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1 Working memory enhances target detection in the blind hemifield

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16 **Word Count:** 2502

17 **Abstract**

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

30

31

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

33

34 **Introduction**

35 The content of working memory (WM) exerts a powerful influence on visual perception by
36 biasing processing in the visual system in favour of items that share features with the item being
37 remembered (Awh, Vogel, & Oh, 2006; Olivers, Meijer, & Theeuwes, 2006; Soto, Hodsoll, Rotshtein,
38 & Humphreys, 2008). With respect to visual search, this bias can facilitate performance when the
39 target matches the WM item, and impair search when the WM item matches a distractor (Olivers et
40 al., 2006). The bias can also facilitate visually guided saccades (Hollingworth, Matsukura, & Luck,
41 2013), enhance perceptual sensitivity (Han, 2015; Pan, Luo, & Cheng, 2016; Soto, Wriglesworth,
42 Bahrami-Balani, & Humphreys, 2010) and improve the accuracy of guesses made about the identity
43 of unconsciously perceived stimuli (Pan, Cheng, & Luo, 2012). Remarkably, the effect of maintaining
44 an object in WM is sufficiently powerful to bring stimuli that are not normally consciously perceived
45 into awareness, such that neuropsychological patients with extinction perceive what would typically
46 be extinguished (Soto & Humphreys, 2006). These studies are consistent with the view that the
47 content of WM acts to enhance the signal associated with objects that share the properties of the
48 memorised item (although see Cosman and Vecera (2011) for an alternative view).

49 The suggestion that the content of WM can enhance visual signals is of particular relevance
50 to the study of patients with visual field defects caused by damage to the visual cortex, such as
51 hemianopia. These patients suffer unilateral loss of vision which is extremely debilitating (e.g. Lane,
52 Smith, & Schenk, 2008), and spontaneous recovery is typically limited (Zhang, Kedar, Lynn, Newman
53 & Biousse, 2006) which makes rehabilitation crucial to improve functioning and quality of life.
54 Patients with hemianopia can possess some preserved but unconscious visual abilities, known as
55 blindsight (Weiskrantz, 1986), and there is good evidence that blindsight is particularly sensitive to
56 certain temporal and spatial parameters (Sahraie, Trevelyan, & MacLeod, 2008; Weiskrantz, 1986).
57 Enhancing blindsight performance for the purposes of rehabilitation has been investigated in a
58 number of studies (for a review see Melnick, Tadin & Huxlin, 2016) and understanding how to
59 maximise such perceptual relearning will help to further this approach. Different manipulations to

60 enhance blindsight performance have been investigated with mixed success. Repeated training can
61 lead to improvements (e.g., Huxlin et al., 2009), with some generalisation to non-trained stimuli
62 possible under certain training configurations (Das, Tadin & Huxlin, 2014). However, whilst
63 proprioceptive signals about arm position appeared to enhance low vision (Schendel & Robertson,
64 2004), they did not lead to improvements in conscious or unconscious perception in individuals with
65 hemianopia (Smith, Lane, & Schenk, 2008). One manipulation which does not appear to have been
66 widely examined is matching a blind-hemifield probe stimulus with an active WM item. Given that
67 this manipulation improves perceptual sensitivity and unconscious guessing in healthy participants
68 (Pan et al., 2012; Soto et al., 2010), and conscious perception in patients with visual extinction
69 following parietal lesions (Soto & Humphreys, 2006), it was predicted that it would also enhance
70 unconscious perception in hemianopia.

