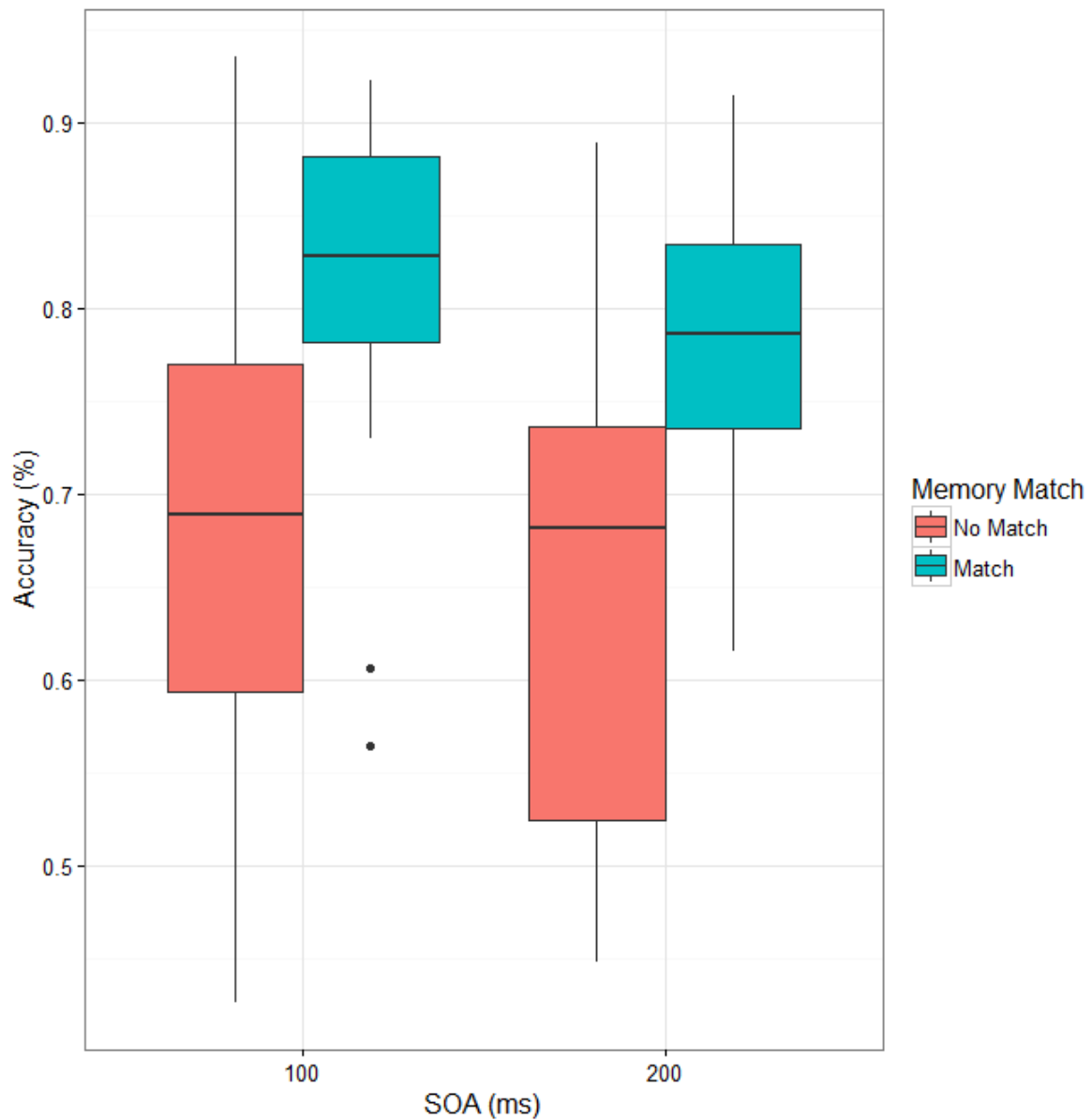


Figure 6. Mean accuracy values separated by Memory Match and SOA. This figure clearly shows the main effect of Memory Match, as the horizontal line representing the median for match trials is significantly higher than for no-match trials at both the 100 ms and 200 ms TMS SOA. However, the interaction between Memory Match and SOA is not significant, as the difference between the match and no-match medians does not differ according to SOA.

3.3 Interim discussion for Experiment 1

We observed a reliable effect of Memory Match in Experiment 1, in that participants' responses were significantly more accurate for targets that matched the memory cue, compared to targets that did not. We also observed a reliable effect of SOA, however, the direction of this effect was not in line with our initial expectations. Specifically, we predicted accuracy to be at chance for an SOA of 100 ms and significantly above chance at 200 ms. In contrast, we found that overall mean accuracy was higher for trials in which TMS was applied at 100 ms after target onset, relative to 200 ms. Whilst this finding could be driven by the higher proportion correct recorded for match trials at an SOA of 100 ms than at 200 ms, this account is unlikely given that we also observed a higher proportion correct for no-match trials at 100 ms, relative to 200 ms. This suggested to us that we were not successful in our attempt to use TMS to block reentrant processing and mask visual perception.

Given that we did not find a reliable interaction between Memory Match and SOA, such that we observed higher accuracy for memory match trials across both durations of TMS, it seemed unlikely that the contents of working memory served to enhance visual awareness for degraded targets. On closer inspection of our data, it appeared that the pattern of responses was due to a response bias. Specifically, participants showed a strong tendency to select the response option that matched the memory cue, even on trials in which the target was a different shape to the to-be-remembered memory cue. In order to confirm this story, we re-analysed the data by pulling out trials in which the target item did not match the memory cue (i.e., no-match trials). We then divided participants' responses on these no-match trials according to whether or not one of the response options (i.e., "*Which one was it: Circle or Triangle?*") matched the memory cue. This enabled us to obtain participants' mean accuracy as a function of whether the memory cue was available as a response option on the no-match classification trial (i.e., when target was different from the memory cue). If participants were

selecting the memory cue response option at greater than chance levels, then their accuracy should be significantly worse on no-match trials when one of the response options matched the memory cue, compared to when it did not. Indeed, across all participants in Experiment 1 we observed a significant perceptual bias in favour of the memory cue (see Figure 7). That is, on no-match trials in which the target shape did not match the to-be-remembered memory cue, participants' target-classification accuracy was significantly worse when the memory cue was nevertheless presented as a response option (61.52%), as opposed to when it was not (69.10%), $\chi^2(1) = 27.00$, $p < .0001$, $b = -0.39$, $SE = 0.07$, $z = 5.21$. This shows a clear response bias to choose the item currently held in memory and should not be interpreted as a facilitation in perceiving items that match the contents of working memory.

The finding of a significant perceptual response bias in itself is somewhat interesting. It suggests that behavioural responses are biased towards representations held in mind (or expectations about upcoming stimuli) even when this information does not facilitate successful task performance. The notion that behaviour can be influenced by task-irrelevant information from the active maintenance of items in working memory is an interesting avenue for future research to consider. However, the point of this study was to determine whether the contents of working memory can facilitate efficient visual perception by biasing the visual system in favour of a preactivated object representation. Thus, we chose to modify the design of Experiment 1 to eliminate the possibility of a response bias.

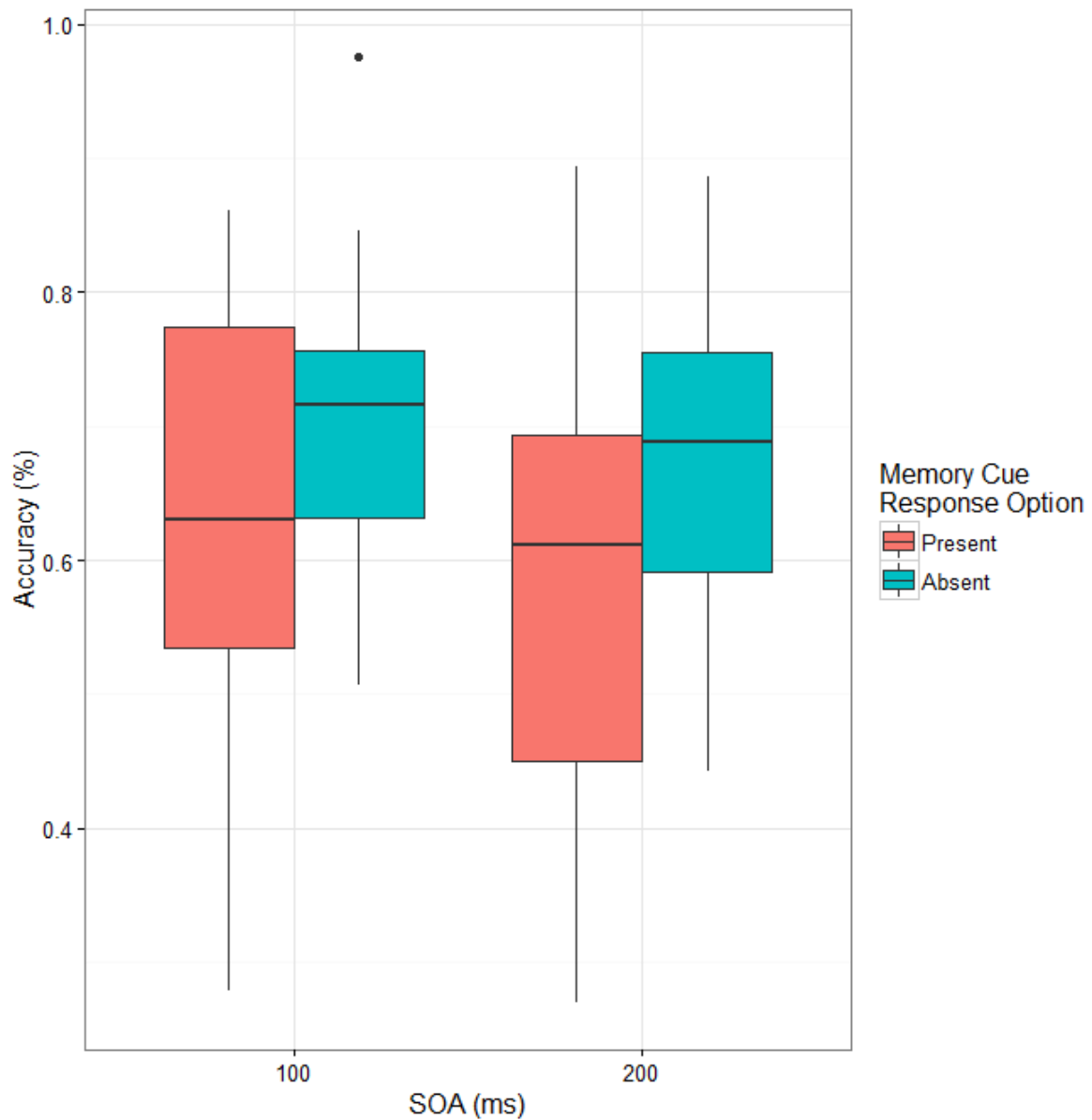


Figure 7. Mean accuracy values separated by whether the memory cue was present or not as a response option and SOA in Experiment 1. This figure shows the significant perceptual bias in favour of selecting the memory cue option even though this option was the incorrect response. The horizontal line representing the median for memory cue present is significantly lower than that of the median for memory cue absent in both the 100 ms and 200 ms SOA conditions.

4. Experiment 2

4.1 Methods

To determine whether the contents of working memory can facilitate efficient visual perception by biasing the visual system in favour of a preactivated representation, we modified the task in Experiment 2 to one where participants' decisions were no longer centred on the visual features of the stimuli themselves. In this way, we aimed to eliminate the utility of the memory response item in producing a correct behavioural response. As in Experiment 1, participants were presented with a memory cue that they would be asked to recall later. However, in Experiment 2 we used a two-interval forced-choice procedure in which participants were required to indicate whether a target item appeared in either the first or second of two temporal intervals.

We also modified certain TMS parameters to increase the likelihood of masking visual perception through the administration of magnetic stimulation to the occipital pole. For example, TMS was applied according to three different SOAs, being 33 ms, 100 ms, and 200 ms after stimulus onset. These SOAs were selected based on the literature regarding the various stages of visual awareness, with the expectation that TMS applied at 33 ms would disrupt the feedforward sweep of visual input towards higher cortical regions, at 100 ms would block reentrant processes from reaching V1, and at 200 ms would arrive at a time point at which the process of perceptual verification should theoretically have been completed (Lamme, 2001). With this in mind, we hypothesised that visual awareness would be suppressed when TMS was applied at 33 ms and 100 ms, but not at 200 ms.

We again hypothesised that the contents of working memory would bias the visual system in favour of a preactivated representation held in mind. If the generation of this preactivated representation meant that the process of perceptual verification could occur more

efficiently, then items that matched the contents of working memory should be less susceptible to masking by TMS at 100 ms after target onset. In contrast, targets that did not match the memory cue would require more processing time and perception of these targets would be degraded by TMS at 100 ms after target onset. We therefore predicted to see a significant interaction between Memory Match and SOA. Specifically, we predicted that detection accuracy would be at chance level for both match and no-match trials at an SOA of 33 ms, as TMS at this SOA would disrupt processing at a point where visual input was still within the early stages of the feedforward sweep. At an SOA of 100 ms, we predicted greater accuracy on match trials relative to no-match trials due to the efficient processing of items that matched the contents of working memory. At an SOA of 200 ms, the process of visual awareness should already have been completed and TMS was predicted to have no effect on visual awareness, with greater than chance accuracy across both levels of the Memory Match factor.

4.1.1 Design

Experiment 2 used a 2 x 3 fully-crossed factorial design. The factors were Memory Match (match vs. no-match) and SOA (33 ms vs. 100 ms vs. 200 ms). Participants completed three practice blocks (not included in the analysis) and 20 experimental blocks over a 90-minute testing session. Each block was comprised of six experimental runs; with each run including one memory probe and four TMS detection trials. Therefore, there were 24 detection trials per block and there was a total of 480 detection trials over the entire experiment (i.e., 24 trials per block x 20 blocks).

