

1 Pop-in: the inversion of pop-out for a feature dimension 2 during visual search in area V4 of the monkey cortex

3 P. Christiaan Klink^{1,2,3,4*} †, Rob R.M. Teeuwen^{1*}, Jeannette A.M. Lorteije¹,
4 & Pieter R. Roelfsema^{1,3,4,5} †

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6
7 ¹Dept. Vision & Cognition, Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts & Sciences,
8 Amsterdam, The Netherlands

9 ²Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, The Netherlands

10 ³Laboratory of Visual Brain Therapy, Sorbonne Université, Institut National de la Santé et de la Recherche Médicale,
11 Centre National de la Recherche Scientifique, Institut de la Vision, Paris F-75012, France

12 ⁴Dept. of Integrative Neurophysiology, Centre for Neurogenomics and Cognitive Research, VU University, Amsterdam,
13 The Netherlands

14 ⁵Dept. of Psychiatry, Academic Medical Center, University of Amsterdam. Amsterdam, The Netherlands

15 *Authors contributed equally

16 †Correspondence: P.C. Klink (c.klink@nin.knaw.nl), P.R. Roelfsema (p.roelfsema@nin.knaw.nl)

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18 **ORCID**s: P.C. Klink: 0000-0002-6784-7842; J.A.M. Lorteije: 0000-0003-0800-0278; P.R. Roelfsema: 0000-0002-
19 1625-0034

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25 Draft Preparation, Writing – Review & Editing, Visualization; J.A.M. Lorteije: Conceptualization, Investigation,
26 Writing – Review & Editing; P.R. Roelfsema: Conceptualization, Resources, Supervision, Funding Acquisition,
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29 [node.org/ChrisKlink/NHP_VisualSearch_Pop-in](https://gin.g-node.org/ChrisKlink/NHP_VisualSearch_Pop-in)). A doi will be associated with the dataset upon acceptance of the final
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31 Abstract

32 During visual search, it is important to reduce the interference of distracting objects in the scene. The
33 neuronal responses elicited by the search target stimulus are typically enhanced. However, it is equally
34 important to suppress the representations of distracting stimuli, especially if they are salient and capture
35 attention. We trained monkeys to make an eye movement to a unique ‘pop-out’ shape stimulus among an
36 array of distracting stimuli. One of these distractors had a salient color that varied across trials and differed
37 from the color of the other stimuli, causing it to also pop-out. The monkeys were able to select the pop-out
38 shape target with high accuracy and actively avoided the pop-out color distractor. This behavioral pattern
39 was reflected in the activity of neurons in area V4. Responses to the shape targets were enhanced, while the
40 activity evoked by the pop-out color distractor was only briefly enhanced, directly followed by a sustained
41 period of pronounced suppression. These behavioral and neuronal results demonstrate a cortical selection
42 mechanism that rapidly inverts a pop-out signal to ‘pop-in’ for an entire feature dimension thereby
43 facilitating goal-directed visual search in the presence of salient distractors.

44 **Keywords:** Visual search, V4, monkey, suppression, enhancement.

45

46 Significance statement

47 Goal-directed behaviors like visual search involve both the selection of behaviorally relevant targets and the
48 suppression of task-irrelevant distractors. This is especially important if distractors are salient and capture
49 attention. Here we demonstrate that non-human primates suppress a salient color distractor while searching
50 for a target that is defined by shape, i.e. another feature dimension. The neuronal activity of V4 neurons
51 revealed the temporal evolution of target selection and distractor suppression. The neuronal responses
52 elicited by the pop-out target stimuli were enhanced whereas responses elicited by salient pop-out color
53 distractors were suppressed, after an initial brief phase of response enhancement. Our results reveal a ‘pop-
54 in’ mechanism by which the visual cortex inverts an attentional capture signal into suppression to facilitate
55 visual search.

56 Introduction

57 Humans and animals usually need to select one of several stimuli for action. This selection process relies on
58 priority signals in the brain such as the salience of stimuli and the subject's goals (1–7). In the visual domain,
59 for example, one could be faced with the task of locating a target object among distractor objects, e.g., trying
60 to find one's keys on a cluttered desk (Fig. 1A). A combination of bottom-up and top-down processes often
61 solves this problem (3). If the keys have a high saliency because they are bright red, for example, they 'pop
62 out' from the background, which would be considered a bottom-up contribution. However, top-down factors
63 also play an important role. You may, for example, imagine the shape of your keychain or try to remember
64 where the keys most likely are. Visual search is therefore a very useful experimental paradigm to study the
65 role of bottom-up and top-down factors in visual selection.

66 In many bottom-up search paradigms, the target pops out, because it has a unique feature. For example, it is
67 the only bright red item among grey distractors, or it is the only circle in the display in which all other
68 elements are squares. There are versions of this paradigm in which subjects do not know beforehand what
69 they will be looking for, but only that it is the unique item. For example, the display might have either one
70 square among circle distractors or one circle among square distractors. The search for items with unique
71 properties is usually parallel, which means that the time to find an item does not depend strongly on the total
72 number of distractors in a search display (7). Previous studies on the neuronal correlates of pop-out search
73 demonstrated that the responses elicited by pop-out stimuli are stronger in the visual, parietal, and frontal
74 cortex than the responses to stimuli that do not pop-out (8–18). In top-down search paradigms, the subject
75 looks for a specific item known as 'search-template' (21, 22). The search template represents a top-down
76 influence on visual selection (1, 23) and the representations of the items in the display that match the search
77 template are also enhanced in areas of the visual, parietal, and frontal cortex (19, 22–29).

78 Many displays contain salient distractors that interfere with visual search. This is the case in Figure 1 for the
79 green parrot, which captures attention, making it more difficult to find the keys. Researchers have debated
80 the degree of automaticity of attentional capture, with some researchers arguing that it is mandatory (30)
81 whereas others arguing that it can be prevented by sufficiently strong top-down signals (31). Importantly,
82 conditions exist under which salient display items do not appear to interfere with visual search (32, 33) or
83 cause even less interference than regular, non-salient distractors (34–37).

84 The mechanism by which salient distractors can be suppressed is not yet fully understood and there are
85 contrasting views (38). One possibility is that salient distractors initially capture attention, but that it is
86 rapidly curtailed by top-down suppression mechanisms (39). Support for such reactive suppression comes
87 from human EEG studies employing markers of distractor selection and suppression (40–43). The signal
88 suppression hypothesis (35–37) proposed another account, in which a top-down influence prevents the
89 capture of attention by salient distractors so that there is no need for disengagement. This viewpoint received

90 support from behavioral studies (34, 35, 44) and other human EEG studies (34, 36, 37, 45, 46). We note,
91 however, that the relation between this putative suppressive signal and its EEG signatures is under dispute
92 (43, 47).

93 The degree to which salient distractors attract attention and, hence the need for disengagement, depends on
94 how predictable they are. Salient distractors are more efficiently suppressed if their features are predictable,
95 for example, because they are the same across trials or are known in advance (48, 49). Bichot et al. (50)
96 demonstrated that the representations of stimuli that consistently appear as distractors, across many days, are
97 strongly suppressed in the frontal cortex of monkeys. Like distractor predictability, foreknowledge about the
98 target also decreases the influence of salient distractors. If the subject knows the target, a search template can
99 be established before the display appears and the influence of salient distractors is weaker than in pop-out
100 search in which the target properties are not specified. Researchers proposed that pop-out search demands a
101 special ‘singleton detection mode’ (32). If subjects search for a salient target with unknown features, they are
102 more susceptible for interference by salient distractors. The degree of interference by the distractor depends
103 on the relation between the features of the target and the distractor (35, 36, 38, 51, 52). Interference is strong
104 if the target and salient distractor are defined on the same feature dimension, e.g., if they both have an
105 orientation that differs from that of all other distractors. Interference is weaker if they are defined on a
106 different feature dimension, e.g., the target differs in orientation from the other items whereas the salient
107 distractor differs in color. In this situation, the features can be weighted. The target dimension receives a
108 higher weight than the salient distractor so that the degree of distraction can be diminished (40, 52–54).

