Working memory enhances target detection in the blind hemifield

Daniel T. Smith and Alison R. Lane

Department of Psychology, Durham University, UK

Corresponding Author:

Daniel T. Smith, PhD

E011 Wolfson Building

Department of Psychology

Durham University

TS176BH

(00)44 1913340436

daniel.smith2@durham.ac.uk

Word Count: 2502

Abstract

Visual perception can be influenced by the content of working memory. Previous studies have shown this influence can be enough to improve unconscious visual discrimination in healthy participants and conscious visual discrimination in neuropsychological patients with extinction. Here, these findings are extended by examining the effects of holding an object in working memory on unconscious visual perception in a person with hemianopia. The results revealed significantly enhanced detection accuracy when there was an exact match between the colour and orientation of the discrimination target and the item in working memory. However, the facilitatory effect was greatly reduced when only colour or orientation was matched with the item being held in memory. A control experiment confirmed these effects were not due to visual priming. These results are consistent with the proposal that working memory guided perceptual facilitation is driven by signal enhancement. More broadly, the data are interpreted in terms of a biased competition account of visual perception.

Keywords: Hemianopia, working memory, attention, blindsight, occipital

Introduction

The content of working memory (WM) exerts a powerful influence on visual perception by biasing processing in the visual system in favour of items that share features with the item being remembered (Awh, Vogel, & Oh, 2006; Olivers, Meijer, & Theeuwes, 2006; Soto, Hodsoll, Rotshtein, & Humphreys, 2008). With respect to visual search, this bias can facilitate performance when the target matches the WM item, and impair search when the WM item matches a distractor (Olivers et al., 2006). The bias can also facilitate visually guided saccades (Hollingworth, Matsukura, & Luck, 2013), enhance perceptual sensitivity (Han, 2015; Pan, Luo, & Cheng, 2016; Soto, Wriglesworth, Bahrami-Balani, & Humphreys, 2010) and improve the accuracy of guesses made about the identity of unconsciously perceived stimuli (Pan, Cheng, & Luo, 2012). Remarkably, the effect of maintaining an object in WM is sufficiently powerful to bring stimuli that are not normally consciously perceived into awareness, such that neuropsychological patients with extinction perceive what would typically be extinguished (Soto & Humphreys, 2006). These studies are consistent with the view that the content of WM acts to enhance the signal associated with objects that share the properties of the memorised item (although see Cosman and Vecera (2011) for an alternative view).

The suggestion that the content of WM can enhance visual signals is of particular relevance to the study of patients with visual field defects caused by damage to the visual cortex, such as hemianopia. These patients suffer unilateral loss of vision which is extremely debilitating (e.g. Lane, Smith, & Schenk, 2008), and spontaneous recovery is typically limited (Zhang, Kedar, Lynn, Newman & Biousse, 2006) which makes rehabilitation crucial to improve functioning and quality of life. Patients with hemianopia can possess some preserved but unconscious visual abilities, known as blindsight (Weiskrantz, 1986), and there is good evidence that blindsight is particularly sensitive to certain temporal and spatial parameters (Sahraie, Trevethan, & MacLeod, 2008; Weiskrantz, 1986). Enhancing blindsight performance for the purposes of rehabilitation has been investigated in a number of studies (for a review see Melnick, Tadin & Huxlin, 2016) and understanding how to maximise such perceptual relearning will help to further this approach. Different manipulations to enhance blindsight performance have been investigated with mixed success. Repeated training can lead to improvements (e.g., Huxlin et al., 2009), with some generalisation to non-trained stimuli possible under certain training configurations (Das, Tadin & Huxlin, 2014). However, whilst proprioceptive signals about arm position appeared to enhance low vision (Schendel & Robertson, 2004), they did not lead to improvements in conscious or unconscious perception in individuals with hemianopia (Smith, Lane, & Schenk, 2008). One manipulation which does not appear to have been widely examined is matching a blind-hemifield probe stimulus with an active WM item. Given that this manipulation improves perceptual sensitivity and unconscious guessing in healthy participants (Pan et al., 2012; Soto et al., 2010), and conscious perception in patients with visual extinction following parietal lesions (Soto & Humphreys, 2006), it was predicted that it would also enhance unconscious perception in hemianopia.