4.1.2 Participants

A different group of 16 Macquarie University undergraduate students aged between 18 and 26 years ($M = 22.10$ years, females = 13) were recruited to participate in Experiment 2 for course credit or financial reimbursement. All participants reported to be strongly right-handed, with normal or corrected-to-normal vision, and provided their written informed consent. The study was approved by the Macquarie University Human Research Ethics Committee (reference numbers = 5201300060 and 5201400585) and procedures were in accordance with the Declaration of Helsinki. All participants were provided with extensive information regarding the nature of TMS and completed the TMS Adult Safety Screen Questionnaire (Keel et al., 2001) to ensure that there was no contraindication for TMS.

4.1.3 TMS Parameters

The TMS coil was fixed in position using a clamp and tripod. Magnetic stimuli were applied approximately 2 cm above the inion of the occipital bone, with the main axis of the coil oriented parallel to the sagittal plane and the handle positioned upright to induce current flow along the inferior-superior axis. Intensity was set at 50 percent of maximum output for all participants, which equalled 1.75 Tesla. Previous research has indicated that 1.5 Tesla and above is sufficient to suppress visual awareness (Kammer et al., 2005). During each block, participants received 48 magnetic stimuli. Throughout the entire testing session, participants received a total of 1104 magnetic stimulations (i.e., 48 pulses per block x 23 blocks). This is in accordance with safety and ethical guidelines for the use of TMS (Rossi et al., 2008).

4.1.4 Apparatus

Participants sat upright at the same rigid table and LED monitor as in Experiment 1, but were positioned 48 cm from the front edge of the desk. As before, the participant's head was fixed within a chinrest. To further stabilise participants' head movements, all responses were made by clicking a computer mouse.

4.1.5 Stimuli and Procedure

The visual trial structure for Experiment 2 can be seen in Figure 8. Each trial was self-initiated by clicking the computer mouse. Participants were instructed to remember an initial memory cue that appeared at fixation and persisted on the screen until participants clicked the mouse again. Both the memory cue and the critical targets were comprised of a string of three randomly selected letters that extended 0.25 degrees of visual angle. Participants were then presented with four target-detection trials in which they had to indicate whether a target displayed for 8.3 ms (i.e., one refresh cycle) appeared in either the first or second interval. Each interval was 500 ms long and was identified by the colour of a central fixation point (i.e., red for the first interval and yellow for the second interval). Participants were instructed to keep their eyes fixed on this central point throughout the detection trials. The target always appeared 3 degrees below fixation, as studies suggest that selective stimulation of V1 produces visual scotomas that occur between 1–3 degrees below central fixation (Kastner, Demmer & Ziemann, 1998). On one out of every four detections trials the target letter string was identical to the one that participants were required to remember. A single pulse of magnetic stimulation was administered in both intervals at one of three SOAs during the detection trials (i.e., 33 ms, 100 ms, and 200 ms). On any given trial, the SOA for the first interval was always the same as for the second interval. Participants' memory for the memory letter string was then probed using a circular display to present a total of twelve letters (i.e., three memory letters and nine distractor letters).

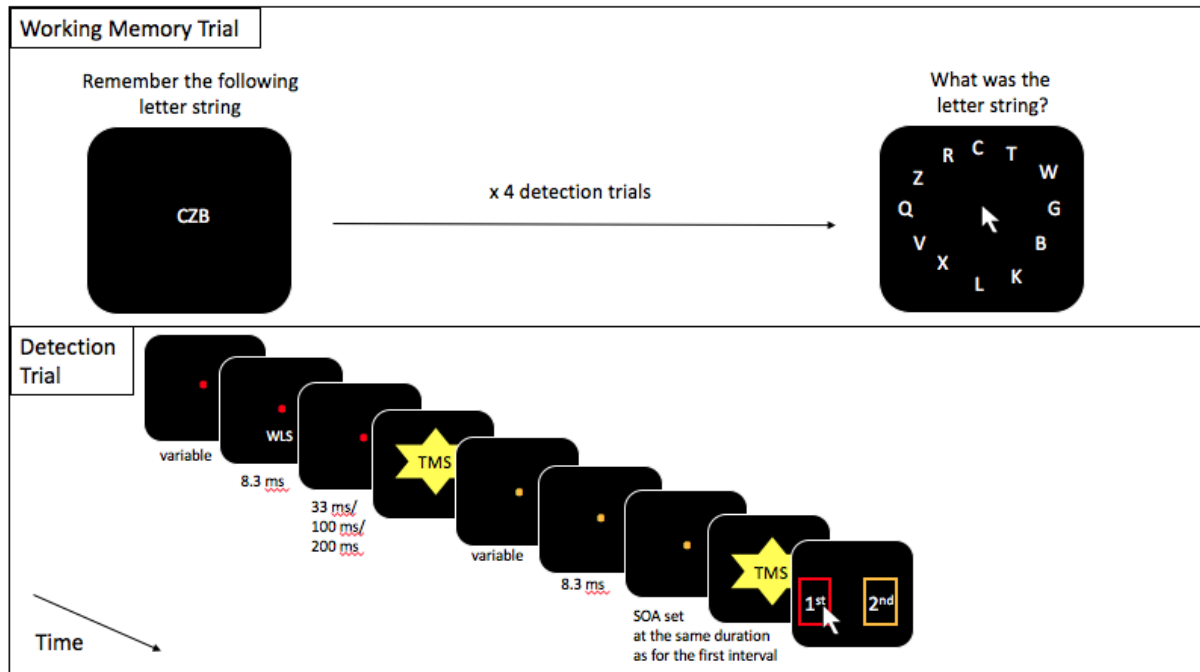


Figure 8. Visual run structure for Experiment 2. Participants were presented with a memory cue that they would be required to recall at the end of the run (top panel). They were then presented with four target-detection trials in which they had to indicate whether a target letter string appeared in either the first (i.e., red fixation point) or second (i.e., yellow fixation point) interval (bottom panel). On one out of every four trials the target letter string was identical to the memory cue. TMS was applied at an SOA of either 33 ms, 100 ms, or 200 ms after target onset. On any given trial, the SOA for the first interval was always the same as for the second interval. For example, the figure above depicts a target-detection trial in which the target did not match the memory cue and was presented in the first interval. To test participants' memory of the initial letter string, they were asked to reconstruct the string by clicking on the correct letters in the correct order.

4.2 Experiment 2 Results

Practice trials were excluded from the analysis. All data were analysed using custom software written in R (www.rproject.org) according to the same parameters described for Experiment 1. The significance level for all analyses was set at $\alpha = 0.05$.

4.2.1 Data Analysis

Data were again analysed by implementing linear mixed-effects modelling (LMM, Baayen, Davidson, & Bates, 2008; Bates, 2005) using the lmer4 package (<http://lme4.r-forge.r-project.org>, cf. Bates, Maechler, & Bolker, 2001). We used an incremental model comparison procedure that relied on goodness-of-fit statistics (i.e., AIC, BIC, and Log Likelihood values, Akaike, 1974; Schwarz, 1978) to evaluate the reliability of each effect of interest. This procedure enabled us to determine whether a model that included the term under inspection, or the same model without this term, fit our data best. In model comparison procedures, the model that best fits the data is the one which minimises AIC and BIC, and maximises Log Likelihood. Individual differences in our sample were modelled jointly by means of a participant random effect (Baayen et al., 2008). Below we report the results of the Likelihood ratio test. We have also reported the coefficients, standard errors (SEs), and z-scores for terms included in the final model.

4.2.2 Results

Mean accuracy for memory probe trials averaged across all participants was 89.76%, indicating that participants were successfully holding the memory cue in mind during the detection trials. To determine whether there was a correlation between participants' ability to remember the memory cue and their performance on the detection trials, we calculated the effect of Memory Match by subtracting each participant's mean accuracy on no-match trials

from their accuracy on match trials. We then tested for a correlation between this variable and mean recall accuracy and found that the relationship was not significant ($r_{(14)} = 0.22$, $p = 0.42$, see Figure 9). This lack of a correlation suggests that participants with greater ability to remember the memory cue were no more likely to correctly indicate the interval in which a memory-match target appeared, compared to participants who performed poorly on the memory probe trials. Our primary analysis revealed that the main effect of Memory Match was not reliable, $\chi^2(1) = 3.44$, $p = 0.06$, indicating that detection accuracy was no more likely to be correct for memory match targets (95.09%), compared to no-match targets (94.05%). The main effect of SOA was also not reliable, $\chi^2(1) = 2.48$, $p = 0.29$, with detection accuracy being 95.04% for an SOA of 33 ms, 95.14% for an SOA of 100 ms, and 94.31% for the final SOA of 200 ms. Finally, the interaction between Memory Match and SOA was not significant, $\chi^2(1) = 0.21$, $p = 0.89$, as the difference in mean accuracy between match and no-match trials averaged across participants did not differ by SOA. Specifically, mean accuracy for match trials was 94.24% at an SOA of 33 ms, 93.87% at an SOA of 100 ms, and 94.03% at an SOA of 200 ms and mean accuracy for no-match trials was 95.33% at an SOA of 33 ms, 95.57% at an SOA of 100 ms, and 94.40% at an SOA of 200 ms (see Figure 10).

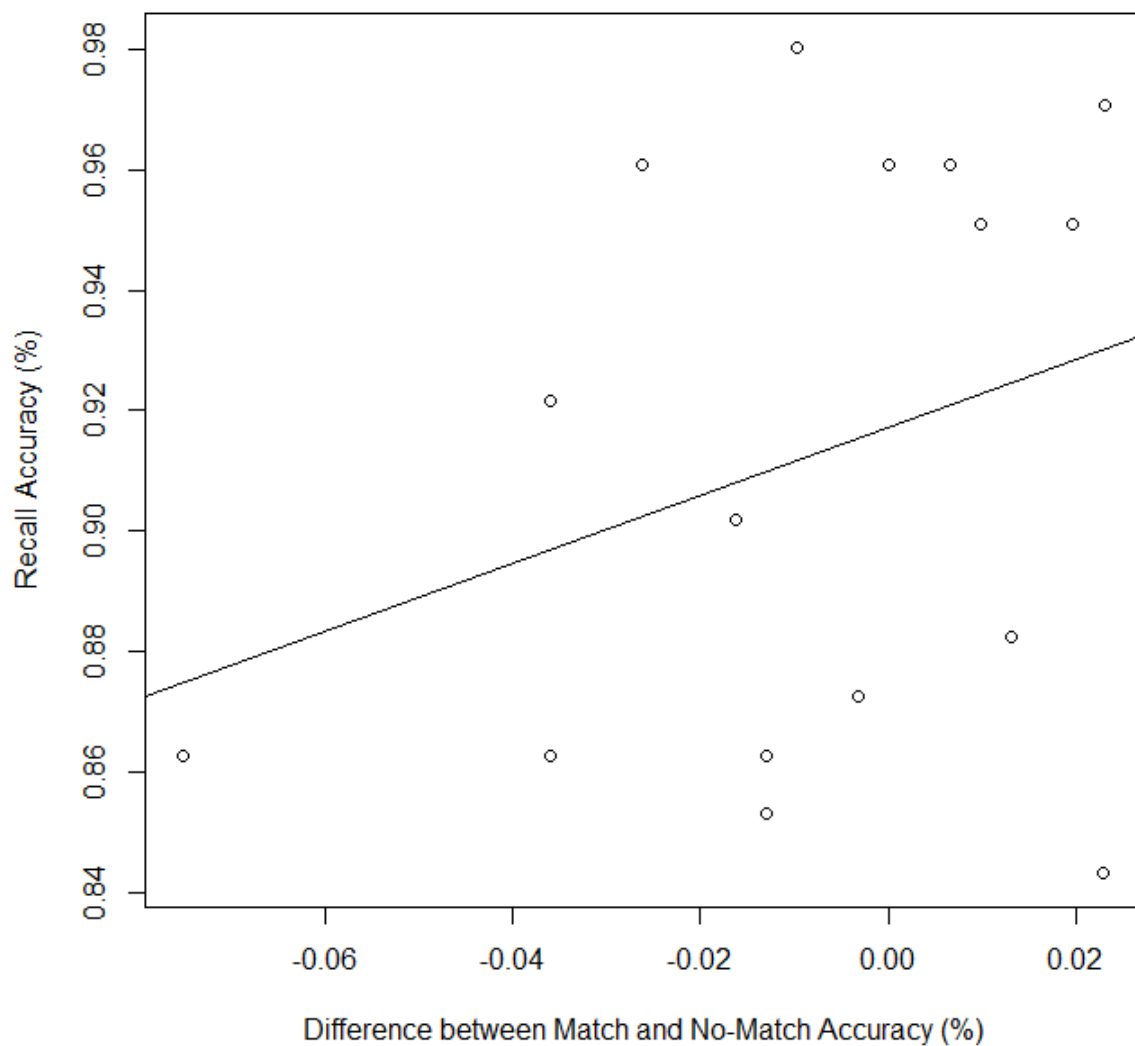


Figure 9. Scatterplot depicting the correlation between memory recall and the effect of Memory Match on detection accuracy. This figure shows that participants' ability to remember the memory cue was not correlated with the effect of Memory Match on their ability to detect the presence/absence of a target stimulus. Participants with greater ability to remember the memory cue were no more likely to detect the temporal interval that a memory-match target appeared in, compared to participants who performed poorly on the memory probe trials.