109 Two previous studies have examined the neuronal mechanisms for the suppression of salient distractors
110 during visual search. Ipata et al. (55) had monkeys searching for a black target shape among black
111 distractors. They added a salient distractor, which was green and bright, and recorded neurons in the lateral
112 intraparietal area (LIP) of the parietal cortex. As expected, targets elicited stronger neuronal responses than
113 the black distractors, but the activity elicited by the salient green items was even weaker than that elicited by
114 the regular black distractors. Hence, the representation of the salient distractor is efficiently suppressed in the
115 parietal cortex. A later study by Cosman et al. (56) replicated this finding in the frontal eye fields (FEF) in a
116 task where the monkeys searched for a white target letter while the salient distractor was colored. Again, the
117 target letter elicited strongest activity, followed by the regular distractors and the salient distractor elicited
118 weakest activity. These results are in accordance with those of Bichot et al. (50) showing the effective
119 suppression of a specific feature that is always distracting in the frontal cortex. (57, 58). However, parietal
120 and frontal cortex are relatively high up in the cortical processing hierarchy and activity elicited by salient
121 distractors might still be enhanced in the visual cortex, even after extensive training. The representation of
122 salient distractors in visual cortex remains to be investigated.

123 In the present study we tested the generality of the suppression mechanisms by asking three questions: (1)
124 Are salient distractors suppressed in the visual cortex? (2) Is the efficient suppression of a salient distractor

125 stimulus also possible when its features vary across trials? (3) Can salient distractor suppression occur when
126 the subject searches for a pop-out stimulus on a different feature dimension?

127 We trained monkeys in a task in which they carried out a pop-out search for a shape while we presented a
128 salient color distractor with a color that varied across trials. They had to select the shape singleton as target
129 for an eye movement to obtain a juice reward. As expected, the shape singleton elicited stronger V4 activity
130 than the distractors with a different shape. Remarkably, the V4 representation of salient color singleton was
131 briefly enhanced followed by a period of pronounced suppression below the level of representation of the
132 regular non-pop-out distractors, even though its color was unpredictable. At a behavioral level, the monkeys
133 also selected the salient distractor less often than the regular distractors, indicating active avoidance. We
134 conclude that after extensive training, the neuronal mechanisms for visual search can exploit the presence of
135 a color singleton if it is always a distractor, and rapidly cause it to ‘pop-in’ instead of pop-out, thus avoiding
136 capture and promoting efficient goal-directed behavior.

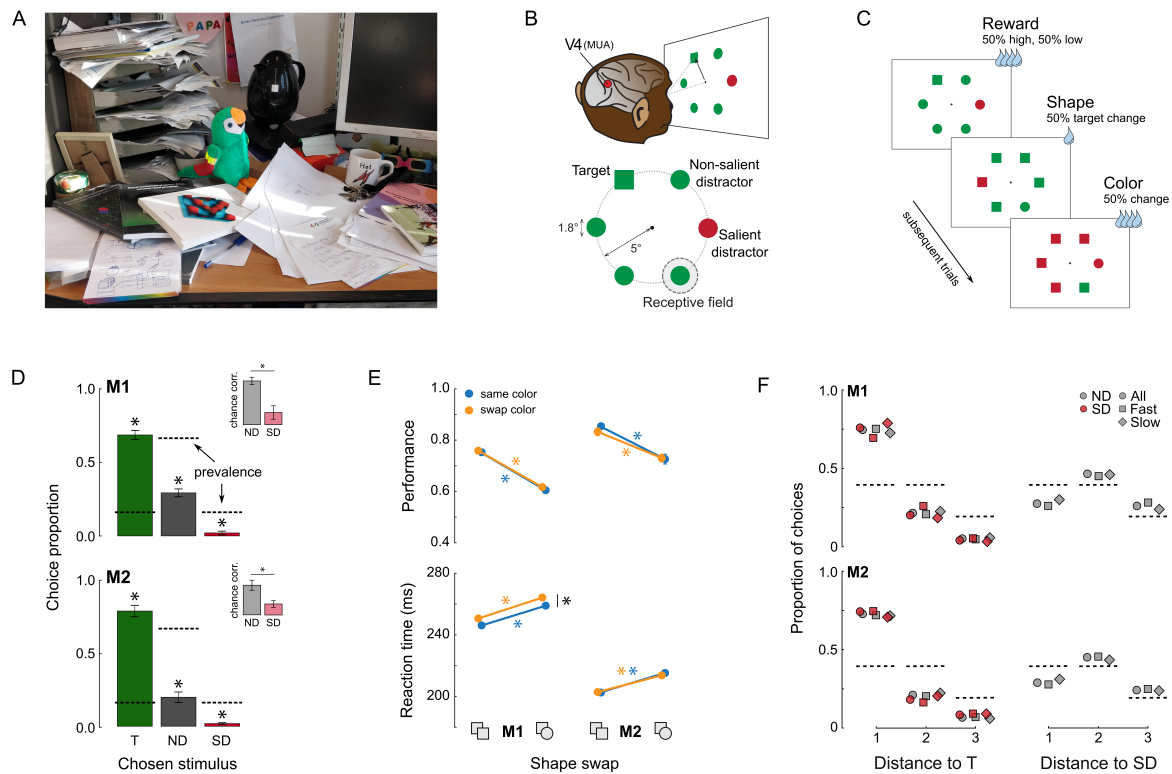


Figure 1. Task description and behavioral results. **A)** Real-life example of visual search with a salient distractor. When looking for your keys on a crowded desk, you may be looking for small key-shaped objects. Your attention may however be captured by salient objects like the bright green parrot, which might interfere with the process of finding your keys. **B)** We recorded from area V4 while monkeys performed a visual search task in which they selected the odd-shape-out (here a square among circles) with an eye movement. One of the six visual items was in the V4 receptive field. The target was the stimulus that differed from the others by shape. Non-salient distractor stimuli had the same color as the target, while a single salient distractor stimulus popped out because it had a different color. **C)** Example series of three trials. In the second trial the target and distractor shapes swapped with respect to the first trial (this occurred 50% of the time). In the third trial, the target and distractor colors swapped (this also occurred 50% of the time). In addition, the reward magnitude was randomly varied (50% high, 50% low). **D)** Accuracy (green bars) and the proportion of trials on which the monkeys made an error by choosing a non-salient distractor (ND, grey bars) or the salient distractor (SD, red bars). Non-salient distractors are 4 times more prevalent than targets and salient distractors (prevalence indicated with dashed horizontal lines). The insets show the proportion of choices of distractor stimuli corrected for prevalence. Even after this correction, the animals chose the salient distractor less often than the non-salient distractors (* indicates $p < 0.001$ for a one-tailed t-test $SD < ND$). Error bars indicate the standard deviation over recording sessions. **E)** The effects of color and shape swaps on accuracy (top panel) and reaction time (bottom panel) for both monkeys. Yellow lines indicate trials in which the target and salient distractor colors swapped relative to the previous trial; blue lines are trials in which those colors stayed the same. The horizontal axis indicates whether the target shape changed relative to the previous trial. Error bars (often smaller than the data points) indicate S.E.M., asterisks denote $p < 0.001$ for main effects as indicated by two-way ANOVAs (no interaction effects were significant at $p < 0.05$). **F)** Dependence of erroneous choices on the relative locations of the target (T) or salient distractor (SD) stimuli. The proportion of choices on error trials is plotted as function of the distance between the chosen stimulus in the search array (a distance of one indicates the two stimuli were next to each other, a distance of two means there was one stimulus in between, etc.), the identity of the chosen stimulus (grey: ND; red: SD), and the reaction time (30% fastest and slowest response indicated with square and diamond symbols respectively). The dashed lines indicate chance level.

138 Results

139 Two monkeys were extensively trained to perform a visual search task (Fig. 1B,C) in which they had to
140 select a single odd-shape-out (target) from an array of six stimuli. On any given trial, the target could either
141 be a circle among squares, or a square among circles. To study whether V4 neurons show suppression of
142 salient distractors, one of the distractor stimuli had a different color than the others (either green among red,
143 or red among green) (Fig. 1B, bottom). The shapes, colors, and locations of the target and salient distractor
144 were randomly assigned on each trial so that the animal could not predict the shape or color of the target and
145 salient distractor. As a result, consecutive trials could have the same shape and colors assigned to the target
146 and distractor, both could change, or one of the feature assignments could stay the same while the other
147 changed. Moreover, to examine a previously reported interaction between stimulus salience and reward in
148 human visual search behavior (59), we randomly rewarded correct responses with either small or large juice
149 rewards (with the large reward being approximately four times the small reward amount). After an initial
150 training phase to learn the task, both monkeys were extensively trained to reach high performance levels (22
151 training sessions for M1, 56 for M2).