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

77

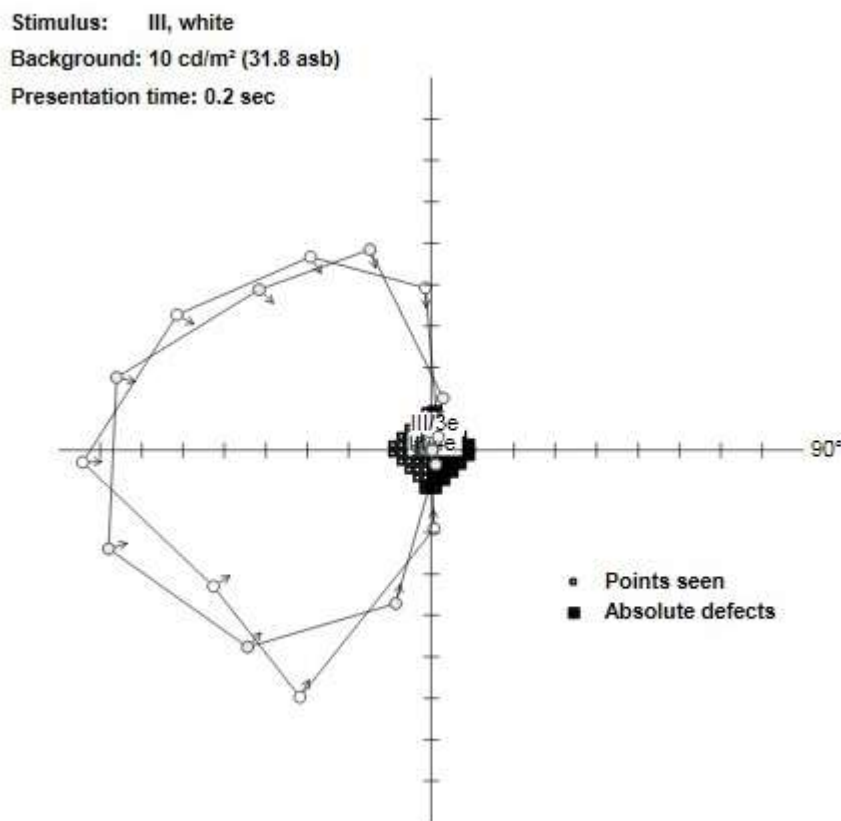
78 **Methods**

79

80 *Participant*

81 SK was a 39 year old, right-handed male. He presented with a stable right-sided hemianopia with
82 macular splitting and had been referred to us to participate in an experimental rehabilitation
83 programme for hemianopia (Lane, Smith, Ellison, & Schenk, 2010). His visual field defect was
84 confirmed with binocular perimetry using an Oculus Twinfield 2 automatic perimeter (Oculus
85 Optikgerate GmbH, Wetzlar-Dutenhofen, Germany; see Figure 1), and was the result of an

86 occipitotemporal brain haemorrhage 32 months prior to testing. There were no co-morbid spatial
87 deficits, as assessed by the star cancellation task (Halligan, Cockburn, & Wilson, 1991). The
88 experiments described in this study were conducted roughly two years after SK had finished the
89 rehabilitation programme. Although travel costs were reimbursed, SK received no other inducement
90 for his participation in the study, which was conducted in accordance with BPS code of ethics and
91 the Declaration of Helsinki. The study was approved by the Department of Psychology Research
92 Ethics Committee.



93

94 **Figure 1:** Visual field plot showing SK's right-sided hemianopia. Kinetic perimetry was conducted
95 with the target moving inwards at 2°/s until detected, and the twelve meridians tested in a pseudo-
96 random order. Static perimetry involved the presentation of the target randomly at 60 points within
97 10° of fixation, each point separated by 2°.

98

99 *Stimuli & Apparatus*

100 The background was a black screen. The detection targets (DT) were equiluminant (25 cdm²),

101 circular (diameter 6.5°), blue and black or red and black square wave gratings with a spatial

102 frequency of 1 cycle/degree that drifted at a speed of 10 Hz (Sahraie et al., 2008). Individual gratings
103 could be oriented at an angle of 0°, 90°, 45° or 135°, and the centre of the DT was 10° to the right of
104 fixation. The end of the first target period was signalled by an auditory cue (two 100ms tones played
105 at 750 Hz and separated by 50ms). The response cue was a green square (0.5°) presented at fixation.
106 Stimuli in the match-to-sample task were static gratings with the same colour, size and spatial
107 frequency as the DT. Items in the match-to-sample task were presented at fixation. All stimuli were
108 generated using a Cambridge Research Systems ViSaGe and presented on a Sony Trinitron monitor
109 with a 100Hz refresh rate. Responses were collected with a 2-button response box. Fixation was
110 monitored with 2-channel BioPac 150 recording horizontal electro-oculography at 250 Hz. A chinrest
111 placed 57cm from the monitor supported the head.