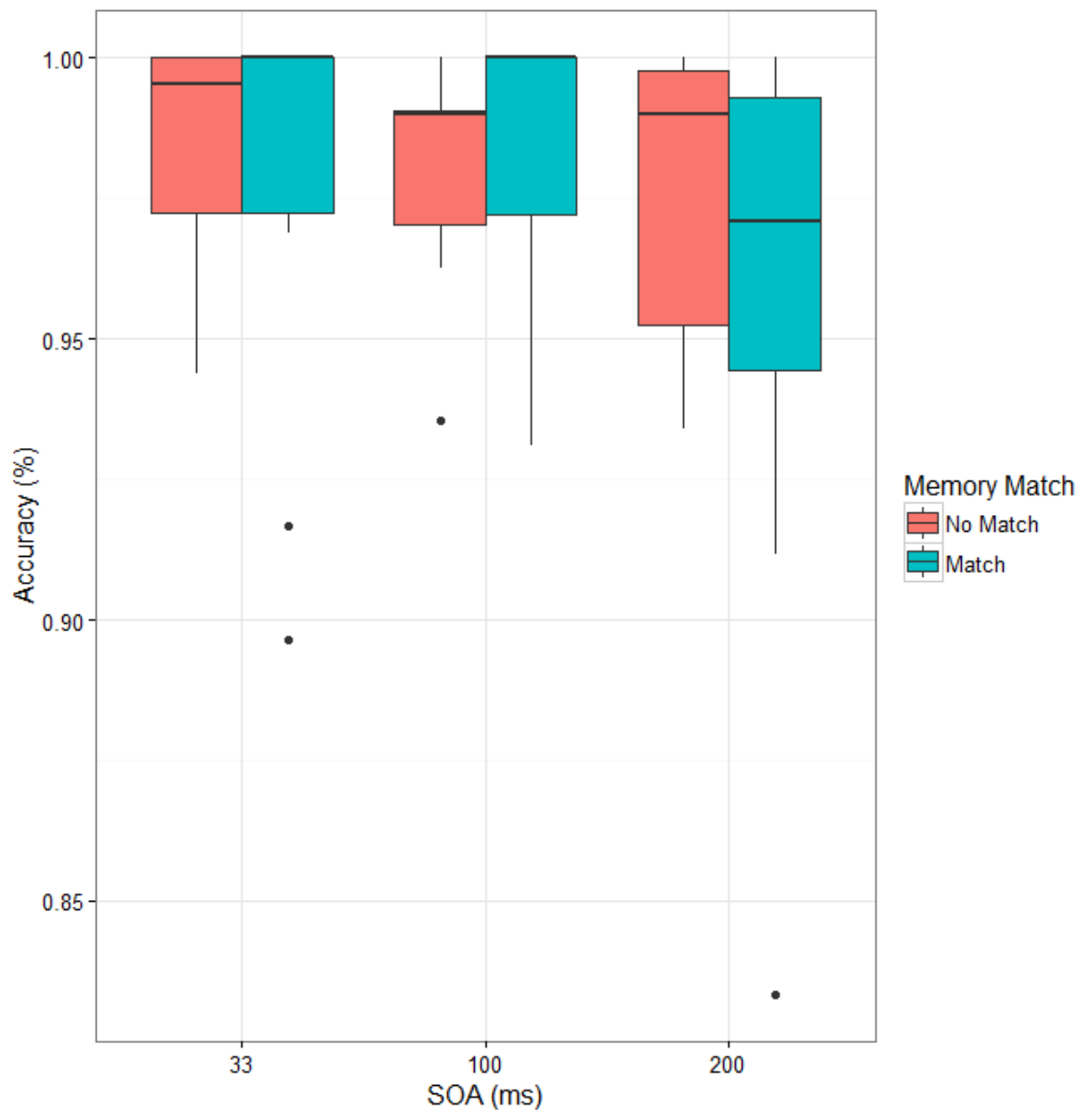


Figure 10. Mean accuracy values separated by Memory Match and SOA. This figure shows the striking ceiling effect in the data. It can clearly be seen that both the main effects and the interaction between them are not reliable, as the difference between the match and no-match horizontal lines representing the medians does not differ according to SOA.

4.3 Interim discussion for Experiment 2

The results of Experiment 2 did not reveal any significant differences in mean accuracy between the levels of the SOA and Memory Match factors. Instead, participants in Experiment 2 performed near perfectly across all experimental conditions. This ceiling effect in the data indicated to us that we had not been successful in using TMS to suppress visual awareness, even though we had precisely replicated the necessary parameters required for visual suppression by TMS. These included setting magnetic field intensity at equal to or greater than 1.5 Tesla (Kammer et al., 2005), administering magnetic stimuli within a 100–120 ms temporal window (Kammer, 2007), presenting targets for one refresh rate or 8.3 ms (Amassian et al., 1989), constraining targets to 0.25 degrees of visual angle (Boyer et al., 2005), and presenting targets at 3 degrees below visual fixation (Kastner et al., 1998).

One reason why TMS did not degrade visual awareness might have been because visual scotomas by occipital lobe TMS cannot be achieved in all participants. For example, Salminen-Vaparanta et al. (2012) used multifocal fMRI combined with electric field modelling during TMS stimulation to identify participants' individual retinotopic mapping. It was found that selective stimulation of V1 was only possible in approximately half of the participants. In the other half, selective stimulation of V1 was obstructed by the intermediate anatomical location of dorsal V2. This is consistent with the findings of Kastner et al. (1998), who administered TMS to a total of 18 subjects and observed reliable masking in only eight of them. Furthermore, Salminen-Vaparanta and colleagues found that when theinion was used as an external anatomical landmark to localise V1 (as was done in the present study), cortical stimulation occurred at various functional areas in different individuals, with dorsal V2 being the most affected area overall, rather than V1.

If visual scotomas can only be induced in certain participants with favourable scalp anatomy, then it is not unreasonable to assume that our sample was comprised of participants who all had an “unfavourable” scalp configuration for visual suppression by TMS. It is entirely possible that selective stimulation of V1 simply was not achievable in this particular group of subjects. No doubt, we are likely not to be the only researchers who have experienced this lack of success. In fact, it seems that the most effective strategy when using this paradigm has been to sample multiple subjects and to stockpile those few that demonstrate reliable masking by TMS to the occipital pole. For example, Kammer’s research group reports testing four particular subjects that show reliable visual scotomas across various experimental tasks with multiple testing sessions for each participant (Kammer & Nusseck, 1998; Kammer et al., 2005a; 2005b). Given that we were unlikely to localise V1 using external anatomical landmarks (Salminen-Vaparanta et al., 2012), we decided to forgo further testing with TMS.

To continue our investigation of whether the contents of working memory can enhance awareness by facilitating efficient visual perception, we required another method that could be used to degrade awareness to a point where subtle improvements in performance could be noted. In this way, we aimed to treat visual awareness as a “ceiling effect” in visual processing, with some method of visual masking used to draw performance away from the upper limit of conscious vision. An appropriate methodology to achieve this aim is object substitution masking (OSM, Enns & Di Lollo, 1997).

5. Experiment 3

5.1 Masking by Object Substitution

Unlike traditional forms of masking, where the mask overlaps the target in either space or time, OSM is unique in that the mask does not occlude the target (Enns & Di Lollo, 1997). Rather, masking by object substitution occurs when four dots that surround a briefly presented target item remain on the screen for some time after target offset. This form of masking is attentional, in that it is critically dependent on the spatial distribution of attention (Enns, 2004). Specifically, if attention can be directly focused on the location of the target item before it appears on the screen, then a trailing four-dot mask has no effect on target detection (Enns & Di Lollo, 1997). However, if the target is presented in an unpredictable location, such that participants cannot direct their attention to a predetermined location, masking occurs that is comparable in strength to that obtained by a tightly fitting metacontrast frame (Enns, 2004).

To illustrate, consider the OSM visual display sequence depicted in Figure 11. The initial display screen contains several different spatially distributed shapes, with one item being identified as the target by four small dots at the corners of an imaginary square surrounding that shape (i.e., the star). The display is flashed very briefly and participants are required to report the identity of the target shape. On half of the trials, the target item and four surrounding dots terminate at the same time (simultaneous-offset trials). On the other half, the four dots remain visible on the screen after the target has been removed from the display (i.e., delayed-offset trials). Visual masking occurs when the four dots that surround the target persist on the screen for some time after target offset, whereas target detection is unimpaired by the simultaneous offset of the mask and target (Enns & Di Lollo, 1997).

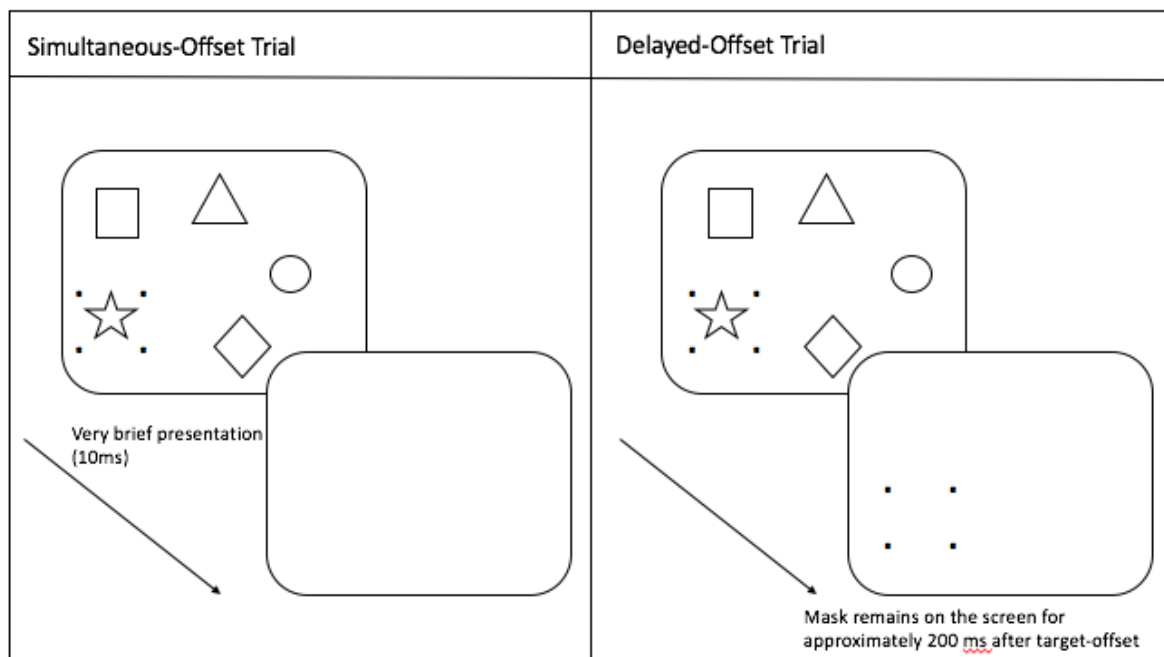


Figure 11. Visual display sequence of a typical OSM trial. Participants are presented with a very brief display screen containing a number of spatially distributed shapes. The target shape is indicated by four small dots at the corners of a hypothetical square surrounding that shape. On half of the trials, the entire display screen (including both the target and the four dots) terminates after approximately 10 ms. On the other half, the four dots remain visible on the screen for approximately 200 ms after target offset. Visual masking occurs in this latter condition, with target detection being unimpaired by the former.

An example of a typical OSM paradigm can be seen in the work of Di Lollo, Enns and Rensink (2000). Participants were presented with a very brief display consisting of up to sixteen concentric rings that each had a small missing segment (i.e., a Landolt C). Their task was to specify the side of the gap in the Landolt C that was surrounded by four dots at the corners of an imaginary square. The four dots also served as the masking stimulus. Unlike conventional forms of behavioural masking, in which the mask stimulus is presented after the target item, the four-dot mask was presented simultaneously with the target. The mask remained on the screen for various durations between zero ms (i.e., the mask was turned off at the same time as the target) and 320 ms (i.e., the mask persisted on the screen for 320 ms after target offset). It was found that masking developed as a joint function of set size and mask duration, such that accuracy rates declined as set size increased and mask durations exceeded 40 ms.

5.1.2 The mechanisms of OSM

Di Lollo et al.'s finding that a temporally trailing mask degraded visual perception is difficult to reconcile with feedforward accounts of visual processing. This is because masking by object substitution cannot be explained in terms of lateral inhibition of the target by the mask. Specifically, the lateral inhibition account specifies that masking is the result of interchannel inhibition between fast-acting transient channels representing information from the mask and slower sustained channels representing information from the target (Beitmeyer & Ganz, 1976; Francis, 1997). However, this account cannot be used to explain the effect of masking by object substitution, as the four-dot mask in a typical OSM paradigm does not spatially overlap with the target and does not surround the target to the same extent as in metacontrast masking.

Instead, OSM has been explained in terms of reentrant models of vision. According to reentrant accounts, neural activity triggered by the initial stimulus display ascends to higher brain regions, where it activates several perceptual hypotheses regarding the likely nature of incoming sensory input (Di Lollo, Enns & Rensink, 2000; Enns & Di Lollo, 2000). These perceptual hypotheses are then thought to descend to lower-level regions in an attempt to match themselves with the actual pattern of incoming sensory input. It is assumed that in cases where the mask persists on the screen for some time after target offset, reentrant representations of the target-mask pair yield a low correlation with the pattern of low-level sensory input coming from the display (i.e., mask alone). This is because sensory activity from the briefly presented target has decayed from the visual system, but the mask has remained at full strength due to its persisting presentation (Di Lollo, 2014). This might result in the visual system discarding its initial interpretation of the target-mask pair and replacing it with a representation of the mask alone (Di Lollo, Enns & Rensink, 2002). In contrast, on trials where the mask terminated simultaneously with the target, reentrant processes would not have encountered conflicting sensory information on the display screen (i.e., the mask only), but rather would encounter a blank stimulus display. This would mean that the initial perceptual hypothesis of the target-mask pair would not need to be discarded, but could continue to be processed until awareness is achieved (Di Lollo, Enns & Rensink, 2002). OSM therefore is argued to provide an ideal psychophysical method for examining the effects of top-down feedback on visual awareness.

An alternative account of OSM is that of the object-updating hypothesis, which states that the simultaneous onset of the target and mask attenuates the visual system's ability to *individuate* these two items into distinct perceptual objects (Enns, Lleras & Moore, 2010). The contours of the target and mask are therefore bound together to form a single object representation. When the mask persists on the screen after target offset, the initial target-mask

representation will be overwritten (or updated) to represent the trailing mask alone (Pilling & Gellatly, 2010). In this way, objects are susceptible to four-dot masking when the visual system fails to establish separate representations of the target and the mask before target offset. On the other hand, when the target and the mask are successfully individuated by the visual system, then target information is protected from being overwritten by the trailing mask (Moore & Lleras, 2005).

