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No evidence for enhanced distractor template representation in early visual cortexReshanne R. Reeder*¹, Christian N. L. Olivers², Michael Hanke^{3,4}, & Stefan Pollmann^{1,4}

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1 Humans can retain task-relevant visual information in working memory and use it to compare against
2 visual information selected from the environment. Behaviorally, this speeds target detection (Desimone
3 & Duncan, 1995). In the brain, this manifests as distinct target-related cortical activity patterns in
4 visual cortex in preparation for visual stimulation (Gayet et al., 2017; Harrison & Tong, 2009). In
5 recent years, it has been hotly contested whether, in addition to these “target templates”, the brain also
6 makes use of “templates for rejection” – representations of distracting information to benefit
7 subsequent target detection (Arita et al., 2012; Beck & Hollingworth, 2015; Beck et al., 2017; Moher &
8 Egeth, 2012; Reeder et al., 2017). A difference in how distractor information is retained compared to
9 target information would suggest the use of a different preparatory template. Our questions for the
10 current paper focus on the nature of such preparatory representations of targets and distractors for
11 search. Is a distractor represented distinctly like a target in visual working memory (VWM) with an
12 additional “tag” that this should be rejected once it has been identified during search? Or is there no
13 distinct representation, perhaps even suppression, of the distractor feature in sensory brain areas during
14 the preparatory period? The current study is the first to provide evidence that visual features of
15 anticipated distractors are not represented more distinctly than irrelevant features (that will not appear
16 in the search display) in early visual cortex (EVC), supporting the hypothesis that a template for
17 rejection is functionally different from a target template.

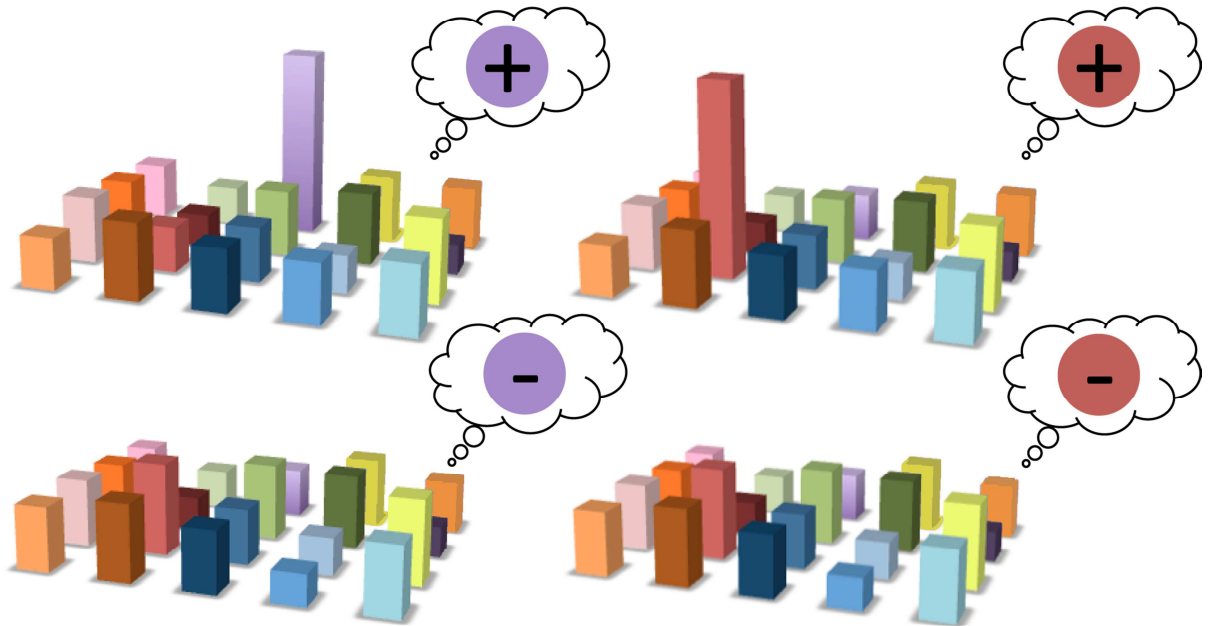
18 We asked subjects to detect a target in an array containing four items of one color and four
19 items of a second color, while undergoing fMRI (see Figure S1 in the Supplementary Methods). One of
20 the two colors was cued beforehand as positive (“the target will appear in this color”), negative (“only
21 distractors will appear in this color”), or neutral (“this color will not appear in the search display”). The
22 two colors that appeared in the search display on each trial were chosen from a selection of five colors.
23 Each of the five colors appeared as a positive, negative, or neutral cue an equal number of times. Initial
24 univariate analyses of the blood-oxygenation-level-dependent (BOLD) signal revealed a lower BOLD
25 response for negative cues compared to positive and neutral cues in EVC, despite a behavioral benefit