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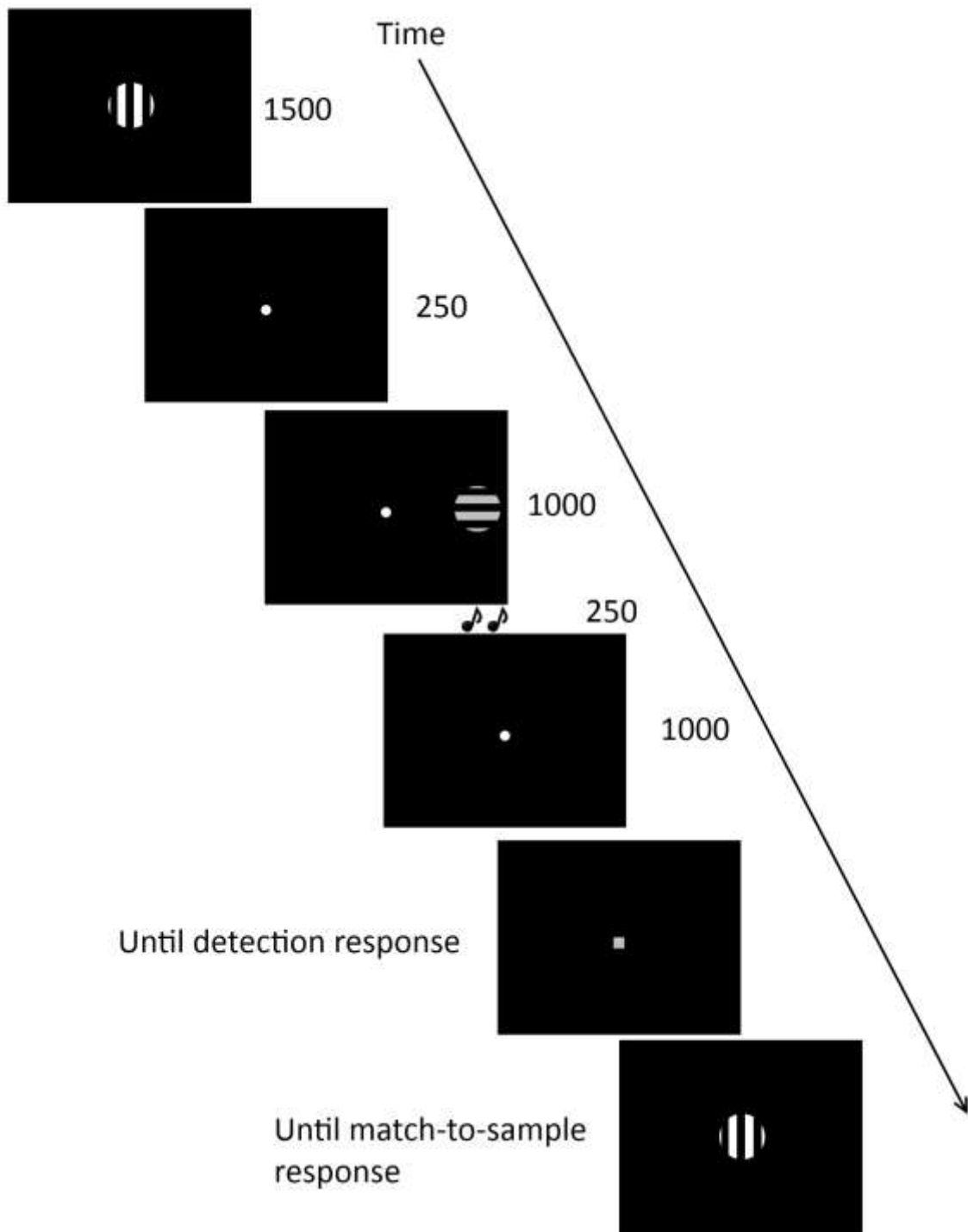
113 *Procedure*