152 We recorded 34,543 trials in monkey 1 (M1) and 13,815 trials in monkey 2 (M2) in 28 and 16 sessions,
153 respectively. Both monkeys displayed similar eye movement patterns (Fig. 1D), most often choosing the
154 target stimulus (M1: 69%, M2: 78% of choices), followed by non-salient distractors (M1: 29%, M2: 20%),
155 and only rarely choosing the salient distractor stimulus (M1: 2%, M2: 2%). The lower probability of
156 choosing a salient distractor than a non-salient distractor remained when we accounted for the fact that there
157 were four non-salient distractors and only one salient distractor (see Fig. 1D insets, corrected for prevalence).
158 The probability of choosing the target was much higher than chance (one-tailed t-test, M1: $t(26) = 87.4$, $p <$
159 0.001 ; M2: $t(15) = 53.5$, $p < 0.001$). On error trials, both animals were significantly less likely to choose the
160 salient distractor than a non-salient distractor (prevalence-corrected, one-tailed paired t-test, M1: $t(26) = -$
161 51.6 , $p < 0.001$; M2: $t(15) = -21.6$, $p < 0.001$).

162 Swapping the colors of the target and salient distractor on successive trials did not affect accuracy for either
163 animal as indicated by a two-way ANOVA with color-swap and reward quantity as independent variables
164 (all p s > 0.48). It did slow down M1 by a few milliseconds (Fig. 1E; $F(1, 12210) = 38.8$, $p < 0.001$), but had
165 no effect on M2's reaction time ($F(1, 7484) = 1.59$, $p = 0.83$). A change of the target shape had a much more
166 pronounced effect of performance. It decreased the accuracy of both animals and increased the reaction times
167 (Fig. 1E; all $p < 0.001$). There were no interactions between the effects of color and shape changes. These
168 results imply a shape-based priming of pop-out effect across trials (60), but an absence of color-based
169 priming, which is consistent with the animals being in 'shape-searching' mode due to extensive training on
170 the 'odd-shape-out' search task. Unlike previous work in humans (59), we did not observe any main or
171 interaction effects of reward quantity on visual search performance (Supplemental Fig. 1).

172 What happened when the monkeys made an error? They predominantly selected the distractor stimulus that
173 was adjacent to the target in the search array (Fig. 1F), a pattern that was neither influenced by the location
174 of the salient distractor, nor by the saccadic reaction time (comparing the 30% fastest and 30% slowest
175 saccades) (squares and diamonds in Fig. 1F). The distribution of erroneous saccades relative to the target
176 position was the same for salient and non-salient distractors (red and grey symbols in Fig. 1F), which
177 indicates that the probability of choosing the salient distractors was decreased uniformly (Fig. 1D) with little
178 influence of the target location.

179 Whereas the signal suppression hypothesis (34) proposes that a salient distractor can be proactively
180 suppressed to avoid attentional capture, the stimulus-driven rapid-disengagement account suggests that
181 capture does temporarily occur but that it is then quickly suppressed. The latter scenario should be associated
182 with a brief period of pop-out for the salient distractor followed by a sustained period of distractor
183 suppression. Because visually guided saccades can occur at very low latencies in both humans and monkeys
184 (61–65), especially after prolonged training (66), we wondered whether an early neuronal pop-out of the
185 salient distractor would result in very rapid saccadic responses to the salient distractor before the distractor
186 suppression could have manifested. To investigate this possibility, we compared the distributions of saccade
187 reaction times (SRTs, Supplemental Fig. 2) for target and salient distractor choices. A larger proportion of
188 the salient distractor choices than the target choices occurred at the shortest reaction times in both monkeys
189 (Fig. 2A). We calculated the proportion of salient distractor choices ($p_{SD} = n_{SD}/n_{ALL}$) as function of SRT (Fig.
190 2B). In both animals, the proportion SD choices was significantly higher for the 12.5% shortest SRTs (first
191 octile) than for SRTs in the 2nd-4th octiles (chi-squared test, M1: $X^2(1) = 8.55$, $p < 0.01$; M2: $X^2(1) = 21.41$, p
192 < 0.001). In M1 there was even a brief epoch in which the salient distractor was chosen more often than the
193 target, but saccades to the salient distractor were strongly suppressed for longer SRTs. Also, in M2 the
194 salient distractor choices decreased for longer SRTs, but the target was always chosen with the highest
195 probability (Supplemental Fig. 2). This result indicates that the distractor pops out in an early interval after
196 stimulus presentation, but that the pop-out signal is rapidly suppressed to prevent erroneous choices.

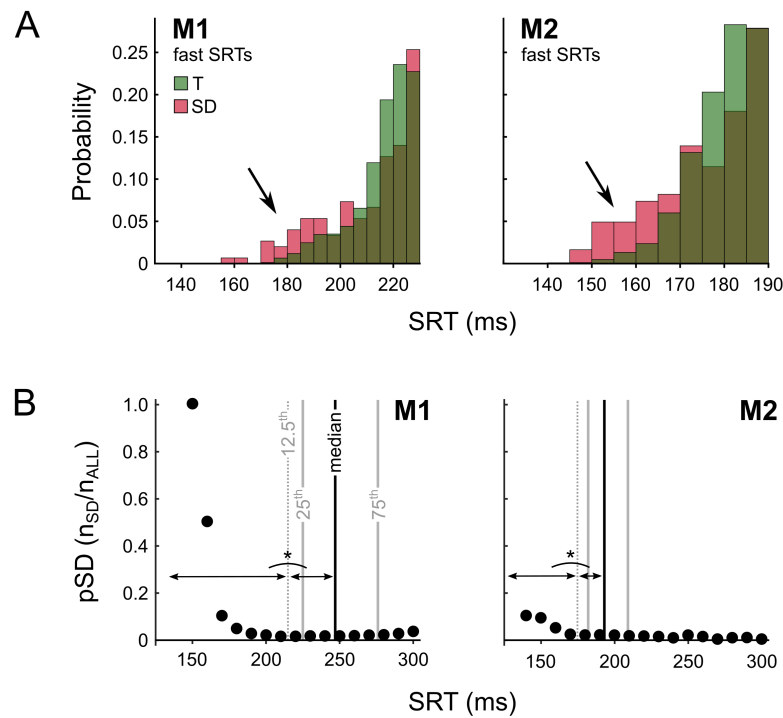


Figure 2. Saccadic reaction times and choices. **A**) Distributions of shortest saccadic reaction times (SRTs, fastest 25th percentile) for target (T, green) and salient distractor choices (SD, red) in the two monkeys. The distributions were normalized such that both the red and green bars sum up to 100% (see Supplemental Fig. 2 for the full SRT distributions, normalized within choice type (as here) and also by to the total number of saccades). The dark colors indicate overlap between the red and green distributions. The probability of choosing the salient distractor was increased at short SRTs (black arrows). **B**) Proportion of salient distractor choices (pSD) calculated in a sliding 20 ms window, moving at 10 ms increments. Solid vertical lines are the median, 25th, and 75th percentiles of the full SRT distributions. In both monkeys, the proportion of salient distractor choices is significantly higher for the 12.5% fastest responses (first octile, left of the dashed vertical line) than in the second through fourth octiles (chi-squared test, M1: $X^2(1) = 8.55$, $p < 0.01$; M2: $X^2(1) = 21.41$, $p < 0.001$).

198 Next, we compared the neuronal responses in V4 elicited by target stimuli, non-salient distractor stimuli and
199 salient distractor stimuli on correct trials (Fig. 3A, top panels). We pooled the data across animals (Fig. 3,
200 left panels) because the results were similar for M1 and M2 (Fig. 3, middle and right panels). The late V4
201 response elicited by target stimuli was stronger than that elicited by non-salient distractor stimuli (time
202 window 150-200 ms after stimulus onset, $t(34) = 8.9$, $p < 0.001$; M1: $t(9) = 5.6$, $p < 0.001$; M2: $t(24) = 7.0$, p
203 < 0.001). The response elicited by the salient distractor stimulus was weaker than that elicited by the target
204 stimulus and, importantly, also weaker than that elicited by the non-salient distractor stimulus ($t(34) = -9.9$, p
205 < 0.001 ; M1: $t(9) = -5.4$, $p < 0.001$; M2: $t(24) = -9.1$, $p < 0.001$). This ordering of response strength was very
206 consistent among recording sites (Supplemental Fig. 3).