26 to having foreknowledge of the upcoming distractor color (Reeder et al., 2017). This pattern is not
27 predicted by the equal representation plus negative tag hypothesis, but rather supports the distractor
28 inhibition hypothesis of templates for rejection. Nevertheless, the regional activation modulation that
29 we reported previously is too unspecific to demonstrate differences in target and distractor feature
30 representations. For instance, a stronger BOLD response following positive cues may reflect a global
31 preparatory increase of neuronal activation instead of a selective increase of activation in those neurons
32 representing the target feature. Likewise, a drop in the regional BOLD amplitude may reflect inhibition
33 of preparatory attention rather than selective suppression of the cued feature. If these regional BOLD
34 amplitude modulations are driven by feature-selective modulation of neuronal delay activity, we should
35 see more distinct patterns of activity for target templates than for task-irrelevant features. If distractor
36 templates are characterized by inhibition of the distractor feature rather than facilitation, they should
37 lack the distinctiveness of target templates. Instead, distractor features should show comparable
38 distinctiveness to irrelevant features (Figure 1) or even an anti-correlated pattern, i.e., decreased
39 activation in voxels that show increased activation from baseline when the same feature is cued as a
40 target.

41
42 Figure 1. a.) An illustration of the study's hypotheses: the activation of a target template (represented
43 by "+" inside the colored bubble) leads to selective activation of EVC neurons representing the target
44 color. This, in turn, leads to distinct activation patterns for the different target colors. Contrarily, the
45 activation of a template for rejection (represented by "-" inside the colored bubble) leads to decreased
46 activation of EVC neurons and therefore decreased variability in stimulus-related activity. Thus,
47 different negatively cued colors will elicit weaker activity patterns that are more similar to those
48 elicited by task-irrelevant colors. b.) A brain in MNI space showing the extent of the EVC region
49 analyzed (in blue). Left hemisphere is displayed on the right. c.) A bar graph showing the average r to
50 Z values across colors presented as positive, neutral, and negative cues. Error bars represent the

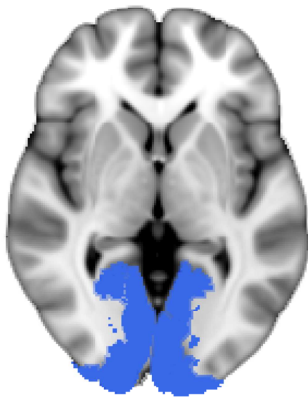
51 standard error of the mean.

a.



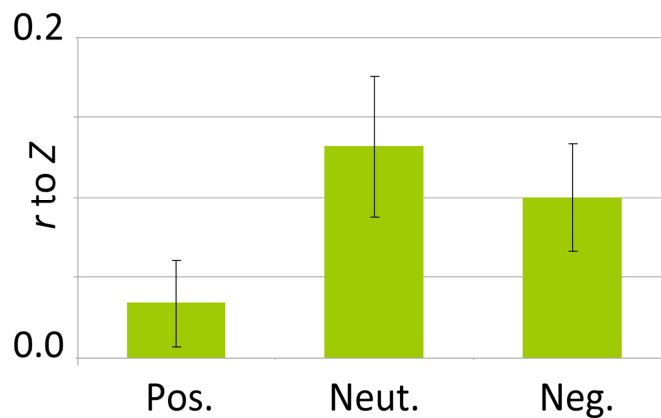
b.

