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The attentional template in high and low similarity search: Optimal tuning or tuning to relations?

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ABSTRACT

The attentional template is often described as the mental representation that drives attentional selection and guidance, for instance, in visual search. Recent research suggests that this template is not a veridical representation of the sought-for target, but instead an altered representation that allows more efficient search. The current paper contrasts two such theories. Firstly, the Optimal Tuning account which posits that the attentional template *shifts* to an exaggerated target value to maximise the signal-to-noise ratio between similar targets and non-targets. Secondly, the Relational account which states that instead of tuning to feature values, attention is directed to the relative value created by the search context, e.g. all *redder* items or the *reddest* item. Both theories are empirically supported, but used different paradigms (perceptual decision tasks vs. visual search), and different attentional measures (probe response accuracy vs. gaze capture). The current design incorporates both paradigms and measures. The results reveal that while Optimal Tuning shifts are observed in probe trials they do not drive early attention or eye- movement behaviour in visual search. Instead, early attention follows the Relational Account, selecting all items with the relative target colour (e.g., redder). This suggests that the masked probe trials used in Optimal Tuning do not probe the attentional template that guides attention. In Experiment 3 we find that optimal tuning shifts correspond in magnitude to purely *perceptual* shifts created by contrast biases in the visual search arrays. This suggests that the shift in probe responses may in fact be a perceptual artefact rather than a strategic adaptation to optimise the signal-to-noise ratio. These results highlight the distinction between early attentional mechanisms and later, target identification mechanisms.

Significance statement: Classical theories of attention suggest that attention is guided by a feature-specific target template. In recent designs this has been challenged by an apparent non- veridical tuning of the template in situations where the target stimulus is similar to non-targets. The current studies compare two theories that propose different explanations for non-veridical tuning; the Relational and the Optimal Tuning account. We show that the Relational account describes the mechanism that guides early search behaviour, while the Optimal Tuning account describes perceptual decision-making. Optimal Tuning effects may be due to an artefact that has not been described in visual search before (simultaneous contrast).

1. Introduction

A fundamental tenet of the attention literature is that visual search can be very fast and efficient or slow and effortful (e.g., Treisman & Gelade, 1980; Wolfe, 1994). Two factors have been identified that play a large role in determining search efficiency: bottom-up saliency and top-down knowledge. When a search target is the only salient item in the visual field, such as a red item among all white items, the target can typically be immediately spotted. When there are multiple differently coloured items, search can be slightly slower – all the more so if we do not know the colour of the target. However, if we know the colour we are looking for, and our search target has a unique feature (e.g., the only red item), search is still very efficient (e.g., Treisman & Gelade, 1980; Wolfe, 1994). Knowledge about a sought-after item can *guide* visual attention to corresponding items in the visual field to facilitate search. One important question is *how* knowledge about the target feature(s) can guide visual attention.

Foundational theories of visual search, such as Guided Search (Wolfe, 1994) proposed that the intention to find a target with a particular feature value biases sensory neurons to enhance sensitivity

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towards this specific feature value. A wide-spread view is that attention is guided by a mental representation of the target (i.e., the *attentional template*) that is stored in visual short-term memory (VSTM), which directs attention to goal-relevant stimuli by increasing the responses of neurons that are maximally tuned to this feature value (Desimone & Duncan, 1995). For instance, if the search target is orange, the visual system would increase the responses of neurons that maximally respond to orange, and/or inhibit responses of neurons that respond to other features (e.g., blue, green, yellow, red), thus ensuring that only target-matching items are selected. Hence, originally, it was believed that the template guiding attention would contain the veridical features of the target (e.g., orange, when the target is orange), and the corresponding theories have long dominated the framework for current research. However, recent studies challenge the central tenet that attention is always biased to the exact target feature value (Becker, 2010; Navalpakkam & Itti, 2007). The current study investigates two such frameworks that explore feature based templates: Optimal Tuning and the Relational Account.