207 We examined the time-course of target enhancement and salient distractor suppression by subtracting V4
208 activity elicited by the non-salient distractor stimuli from the other two conditions (Fig. 3A, bottom panels).
209 We measured the latency of the enhancement and suppression of targets and salient distractors with a fitting
210 procedure that has been described before (67) (see Methods and Supplemental Fig. 4). The latency of target
211 enhancement was 112 ± 9 ms (averaged across monkeys, standard deviation determined with bootstrapping)
212 and the latency of suppression of salient distractors was 158 ± 25 ms. This pattern was also present in
213 individual animals (M1_T: 124 ± 20 ms, M2_T: 108 ± 15 ms; M1_{SD}: 184 ± 14 ms, M2_{SD}: 159 ± 11 ms) and the
214 salient distractor suppression was significantly later than the target enhancement (paired t-test, M1: $t(75) = -$
215 26.3 , $p < 0.001$; M2: $t(72) = -22.1$, $p < 0.001$; Pooled data: $t(67) = -17.7$, $p < 0.001$). Thus, the pop-in effect
216 was expressed in area V4 as a decreased response to the irrelevant singleton, even though its color was
217 unpredictable.

218 The brief early epoch with an enhanced probability of saccades to the salient distractor suggests that the
219 distractor representation might be briefly enhanced in V4 (33, 35, 37) before it is suppressed. We therefore
220 examined the possibility of an early response enhancement. We observed that the salient distractor (Fig. 3B,
221 red bars) indeed caused a brief epoch of enhanced activity before suppression became evident, in a time-
222 window up to 100 ms after stimulus onset (Fig. 3B shows significant modulation in several 10 ms non-
223 overlapping time bins in both monkeys; t-tests at $p < 0.05$, Bonferroni corrected).

224 We also examined a possible influence of the behavioral priming effect, which occurred when the target
225 shape was the same on consecutive trials, on V4 activity. The priming effect did not have a consistent
226 influence on V4 activity (Supplemental Fig. 5), which suggests that the increase in SRT may originate in
227 downstream brain regions, as a post-selective process (54). Furthermore, V4 activity on error trials was more
228 variable than on correct trials (Supplemental Fig. 3).

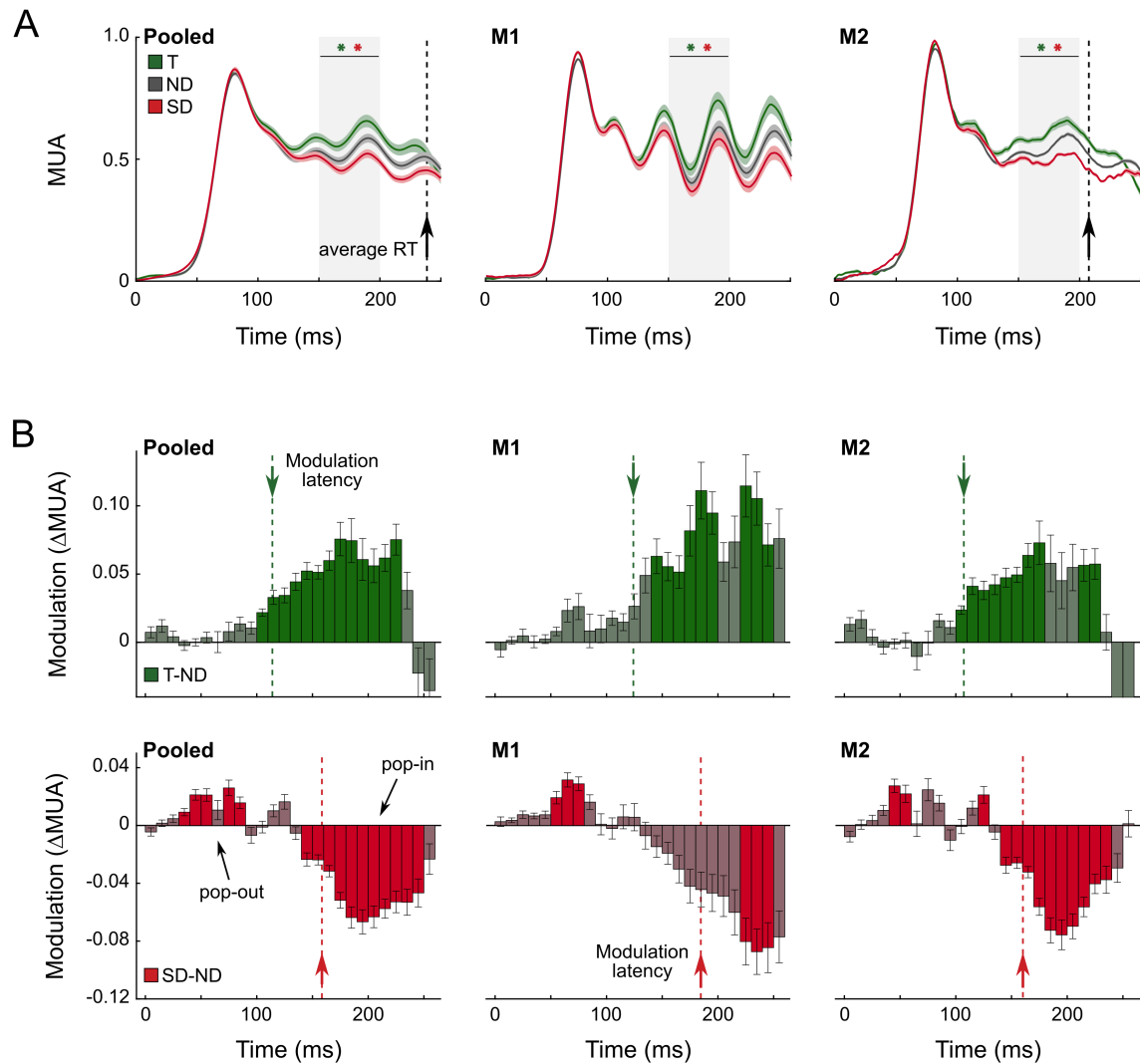


Figure 3. V4 activity during visual search reveals the time-course of pop-out and pop-in. **A**) Neuronal responses in area V4 responses on correct trials. Average V4 activity elicited by the target (T, green trace), non-salient distractors (ND, gray trace) and the salient distractor (SD, red trace) averaged across animals (left panel) and for individual monkeys (M1: middle panel; M2: right panel). Shaded area corresponds to S.E.M. across recording sites. Black arrows indicate the average reaction time (for M1 this was later than 250 ms and is not depicted). The light grey areas indicate the time window used for statistical testing of the response modulation, with * indicating $p < 0.001$ with a paired t-test (green: T-ND; red: SD-ND). **B**) Time-course of neuronal target and salient distractor modulation. Top row, difference in activity elicited by the target and non-salient distractor (T-ND; non-overlapping 10 ms time bins) pooled across monkeys (left) and individual animals (middle and right panels). Green bars indicate significant epochs at $p < 0.05$ (t-test with Bonferroni correction for multiple comparisons). Bottom row, difference in activity elicited by the salient distractor and non-salient distractor (SD-ND) with the red bars indicating $p < 0.05$ (t-test, Bonferroni correction). In both animals, there is an initial epoch of salient distractor enhancement, followed by suppression, later than 150 ms. Colored arrows indicate the latency of target enhancement (green) and salient distractor suppression (red).

230 Discussion

231 Goal-directed behaviors require a selection process that highlights relevant stimuli and suppresses
232 distractors. Here, we used a visual search paradigm to investigate the representations of relevant and
233 irrelevant pop-out stimuli (7) in area V4 of the monkey visual cortex. We presented a salient pop-out color
234 distractor with an unpredictable color while the monkeys searched for a singleton shape. Our results
235 demonstrate that the visual brain can suppress the representation of pop-out stimuli on an irrelevant feature
236 dimension while enhancing the representation of pop-out stimuli on a relevant feature dimension. A brief
237 neuronal activity enhancement preceded the suppression of distractor representations (Fig. 4), suggesting that
238 an initial pop-out process is required before it can invert into pop-in. To our knowledge, this is the first
239 demonstration of ‘pop-in’ for an irrelevant feature dimension, which presumably emerged during the
240 monkeys’ considerable training.