EVC



z=0

c.



52

53 To investigate how distinctly the cue colors were represented in preparation for search, we used
 54 representational similarity analysis (RSA; Kriegeskorte et al., 2008) combined with a searchlight
 55 method implemented in PyMVPA (Hanke et al., 2009) within EVC (see Supplementary Methods for a
 56 detailed description of the analysis pipeline). Correlation distance ($1-r$) between beta weights was
 57 calculated for 15 conditions of interest (3 cue types x 5 colors), serving as the “distinctiveness” metric.

58 The data expressing the non-transformed $1-r$ values associated with each color and cue type, as well as
 59 the mean $1-r$ value for each cue type collapsed across colors, are reported in Table 1. $1-r$ values were
 60 then transformed into r values and Fisher Z -transformed to ensure a normal distribution of the data for
 61 statistical hypothesis tests. Lower Z values therefore indicate smaller correlations (i.e., greater
 62 distinctiveness) between color representations (see Figure S2).

63 We first performed a 3 (cue type: positive, negative, neutral) x 5 (color) repeated-measures
 64 ANOVA to test for representational distinctiveness of the different colors for each cue type. This
 65 revealed a significant main effect of cue type ($F(2,32)=4.960, p=0.013, \eta^2_p=0.237$), no main effect of
 66 color ($F(2,32)=1.237, p=0.304, \eta^2_p=0.072$), and no interaction between the two ($F(2,32)=0.812,$
 67 $p=0.593, \eta^2_p=0.048$). We then collapsed the data across color and conducted paired-samples t -tests to
 68 gauge the representational distinctiveness differences between cue types.

69

70 Table 1

71 *Mean $1-r$ distinctiveness values for each color and their standard deviation (SD). The mean and SD of*
 72 *each cue type with all colors combined are shown in the last column*

Cue type	Light Pink		Orange		Chartreuse		Cyan		Orchid		All colors	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Positive	1.004	0.212	0.989	0.109	1.018	0.115	0.949	0.153	0.872	0.143	0.966	0.109
Negative	0.897	0.154	0.901	0.123	0.885	0.192	0.895	0.164	0.931	0.227	0.902	0.133
Neutral	0.828	0.190	0.853	0.177	0.892	0.228	0.898	0.214	0.903	0.207	0.875	0.167

73 *Note. The SD for all colors combined was calculated as the between-subjects SD after obtaining the*
 74 *mean $1-r$ values collapsed across the 5 colors. Hex codes of each color are provided in the*
 75 *Supplementary Methods.*

76

77 To test for increased distinctiveness of cued target features, we first conducted a paired-samples
 78 t -test on positive > neutral cue distinctiveness in EVC. Positive cues were represented more distinctly
 79 than neutral cues ($t(16)=-2.574, p=0.01$, one-tailed, $d=0.953$; Cohen's d is corrected for dependent
 80 samples; Morris & DeShon, 2002). We then conducted a paired-samples t -test on positive > negative
 81 cue distinctiveness, which also showed a significant difference between cue types ($t(16)=-2.180,$
 82 $p=0.023$, one-tailed, $d=0.813$). We then tested if cued distractor features were more distinctively

83 represented than neutral features. A paired-samples t-test showed no difference between negative and
84 neutral cue distinctiveness ($t(16)=-0.794$, $p=0.216$, one-tailed, $d=-0.198$). We followed this up with a
85 Bayes factor (BF) analysis¹ (JASP Team, 2018). Bayes factors are particularly useful to test if the lack
86 of a significant difference is due to equal distinctiveness or low power (see Dienes, 2014). With the
87 Cauchy prior set to the default of 0.707, we found a $BF_{01} = 3.04$ (in favor of the null hypothesis),
88 which provides moderate support for equal distinctiveness of negative and neutral cues (Schönbrodt &
89 Wagenmakers, 2018). A BF robustness test on these data revealed that the likelihood of this lack of a
90 difference increases when the Cauchy prior is increased, suggesting this effect survives variability in
91 the prior width.