The *Optimal Tuning* account provides predictions on search behaviour dependent on knowledge of target and non-target relationships. It is part of recent frameworks which describe search behaviour as following that of the ideal observer, where behaviour is tailored to the specific information known, to produce optimal strategies (Ma, Shen, Dziugaite, & van den Berg, 2015). The distinguishing factor of Optimal Tuning is in circumstances where target and non-target information is known and the feature difference between the two his highly similar. According to the *Optimal Tuning* account, attention will be biased to the feature value that optimally singles out the target from the background of irrelevant non-targets. In most situations, tuning attention to the exact target feature value will be optimal. However, when the target is very similar to the non-targets (e.g. an orange target among similarly coloured, yellow-orange non-targets), tuning attention to the target feature could lead to inefficient search, as feature gains would not just apply to the target, but also to the non-targets (as neurons responding to the target will also respond strongly to the non-targets). To maximise the signal-to-noise ratio with similar non-targets, the attentional target template can *shift* to an exaggerated target feature value, away from non-target colours (to reduce the overlap with the non-target feature values; e.g., Navalpakkam & Itti, 2007; Scolari & Serences, 2009 see also Geng & Witkowski, 2019). Thus, according to the Optimal Tuning account, the top-down attentional bias will typically limit selection to the feature that optimally singles out the target, and this shift in bias is dependent on the similarity of the targets to the non-targets.

An alternative view proposed in the *Relational Account* is that attention is not typically tuned to a specific feature value but to *feature relationships* or *relative features*. According to the Relational account, the visual system quickly evaluates *how* the target differs from the irrelevant items (e.g., redder, when the target is orange, among yellow-orange non-targets) and directs attention to this relative feature (i.e. all *redder* items, or the *reddest* item; Becker, 2010). As attention will usually be attracted to the item with the best-matching relative feature (e.g., the reddest item), attention can be potentially attracted to a wide range of different features, including ones that are quite dissimilar from the target (e.g., ranging from full red to red-orange; Becker, 2010; Becker, Folk, & Remington, 2013). According to the Relational Account, this top-down attentional bias will be adopted whenever the target differs in a constant relative feature from the non-targets (e.g., is the reddest item or one of the reddest items on the majority of trials), independent of whether the non-targets are similar or dissimilar to the target. Additionally, capture by relational matching distractors was independent of bottom-up saliency, occurring equally for salient and non-salient items (e.g., conjunction search; Becker, Atalla, & Folk, 2020; Becker, Harris, York, & Choi, 2017), and without being modulated by bottom-up saliency (e.g., feature contrast; e.g., York & Becker, 2020). Thus, the Relational Account proposes a broad top-down attentional setting that allows selection of all relational matching items, independent of their similarity to the target, and independent of the similarity of the non-targets to the target. Across different paradigms and measures, relational tuning has been shown for different stimuli (e.g., colour, size, brightness, shape) in conditions that conclusively ruled out alternative explanations such as a broader search setting, a combination of top-down and bottom-up processes, optimal tuning or inhibition (e.g., Becker, 2010; Becker et al., 2013; see also Becker, 2013; York & Becker, 2020).

The Optimal Tuning and Relational Account make quite different predictions about which item(s) will fulfil the parameters set by the attentional template. Intriguingly, both accounts have been supported by distinct strands of evidence. However, as further detailed below, the corresponding studies used quite different measures and procedures to determine attentional selection. In the studies supporting the Relational Account, participants were asked to search for a particular target, such as an orange disk that was consistently presented among five yellow-orange non-target disks, while ignoring an irrelevant distractor square that could be red, red-orange, orange, yellow-orange or yellow (Becker, Harris, Venini, & Retell, 2014). To index how attention was top-down tuned to the target, eye-movements were tracked during the visual search task; in particular the proportion of first eye-movements to each of the different distractors (see Deubel & Schneider, 1996 and Theeuwes, Kramer, Hahn, & Irwin, 1998 for a similar procedure). The results of several studies showed that the relational matching (e.g., red and red-orange) distractors attracted gaze most strongly, stronger than the target-matching (e.g., orange) distractor while the remaining distractors (e.g., yellow-orange and yellow) attracted gaze weakly. Importantly, the more extreme distractor colours (e.g., red) were quite dissimilar from the target, and outside the area of a shift to a more optimal colour; yet, they attracted gaze just as strongly as more target-similar distractors (e.g., red-orange distractor; see also York & Becker, 2020). Hence, the finding that all relational matching distractors strongly attracted gaze was interpreted as evidence that attention was top- down biased to the relative target feature, not a particular feature value.