241 The efficiency of visual search depends on bottom-up factors that determine the salience of stimuli, such as
242 brightness and local feature contrasts causing pop-out, and the top-down search template, the internal
243 representation of the item that the subject is searching for (1, 3, 4, 22). Researchers have hypothesized that
244 stimulus salience and goal-driven influences on the distribution of attention jointly determine a ‘priority
245 map’ of visual space (3–7, 68–70). There are multiple candidate brain regions for such a priority map,
246 including the LGN (68), pulvinar (71), superior colliculus (72, 73), V1 (74), V4 (66), the parietal (8, 10, 55)
247 and prefrontal cortex (11). Indeed, stimulus-driven pop-out signals have a widespread influence on the
248 neuronal firing rates in early visual cortex (12, 75, 76), parietal cortex (10), frontal cortex (11), and
249 subcortical structures like the superior colliculus (77). Similarly, the top-down influences of the search
250 template on firing rates also occur in most, if not all, of the same brain regions, including V1 (78, 79), V4
251 (15, 18), the parietal (55) and prefrontal cortex (11, 50, 56). It is conceivable that the relative contributions of
252 the multiple priority maps depend on the task, e.g., on the features that matter and on whether the subject
253 reports the location of the target with an eye or hand movement.

254 There are many instances in which the representation of visually salient items needs to be suppressed,
255 because task relevant items are less conspicuous, causing a conflict between bottom-up and top-down
256 factors. The signal suppression hypothesis (36, 37) proposed that top-down suppression signals can prevent
257 attentional capture by salient distractors if their features are known in advance (34–37, 44–46, 51, 56, 80–
258 82). An alternative possibility is that salient distractors attract attention, but that it is rapidly disengaged (39).
259 Previous electrophysiological studies in areas LIP and FEF of monkeys revealed that the neuronal activity
260 elicited by a salient distractor with a predictable color can indeed be suppressed below the activity elicited by
261 regular distractors (55, 56). The suppression of salient distractors has also been measured as a distractor
262 positivity (Pd) component in the EEG of humans (37, 38, 83) but a recent study using the steady-state
263 visually evoked potential (SSVEP) did not find evidence for suppression below the activity elicited by
264 regular distractors (47). This SSVEP study used displays with only few items, however, and it has been

265 suggested that such displays do not emphasize pop out but require other search processes ('clump scanning')
266 (41, 52, 84). The present study went beyond these previous studies by investigating whether suppressive
267 signals influence spiking activity in the visual cortex of monkeys. Furthermore, we used a new task in which
268 the features of the salient distractor were unpredictable, and the monkey was searching for a pop-out
269 stimulus on a different feature dimension.

270 Unlike the previous studies (55, 56), we found that the salient distractor elicited a brief enhancement of V4
271 activity that later inverted into sustained suppression. It seems likely that the early response enhancement
272 occurred because the color of the salient distractor was unpredictable so that it first needed to be registered
273 before it could be suppressed. We also observed a behavioral consequence of this brief pop-out phase
274 because a proportion of the early saccades landed on the salient distractor whereas it was less likely to be
275 selected than regular distractors at later time points, when pop-out has inverted into pop-in. This result
276 provides evidence for short-lived attentional capture, followed by rapid attentional disengagement (38, 39). It
277 supports previous EEG studies indicating that predictable salient distractors cause attentional capture (40)
278 and is not in accordance with the signal suppression theory, which proposed that suppressive top-down
279 signals eliminate attentional capture.

280 In a previous study on the role of area V4 during visual search Ogawa and Komatsu (15) trained monkeys to
281 search for either shape or color singletons in displays that also included a singleton in the other dimension, as
282 a salient distractor. Unlike in the present study, however, the monkeys searched for shape and color
283 singletons in alternating blocks of trials. When they made an error, they selected the salient distractor more
284 often than regular distractors, which is also different from the current results. Accordingly, V4 activity
285 elicited by the target of search was strongest, V4 activity elicited by salient distractors was intermediate and
286 stronger than that elicited by regular distractors (15). In other words, in the previous study both the singleton
287 target and the singleton distractor popped out, while in the present study, the color singleton was never
288 relevant and its V4 representation was suppressed below the activity elicited by regular distractors.

289 Our results indicate that there are at least two processing steps in the present search task (Fig. 4). Initially,
290 there is pop-out in two feature dimensions: color and shape. Later in the trial, the activity elicited by the
291 shape singleton remains enhanced, whereas activity elicited by the color singleton is suppressed, indicating
292 that V4 could contribute to a priority map with enhanced target and suppressed distractor representations
293 (Fig. 4). The source of the suppressive pop-in signal is unknown, but it could rely on feedback projections
294 (85, 86) that might have been strengthened during training. In accordance with this view, microstimulation of
295 FEF interacts with stimulus driven activity in early visual cortex in a topographic manner, with an effect that
296 depends on stimulus strength and the presence of distractors (87). It is remarkable that the neuronal
297 mechanisms for the registration of the salient distractor and its later suppression can co-exist with the
298 mechanisms for pop-out on another feature dimension. Previous studies anticipated that that the degree to
299 which different feature dimensions cause pop-out can be weighted (52–54). However, to our knowledge,

300 these theories did not anticipate that dimension weights could become negative, causing attentional repulsion
301 of singletons on a specific feature dimension.

302 Previous studies demonstrated a profound influence of the recent history of trial types during visual search.
303 Repeatedly searching for the same stimulus features causes priming. It reduces an observer's reaction time,
304 improves accuracy, and increases the difference between the strengths of the neuronal representation of
305 targets and distractors (9, 18, 60, 88–92). We here observed a priming effect of shape. When the shape of the
306 search target remained the same on consecutive trials, the monkeys were faster and more accurate than when
307 it was different. Interestingly, we did not find a behavioral priming effect of color as was observed in
308 previous studies (9, 18, 88), in which the search target was a color singleton. It therefore seems likely that
309 priming only occurs for the feature dimension that defines the search goal.

310 Earlier studies also demonstrated an effect of reward quantity on visual search performance (59, 93–95). A
311 study in human subjects demonstrated that visual search is faster if a preceding trial with the same target and
312 distractor features gave rise to high, as opposed to low, reward (59). We did not replicate this effect in our
313 monkeys, where reward magnitude on the previous trial did not strongly affect performance. One possible
314 explanation is that the animals were highly trained, which may have reduced their sensitivity to reward
315 outcomes on individual trials. However, other explanations, including species differences, are also
316 conceivable.

317 In conclusion, our work shows parallel mechanisms of target enhancement and salient distractor suppression
318 during visual search in V4 that rapidly develop and manifest behaviorally as efficient distractor avoidance
319 and goal-directed target selection. It seems likely that the conversion of initial distractor enhancement into
320 functional and profound that occurs round 150 ms after stimulus onset reflects a top-down dynamic
321 adjustment of the weights of individual feature dimensions. The extended training history, during which the
322 salient color never coincided with the search target, must have engaged plasticity mechanisms inverting pop-
323 out into pop-in, making the mechanisms of visual search more versatile than might have been anticipated.

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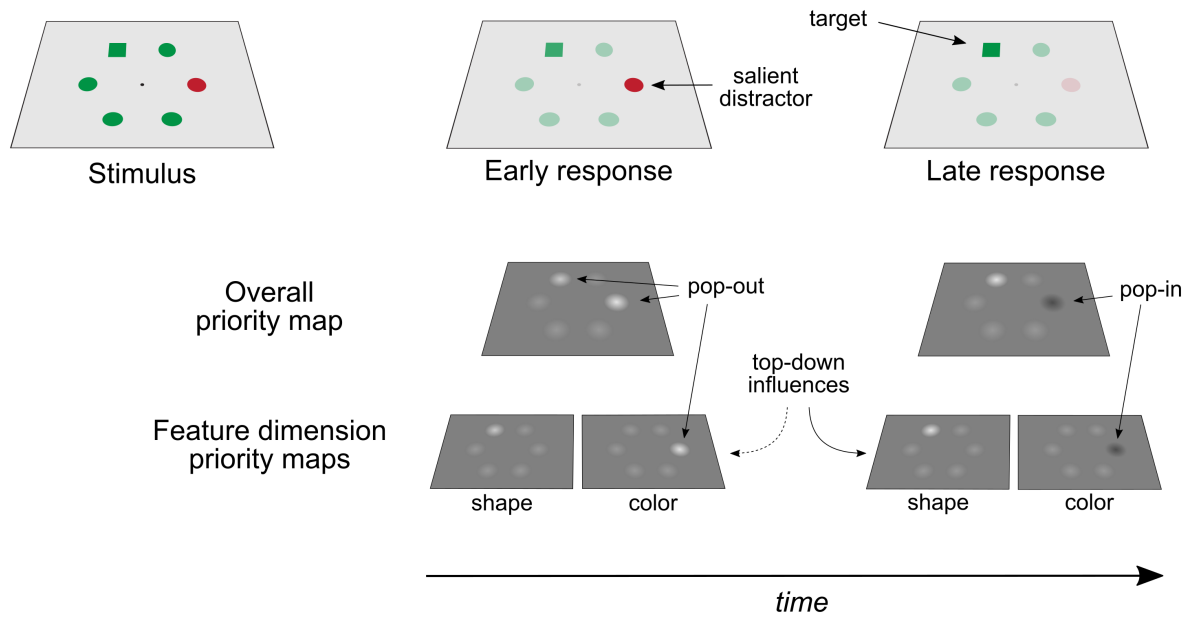


Figure 4. Pop-out and pop-in. During the early phase of the V4 response (middle) to a visual search stimulus (left), both the shape and color singletons pop-out. In a later phase of the response (right), top-down influences invert the pop-out of the salient color distractor into pop-in.