This prediction was tested in a single neuropsychological patient (SK) with dense right-sided hemianopia. He was asked to memorise either the colour of a grating, orientation of a grating, or colour and orientation of a grating, then decide which of two time intervals contained the target. Comparing trials in which one or both features of the grating were congruent with the item in WM with trials in which features were entirely incongruent allowed the relative contribution of different features on blindsight performance to be examined.

Methods

Participant

SK was a 39 year old, right-handed male. He presented with a stable right-sided hemianopia with macular splitting and had been referred to us to participate in an experimental rehabilitation programme for hemianopia (Lane, Smith, Ellison, & Schenk, 2010). His visual field defect was confirmed with binocular perimetry using an Oculus Twinfield 2 automatic perimeter (Oculus Optikgerate GmbH, Wetzlar-Dutenhofen, Germany; see Figure 1), and was the result of an occipitotemporal brain haemorrhage 32 months prior to testing. There were no co-morbid spatial deficits, as assessed by the star cancellation task (Halligan, Cockburn, & Wilson, 1991). The experiments described in this study were conducted roughly two years after SK had finished the rehabilitation programme. Although travel costs were reimbursed, SK received no other inducement for his participation in the study, which was conducted in accordance with BPS code of ethics and the Declaration of Helsinki. The study was approved by the Department of Psychology Research Ethics Committee.

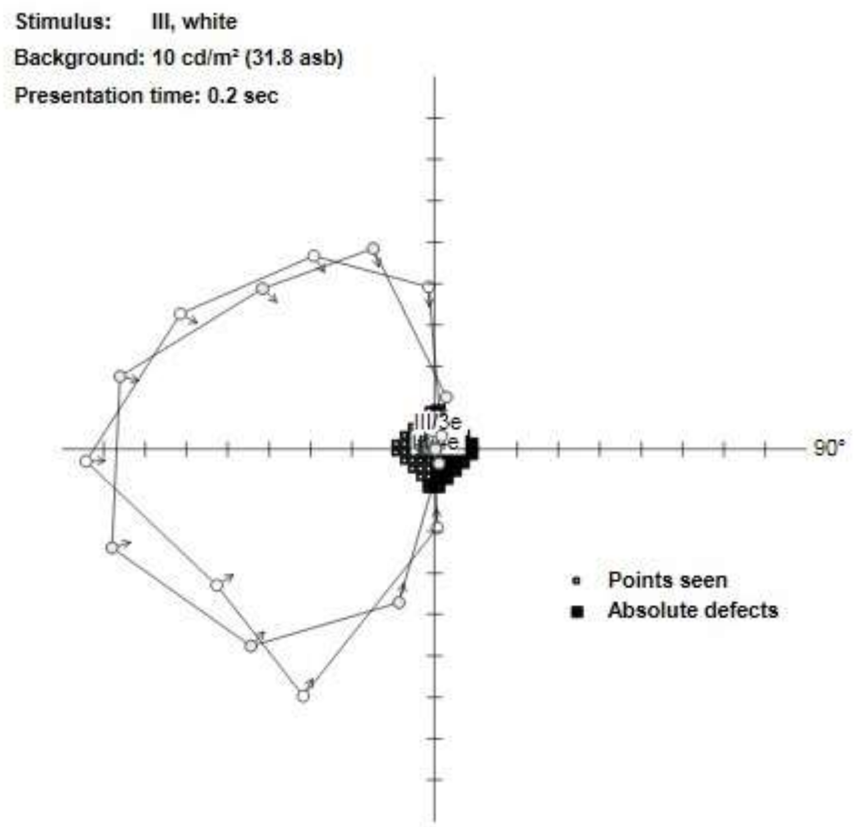

Figure 1: Visual field plot showing SK's right-sided hemianopia. Kinetic perimetry was conducted with the target moving inwards at 2°/s until detected, and the twelve meridians tested in a pseudo-random order. Static perimetry involved the presentation of the target randomly at 60 points within 10° of fixation, each point separated by 2°.