The object substitution and object updating accounts find common ground in the assumption that masking is in some way driven by feedback signals from top-down mechanisms. For this reason, the precise mechanisms that drive the effects of OSM masking are irrelevant to testing the aims of the present thesis – to investigate whether top-down mechanisms prompted by top-down signals from visual working memory can influence visual perception. We questioned whether objects that match the contents of visual working memory are more challenging to mask (or less susceptible to visual masking) than novel items.

5.1.3 OSM and Working Memory

In the present study, OSM provided a particularly well suited means of addressing our research question regarding whether top-down effects from working memory could influence visual awareness, as empirical evidence from electrophysiological investigations has convincingly demonstrated the role of working memory in performance during OSM tasks. For example, Prime, Pluchino, Eimer, Dell’Acqua and Jolicoeur (2011) measured event-related potential (ERP) components known to index attentional selection of visual targets (i.e., the N2pc) and storage in working memory (i.e., the sustained posterior contralateral negativity, SPCN) during a target-detection OSM task. They hypothesised that if OSM resulted from overwriting of the target representation by the mask representation during reentrant processes, then delayed-offset masks should interfere with encoding of the target

representation in working memory. Support for this hypothesis was provided by the finding that a spike in the amplitude of the SPCN was observed on trials with correct responses, but not incorrect responses. Furthermore, the amplitude of the N2pc in the delayed-offset condition did not differ by response accuracy, which suggested that participants were able to locate and attend to masked targets even if they were unable to accurately identify the shape. Together, these findings suggest that reduced performance on delayed-offset trials arises from a failure to encode the target stimulus in working memory, rather than a lack of attention at the target location. With this in mind, in Experiment 3 we wondered whether pre-exposure to a memory cue would facilitate efficient encoding of a matching target in working memory, thereby enhancing visual awareness for these match items.

5.1.4 OSM and Signal Detection Tasks

In all of the OSM studies reviewed above, participants were tasked with identifying a specific feature of a target that was indicated by four surrounding dots (e.g., the side of the gap in a Landolt C). However, research has also demonstrated that masking by object substitution can be achieved when participants are asked not to identify specific features of the target, but rather, to detect the presence or absence of the target item. For example, Di Lollo et al. (2000) presented participants with a very brief display consisting of up to sixteen rings. Half of the rings had a vertical bar bisecting the bottom of the shape and participants' were required to indicate whether this bar was present or absent from the target ring. The target ring was identified by the four-dot mask, which either persisted on the screen between 45 ms to 180 ms after target offset or was removed from the display at the same time as the target. Similar to previous findings from target-identification tasks masked by object substitution, it was found that masking developed as a joint function of set size and mask

duration. Specifically, accuracy rates declined as set size increased and mask durations exceeded 45 ms.

Whilst the work above suggests that OSM is an appropriate method of visual masking to be used in conjunction with signal detection tasks, the use of accuracy rates as an index of performance left the results vulnerable to two types of response bias common to target-detection tasks. Specifically, it is possible that participants' responses were biased by their own personal decision criteria regarding the amount of sensory evidence required to confirm the presence/absence of a target item (Stanislaw & Todorov, 1999). However, the dependent measure used by Di Lollo et al. (i.e., mean accuracy values) could not account for the possibility that responses could be biased towards a conservative approach (i.e., participants respond "target absent" even on target-present trials) or a liberal approach (i.e., participants respond "target present" regardless of the strength of the target signal) depending on participants' individual decision criterion.

This limitation has since been remedied by Camp, Pilling, Argyropoulos and Gellatly (2015), who combined OSM with a digit-detection task. Participants were presented with a brief display containing twelve digits positioned in a concentric arrangement. As with the typical OSM paradigm, the target stimulus was identified by four small dots at the corners of a hypothetical square surrounding that item. However, unlike the traditional OSM identification task, the space within the four-dot mask contained a digit on only half of the trials. On the other half, the space within the four dots was left blank. Participants were required to indicate whether the target digit was present or absent at the mask location. To ensure that the data reflected sensitivity to the target, rather than response bias, the researchers utilised d' as their dependent measure, which is known to distinguish between the two (Stanislaw & Todorov, 1999). Good detection ability is indicated by higher values of d' , whereas values of d' that are equal to or approaching zero indicate that the participant was

unable to detect the presence of the target. Consistent with typical OSM effects, Camp et al. found that d' decreased as set size and mask duration increased. Specifically, participants' ability to determine whether the target item was present or absent was significantly hindered by the presence of multiple distractors and a delayed mask-offset of 180 ms. This finding is particularly important, as it attests to the generality of masking by object substitution to signal detection tasks.

5.3 Aims and Hypotheses

Based on the findings of Di Lollo and colleagues, our first hypothesis was that the delayed offset of the four-dot mask would suppress visual awareness, whereas this would not be the case for simultaneous mask-target offsets. This would be demonstrated by a significant main effect of Mask Offset, with higher detection sensitivity on trials with simultaneous mask-target offsets, relative to delayed-offset trials. Our second hypothesis was based on reentrant accounts of OSM effects and empirical evidence demonstrating the involvement of working memory in masking by object substitution (Prime et al., 2011). We reasoned that if a target shape could be processed more efficiently, then fewer reentrant iterations would be required to achieve visual awareness. The target representation would therefore be less likely to have decayed (and be replaced with a representation of the mask alone) before a perceptual match occurred between lower- and higher-order codes. Based on research that suggests that items held in visual working memory capture attention and, hence, are 'noticed' more efficiently (Soto et al., 2005; Kumar et al., 2009; Han & Kim, 2009), we hypothesised that targets that matched the memory cue would be processed over fewer iterations and be more likely to enter visual awareness than no-match targets on delayed-offset trials. We predicted that there would be a significant interaction between Mask Offset and Memory Match, such

that the difference in detection sensitivity between simultaneous and delayed-offset conditions would be smaller for match items than for no-match items.

5.3 Methods

5.3.1 Design

Experiment 3 used a 2 x 2 x 2 fully-crossed factorial design. The factors were Memory Match (match vs. no-match), Mask Offset (simultaneous-offset vs. delayed-offset), and Target Presence (present vs. absent). Participants completed three practice blocks (not included in the analysis) and 12 experimental blocks over a 45-minute testing session. Each block was comprised of twelve experimental runs; with each run including one memory probe and four OSM detection trials. Therefore, there were 48 detection trials per block and there was a total of 576 detection trials over the entire experiment (i.e., 48 trials per block x 12 blocks).

5.3.2 Participants

A different group of 16 Macquarie University undergraduate students aged between 18 and 31 years ($M = 22.94$ years, females = 12) were recruited to participate in Experiment 3 for course credit or financial reimbursement. This number is consistent with previous studies that have found significant masking effects using OSM (Di Lollo & Enns, 1997; Enns & Di Lollo, 1997; Di Lollo, Enns & Rensink, 2000). All participants reported to be strongly right-handed, with normal or corrected-to-normal vision, and provided their written informed consent. The study was approved by the Macquarie University Human Research Ethics Committee (reference number = 5201300060) and procedures were in accordance with the Declaration of Helsinki.

5.3.3 Apparatus, Stimuli, and Procedure

Participants sat upright at a rigid table in front of a 60 cm x 34 cm LED monitor positioned 70 cm from the front edge of the desk. As in Experiment 2, participants responded to all trials using a computer mouse click.

The visual trial structure for Experiment 3 can be seen in Figure 12. Each trial was self-initiated by clicking the computer mouse. Participants were instructed to remember an initial memory cue that appeared at fixation and persisted on the screen until participants clicked the mouse to continue. Both the memory cue and the critical targets were randomly selected from a total of 12 shapes. The memory cue and targets extended 1.07 degrees of visual angle. Participants were then presented with four OSM detection trials in which they were required to indicate whether a target displayed for 16 ms was either present or absent. The target was presented on the screen on 50% of the trials and it was absent on the remaining 50%. The target location was indicated by four small dots at the corners of a hypothetical square surrounding the location of the target shape. Target and distractor stimuli were randomly assigned to one of twelve possible locations and were arranged in a circular pattern, with each item positioned 5.73 degrees from central fixation. Mask durations varied according to two offsets; either the mask was removed from the screen at the same time as the target (when it was present) and distractors (i.e., simultaneous-offset) or the mask persisted on the screen for 200 ms after display offset (i.e., delayed-offset).

Participants were instructed to keep their eyes fixed on a central point throughout the OSM trials. On one out of every four OSM trials the target shape was identical to the memory cue. Each of the 12 shapes were presented as a critical match target once per block (i.e., four OSM trials per run; 12 runs per block). Participants' memory for the memory cue was then probed using the same circular arrangement of twelve shapes (i.e., one target shape and eleven

distractor shapes) which remained on the screen until response. A single experimental run therefore involved the presentation of a memory cue, four OSM detection trials, and a memory probe.

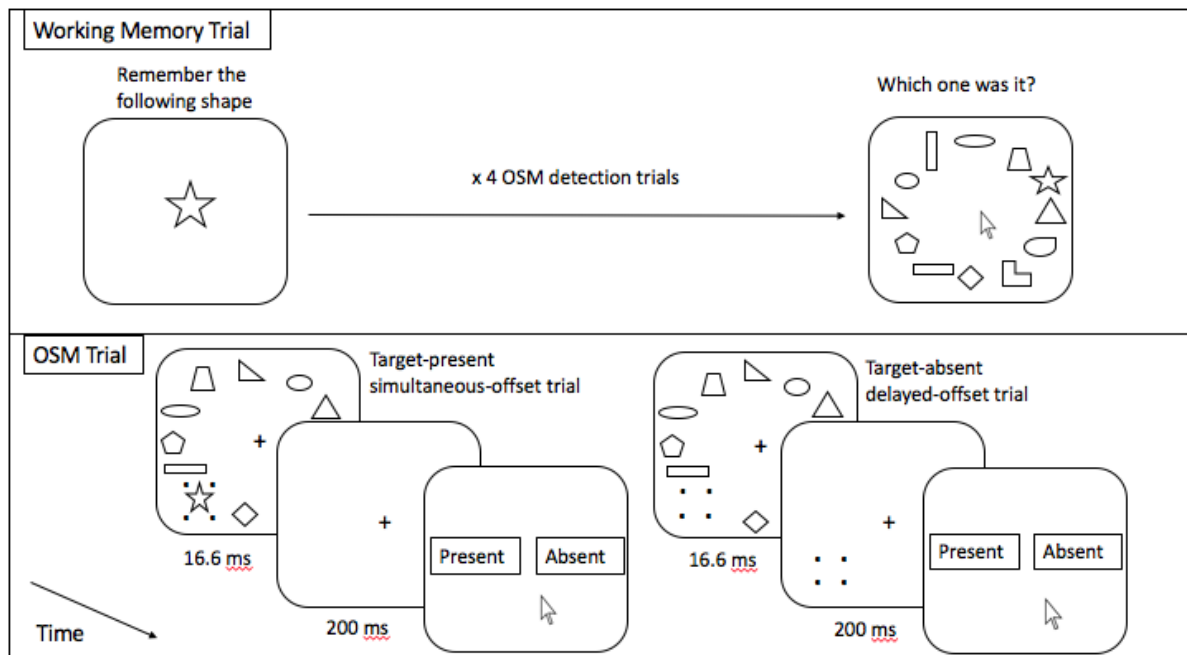


Figure 12. Visual run structure for Experiment 3. Participants were presented with a memory cue that they were required to recall at the end of the run (top panel). They were then presented with four OSM trials in which they had to indicate whether a target shape was either present (left sequence of bottom panel) or absent (right sequence of bottom panel). The target location was indicated by four dots surrounding the shape. Mask offset was either simultaneous with the target (left sequence of bottom panel) or delayed by 200 ms (right sequence of bottom panel). On one out of every four target-present trials the target shape was identical to the memory cue. Memory for the initial shape was then probed using a circular arrangement of twelve shapes.

5.4. Experiment 3 Results

Practice trials were excluded from the analysis. All data were analysed using custom software written in R (www.rproject.org). The significance level for all analyses was set at $\alpha = 0.05$.

5.4.1 Data Analysis

Experiment 3 required participants to distinguish between target-present and target-absent trials. Decisions were based on participants' own personal decision criterion for determining whether sensory evidence was sufficient to conclude that a target was present. This type of design was vulnerable to two types of response bias; responses could either be biased towards a conservative approach or a liberal approach depending on the participant's personal decision criterion. For example, a liberal criterion can bias participants to respond "target present" regardless of the strength of the target signal. In contrast, a conservative criterion can cause participants to respond "target absent" even on target-present trials. The *hit* rate (i.e., the probability of responding "target present" on target-present trials) and *false-alarm* rate (i.e., the probability of responding "target present" on target-absent trials) can therefore be considered as reflecting two things: response bias and true sensitivity to the target stimulus (Stanislaw & Todorov, 1999).

To ensure that our data reflected sensitivity to the target, rather than response bias, we utilised d' as our dependent measure, which is known to distinguish between the two (Stanislaw & Todorov, 1999). Good detection ability is indicated by higher values of d' . In contrast, when d' is equal to or approaching zero, then this indicates that the participant was unable to detect the presence of the target. We calculated d' by subtracting the z-score that corresponded to the *false-alarm* rate from the z-score that corresponded to the *hit* rate (Macmillan, 1993). However, a *hit* or *false-alarm* rate of zero or one is equal to a z-score of plus or minus infinity. This makes it difficult to obtain a sensible estimate of d' for these

cases. To correct for *hit* and *false-alarm* rates that equalled either zero or one, we used the log-linear rule as described by Hautus (1995). Specifically, we added 0.5 to the number of *hits* and the number of *false-alarms* before calculating d' .