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335 **Methods**

336 **Subjects**

337 All animal procedures complied with the NIH Guide for Care and Use of Laboratory Animals, and were
338 approved by the institutional animal care and use committee of the Royal Netherlands Academy of Arts and
339 Sciences. Two male macaque monkeys participated in the experiment. They were 5 (M1) and 8 (M2) years
340 old at the start of the experiments and weighted between 7-8 (M1) and 8-9 (M2) kg over the course of the
341 recordings. The monkeys were socially housed in pairs in a specialized primate facility with natural daylight,
342 controlled humidity and temperature. The home-cage was a large floor-to-ceiling cage that allowed natural
343 climbing and swinging behavior. The cage had a solid floor, covered with sawdust, and was enriched with
344 toys and foraging items. The diet consisted of monkey chow supplemented with fresh fruit. The access to
345 fluid was controlled, according to a carefully designed regime for fluid uptake. During weekdays the animals
346 received diluted fruit juice in the experimental set-up upon correctly performed trials. We ensured that the
347 animals drank sufficient fluid in the set-up and supplemented extra fluid after the recording session if the
348 monkeys did not drink enough. In the weekend the animals received at least 700 ml of water in the home-
349 cage supplied in a drinking bottle. The animals were regularly checked by veterinary staff and animal
350 caretakers and their weight and general appearance were recorded in an electronic logbook daily during
351 fluid-control periods.

352 **Surgical procedures and training**

353 We implanted both monkeys with a titanium head-post (Crist instruments) under aseptic conditions and
354 general anesthesia as reported previously (96–98). The monkeys were first trained to fixate a 0.5 diameter
355 fixation dot and hold their eyes within a small fixation window (1.2 diameter). They then underwent a
356 second operation to implant arrays of 4x4, 4x5 and 5x5 micro-electrodes (Blackrock Microsystems) in V4.
357 The inter-electrode spacing of the arrays was 400 μm . The animals were later extensively trained to perform
358 the visual search task at adequate performance levels (22 training sessions with the final task for M1, 56
359 sessions for M2). During the early phase of the training the animals were required to make an eye movement
360 from the fixation point to a single target, and in later phases the distractors were introduced at low contrast
361 which over sessions gradually increased to the same contrast as the target.

362 **Electrophysiology**

363 Recordings from the chronically implanted electrode arrays were made with TDT (Tucker Davis
364 Technology) recording equipment using a high-impedance head-stage (RA16AC) and a preamplifier (either
365 RA16SD or PZ2). The signal was referenced to a subdural electrode and digitized at 24.4 kHz. It was band-
366 pass filtered (2nd order Butterworth filter, 500 Hz – 5 kHz) to isolate high-frequency (spiking) activity. This
367 signal was rectified (negative becomes positive) and low-pass filtered (corner frequency = 200 Hz) to
368 produce multi-unit activity (MUA), which is the envelope of the high-frequency activity (99). MUA reflects

369 the spiking of neurons within 100-150 mm of the electrode and MUA population responses are very similar
370 to those obtained by pooling across single units (98–102). We used a video-camera based eye-tracker
371 (Thomas Recording) to measure the eye position at a sampling frequency of 250 Hz. V4 receptive fields
372 were mapped by presenting white squares (1° , luminance 115 cd/m^2) on a dark background (2 cd/m^2) at
373 different positions of a grid (1° spacing). We defined the RF borders as the locations where activity fell
374 below 50% of the maximum (103).

375 We removed trials with artifacts first by calculating the time-average for each trial and removing trials with
376 extreme average MUA responses. We used an iterative z-scoring procedure (values higher than 3 were
377 removed). If z-scores higher than 20 remained in the cleaned collection of trials, the process was repeated,
378 leading to the removal of less than 2% of all the trials. We also removed trials that included any samples
379 (without averaging) that had a z-score higher than 10. To normalize MUA, we subtracted the spontaneous
380 activity level in a 100 ms time window prior to the onset of the stimulus and divided by the peak response
381 after LOWESS smoothing (26 ms window). We only included recording sites with a signal-to-noise (SNR)
382 higher than 2.5. SNR was computed for individual recording sessions by dividing the peak of the smoothed
383 response by the standard deviation of the spontaneous activity level across trials. We excluded recording
384 sites with fewer than 3 recording sessions that met the SNR criterion. For the other recording sites, we
385 averaged the activity per recording site across sessions so that every recording site contributed only once to
386 the statistics.

387 Behavioral task and stimuli

388 Stimuli were presented on a 21" CRT monitor (Dell Trinitron) with a refresh rate of 85 Hz and a resolution
389 of 1024×768 pixels, viewed at a distance of 87 cm. All stimuli were created using the COGENT graphics
390 toolbox (developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience)
391 running in MATLAB (Mathworks Inc.) with custom experimental control software (104). The monkeys were
392 trained to perform a visual search task. A trial started when the monkey acquired fixation on a 0.3° red (26.2
393 cd/m^2) fixation dot in the center of the screen. After 200 ms of fixation within a 1.2° diameter window, 6
394 stimuli appeared, arranged in a circle around the fixation point, at 5.3° eccentricity. Simultaneously, the
395 fixation dot became green (98.6 cd/m^2) cueing the monkey to make a saccade. The stimuli were visible for
396 2,000 ms, during which the monkey was required to respond. If the monkey failed to respond in time, the
397 trial was classified as aborted. Each stimulus could be either a square or a circle and was either red (76.0
398 cd/m^2) or green (114.1 cd/m^2), presented on a gray background (54.2 cd/m^2). Stimuli had a size of 1.8°
399 diameter. On each trial, one stimulus had a different shape (the target stimulus), one stimulus had a different
400 color (the salient distractor stimulus), and the 4 remaining stimuli (non-salient distractors) had the same color
401 as the target stimulus and the same shape as the salient distractor. The task of the monkey was to make an
402 eye movement to the target stimulus, while ignoring the salient and non-salient distractors. Choices were
403 detected as the eye-position entering a 4° diameter circular window around one of the stimuli. Upon a correct

404 response, the monkey received a juice reward. This reward was randomly selected to be either small or large
405 (~4 times the small amount). The trials were ordered in a pseudorandom fashion. We recorded 34,543 trials
406 across 28 sessions in monkey 1 and 13,815 trials across 16 sessions in monkey 2.

407 **Computation of target and salient distractor modulation**

408 Average MUA responses for target, non-salient distractor, and salient distractor stimuli were calculated for
409 individual monkeys and the pooled data. To compute target and salient distractor modulation we subtracted
410 the response to non-salient distractors from the response to targets and salient distractors, respectively, for
411 each recording site in a 150-200 ms time window after stimulus onset. As statistical test we used paired t-
412 tests over recording sites. The time-courses of target and salient distractor modulation were furthermore
413 evaluated by recalculating the modulation in 10 ms non-overlapping bins and statistically tested with a series
414 of t-tests, using Bonferroni correction for multiple comparisons.