Stimuli & Apparatus

The background was a black screen. The detection targets (DT) were equiluminent (25 cdm2), circular (diameter 6.5^{o}), blue and black or red and black square wave gratings with a spatial frequency of 1 cycle/degree that drifted at a speed of 10 Hz (Sahraie et al., 2008). Individual gratings could be oriented at an angle of 0^{o}, 90^{o}, 45^{o} or 135^{o}, and the centre of the DT was 10^{o} to the right of fixation. The end of the first target period was signalled by an auditory cue (two 100ms tones played at 750 Hz and separated by 50ms). The response cue was a green square (0.5^{o}) presented at fixation. Stimuli in the match-to-sample task were static gratings with the same colour, size and spatial frequency as the DT. Items in the match-to-sample task were presented at fixation. All stimuli were generated using a Cambridge Research Systems ViSaGe and presented on a Sony Trinitron monitor with a 100Hz refresh rate. Responses were collected with a 2-button response box. Fixation was monitored with 2-channel BioPac 150 recording horizontal electro-oculography at 250 Hz. A chinrest placed 57cm from the monitor supported the head.

Procedure

SK sat 57cm from the display with viewing distance maintained by a chinrest. Trials began with the onset of a central fixation point for 1000ms. The fixation point was then replaced with the memory target for 1500ms, after which the fixation point reappeared. Following a delay of 1250ms two 750 Hz tones were played for 100ms, separated by 50ms silence. The DT was presented in the blind hemifield for 1000ms either 250ms after the onset of the fixation point, or immediately following the presentation of the two tones. 1000ms after the tones were presented the fixation point turned green. This cue signalled the participant to indicate whether the target had been presented before or after the tone. There were four conditions in the detection task; the memory target could (a) match both the colour and orientation of the DT (AllCongruent), (b) match the colour but not the orientation of the DT (ColourCongruent), (c) match the orientation but not the colour of the DT (OrientationCongruent) or (d) match neither the colour nor orientation of the DT (Incongruent). These conditions were randomly interleaved and were presented an equal number of times. The DT was equally likely to appear before or after the tone. After the detection response had been provided, SK was presented with a match-to-sample task in which he reported whether the sample matched the working memory target or not. The sample matched both the colour and orientation of the memory target on 50% of trials. On the mismatching trials the sample differed from the memory target on both dimensions. SK was presented with feedback about his performance on the match-to-sample task for 1000ms then the next trial began. SK completed 5 blocks of 32 trials in each of two separate sessions. There were therefore 80 trials per condition. Session 1 began with 2 blocks of 32 practice trials and session 2 began with 1 block of 32 practice trials. Figure 2 illustrates a typical trial.