5.4.2 Results

The results of Experiment 3, averaged over all 12 target locations, are presented here¹. The mean accuracy for the memory probe trials averaged across all participants was 88.82%, indicating that participants were successfully holding the memory cue in mind during the OSM detection trials. To determine whether there was a correlation between participants' ability to remember the memory cue and their performance on the OSM trials, we calculated the effect of memory match by subtracting each participant's mean accuracy on no-match trials from accuracy on match trials. We then tested for a correlation between this variable and mean recall accuracy and found that the relationship was not significant ($r_{(14)} = -0.07$, $p = 0.78$, see Figure 13). The lack of a correlation here suggests that participants with greater ability to remember the memory cue were no more likely to detect the presence or absence of a memory-match target shape, compared to participants who performed poorly on the memory probe trials. We found a significant main effect of Mask Offset [$F_{(1, 15)} = 59.4$, $p < 0.0001$]. Detection sensitivity was higher on simultaneous-offset trials ($d' = 2.087$), relative to delayed-offset trials ($d' = 0.666$). In contrast, the main effect of Memory Match [$F_{(1, 15)} = 0.052$, $p = 0.823$] was not significant, as detection sensitivity did not differ according to match ($d' = 1.385$) and no-match trials ($d' = 1.367$). The interaction between Memory Match and Mask Offset [$F_{(1, 15)} = 2.376$, $p = 0.144$] was also not significant (see Figure 14).

¹ Target Presence was not included in the main analysis, as the difference between detection sensitivity for target-present (68.81%) and target-absent trials (71.19%) was not significant [$F_{(1, 15)} = 1.795$, $p = 0.20$].

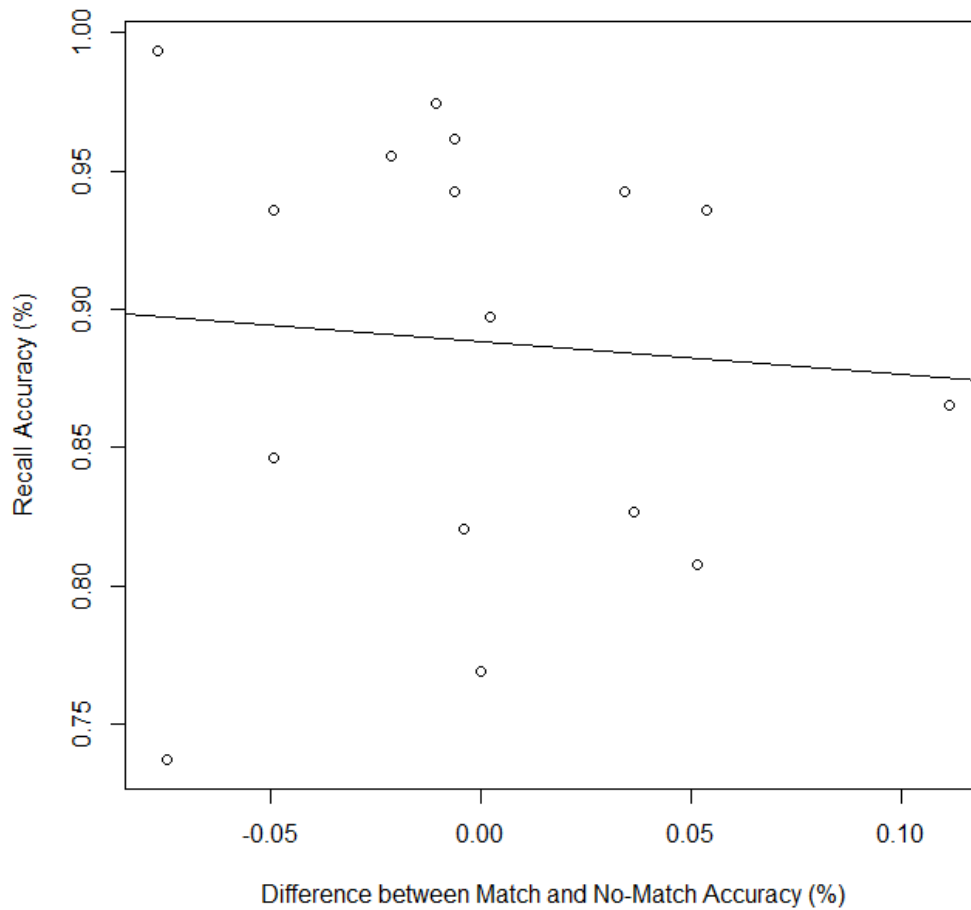


Figure 13. Scatterplot depicting the correlation between memory recall and the effect of Memory Match on detection accuracy. This figure shows that participants' ability to remember the memory cue was not correlated with the effect of Memory Match on their ability to detect the presence/absence of a target stimulus. Participants with greater ability to remember the memory cue were no more likely to detect a memory-match target on OSM trials, compared to participants who performed poorly on the memory probe trials.

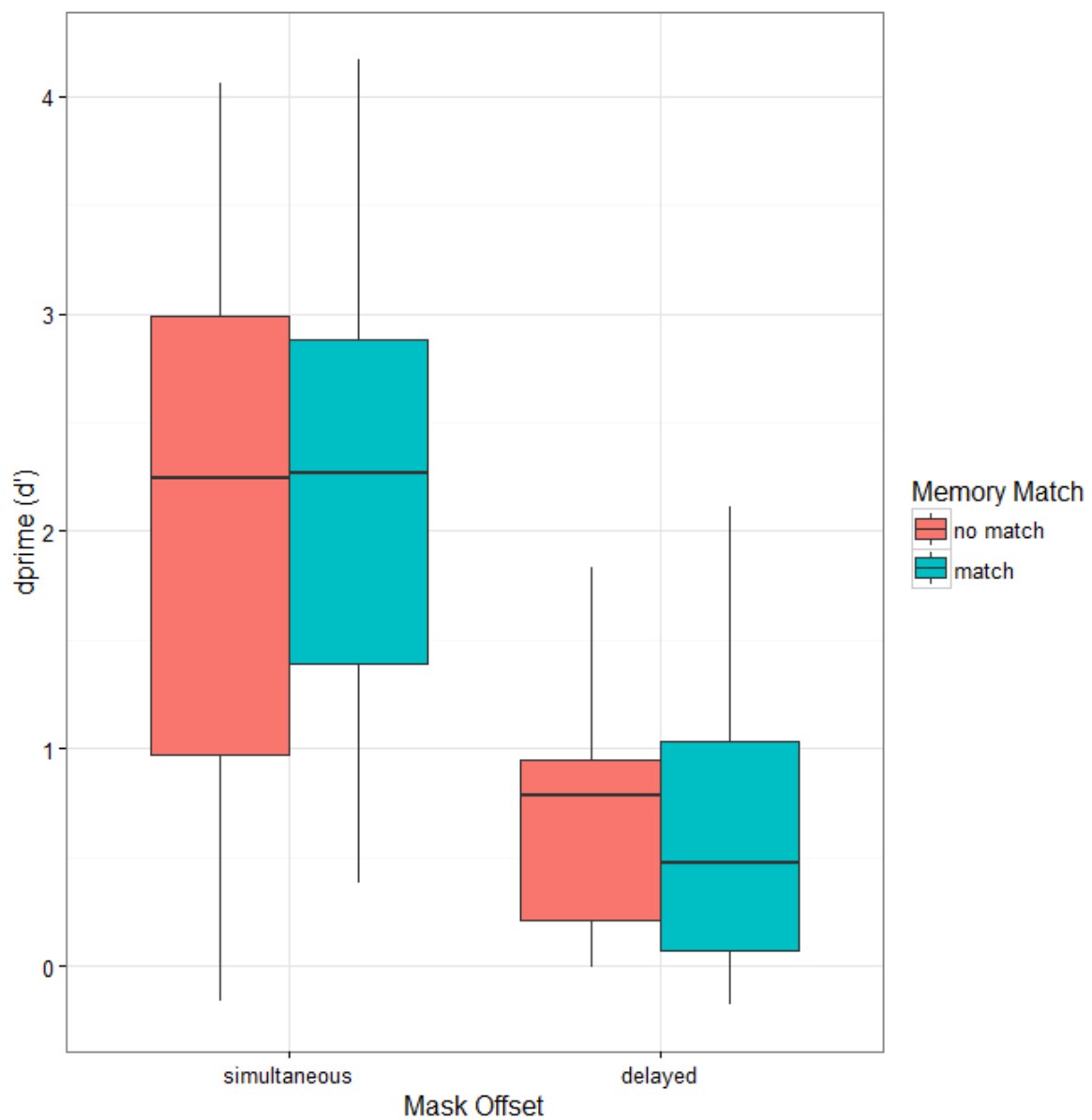


Figure 14. Values of d' separated by whether mask offset was simultaneous or delayed, relative to target offset. This figure shows a clear main effect of Mask Offset, in that the horizontal line representing the median for simultaneous mask offset is significantly higher than that of the median for delayed mask offset for both match and no-match targets. However, the medians for match and no-match trials were not significantly different for both simultaneous and delayed mask offsets.

5.4.3 Post Hoc Examination of Non-Significant Results

Inferential statistics do not allow for the interpretation of null findings (i.e., p value greater than 0.05). This is because a non-significant result can mean two things: either that the data are insensitive in distinguishing the alternative hypothesis from the null hypothesis; or that there is in fact sufficient evidence to conclude in favour of the null hypothesis (Dienes, 2014). We therefore could not interpret the large p values obtained for the effect of interest and interaction term in Experiment 3. To determine whether we had indeed obtained substantial evidence in favour of the null hypothesis, or whether our data was insensitive to disentangle the alternative hypothesis from the null hypothesis, we used the Bayes Factor package in R (Morey & Rouder, 2011; Morey, Rouder & Jamil, 2015) to run a repeated measures ANOVA with Participant as a random factor that compared Mask Offset, Memory Match, and all interaction contrasts. A Bayes Factor (B) close to or greater than 3 indicates that there is substantial evidence in favour of the alternative hypothesis; B close to or less than $1/3$ indicates that there is substantial evidence in favour of the null hypothesis; and values of B that fall between $1/3$ and 3 indicate that there is insufficient evidence to discriminate between the null and alternative hypothesis (Jeffreys, 1961; Dienes, 2014). In line with previous findings, we found substantial evidence supporting the effect of Mask Offset on detection sensitivity ($B > 1000000$). We found substantial evidence supporting the null hypothesis that Memory Match did not impact upon detection sensitivity ($B = 0.252$), which extends upon the results above. We also found evidence in favour of the null hypothesis that the difference between performance for trials with simultaneous- and delayed-offset masks was not modulated by whether or not the target matched the contents of working memory ($B = 0.368$).

5.5 Interim Discussion for Experiment 3

As predicted, the results of Experiment 3 revealed a reliable effect of Mask Offset, in that target detection was significantly worse in the delayed-offset condition, relative to when the offsets of the target and mask were simultaneous. This finding replicated previous results (Di Lollo et al., 2000; Di Lollo et al., 2002; Camp et al., 2015) and provided convincing evidence that we had effectively suppressed visual awareness using an OSM paradigm. In contrast, both the main effect of Memory Match and the interaction between Memory Match and Mask Offset were not significant. As inferential statistics do not allow for the interpretation of non-significant results, we used Bayesian statistics to determine whether the observed null effects reflected substantial evidence in favour of the null hypothesis or rather reflected an insensitivity within the data to distinguish between the null and alternative hypotheses. In doing so, we eliminated the possibility that the data were insensitive to the different distributions encompassing the null and alternative hypotheses. Instead, we found substantial evidence supporting the null hypothesis that detection sensitivity in an OSM paradigm was not modulated by whether or not the target shape matched the contents of working memory.

5.5.1 Discussion

This null result was particularly unexpected and seemingly inconsistent with work by Soto and Humphreys (2006). These researchers had previously reported that enhanced awareness could be achieved in patients with visual extinction when there was a match between the contents of their working memory and the stimuli presented to their otherwise neglected visual field. However, there are reasons to think that the apparent discrepancy between our own results and previous research can be attributed to slight differences in the

experimental paradigms between the different studies. Consider, for example, the ways in which participants located the target shape across the two studies. Specifically, Soto and Humphreys presented patients with targets that appeared in the same two locations throughout the task (i.e., the left and right sides of the visual display, in line with fixation). This meant that patients were required to monitor only two positions in space when attempting to identify the target. Due to their lesion they were less able to direct their attention to the contralateral target location, but this was facilitated by a match between the target item and memory cue. In contrast, in the present study participants located the target by searching for four salient black dots that could be displayed in one of twelve spatial locations. This required attention to be distributed across the entire display, rather than being focused on two specific spatial locations. Furthermore, attentional selection was most likely guided by a preactivated search template of the four-dot mask and not of the target itself. Once participants had located the four dots, they could provide a correct response simply by detecting whether a flicker of light did or did not appear within the four dots. This meant that participants were never directly searching for the target shape, were never required to process its visual features, and, hence, did not benefit when the target shape matched the shape held in working memory.

6. General Discussion

The aim of the present study was to test whether top-down effects from working memory can facilitate efficient visual perception for targets that matched preactivated representations of items held in mind. To achieve this aim, we modified Soto and Humphreys' (2006) working memory task by incorporating visual masking in the form of TMS to the occipital pole. However, we were unable to adequately suppress visual awareness using this technique and we instead provide a detailed discussion of the difficulties in localising area V1 using external anatomical landmarks. In Experiment 3, we adapted Enns and Di Lollo's OSM paradigm to incorporate a working memory component. Participants were presented with a memory cue that they were required to recall at the end of the experimental run. They were then presented with four OSM detection trials that were each comprised of a circular search array containing a target shape. The task was to determine whether the target shape was either present or absent from the display screen. The location of the target was indicated by four small dots positioned on the corners of a small imaginary square. These dots not only identified the target, but also acted as the masking stimulus. For instance, on approximately half the trials the mask persisted on the screen for some time after target offset. On these trials, we predicted that detection sensitivity would be reduced due to degraded visual perception. On the other 50 percent of trials, the target and mask shared a simultaneous-offset and we expected that target detection would be unimpaired. The critical manipulation was whether or not the target shape was a direct match to the memory cue or not. Specifically, on one out of every four target-present trials the target shape matched the memory cue and we predicted that these targets would be less susceptible to masking by object-substitution than non-matching targets.