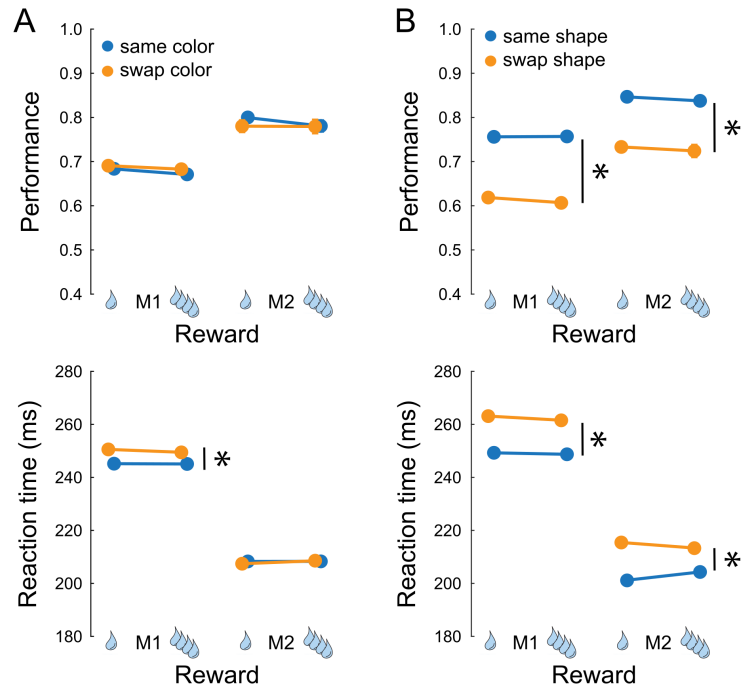
415 **Latency of target selection and distractor suppression**

416 To estimate the latency of the enhancement of the representation of the target and the suppression of the
417 representation of the salient distractor we used a fitting procedure that has been described before (67).
418 Briefly, a cumulative gaussian function was fit to the difference between either the target and the non-salient
419 distractor response (i.e., target modulation) or the non-salient distractor and the salient distractor response
420 (i.e., salient distractor modulation). The latency is estimated as the time point at which the fit reaches 33% of
421 its maximum (Supplemental Fig. 4). The fits were calculated based on the population responses, i.e., after
422 averaging across recording sites. We used a bootstrapping procedure (100 times) with replacement to
423 estimate the mean and standard deviation of these latency estimates and compared latencies of target and
424 salient distractor modulations with paired t-tests.

425 **Saccadic reaction times**

426 We investigated the susceptibility to attentional capture by the salient distractor as a function of saccadic
427 reaction time (SRT). We removed SRTs that were faster than 75 ms because we deemed such responses to be
428 too fast to be visually guided based on previous reports . This resulted in the removal of 6 target (M1: 2, M2:
429 4) and 9 salient distractor responses (M1: 7, M2: 2). For the remaining responses we calculated the 25th
430 percentile SRT per animal and classified all faster responses as ‘fast SRTs’. The values of these fast SRTs
431 for target and salient distractor choices were compared with Wilcoxon rank sum tests. We also used the full
432 range of SRTs to calculate a proportion of salient distractor choices ($p_{SD} = N_{SD}/N_{ALL}$) within a 20 ms sliding
433 window moving through the range of SRTs with 10 ms increments.

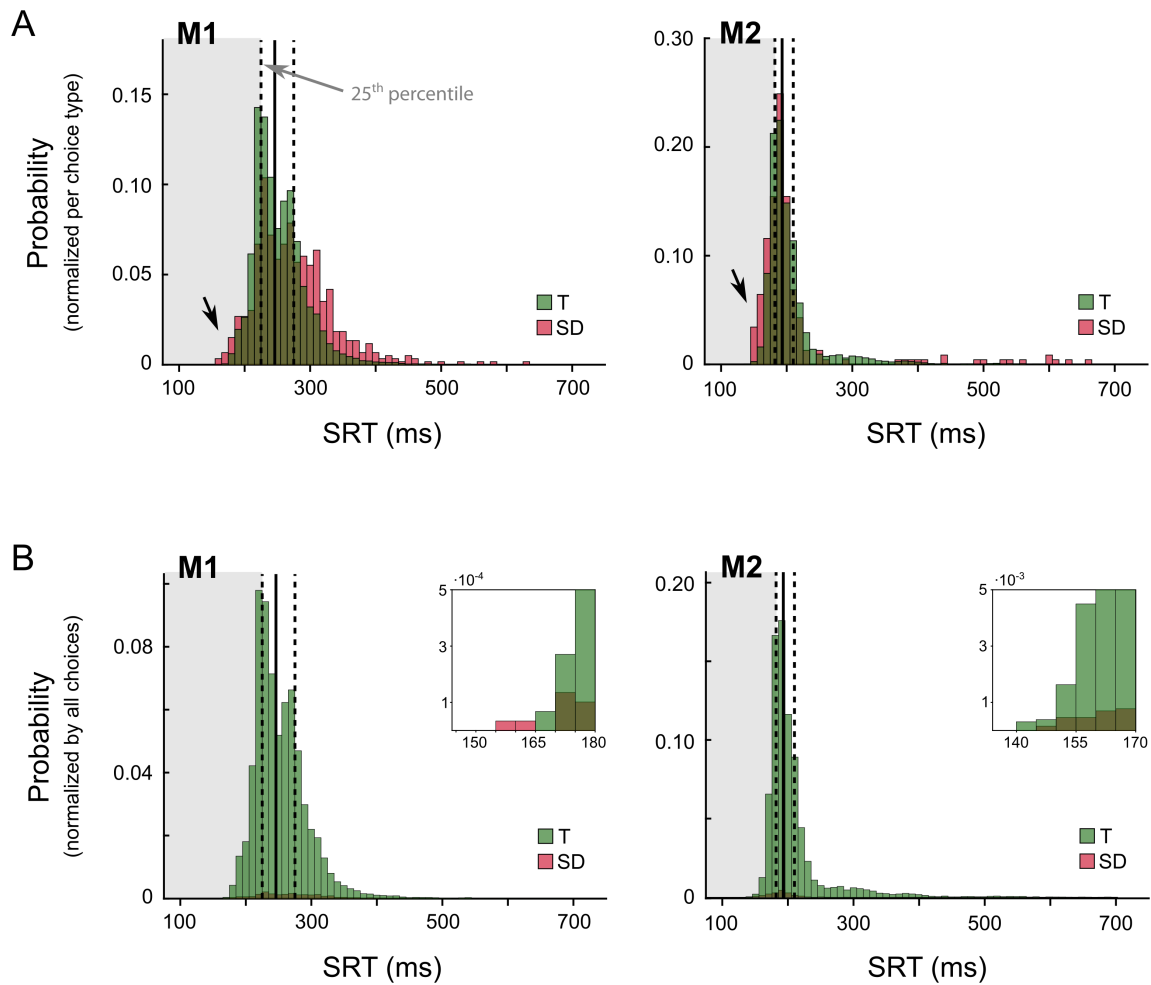
434 Supplemental figures



Supplemental Figure 1. Influence of previous trial on behavioral performance. **A)** The effects of preceding reward quantity and the swapping of target and salient distractor colors (top panel) and reaction time (bottom panel) for both monkeys. Yellow lines indicate trials in which the target and distractor colors swapped relative to the previous trial; blue lines are trials in which the colors of the target and salient distractor stayed the same. Reward quantity is indicated on the horizontal axis (large rewards were four times larger than small rewards). **B)** The effects of preceding reward quantity and shape swaps on accuracy (top panel) and reaction time (bottom panel) for both monkeys. Yellow lines indicate trials in which the target and distractor shapes swapped relative to the previous trial; blue lines are trials in which the shape assignment stayed the same. Error bars (often smaller than the data points) indicate S.E.M., asterisks denote $p < 0.001$ for main effects as indicated by two-way ANOVAs (no interaction effects were significant at $p < 0.05$).