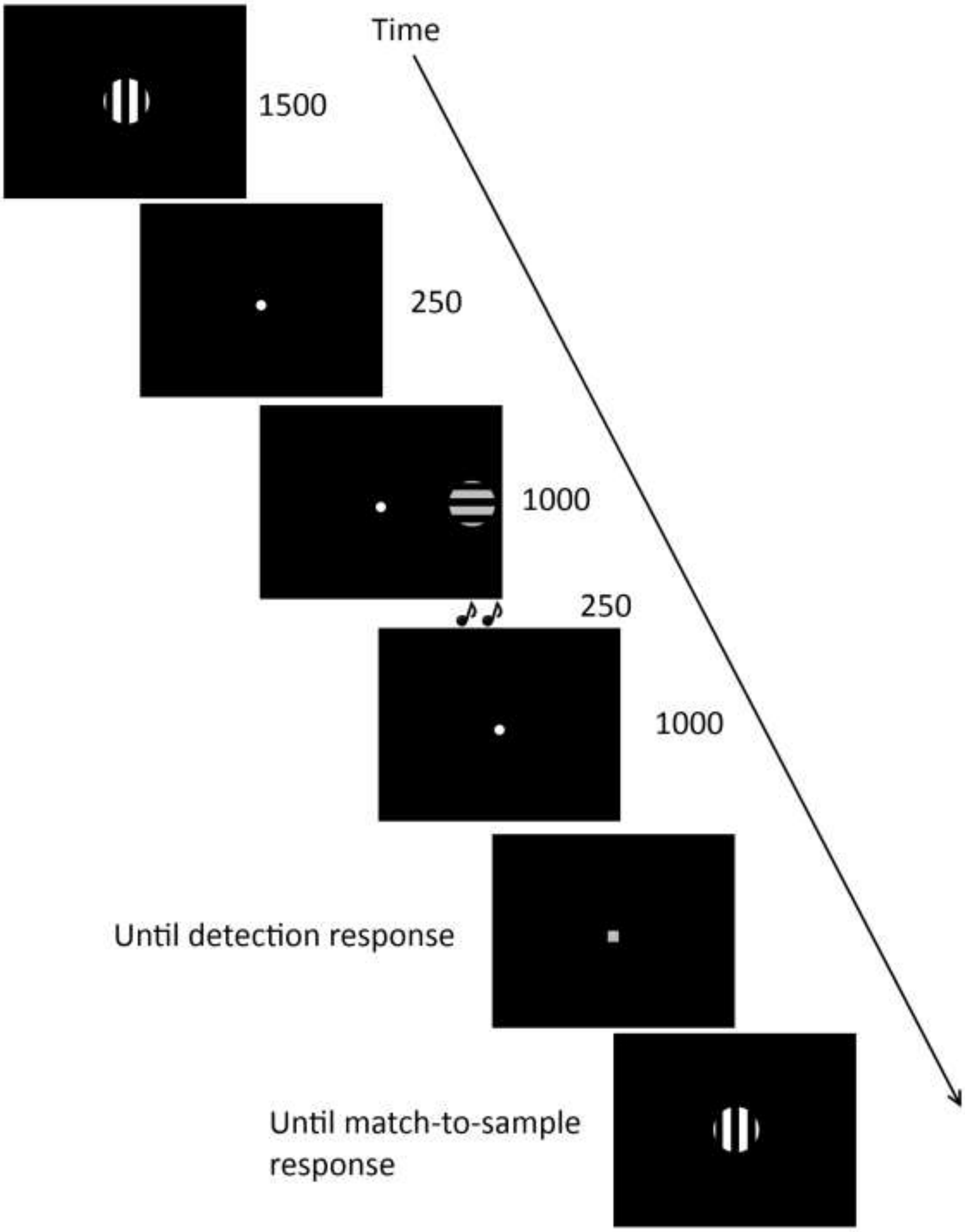

Figure 2: Illustration of a typical trial. In this example the Discrimination Target (the light grey and black grating) had incongruent colour and orientation and appeared in the 1st time interval. The Memory Target is a match to the sample. The initial fixation point is not shown.

Results

The data were filtered to exclude trials where performance on the match-to sample task was inaccurate (n = 6) as this demonstrated that the item may not have been held correctly in WM during the trial, trials with RT >3SD+mean (6103ms, 6 trials), and trials where a saccade was made and thus it cannot be guaranteed that the DT was presented to the blind hemifield (n = 16). Saccades were analysed offline and a trial was discarded if there was an eye-movement with a magnitude greater than 3^{o}.

Performance on each of the three congruent conditions was contrasted with performance on the incongruent condition using a series of Bayesian tests. These tests were selected because (a) they allow us to make claims about the likelihood of the key hypothesis and (b) multiple such tests can be performed without risking inflating the possibility of a type I error (Dienes, 2008, 2014). Bayesian analyses require a specific statement of priors relating to experimental hypothesis. In this case it was expected that accuracy in the congruent conditions would be better than accuracy in the Incongruent condition, and that the magnitude of this advantage would be ~30% points, based on Soto and Humphreys (2006). Table 1 shows the Bayes factors for each of the three comparisons.

Condition	**Expected difference under H_1**	**Observed Difference (%)**	**SE of difference**	**Bayes factor**	**Interpretation**
AllCongruent	0.3	18	0.08	5.4	Evidence for H_1
ColourCongruent	0.3	4.9	0.08	0.41	Inconclusive
OrientationCongruent	0.3	9.1	0.08	0.8	Inconclusive
Priming only (Experiment 2)	0.3	0	0.1	0.32	Evidence for H_0

Table 1: Priors, observed differences and Standard Errors used to calculate the Bayes factors for each condition.

Only in the case where both colour and orientation matched the content of working memory (AllCongruent) was there evidence for the idea that the content of WM enhanced performance. As can be seen in Figure 3, performance in the AllCongruent condition is significantly better than chance.