6.1 Findings

There are two notable findings reported in the present study. Our first finding was consistent with our hypothesis that performance in an OSM paradigm would be modulated by whether or not the offset of the mask was simultaneous or delayed relative to target offset. We found that participants were more likely to detect the presence of a target when the mask and target had a simultaneous offset, relative to when the mask persisted on the screen for 200 ms after target offset. This finding replicated previous work showing that a temporally trailing four-dot mask obscured the visibility of a briefly presented target shape (Di Lollo et al., 2000; Di Lollo et al., 2002). We were therefore confident that our implementation of masking by object-substitution was effective in degrading visual perception.

Consistent with the views of Enns and Di Lollo (2000), we believe that this finding is the result of iterative reentrant processing in the visual system, such that masking occurred when there was a mismatch between the reentrant visual representation and the low-level sensory information from the display. Specifically, on trials where the mask persisted on the screen after target offset, reentrant representations of the target-mask pair yielded a low correlation with the actual pattern of low-level activity from the mask alone. This is because sensory activity from the briefly presented target had presumably decayed from the visual system, but the mask had remained at full strength due to its persisting presentation. Object substitution theory proposes that in these instances the visual system discards its initial interpretation of the target-mask pair and replaces it with a representation of the mask alone (Di Lollo, 2014). In the present experiment, this would have resulted in participants being much more likely to see only the mask item on delayed-offset trials, without any awareness (or ‘forgetting’) that a target stimulus had been presented. In contrast, on trials where the mask terminated simultaneously with the target, reentrant processes would not have conflicted with an interfering stimulus present on the screen (i.e., the mask only), but rather would have

encountered a blank stimulus display. This meant that the initial perceptual hypothesis of the target-mask pair would not be discarded, but would continue to be processed until awareness was achieved.

An alternative account of OSM is that of the object-updating hypothesis, which states that the simultaneous onset of the target and mask attenuates the visual system's ability to *individuate* these two items into distinct perceptual objects (Enns, Lleras & Moore, 2010). The contours of the target and mask are therefore bound together to form a single object representation. When the mask persists on the screen after target offset, the initial target-mask representation will be overwritten (or updated) to represent the trailing mask alone (Pilling & Gellatly, 2010). In this way, objects are susceptible to four-dot masking when the visual system fails to establish separate representations of the target and the mask before target offset. On the other hand, when the target and the mask are successfully individuated by the visual system, then target information is protected from being overwritten by the trailing mask (Moore & Lleras, 2005). The object substitution and object updating accounts find common ground in the assumption that masking is in some way driven by feedback signals and top-down mechanisms. The precise ways in which this occurs is beyond the scope and irrelevant to the findings of the present thesis. This is because OSM was selected as a tool to investigate whether objects that match the contents of visual working memory are more challenging to mask (or less susceptible to visual masking) than novel items.

Interestingly, the second result to be discussed is the finding of no evidence of a Memory Match effect. We had initially predicted that targets that matched the contents of working memory would be less susceptible to OSM, relative to non-matching targets. However, we were unable to reject the null hypothesis that there was no difference between matching and non-matching targets, as we obtained statistically non-significant *p*-values for the main effect of Memory Match and the interaction between Mask Offset and Memory

Match. For this reason, we utilised Bayesian statistics to examine the relative strength of evidence in favour of both the null and alternative hypotheses. Recall that the calculation of a Bayes Factor enables researchers to interpret null findings by providing an indication of whether the data were simply insensitive to distinguish between the null and alternative hypotheses (i.e., $1/3 < B < 3$) or whether there was ample evidence in favour of the null hypothesis ($B < 1/3$, Jeffreys, 1961). In using this measure, we found substantial evidence in favour of the null hypothesis and concluded that the impact of Mask Offset on detection sensitivity was not modulated by whether or not targets matched the contents of working memory.

At first glance, this null effect seems to conflict with the previous finding reported by Soto and Humphreys (2006) that items held in mind facilitated enhanced awareness of targets within the otherwise neglected visual field in patients with visual extinction. But there are reasons to think that the apparent discrepancy between our own results and previous research can be attributed to slight differences in the experimental paradigms between the different studies. For example, Soto and Humphreys presented patients with targets that appeared in the same two locations throughout the task (i.e., the left and right sides of the visual display, in line with fixation). This meant that patients were required to monitor only two positions in space when attempting to identify the target. In contrast, participants in Experiment 3 of the present study located the target by searching for four salient black dots that could be displayed in one of twelve spatial locations. This required attention to be distributed across the entire display, rather than being focused on two specific spatial locations. Furthermore, Soto and Humphreys utilised a target identification task, such that the target needed to be processed to the level of identification for successful task completion. In the present study, we used a target-detection task that required participants simply to indicate whether a target was either present or absent from the display screen.

Critically, this difference may have led to participants adopting two very different task sets across the two studies. In our task, participants may have adopted a “detect four dots” task set initially, followed by a “detect object presence” task set. Note that if participants did in fact adopt these task sets, then they would still be able to perform the task in Experiment 3 without, importantly, having to match the target with the item being held in working memory. Thus, it may not be surprising that our participants did not exhibit a memory effect. Indeed, where significant effects of working memory have been found participants were required to **identify** visual features of the target stimulus (Soto, Heinke, Humphreys and Blanco, 2005; Soto, Humphreys & Heinke, 2006; Kumar, Soto & Humphreys, 2013), whereas studies that failed to show a processing advantage for working memory items used similar **detection** tasks to that of the present research (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006).

With this in mind, it might be tempting to question why we used a detection task in our final experiment. The reasoning comes from the findings of Experiment 1, in which identification of targets presented under masked conditions resulted in a striking response bias in which participants responded in favour of the memory cue option, regardless of the true target identity. To explain why the results of Soto and Humphreys were not vulnerable to the same response bias it is necessary to consider a final discrepancy between their study and our own. In the previous research, patients with visual extinction were presented with either a one-object trial (i.e., target shape appeared on the left OR right) or two-object trial (i.e., target shape appeared on the left AND right). These two trial types were randomly interleaved within an experimental block, such that the patients were not able to predict whether they would be required to report on the identity of one shape or of two shapes. This meant that when presented with a two-object trial in which the contralateral target did not match the memory cue, patients could report the colour and shape of the ipsilesional target only, without being prompted to guess the identity of the contralateral target. In contrast, in the present

study participants were always required to make a response about the identity of the target shape, even if they did not see it. This left participants vulnerable to utilising a form of sophisticated guessing, in which they responded in favour of the memory item when it was presented as a response option. A challenge for future researchers using masked identification tasks will be to disentangle this potential for response bias from enhanced visual awareness for items that match the contents of the mind.

6.2 Limitations and Future Directions

The present research was faced with two notable limitations. Firstly, the results of both Experiment 1 and Experiment 2 revealed that we were not successful in our attempts to suppress visual awareness using TMS to the occipital pole. Although we observed a reliable effect of SOA in Experiment 1, we found that participants' responses were more likely to be correct when TMS was applied at 200 ms after target onset, rather than 100 ms. The direction of this effect was in conflict with the many studies that claim to have suppressed visual awareness using TMS to the occipital pole at precisely 100 ms post target onset, with no impact on visual processing at 200 ms after the arrival of the target (Amassian et al., 1989; Boyer et al., 2005; Kammer et al., 2005; Kammer, 2007). Furthermore, in Experiment 2 our data were subject to a striking ceiling effect, in that participants performed near perfectly across all experimental conditions. This reaffirmed that we had not suppressed visual awareness using occipital lobe TMS. Again, this was surprising as we had precisely replicated the necessary parameters required for visual suppression by TMS, which included setting magnetic field intensity at equal to or greater than 1.5 Tesla (Kammer et al., 2005), administering magnetic stimuli within an 80–120 ms temporal window (Kammer, 2007), presenting targets for one refresh rate or 8.3 ms (Amassian et al., 1989; Boyer et al., 2005),

constraining targets to 0.25 degrees of visual angle (Boyer et al., 2005), and presenting targets at 3 degrees below visual fixation (Kastner et al., 1998).

We believe that there are two main reasons that explain why we were unable to mask target stimuli using occipital lobe TMS. Firstly, research has shown that visual scotomas can only be induced in participants with a favourable scalp anatomy, with these participants making up approximately half of the population (Kastner et al., 1998). Although unfortunate, it is not unreasonable to assume that participants in our investigations all had an “unfavourable” scalp configuration for visual suppression by TMS. Secondly, it has also been demonstrated that using theinion as an external anatomical landmark (as was done in the present research) is unlikely to result in cortical stimulation of V1, which is required for visual suppression by TMS (Salminen-Vaparanta et al., 2012). Those who wish to utilise occipital lobe TMS in the future might fare better in using fMRI in combination with a stereotactic navigation system to more accurately localise V1 (Kammer, 2007). Nevertheless, to address the concern that we were unlikely to mask visual perception using external anatomical landmarks to guide the application of TMS, we decided to utilise an alternative method of visual masking that precluded explanation by feedforward accounts of visual awareness, being masking by object-substitution (Enns & Di Lollo, 1997). In a typical OSM paradigm, both the target and mask are equally represented within the feedforward stream, such that visual processing is assumed to be disrupted at the re-entry stage (Di Lollo et al., 2000; 2002; Di Lollo, 2014). Given that we observed a reliable effect of Mask Offset, with target detection being significantly worse for delayed-offset than simultaneous-offset trials, we were confident that we had sufficiently masked our targets and remedied the limitations of Experiment 1 and 2.

A second limitation of the present study stemmed from the observation in Experiment 1 that accuracy was significantly higher for match than no-match targets, even though we were confident that TMS had **not** masked visual awareness. Without a convincing demonstration of masking by TMS, we could not conclude that our significant main effect of Memory Match provided evidence in favour of our hypothesis that working memory enhanced visual awareness for otherwise degraded targets. Therefore, the question still remained as to what was driving this effect? The answer to this query became strikingly clear upon closer inspection and re-analysis of the data. We pulled out trials in which the target item did not match the memory cue and then divided participants' responses to these no-match trials according to whether or not one of the response options matched the memory cue. This enabled us to obtain participants' mean accuracy as a function of whether the memory cue was available as a response option on the classification trial. We reasoned that if participants were selecting the memory cue response option at greater than chance levels, then their accuracy should be significantly worse when the memory cue was present, compared to when it was not. Consistent with this, we found a significant perceptual bias in favour of the memory cue across all participants in this experiment.

Consequently, the results of our first experiment did not reflect enhanced awareness for items that matched the contents of working memory, but rather, were driven by a strong bias to select the response option that matched the memory cue regardless of the item that was presented on target-classification trials. This finding in itself is somewhat interesting; it suggests that our responses are biased towards representations held in mind (or expectations about upcoming stimuli) even when this information is detrimental to successful task performance. Such a result is reminiscent of the findings reported by Soto et al., (2005; 2006; 2013) that active maintenance of an item in working memory elicited faster responding to matching distractor items. The notion that behaviour can be influenced by task-irrelevant

information from the active maintenance of items in working memory is an interesting avenue for future research to consider. Nevertheless, the existence of such a prominent perceptual bias in our study meant that Experiment 1 was severely limited by poor internal validity, in that the data could be plausibly accounted for by an alternative explanation. To eliminate the influence of a perceptual bias, and improve upon internal validity, we chose to modify the design of Experiment 1 so that the decision required from participants was no longer centred on the visual properties of the stimuli themselves. Whilst Experiment 2 provided no clarification about whether we had remedied this limitation due to the massive ceiling effect in the data, the null findings of Experiment 3 (although disappointing) confirmed to us that we had effectively eliminated any response bias within the data.

6.3 Conclusion

In summary, the results of the present study suggest that merely holding something in working memory is not sufficient to enhance awareness of otherwise difficult to detect visual targets. Despite the fact that we obtained clear evidence that participants were actively maintaining the memory cues in mind, targets that matched the contents of working memory were equally as susceptible to masking by object substitution as non-matching targets. Importantly, our study has merit in the application of novel statistical techniques to overcome the limitations of obtaining large p -values when using inferential statistics. Specifically, we utilised Bayesian statistics and found substantial evidence in favour of the null hypothesis, which could not be accounted for by data insensitivity or a lack of statistical power. This study highlights the significant challenges in investigating top-down effects from working memory in a neurotypical population. Future research will need to address ways in which

enhanced awareness can be disentangled from response bias when using identification tasks with targets presented under masked conditions.

References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19, 716-723.
- Amassian, V. E., Cracco, R. Q., Maccabee, P. J., Cracco, J. B., Rudell, A., & Eberle, L. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and Clinical Neurophysiology*, 74(6), 458-462
- Aminoff, E. M., Gronau, N., & Bar, M. (2007). The parahippocampal cortex mediates spatial and nonspatial associations. *Cerebral Cortex*, 17(7), 1493-1503
- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modelling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59, 390-412.
- Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*, 55(5), 485-496
- Bates, D. (2005). Fitting linear mixed models in R. *R News*, 5, 27-30.
- Bates, D., Maechler, M., & Bolker, B. (2011). Linear mixed-effects models using Eigen and R syntax. R package version 0.999375-42, <http://lme4.r-forge.r-project.org/>
- Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, 15(4), 600-609
- Bar, M. (2007). The proactive brain: Using analogies and associations to generate predictions.

Trends in Cognitive Sciences, 11(7), 280-289

Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron*, 38(2), 347-358

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmidt, A. M., Dale, A. M.,

...Haldren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the*

National Academy of Sciences of the United States of America, 103(2), 449-454

Bar, M., Tootell, R., Schacter, D., Greve, D., Fischl, B., Mendola, J., Rosen, B. & Dale, A.

(2001). Cortical mechanisms of explicit visual object recognition. *Neuron*, 29(2), 529

535.

Barker, A. T. (1991). An introduction to the basic principles of magnetic nerve stimulation.

Journal of Clinical Neurophysiology, 8(1), 26-37

Barker, A. T. (2002). The history and basic principles of magnetic nerve stimulation. In A.