92 These analyses looked at the distinctiveness of the five colors given a cue condition, but we can
93 also look at the similarity of activation patterns across cue conditions for a given color. For example, a
94 positive cue may facilitate firing in a neuron that codes a given color and inhibit firing in a neuron that
95 codes a different color, whereas a negative cue may inhibit firing below baseline in the former and
96 increase firing in the latter. This could lead to comparable distinctiveness in the above pattern analyses
97 between colors, but a negative correlation for the same color across cue conditions. We therefore tested
98 the correlation between positive and negative cue distinctiveness and found a moderate positive
99 correlation ($r=0.51$, $p=0.036$), supporting the hypothesis that negative cue activation patterns are less
100 distinct, but qualitatively similar to positive cue representations, rather than inverted (which would be
101 suggested by a negative correlation).

102 These results show that only preparatory target feature representations in EVC are more distinct
103 than neutral feature representations, whereas the preparatory representation of distractor features are
104 not distinct from neutral feature representations. This pattern is incompatible with the hypothesis that
105 target and distractor representations are both enhanced by attention during the preparatory period. The

¹ For completeness, we report the other comparisons: positive vs. neutral cues $BF_{01} = 0.33$, and positive vs. negative cues $BF_{01} = 0.62$.

106 current results suggest that the lower univariate BOLD signal for negatively cued colors compared to
107 positively cued colors in the previous analysis of this dataset (Reeder et al., 2017) was driven by a
108 general suppression of visual processing in EVC, rather than color-specific suppression.

109 While distractor colors and irrelevant colors showed similar levels of distinctiveness, we
110 observed no negative correlation between positively and negatively cued colors that would have
111 resulted if neuronal activation of the distractor feature was a mirror image of the pattern elicited by
112 target features, i.e., distractor suppression in neurons where there is target facilitation, and vice versa.
113 We think this did not occur because of the overall low level of activation during the delay between cue
114 offset and search onset. While attention can cause clear increases and decreases during sensory
115 stimulation (e.g. Treue & Martinez Trujillo, 1999), during the delay period (which we have analyzed
116 here), neuronal activity is typically much reduced even if the cue matches the preferred feature of the
117 neuron (Bichot et al., 2005; Chelazzi et al., 1993; see also decoding of working memory content in the
118 absence of an elevated BOLD-response: Harrison & Tong, 2009; Serences et al., 2009). Inhibition of
119 stimulus features would only reduce the neuronal firing rate from already low delay activity to zero,
120 leaving much less room for distinctive differences in firing rate compared to the facilitatory modulation
121 of firing rate by positive cues.

122 At this point we cannot rule out that features cued as distractors may be represented by a
123 negatively correlated pattern with target features, but our current methods lack the sensitivity to
124 measure it. Increasing sensitivity, e.g., by using higher magnetic field strength fMRI, may lead to
125 further insights. Moreover, note that our irrelevant feature baseline may itself represent inhibition of
126 EVC. The facilitation of reaction times by negative cues compared to neutral cues yields no indication
127 that inhibition was only present in the former. It may simply be due to the fact that distractor inhibition
128 is useful for search whereas inhibition of irrelevant features is not. Thus, defining a different neutral
129 baseline that is less likely to induce inhibition may also be a way to address the effects of distractor
130 inhibition on EVC representations. Finally, it would be worthwhile to investigate whether the

131 modulation of representational distinctiveness depends on the features that are used as cues.

132 The present results show that target templates were distinctly represented in EVC, whereas no
133 distinct representation was observed for distractor templates, compared to baseline. Combined with the
134 previous results showing region-wide preparatory target facilitation and distractor inhibition, we
135 conclude that the representation of target templates and templates for rejection reflect differences in
136 both global and feature-selective brain activity.

137

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178

179 **Author Contributions**

180 RRR, CNLO, and SP conceived the experiment and wrote the paper. RRR designed and conducted the

181 experiment and performed the analyses. MH provided input on all analyses and RRR and MH wrote
182 the Supplementary Methods.

183

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189

190 **Competing interests**

191 The authors declare no competing interests.