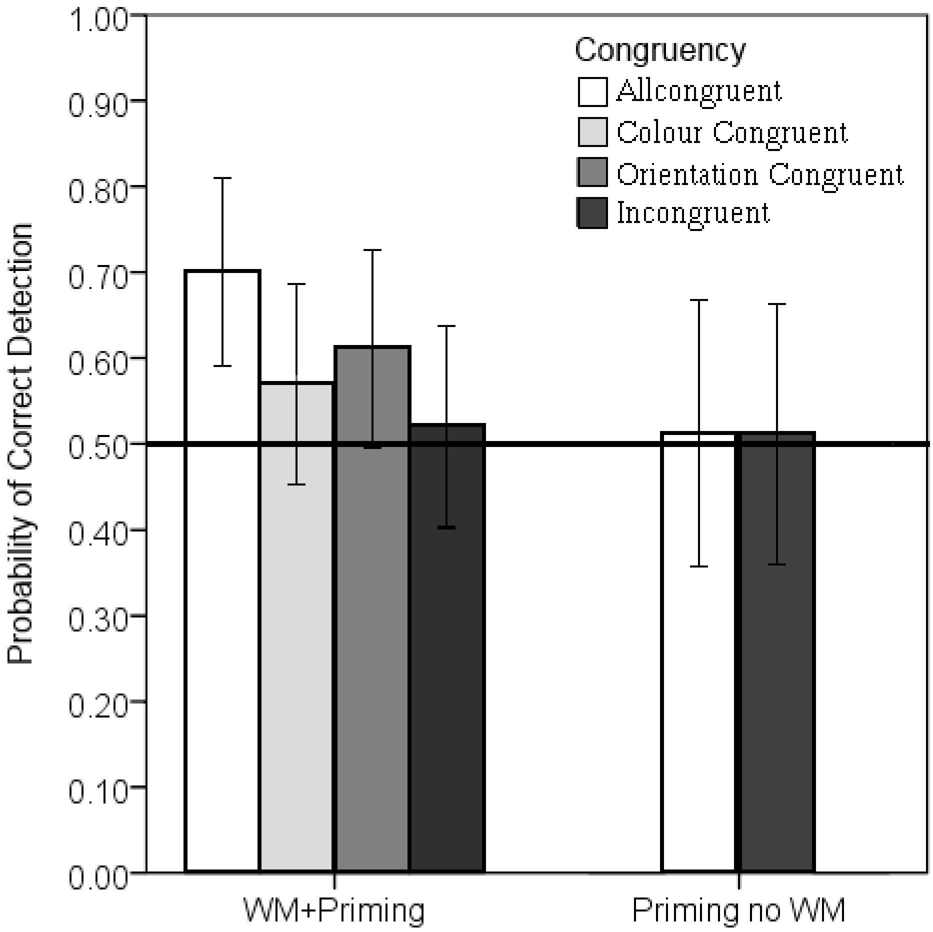

Figure 3: Mean detection accuracy in Experiments 1 and 2. The error bars show 95% confidence intervals and the horizontal reference line shows chance performance.

The results of the Bayesian analysis were consistent with more typical analysis in which performance in the AllCongruent condition was contrasted with performance in the Incongruent condition with a 1-tailed t-test (AllCongruent v Incongruent; $t_{(141)} = 2.22$, $p = .014$). The other contrasts were non-significant after correcting for multiple comparisons (ColourCongruent vs Incongruent: $t_{(143)} = 0.59$, $p = .25$.; OrientationCongruent v Incongruent: $t_{(143)} = 1.1$, $p = .135$).

Table 2 shows SK's mean reaction time in each condition, along with SD. There were no significant differences in RT between the AllCongruent and Incongruent conditions ($t_{(141)}$ = 1.25, p = .22). This shows that the differences in detection accuracy were not influenced by speed of response.

AllCongruent	ColourCongruent	OrientationCongruent	Incongruent
4441.49 (372.62)	4455.75 (336.02)	4367.17 (227.09)	4374.96 (258.08)

Table 2: Means (Standard Deviations) of SK's reaction times in experiment 1 (milliseconds).

To ensure that the effects observed in Experiment 1 were not due to priming, SK was invited back for a third session in which a control experiment was conducted. The task was similar to Experiment 1, with two exceptions. Firstly, SK was told not to memorise the item shown at the start of the trial and did not perform the match-to-sample task. Secondly, there were only AllCongruent or Incongruent trial types. SK performed 1 block of practice trials and 3 blocks of 32 experimental trials, producing 48 trials per condition. Trials were excluded where a saccade was made (n = 6) and trials with RT >3SD+mean (5691, 9 trials), then calculated the Bayes factor (see Table 1). The Bayes factor of 0.32 is evidence for the null hypothesis, suggesting that priming a stimulus does not lead to enhanced detection in this task (see Figure 3). A t-test comparing Allcongruent with Incongruent was non-significant (Allcongruent 52%, AllDifferent 52%, $t_{(94)}$ = 0, p = 1).