Pascual-Leone., N. Davey., J. Rothwell., E. M. Wasserman., B. K. Puri. (Eds.),

Handbook of transcranial magnetic stimulation (pp. 3–17) New York, NY: Oxford

University Press.

Boyer, J. L., Harrison, S., & Ro, T. (2005). Unconscious processing of orientation and color

without primary visual cortex. *Proceedings of the National Academy of Sciences of the*

United States of America, 102(46), 16875-16879

Breitmeyer, B., & Ganz., L. (1976). Implications of sustained and transient channels for

theories of visual pattern masking, saccadic suppression, and information processing.

Psychological Review, 83(1), 1–36.

- Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, 36(1), 96-107
- Camp, S. J., Pilling, M., Argyropoulos, I., & Gellatly, A. (2015). The role of distractors in object substitution masking. *Journal of Experimental Psychology: Human Perception and Performance*, 41(4), 940-957
- Carlsson, K., Petrovic, P., Skare, S., Petersson, K. M., Ingvar, & M. (2000). Tickling expectations: Neural processing in anticipation of a sensory stimulus. *Journal of Cognitive Neuroscience*, 12(4), 691–703
- Cavaada, C., Company, T., Tejedor, J., Cruz –Rizzolo, R. J., Reinoso-Suarez, & F. (2000). The anatomical connections of the macaque monkey orbitofrontal cortex: A review. *Cerebral Cortex*, 10(3), 220–242
- Courthout, E., Uttl, B., Walsh, V., Hallett, M., & Cowey, A. Timing of activity in early visual cortex as revealed by transcranial magnetic stimulation. *NeuroReport: Cognitive Neuroscience and Neurophysiology*, 10(12), 2631-2634
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective attention. *Annual Review of Neuroscience*, 18, 193-222
- Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, 5(781), 1-17
- Di Lollo, V. (2014). Reentrant processing mediates object substitution masking: A comment on Pöder (2013). *Frontiers in Psychology*, 5(819), 1-5

- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Physiology: General*, 129(4), 481-507
- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2002). Object substitution without reentry? *Journal of Experimental Physiology: General*, 131(4), 594-596
- Downing, P. E, & Dodds, C. M. (2004). Competition in visual working memory for control of search. *Visual Cognition*, 11(6), 689-703
- Enns, J. T. (2004). Object substitution and its relation to other forms of visual masking. *Vision Research*, 44(12), 1321-1331
- Enns, J. T., & Di Lollo, V. (1997). Object substitution: A new form of masking in unattended visual locations. *Psychological Science*, 8(2), 135-139
- Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Sciences*, 4(9), 345-352
- Francis, G. (1997). Cortical dynamics of lateral inhibition: Metacontrast masking. *Psychological Review*, 104(3), 572-594
- Felleman, D. J., & Van Essen. D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1047-3211
- Han, S. W., & Kim. M. S. (2009). Do the contents of working memory capture attention? Yes, but cognitive control matters. *Journal of Experimental Psychology: Human*

Perception and Performance, 35(5), 1292-1302

- Hautus, M. (1995). Corrections for extreme proportions and their biasing effects on estimated values of d' . *Behavior Research Methods, Instruments, & Computers*, 27(1), 46-51
- Hinds, O., Polimeni, J. R., Rajendran, N., Balasubramanian, M., Wald, L. L., Augustinack, J. C., ... Schwartz, E. L. (2008). The intrinsic shape of human and macaque primary visual cortex. *Cerebral Cortex*, 18(11), 2596-2595
- Houtkamp, R., & Roelfsema, P. R. (2006). The effect of items in working memory on the deployment of attention and the eyes during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 32(2), 423-442
- Hubel, D. H., & Wiesel. T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat visual cortex. *Journal of Physiology*, 160, 106-154
- Hubel, D. H., & Wiesel. T. N. (1968a). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215-243
- Hubel, D. H., & Wiesel. T. N. (1968b). Sequence regularity and geometry of orientation columns in the monkey striate cortex. *Journal of Comparative Neurology*, 158(3), 267-293
- Hupé, J. M., James, A. C., Girard, J., Payne, B. R., & Bullier, J. (2001). Feedback connections act on the early part of the responses in monkey visual cortex. *Journal of Neurophysiology*, 85(1), 134-145

Jeffreys, H. (1961). *The Theory of Probability*. Oxford, England: Oxford

University Press.

Kammer, T. (2007). Masking visual stimuli by transcranial magnetic stimulation.

Psychological Research, 71(1), 659-666

Kammer, T., Puls, K., Strasburger, H., Hill, N. J., & Wichmann, F. A. (2005). Transcranial

magnetic stimulation in the visual system. I. The psychophysics of visual suppression.

Experimental Brain Research, 160(1), 118-128

Kammer, T., & Nusseck, H. (1998). Are recognition deficits following occipital lobe TMS

explained by raised detection thresholds? *Neuropsychologia*, 36(11), 1161-1166

Kanwisher, N., McDermott, J., & Chun, M. M (1997). The Fusiform Face Area: A module in

human extrastriate cortex specialised for face perception. *The Journal of*

Neuroscience, 17(11), 4302-4311

Karnath, H-O. (1988). Deficits of attention in acute and recovered visual hemi-neglect.

Neuropsychologia, 26(1), 27-43

Kastner, S., Demmer, I., & Ziemann, U. (1998). Transient visual field defects induced by

transcranial magnetic stimulation over human occipital pole. *Experimental Brain*

Research, 118(1), 19-26

Keel, J. C., Smith, M. J., & Wassermann, E. M. (2001). A safety screening questionnaire for

transcranial magnetic stimulation: Letter to the editor. *Clinical Neurophysiology*, 112,

720

- Kennedy, H., & Bullier, J. (1985). A double-labelling investigation of the afferent connectivity to cortical areas V1 and V2 of the macaque monkey. *Journal of Neuroscience*, 5(1), 2815-2830
- Kim, M. S., & Cave, K. R. (1999). Top-down and bottom-up attentional control: On the nature of interference from a salient distractor. *Perception & Psychophysics*, 61(6), 1009-23.
- Kumar, S., Soto, D., & Humphreys, G. W. (2013). Electrophysiological evidence for attentional guidance by the contents of working memory. *European Journal of Neuroscience*, 30(2), 307-317
- Lamme, V. A. F. (2001). Zap! Magnetic tricks on conscious and unconscious vision. *Trends in Cognitive Sciences*, 10(5), 193-195
- Lamme, V. A. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, 10(11), 494-501.
- Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23(11), 571-579
- Macmillan, N. A. (1993). Signal detection theory as data analysis method and psychological decision model. In G. Keren & C. Lewis (Eds.), *A handbook for data analysis in the behavioral sciences: Methodological issues* (pp. 21-57). Hillsdale, NJ: Erlbaum.
- Malach, R., Reppas, J. B., Benson, R. B., Kwong, K. K., Jiang, H., Kennedy, W. A.,

- ... Tootell, R. B. H. (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 92(18), 8135– 8138
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information* (pp. 1–18). San Francisco, CA: Freeman and Company
- Maunsell, J. H. R., & Van Essen, D. C. (1983). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *The Journal of Neuroscience*, 3(12), 2563-2586
- Miller, M. B., Fendrich, R., Eliassen, J. C., Demirel, S., & Gazzaniga, M. S. (1996). Transcranial magnetic stimulation: Delays in visual suppression due to luminance changes. *NeuroReport: Cognitive Neuroscience and Neurophysiology*, 7(1), 1740-1744
- Morey, R. D., & Rouder, J. N. (2011). Bayes factor approaches for testing interval null hypotheses. *Psychological Methods*, 16(4), 406-419
- Morey, R. D., Rouder, J. N., & Jamil, T. (2014). BayesFactor: Computation of Bayes factors for common designs. R package version 0.9.12-2, <https://cran.r-project.org/web/packages/BayesFactor/BayesFactor.pdf>
- Pan, Y., Lin, B., Zhao, Y., & Soto, D. (2013). Working memory biasing of visual perception without awareness. *Attention, Perception & Psychophysics*, 76 (7), 2051-62

- Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, 20(292), 510-2
- Pascual-Leone, A., Walsh, V. (2003). Transcranial magnetic stimulation studies of asymmetry of cognitive functions in the brain. In, Hugdahl, K. and Davidson, R. J. (Eds.), *The Asymmetrical Brain* (pp. 232-245). Cambridge, MA: The MIT Press
- Prime, D. J., Pluchino, P., Eimer, M., Dell'Acqua, R., & Jolicoeur, P. (2011). Object substitution masking modulates spatial attention deployment and the encoding of information in visual short-term memory: Insights from occipito-parietal ERP components. *Psychophysiology*, 48(5), 687-696
- Riddoch, M. J., Humphreys, G. W., Edwards, S., Baker, T., & Willson, K. (2003). Seeing the action: Neuropsychological evidence for action-based effects on object selection. *Nature Neuroscience*, 6, 82-89
- Rossi, S., Hallet, M., Rossini, P. M., Pascual-Leone, A., & The Safety of TMS Consensus Group. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, 120(12), 2008-2039
- Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di lorio, R., ... Siebner, H. R. (2015). Non-invasive electrical and magnetic stimulation of the brain, spinal cord, roots and peripheral nerves: Basic principles and procedures for routine clinical and

- research application. An updated report from an I.F.C.N committee. *Clinical Neurophysiology*, 126(1), 1071-1107
- Saad, E., & Silvanto, J. (2013). How visual short-term memory maintenance modulates the encoding of external input: Evidence from concurrent visual adaptation and TMS. *NeuroImage*, 72(1), 243-251
- Salminen-Vaparanta, N., Noreika, V., Revonsuo, A., Koivisto, M., & Vanni, S. (2012). Is selective primary visual cortex stimulation achievable with TMS. *Human Brain Mapping*, 33(3), 652-655
- Shipp, S., & Zeki, S. (1989a). The organization of connections between areas V5 and V1 in macaque monkey visual cortex. *European Journal of Neuroscience*, 1(4), 309-330
- Shipp, S., & Zeki, S. (1989b). The organization of connections between areas V5 and V2 in macaque monkey visual cortex. *European Journal of Neuroscience*, 1(4), 330-354
- Schwarz, G. E. (1978). Estimating the dimension of a model. *Annals of Statistics*, 6, 461-464
- Siebner, H. R., Hartwigsen, G., Kassuba, T., & Rothwell, J. (2009). How does transcranial magnetic stimulation modify neuronal activity in the brain?—Implications for studies of cognition. *Cortex*, 45(9), 1035-1042
- Silvanto, J., Lavie, N., & Walsh, V. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex*, 15(1), 1736-1741
- Soto, D., Heinke, D., Humphreys, G. Q., & Blanco, M. J. (2005). Early, involuntary top

- down guidance of attention from working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 31(2), 248-261
- Soto, D., & Humphreys, G.W. (2006). Seeing the content of the mind: Enhanced awareness through working memory in patients with visual extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 103(12), 4789-4792
- Soto, D., Humphreys, G. W., & Heinke, D. (2006). Working memory can guide pop-out search. *Vision Research*, 46(6-7), 1010-1018.
- Sporns, O., & Zwi, J. D. (2004). The small world of the cerebral cortex. *Neuroinformatics*, 2, 145-162
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures, *Behaviour Research Methodology*, 31(1), 137-149
- Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top-down activation of shape specific population codes in visual cortex during mental imagery. *The Journal of Neuroscience*, 29(5), 1565-1572
- Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, 19, 109-139
- Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Reviews: Neuroscience*, 4, 219-229
- Trapp, S., & Bar, M. (2015). Prediction, context, and competition in visual recognition.

Annals of the New York Academy of Sciences, 1339(1), 190-198

Van Essen, D. C., & Maunsell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neuroscience*, 6(1), 370-375

Walsh, V., & Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: A neurochronometrics of mind*. Cambridge, MA: MIT Press.

Woolsey, C. N. (1981). *Cortical sensory organization, Vol. 2: Multiple Visual Areas*. Clifton, NJ: Humana Press.

Appendix A

Section 1: Ethics Reference Number 5201300060

Fhs Ethics <fhs.ethics@mq.edu.au>

to Associate, Ms, Miss, Ms, Mr, me, Ms ▾

Dear Ms Quek and Dr Finkbeiner,

RE: 'Attention, Intention and Automaticity ' (Ref: 5201300060)

Thank you for your recent correspondence regarding the amendment request. The amendments have been reviewed and we are pleased to advise you that the amendments have been approved.

This approval applies to the following amendments:

1. Change in personnel
 - a) Dr Brenda Ocampo, Mr Anthony Espinosa and Ms Lucy Shi removed from the project;
 - b) Ms Daniell Steinberg, Ms Samantha Parker, Ms Irene Chork added to the project;
2. Revised Information and Consent form.

Please accept this email as formal notification that the amendments have been approved. Please do not hesitate to contact us in case of any further queries.

All the best with your research.

Kind regards,

FHS Ethics

Faculty of Human Sciences - **Ethics**
 Research Office
 Level 3, Research HUB, Building C5C
 Macquarie University
 NSW 2109

Ph: [+61 2 9850 4197](tel:+61298504197)

Fax: [+61 2 9850 4465](tel:+61298504465)

Email: fhs.ethics@mq.edu.au

<http://www.research.mq.edu.au/>

Section 2: Ethics Reference Number 5201400585

APPROVED

By Dr Nitya Phillipson at 1:46 pm, Mar 16, 2016



Human Research Ethics Committee

REQUEST FOR AMENDMENT FORM

Dr Nitya Phillipson
2016.03.16
13:47:28 +11'00'

Please complete this form for all amendments/modifications including extensions to approved ethics projects.

For quick and efficient review of your amendment, please provide sufficient information in this document to allow the amendment to be reviewed as a standalone document (i.e. it does not require the Ethics Secretariat or HREC reviewing the original application).

Please attach tracked and clean copies of all amended documents to the amendment request. Documents could include participant information and consent forms (PICF), advertising material, surveys, interview questions, verbal scripts, support letters from external organizations.

Submitting this form:

HREC approved applications: Please send this form to ethics.secretariat@mq.edu.au.