114 SK sat 57cm from the display with viewing distance maintained by a chinrest. Trials began with the
115 onset of a central fixation point for 1000ms. The fixation point was then replaced with the memory
116 target for 1500ms, after which the fixation point reappeared. Following a delay of 1250ms two 750
117 Hz tones were played for 100ms, separated by 50ms silence. The DT was presented in the blind
118 hemifield for 1000ms either 250ms after the onset of the fixation point, or immediately following
119 the presentation of the two tones. 1000ms after the tones were presented the fixation point turned
120 green. This cue signalled the participant to indicate whether the target had been presented before
121 or after the tone. There were four conditions in the detection task; the memory target could (a)
122 match both the colour and orientation of the DT (AllCongruent), (b) match the colour but not the
123 orientation of the DT (ColourCongruent), (c) match the orientation but not the colour of the DT
124 (OrientationCongruent) or (d) match neither the colour nor orientation of the DT (Incongruent).
125 These conditions were randomly interleaved and were presented an equal number of times. The DT
126 was equally likely to appear before or after the tone. After the detection response had been
127 provided, SK was presented with a match-to-sample task in which he reported whether the sample

128 matched the working memory target or not. The sample matched both the colour and orientation of
129 the memory target on 50% of trials. On the mismatching trials the sample differed from the memory
130 target on both dimensions. SK was presented with feedback about his performance on the match-to-
131 sample task for 1000ms then the next trial began. SK completed 5 blocks of 32 trials in each of two
132 separate sessions. There were therefore 80 trials per condition. Session 1 began with 2 blocks of 32
133 practice trials and session 2 began with 1 block of 32 practice trials. Figure 2 illustrates a typical trial.

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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.

141
142

143 **Results**

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

150

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

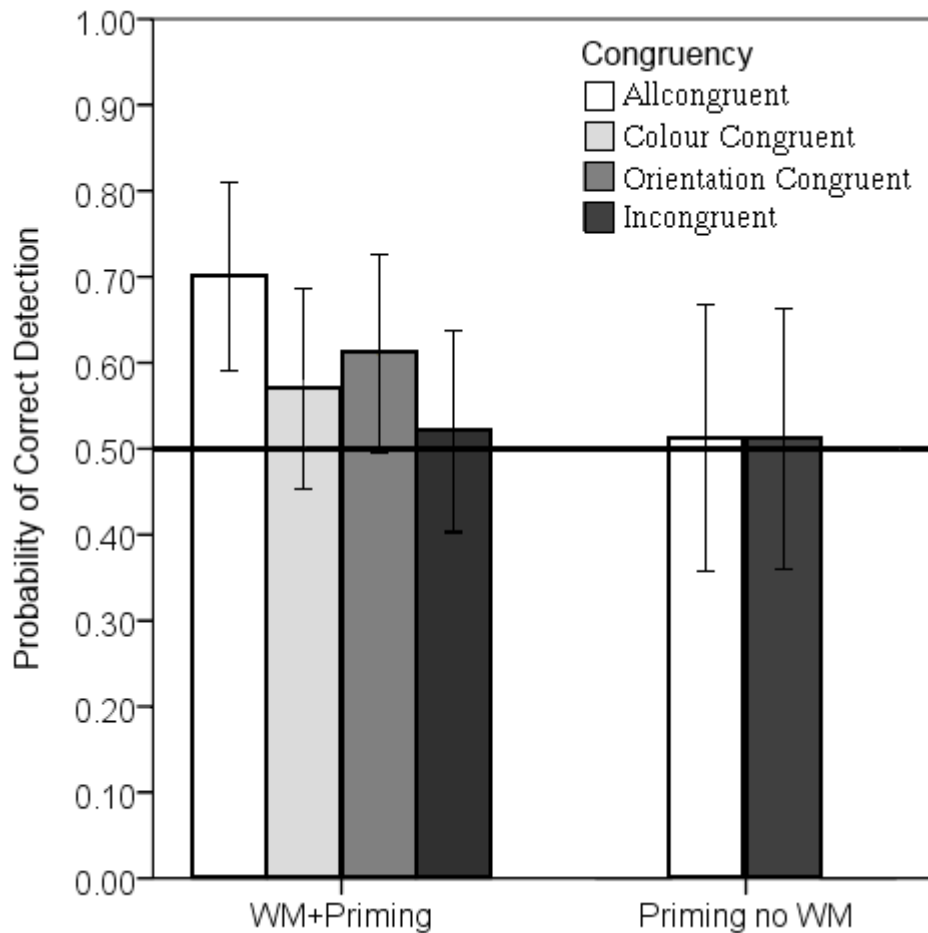
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| Condition | Expected difference under H ₁ | Observed Difference (%) | SE of difference | Bayes factor | Interpretation |
|-----------------------------|--|-------------------------|------------------|--------------|-----------------------------|
| 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 |