Discussion

Our goal was to test the hypothesis that unconscious perception in hemianopia, or 'blindsight', would be enhanced if the DT matched the contents of WM. The results suggest that this hypothesis is correct when there is an exact match between the DT and the item to be remembered. However, the evidence was less clear cut when only one of the features of the DT (colour or orientation) was encoded in memory. In these conditions there was a small improvement in performance of 5-10 percentage points but the Bayes factor was inconclusive. Importantly, a control experiment in which SK was primed with DT but did not have to remember the DT provided evidence *against* the hypothesis that priming could account for the effects observed in Experiment 1.

Overall these data are consistent with previous studies showing that holding an item in WM enhances the strength of the visual signals arising from objects that share features with the WM item (Soto et al., 2010) and fit well with the biased competition account of visual processing (Desimone & Duncan, 1995). This theory holds that sensory signals compete in a winner-takes-all fashion, with the strongest signals gaining access to further processing. The outcome of this competition can be biased by top-down factors, including the current content of WM, which is operationalised by modulating the responsiveness of visual neurons that code the features being held in memory (Chelazzi, Duncan, Miller, & Desimone, 1998). In the current study, maintaining a WM of a coloured grating with a particular orientation biased the visual system towards processing congruent visual signals, which appears to have enhanced the weak signals from the blind hemifield sufficiently to allow them to bias response selection towards the correct time window of target presentation. Unlike the study of Soto et al. (2006), congruency between WM item and DT was not sufficient to bring the blind hemifield stimulus into conscious awareness; SK did not report seeing the stimuli. This difference probably reflects differences in the core deficits of patients with extinction and those with hemianopia. Specifically, extinction patients typically have preserved visual processing, so the incoming visual information from the affected side of space is intact. In this case a biasing signal from WM appears to be sufficient to bring this visual information into awareness. In contrast, SK's hemianopia means that he has limited preserved visual processing on the blind side, so the bias from WM is acting on a weakened signal, which limits the potential for this signal to become consciously accessible. We speculate that this preserved visual information is communicated via intact white-matter tracts between the LGN and extrastriate areas that code motion and colour (Ajina, Pestilli, Rokem, Kennard, & Bridge, 2015).

It is also noteworthy that only an exact match between the WM item and DT led to enhanced detection accuracy, suggesting that colour or orientation information alone was not enough to produce measurable improvement. This finding suggests that different features may combine in an additive way to produce a more powerful bias. Furthermore, Martin et al. (2012) demonstrated that there is a slower accumulation of visual information from the blind hemifield than the sighted, and therefore it is possible that with a longer duration of presentation that either feature alone (colour or orientation) may be sufficient to improve performance. In this respect it may be worth considering the variability that exists in blindsight and the features that can elicit it (e.g., Danckert & Rossetti, 2005), and it could be that some patients would be more influenced by some features and different combinations than others. This could be an avenue for further work. Indeed, further studies examining these effects in other patients are important in order to establish the replicability and generalisability of our results.

More broadly, by showing enhanced unconscious processing of a single target presented without distractors, the current experiments provide direct evidence that the content of WM acts at an early stage of processing to enhance visual perception via signal enhancement (Pan et al., 2016; Yeshurun & Carrasco, 1998). However, it is important to be clear that these data do not exclude the possibility that WM also influences later, post-perceptual stages of visual processing (Cosman & Vecera, 2011).

To summarize, it was predicted that holding an object in WM would increase the detectability of targets appearing in the blind hemifield. This hypothesis was confirmed when there was an exact match between the WM item and the DT, but not when only one of two features matched. These data are consistent with previous neuropsychological studies of extinction patients and fit well with the biased competition account of visual processing. While it is important to be cautious in generalising from a single case to a broader neuropsychological population, these data do provide preliminary support for the idea that WM content may have the potential to improve the processing of visual signals from the blind hemifield and could inform the development of rehabilitation tools for people with visual field defects in the future.

References

Ajina, S., Pestilli, F., Rokem, A., Kennard, C., & Bridge, H. (2015). Human blindsight is mediated by an intact geniculo-extrastriate pathway. *eLife, 4*, e08935. doi: 10.7554/eLife.08935

Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience, 139*(1), 201-208.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *J Neurophysiol, 80*(6), 2918-2940.