Faculty/School-approved applications:

Please send this form to the ethics subcommittee administrator of the relevant Faculty/School

Faculty of Human Sciences: fhs.ethics@mq.edu.au

Faculty of Science and Engineering: sci.ethics@mq.edu.au

Faculty of Arts: artsro@mq.edu.au

Faculty of Business and Economics: fbe-ethics@mq.edu.au

MGSM: ethics@mgsm.edu.au

PACE: pace.ethics@mq.edu.au

Faculty of Medicine and Health Sciences: ethics.secretariat@mq.edu.au.

Handwritten forms will not be accepted.

1. **Human Research Ethics Committee Reference No:** 5201400585

2. **Chief Investigator/Supervisor:** Paul Sowman

Faculty: Human Sciences

Department: Cognitive Science

Email: paul.sowman@mq.edu.au

Date of amendment: 29/02/2016

3. Names of Co-Investigators/Associate Supervisors/Research Assistants: Anina Rich, Matthew Finkbeiner, Mark Williams, Margaret Ryan, Alexandra Woolgar, Anna Hearne, Genevieve Mcarthur, Anne Castles, Saskia Kohlen, Soheil Afshar, Denise Moerel, Andrew Etchell, Leidy Castro-Meneses, Shahd Al Janabi, Manjunath Narra, Lina Teichmann, Rocco Chiou, Jade Jackson, Jordan Wehrman, Nathan Caruana, Yvette Kezilas, Ana Murteira, **Di Zhu and Daniéll Steinberg.**

(Note: If the project is to be undertaken by an Honours/postgraduate/HDR student, the supervisor will be considered the Chief Investigator. The student may be named as a co-investigator.)

Appendix B

Section 1: Participant Consent Form

Participant Information and Consent Form

Title:	Perceptual judgments during TMS
Protocol number:	5201400585
Principal Investigator (PI):	Daniell Steinberg and Matthew Finkbeiner
Sites:	The Department of Cognitive Science, Macquarie University

1. Introduction

This Participant Information and Consent Form (PICF) tells you about the research project. It explains what taking part in this study will involve. Knowing what is involved will help you decide if you want to take part in the research.

Please read this information carefully. Ask questions about anything that you don't understand or want to know more about.

Our research team are happy to go through this information with you and answer any questions you may have. Please feel free to ask questions about anything that you do not understand or that you wish to know more about.

Conducting this research are members of the Department of Cognitive Science: Associate Professor Matthew Finkbiener and Ms. Daniell Steinberg.

2. Purpose of the research

Aims

The aim of this research is to understand more about how the human brain controls attention and cognitive functions such as visual recognition. The research uses a physiological technique known as transcranial magnetic stimulation (TMS). The TMS technique allows us to stimulate a small area of the brain as participants are performing a behavioural task. The behavioural tasks will involve simple perceptual judgements about stimuli that are presented visually and/or simple responses to these stimuli such as button pressing.

3. Do I have to take part in this research project?

Participation in any research project is voluntary. If you decide you want to take part, you will first be asked to sign the consent section at the end of this form prior to any study assessments being performed. By signing it you are telling us that you:

- Understand what you have read
- Consent to take part in the research project
- Consent to have the tests that are described

- Consent to the use of your personal information as described

If you decide to take part and later change your mind, you are free to withdraw from the project at any stage for any reason.

Your decision whether or not to take part in the study will not affect your relationship with Macquarie University. If you choose to withdraw you do not have to offer an explanation for your decision, and you may request that any unprocessed data collected from you be removed from the database.

4. What do I do if I wish to withdraw from the research?

Participation in any research is voluntary. If you do not wish to take part you do not have to. If you decide to take part and later change your mind, you are free to withdraw. You may withdraw even after you have commenced your participation. If you wish to withdraw from this study, please advise the study team. Once the results are published, you will not be able to withdraw from the study but you may ask that you not be invited to participate in future research.

5. What does participation in this research involve?

We will ask you to sit comfortably on a chair and to remain quite still whilst you complete a task. You will have a chinrest to place your head in for comfort and to help with this. A researcher will place the TMS coil gently against your head during this time. If you feel uncomfortable at any time you can ask for a break or to terminate the experiment.

6. What are the risks of taking part in this research?

Transcranial Magnetic Stimulation (TMS)

TMS is a neurophysiological technique that induces a current in a small area of the brain, using a magnetic field to pass the scalp safely and painlessly. In TMS, a current passes through a coil of copper wire that is wound inside a plastic-insulated casing and held over the participant's head. This coil resembles a paddle or large spoon, and is held in place either by the investigator, or by a mechanical stabilisation device similar to a microphone stand or metal frame. As the current passes through the coil it generates a magnetic field that can pass through the scalp and skull, and in turn induces a current in a small area of the participant's brain. There is a clicking noise associated with the current passing through the coil, but the effect of the magnetic field and the induction of current in the brain are not painful.

TMS was introduced in the mid 1980's and is used in clinical neurophysiology to study the conduction of nerve information from the brain cortex through the spinal cord to the muscles. In the last few years it has also been used in many laboratories to study the effects of localised brain stimulation on perception, attention, movement control and higher thought processes (such as language and memory). The technique is considered to be safe for use in neurologically healthy individuals.

Are there any risks associated with TMS?

Although we administer TMS according to strict safety guidelines, there are some risks associated with this technique. In rare instances TMS has induced a seizure (or epileptic convulsion). This risk is extremely low, and is further minimised in our protocol because of our adherence to the safety guidelines. Nevertheless, it is important that you tell us now if

you have ever experienced a seizure yourself, or if there is any history of seizures in your family. To help us determine whether you are eligible to have TMS, you will be asked to complete a safety questionnaire which contains a number of questions about previous medical conditions involving the brain, whether you have any implants that contain metal, and any current medications. If you have any of the known risk factors, you may not be eligible to participate in this research.

It is important to note that experiencing a seizure induced by TMS has never led to the development of epilepsy or posed any risk for subsequent unprovoked seizures. In addition, any TMS induced seizure would occur during stimulation or immediately after; it would not be expected to affect a participant hours or days after the TMS. As an additional safety precaution, we recommend that you avoid driving for 30 minutes following a session of TMS.

Certain factors can predispose an individual to a seizure during TMS. These include fatigue, or recent consumption of alcohol or drugs. Therefore, prior to each session involving TMS, we will ask if you have consumed more than three units of alcohol or any recreational drugs the night before the session, if you have had a good night's sleep, and if you have consumed more than two cups of coffee in the two hours before the session. If your answer predisposes you to an increased risk of seizure, then we will arrange an alternative time for your testing session.

Overall, of the many thousands of TMS studies in the scientific literature, less than 10 seizures caused by TMS have been reported, and most of these occurred in the setting of early studies designed to evaluate the safety of TMS.

Other potential adverse effects of TMS

Other potential adverse effects associated with TMS include the induction of a muscle tension headache or a neck ache in approximately 3 of every 100 participants. These are generally mild discomforts that respond promptly to aspirin, panadol or other common analgesics. If you feel any pain or discomfort during the procedure please alert the experimenter immediately so that testing can be discontinued.

Are there any restrictions for those wishing to take part?

You must be over 18 and generally healthy. Because TMS involves a strong magnet, some people are excluded. These include people with pacemakers and other implanted devices, those with metal foreign bodies (e.g. shrapnel from war injuries) and those who have had certain types of surgery. Because of the theoretical risk of seizure, we also exclude people with any history of seizures. You will be asked to complete a screening questionnaire prior to your participation. People who do not pass this screen may be excluded from the experiments. We cannot recruit anyone with a history of neurological or psychiatric illness, or drug abuse.

7. What will happen to the information collected about me?

By signing this consent form you have consented for the study team and relevant research staff to collect and use your data and the information you give to us for the research project. Any information obtained during the course of this study will remain confidential.

Each participant's data is identified by code rather than name. All computers on which data is stored is password protected so may only be accessed by the researchers involved in this

study. Paper forms are stored in locked cupboard, so that only researchers involved in this study will have access.

The data from the study will be stored for a period of ten years.

In some cases, data collected as part of this study may be shared with other researchers. With your consent, we would like to keep your data for the purposes of future, unspecified research projects. Any research that will be conducted using your data will be approved by a Human Research Ethics Committee and conducted in accordance with the *National Statement on Ethical Conduct in Human Research* (2007 – Updated March 2014)

It is expected that the results of this study will be published or presented in a variety of forums such as books, journal articles or at conferences. In any publication or presentation, information about you will be provided in a way that you cannot be identified, except with your express permission.

8. Who has reviewed this study?

All research in Australia involving human participants is reviewed by an independent group of people, called a Human Research Ethics Committee (HREC). HRECs must review research in accordance with a set of ethical guidelines called the *National Statement on Ethical Conduct in Human Research* (2007 – Updated March 2014) and other relevant legislation and guidelines.

This study has been reviewed and given ethical approval by the Macquarie University HREC (Medical Sciences). This research meets the requirements of the National Statement which is available at the following website:

<http://www.nhmrc.gov.au/files/nhmrc/publications/attachments/e72.pdf>

If you have any complaints or reservations about any ethical aspect of your participation in this research, you may contact the Committee through the Director, Research Ethics (telephone (02) 9850 7854; email ethics@mq.edu.au). Any complaint you make will be treated in confidence and investigated, and you will be informed of the outcome.

Participant Consent

Title: Perceptual judgments during TMS

Investigator: Ms. Daniell Steinberg

Site: A Department of Cognitive Science, MQ University

1. I have read the attached Participant Information Form outlining the nature and purpose of the research study and I understand what I am being asked to do.
2. I have discussed my participation in this study with a member of the study team. I have had the opportunity to ask questions and I am satisfied with the answers I have received.
3. I have been informed about the possible risks of taking part in this study.
4. I freely consent to participate in the research project as described in the attached Participant Information Sheet.
5. I understand that my participation is voluntary and that I am free to withdraw at any time during the study.
6. I have been given a copy of this information and consent form to keep.

Participant's Name: _____

(Block letters)

Participant's Signature: _____ Date: _____

Principal Investigator's Name: Daniell Steinberg

(Block letters)

Investigator's Signature: _____ Date: _____

Demographic Information

Name of Participant:(block letters)

Date of Birth.....

Right or left handed.....

Address.....

Email.....

Withdrawal of Participation

Title: Perceptual judgments during TMS
Investigator : Ms. Daniell Steinberg
Site: The Department of Cognitive Science, MQ University

I hereby wish to **WITHDRAW** my intent to participate further in the above research project and understand that such withdrawal will not jeopardise my future health care.

Participant's Name (printed) _____

Signature _____

Date _____

If a verbal withdrawal:

In the event the participant decided to withdraw verbally, please give a description of the circumstances. Coordinating Investigator to provide further information here:

Coordinating Investigator to sign the withdrawal of consent form on behalf of a participant if verbal withdrawal has been given:

Participant's Name (printed) _____

Signature of Investigator _____

Date _____

Section 2: TMS Screener (Keel et al., 2000)

TMS SCREENING FORM

Date of birth:

IDENTIFIER:

Transcranial Magnetic Stimulation (TMS) is a method for producing an electric current in a small part of the brain. During TMS, a current passes through a copper coil that is wound inside a plastic casing and held over the participant's head. The current in the coil produces a magnetic field, which passes safely through the scalp and causes electrical activity in brain tissue. Before receiving TMS, please read the following questions carefully and provide answers. For a small number of individuals, TMS may carry an increased risk of causing a seizure. The purpose of these questions is to make sure that you are not such a person. You have the right to withdraw from the screening and subsequent scanning if you find the questions unacceptably intrusive. The information you provide will be treated as strictly confidential and will be held in secure conditions. If you are unsure of the answer to any of the questions, please ask the person who gave you this form or the person who will be performing the study. Definitions of some of technical terms are given overleaf.

	<i>Please tick</i>
Have you ever had an adverse reaction to TMS?	☐ Yes ☐ No
Do you experience claustrophobia?	☐ Yes ☐ No
Have you had a seizure?	☐ Yes ☐ No
Have you had a stroke?	☐ Yes ☐ No
Have you had a serious head injury (including neurosurgery)?	☐ Yes ☐ No
Do you have any metal in your head (outside the mouth) such as shrapnel, surgical clips, or fragments from welding or metalwork?	☐ Yes ☐ No
Do you have any implanted devices such as cardiac pacemakers, aneurysm clips, cochlear implants, medical pumps, deep brain stimulators, or intracardiac lines?	☐ Yes ☐ No
Do you suffer from frequent or severe headaches?	☐ Yes ☐ No
Have you ever had any other brain-related condition?	☐ Yes ☐ No
Have you ever had any illness that caused brain injury?	☐ Yes ☐ No
Are you taking any psychiatric or neuroactive medications, or do you have a history of drug abuse?	☐ Yes ☐ No
Are you pregnant?	☐ Yes ☐ No
Do you, or does anyone in your family, have epilepsy?	☐ Yes ☐ No
Do you hold a heavy goods vehicle driving license or bus license?	☐ Yes ☐ No

I have read and understood the questions above and have answered them correctly.

SIGNED..... **DATE**.....

DEFINITIONS OF TECHNICAL TERMS

PACEMAKER: An electronic device that is surgically placed in the patient's body and connected to the heart to regulate the heartbeat.

COCHLEAR IMPLANT: An electronic medical device that bypasses damaged structures in the inner ear and directly stimulates the auditory nerve, allowing some deaf individuals to learn to hear and interpret sounds and speech.

ANEURYSM CLIP: A surgically implanted metal clip used to cut off blood flow through the neck of an aneurysm. An aneurysm is a deformity of a blood vessel in the body, which can swell and burst causing a haemorrhage.

SHUNT: A surgically implanted connector, which allows passage of fluid between two parts of the body. A common use of a shunt is to allow fluid to drain away from the brain, thus reducing pressure in the brain. May also describe a tube which allows blood to be moved from one part of the body to another.

STENT: A surgical implanted device that is inserted into a blood vessel to provide support, keep the vessel open and promote unblocked and enhanced blood flow. Sometimes used in other fluid carrying vessels in the body such as bile ducts etc.