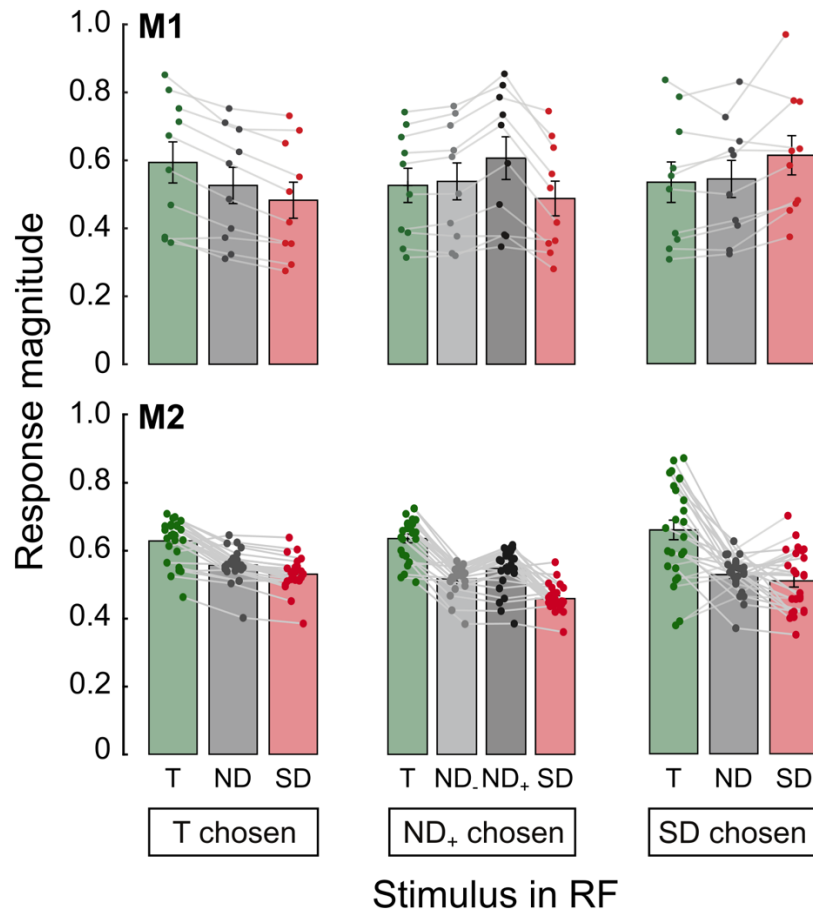
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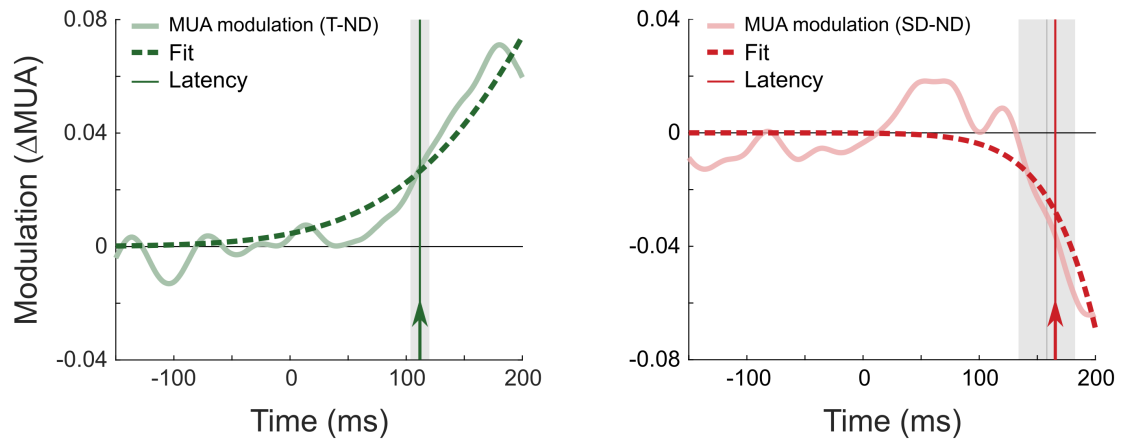


Supplemental Figure 2. Saccadic reaction times and choices. Distributions of saccade reaction times (SRTs) for target (T, green) and salient distractor choices (SD, red) of the two monkeys (M1, M2). Solid and dashed vertical lines represent the median, 25th and 75th percentiles of the RT distribution. Histograms in **A**) show the distributions normalized per choice type (T or SD) as in Figure 2A, while histograms in **B**) show the distributions normalized to the total number of responses (T, SD, and ND combined). Insets in panel **B**) zoom in on the fast tail of the distributions.

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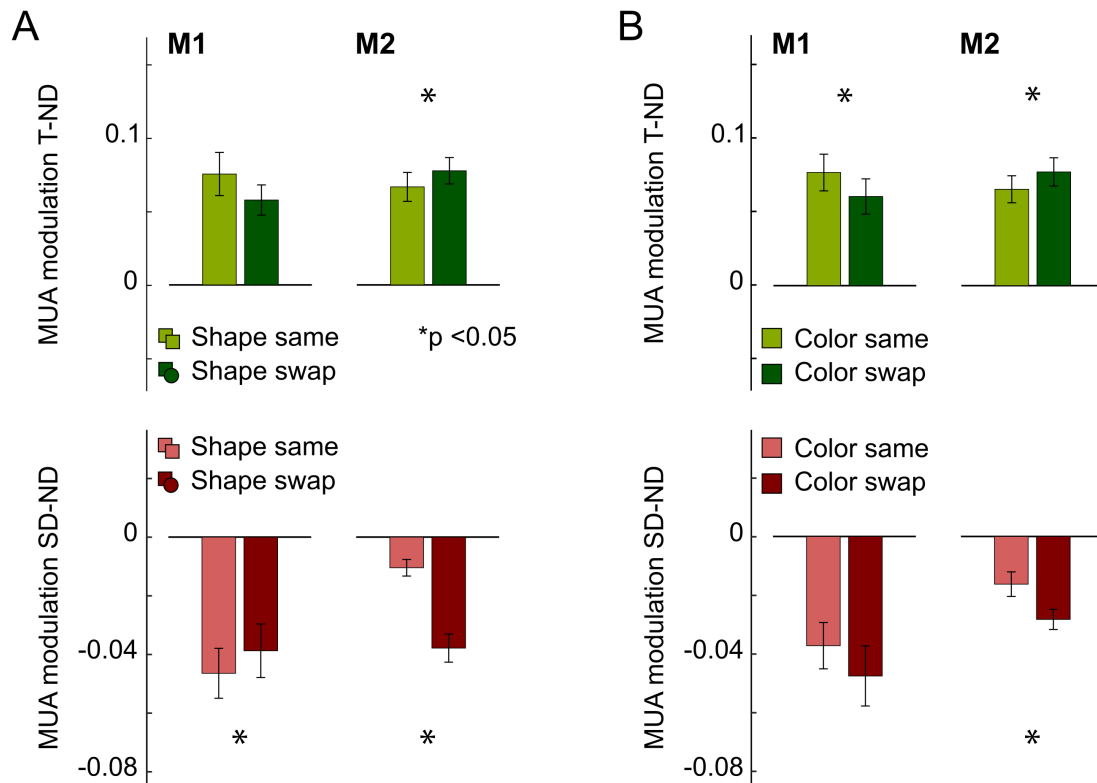


Supplemental Figure 3. V4 activity and its dependence on choice. Average activity of V4 neurons at individual recording sites, 150-200 ms after stimulus onset. Left, correct responses to the target in M1 (top row) and M2 (bottom). Middle, erroneous responses in which the animals selected one of the non-salient distractors (ND₊). ND₋, response elicited by non-salient distractors that were not chosen. Right, erroneous responses in which the salient distractor was chosen. Bar colors represent the stimulus in the RF (green: target, light gray: non-salient distractor, red: salient distractor). Dark grey bars show the response elicited by the chosen non-salient distractors (ND₊). Light grey bars show the response elicited by ND₋. The data of individual recording sites are shown as colored data points, connected by gray lines. Error bars represent S.E.M. across recording sites.



Supplemental Figure 4. Latency analysis of target and salient distractor MUA modulation. Cumulative Gaussian functions were fit to the difference between either the average V4 activity elicited by the target and the non-salient distractor (i.e. target modulation, left panel) or the non-salient and salient distractors (i.e., salient distractor modulation, right panel). The latency (vertical line and arrow) is estimated as the time point at which the fit (dashed line) reaches 33% of its maximum. The grey area and grey vertical line indicate the mean latency and standard deviation of a bootstrap analysis (100 samples with replacement).

439



Supplemental Figure 5. Influence of the previous trial on V4 activity. **A)** The effect of shape assignment changes on consecutive trials on the modulation of V4 activity by the target (T-ND; top row) and salient distractor (SD-ND; bottom row) in the 150-200 ms time window after stimulus onset. Bars are the mean across recording sites and error bars denote S.E.M. Light and dark colors represent trials in which the shape assignment stayed the same or changed, respectively. **B)** The effect of target and salient distractor color swapping on consecutive trials on the modulation of V4 activity by the target (T-ND; top row) and salient distractor (SD-ND; bottom row) in the 150-200 ms time window after stimulus onset. Light and dark colors represent trials in which the color assignment stayed the same or were swapped, respectively. Asterisks, significant differences (paired t-test, $p < 0.05$).