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

162

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



167
 168 **Figure 3:** Mean detection accuracy in Experiments 1 and 2. The error bars show 95% confidence
 169 intervals and the horizontal reference line shows chance performance.
 170

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

176

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

180

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

181 **Table 2:** Means (Standard Deviations) of SK's reaction times in experiment 1 (milliseconds).
 182

183 To ensure that the effects observed in Experiment 1 were not due to priming, SK was invited back for
 184 a third session in which a control experiment was conducted. The task was similar to Experiment 1,
 185 with two exceptions. Firstly, SK was told not to memorise the item shown at the start of the trial and
 186 did not perform the match-to-sample task. Secondly, there were only AllCongruent or Incongruent
 187 trial types. SK performed 1 block of practice trials and 3 blocks of 32 experimental trials, producing
 188 48 trials per condition. Trials were excluded where a saccade was made ($n = 6$) and trials with RT
 189 $>3SD + \text{mean}$ (5691, 9 trials), then calculated the Bayes factor (see Table 1). The Bayes factor of 0.32
 190 is evidence for the null hypothesis, suggesting that priming a stimulus does not lead to enhanced
 191 detection in this task (see Figure 3). A t-test comparing Allcongruent with Incongruent was non-
 192 significant (Allcongruent 52%, AllDifferent 52%, $t_{(94)} = 0, p = 1$).

193

194 **Discussion**

195 Our goal was to test the hypothesis that unconscious perception in hemianopia, or
 196 'blindsight', would be enhanced if the DT matched the contents of WM. The results suggest that this
 197 hypothesis is correct when there is an exact match between the DT and the item to be remembered.
 198 However, the evidence was less clear cut when only one of the features of the DT (colour or
 199 orientation) was encoded in memory. In these conditions there was a small improvement in
 200 performance of 5-10 percentage points but the Bayes factor was inconclusive. Importantly, a control

201 experiment in which SK was primed with DT but did not have to remember the DT provided evidence
202 *against* the hypothesis that priming could account for the effects observed in Experiment 1.

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

225 It is also noteworthy that only an exact match between the WM item and DT led to
226 enhanced detection accuracy, suggesting that colour or orientation information alone was not

227 enough to produce measurable improvement. This finding suggests that different features may
228 combine in an additive way to produce a more powerful bias. Furthermore, Martin et al. (2012)
229 demonstrated that there is a slower accumulation of visual information from the blind hemifield
230 than the sighted, and therefore it is possible that with a longer duration of presentation that either
231 feature alone (colour or orientation) may be sufficient to improve performance. In this respect it
232 may be worth considering the variability that exists in blindsight and the features that can elicit it
233 (e.g., Danckert & Rossetti, 2005), and it could be that some patients would be more influenced by
234 some features and different combinations than others. This could be an avenue for further work.
235 Indeed, further studies examining these effects in other patients are important in order to establish
236 the replicability and generalisability of our results.

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

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

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309

310 **Figure Legends**

311

312

313 **Figure 1:** Visual field plot showing SK's right-sided hemianopia. Kinetic perimetry was conducted

314 with the target moving inwards at 2°/s until detected, and the twelve meridians tested in a pseudo-

315 random order. Static perimetry involved the presentation of the target randomly at 60 points within

316 10° of fixation, each point separated by 2°.

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318 **Figure 2:** Illustration of a typical trial. In this example the Discrimination Target (the light grey and

319 black grating had incongruent colour and orientation and appeared in the 1st time interval. The

320 Memory Target is a match to the sample. The initial fixation point is not shown.

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