Cosman, J. D., & Vecera, S. P. (2011). The contents of visual working memory reduce uncertainty during visual search. *Attention, Perception, & Psychophysics, 73*(4), 996-1002. doi: 10.3758/s13414-011-0093-y

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 192-222.

Dienes, Z. (2008). *Understanding Psychology as a science: An introduction to scientific and statistical inference*. Basingstoke: Palgrave Macmillan.

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology, 5*, 17. doi: 10.3389/fpsyg.2014.00781

Han, S. W. (2015). Working memory contents enhance perception under stimulus-driven competition. *Mem Cognit, 43*(3), 432-440. doi: 10.3758/s13421-014-0460-8

Hollingworth, A., Matsukura, M., & Luck, S. J. (2013). Visual Working Memory Modulates Rapid Eye Movements to Simple Onset Targets. *Psychological Science, 24*(5), 790-796. doi: 10.1177/0956797612459767

Lane, A. R., Smith, D. T., Ellison, A., & Schenk, T. (2010). Visual exploration training is no better than attention training for treating hemianopia. *Brain, 133*(6), 1717-1728. doi: 10.1093/brain/awq088

Lane, A. R., Smith, D. T., & Schenk, T. (2008). Clinical treatment options for patients with homonymous visual field defects. *Clinical Opthalmology, 2*(1), 93-102.

Olivers, C. N. L., Meijer, F., & Theeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology-Human Perception and Performance, 32*(5), 1243-1265. doi: 10.1037/0096-1523.32.5.1243

Pan, Y., Cheng, Q. P., & Luo, Q. Y. (2012). Working memory can enhance unconscious visual perception. *Psychonomic Bulletin & Review, 19*(3), 477-482. doi: 10.3758/s13423-012-0219-9

Pan, Y., Luo, Q., & Cheng, M. (2016). Working memory-driven attention improves spatial resolution: Support for perceptual enhancement. *Attention, Perception, & Psychophysics, 78*(6), 1625-1632. doi: 10.3758/s13414-016-1138-z

Sahraie, A., Trevethan, C. T., & MacLeod, M. J. (2008). Temporal properties of spatial channel of processing in hemianopia. *Neuropsychologia, 46*(3), 879-885. doi: 10.1016/j.neuropsychologia.2007.11.008

Schendel, K., & Robertson, L. C. (2004). Reaching out to see: Arm position can attenuate human visual loss. *Journal of Cognitive Neuroscience, 16*(6), 935-943.

Smith, D. T., Lane, A. R., & Schenk, T. (2008). Arm position does not attenuate visual loss in patients with homonymous field deficits. *Neuropsychologia, 46*, 2320-2325.

Soto, D., Hodsoll, J., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. *Trends in Cognitive Sciences, 12*(9), 342-348.

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. doi: 10.1073/pnas.0510718103

Soto, D., Wriglesworth, A., Bahrami-Balani, A., & Humphreys, G. W. (2010). Working memory enhances visual perception: evidence from signal detection analysis. *J Exp Psychol Learn Mem Cogn, 36*(2), 441-456. doi: 10.1037/a0018686

Weiskrantz, L. (1986). *Blindsight: A case study and implications*. Oxford: Oxford University Press.

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396*(6706), 72-75.

Zhang, X., Kedar, S., Lynn, M. J., Newman, N. J., & Biousse, V. (2006) Natural history of homonymous hemianopia. *Neurology, 66* (6), 901-905. doi: 10.1212/01.wnl.0000203338.54323.22

Figure Legends

Figure 1: Visual field plot showing SK's right-sided hemianopia. Kinetic perimetry was conducted with the target moving inwards at 2°/s until detected, and the twelve meridians tested in a pseudo-random order. Static perimetry involved the presentation of the target randomly at 60 points within 10° of fixation, each point separated by 2°.

Figure 2: Illustration of a typical trial. In this example the Discrimination Target (the light grey and black grating had incongruent colour and orientation and appeared in the 1st time interval. The Memory Target is a match to the sample. The initial fixation point is not shown.

Figure 3: Mean detection accuracy in Experiments 1 and 2. The error bars show 95% confidence intervals and the horizontal reference line shows chance performance.

Table 1: Priors, observed differences and Standard Errors used to calculate the Bayes factors for each condition.

Table 2: Means (Standard Deviations) of SK's reaction times in experiment 1 (milliseconds).