The Optimal Tuning studies reported a significantly different result pattern, but used distinct procedures. In Optimal Tuning studies, participants were asked to search for a target of a specific colour (e.g. bluish-green) among non-targets that were either similar to the target (e.g., slightly more green) or dissimilar (e.g., green; Yu & Geng, 2019). These visual search trials were only included to induce a particular attentional bias and were not analysed. How attention was tuned to the target in visual search was tested on rare *probe trials*, in which multiple different colours were briefly presented and backward-masked, and participants had to report the position of the target colour (in a four alternative forced choice task; Yu & Geng, 2019). In other studies, a single probe was presented, and participants had to decide whether the colour matched the target colour or not (Geng & Witkowski, 2019). Results showed that participants most frequently picked an exaggerated target colour that was slightly shifted away from non-target colours when the non-targets were similar to the search target (on the visual search trials), whereas participants were less biased to the exaggerated colour when the non-targets were dissimilar to the target. According to the Optimal Tuning Account, this shift in the response on probe trials reflects a change in how attention was top-down tuned to the target in visual search trials. This, ultimately supported the claim that the attentional template was shifted to an optimal feature value that in turn allowed for efficient search (Navalpakkam & Itti, 2007; see also Geng, Di Quattro, & Helm, 2017).

A potential critique of the Optimal Tuning studies is that the masked probe trials are not an adequate measure of the attentional template. Wolfe (2020) argues that there are two types of templates which are responsible for behaviour in visual search. A *Guidance* template which directs attention to specific items in the array and a *Target* template which contrasts the selected item to a mental representation of that item. Importantly this draws a distinction between early attentional guidance, relating to pure attentional selection, and later mechanism which involves target discrimination, potentially incorporating long term memory resources (Wolfe, 2020). In terms of the current study there is the possibility of two involved templates: a broad (relational) guidance template that drives early visual selection (as indexed by the first eye movements on a trial), and a feature-specific ('optimal') target template that determines perceptual decision-making processes once an item has been selected (indexed by probe responses). If this is correct, probe responses would not reflect a strategic adaptation that is used in visual search to find the target. Rather, probe responses would reflect the results of a decision- making process that centrally involves comparing the features of the selected item to the target template in memory.

With this, probe responses may centrally reflect the properties of the memory representation of the target. Moreover, the shift in the target representation with similar non- targets may not reflect a strategic adaptation, but perceptual artefacts or other influences from higher-level, long-term memory representations that do not directly serve a particular goal but are passive adaptations to the displays. A potential source of a passively induced shift in the target representation may be perceptual contrast effects between the highly similar search target and the non-targets (Eagleman, 2001). *Simultaneous contrast* effects can skew the perception of similar colours to render them more distinct when the colours are placed side by side or when one is juxtaposed on top of the other (Brown & MacLeod, 1997). Although simultaneous contrast effects have not been reported in visual search displays with multiple, spatially separated objects, the similar non-targets could potentially skew the perception of an orange target to make it appear redder (due to lateral inhibitory connections between neurons that respond to similar colours; Blakemore & Tobin, 1972). Such a shift in the perception of the target on search trial could explain the shift of responses in the probe trials, but this would be an automatic, hard- wired response, not a strategic adaptation.

The present study has two broad aims; first, to assess whether the discrepant results of the Relational and Optimal Tuning studies are due to measuring early visual selection vs. decision- making processes that are based on two different templates (that drive early visual selection in visual search vs. later decision-making on probe trials). To assess this question, we combined the paradigms used in previous studies and assessed eye-movements in visual search trials (with distractor trials) to index early processes of visual selection, and responses on probe detection trials to index later, decisional processes. A second aim of the present study was to assess whether the shift observed with similar non-targets is due to a strategic adaptation of visual processes, or to a passive, automatic shift in the perception of the target when it is surrounded by similar non-targets (in the fashion of simultaneous contrast effects).

2. Experiment 1

Experiment 1 combined elements from both the visual search paradigm and probe trials used in previous studies on Relational and Optimal Tuning. Thus we measured visual selection on visual search trials both in a similar and dissimilar search context, and assessed target selection among different colours on probe detection trials that were randomly interleaved with the search trials. In visual search trials three types of stimuli were used. The ***target*** item, to which participants were searching for, ***non-target*** items present on every trial and thirdly rare singleton ***distractor*** items which varied in colour. The proportion of first eye-movements to each distractor was used to index which colour values would attract attention, thus providing a portrayal of the attentional template guiding search.

Intermixed with the search trials were two types of masked probe trials. Firstly, *multi- probe trials* in which the target colour was presented among three differently coloured probes and participants were asked to indicate the location of the target (by a button-press response; see Navalpakkam & Itti, 2007, for a similar design) Secondly, *single-probe trials* in which we presented a single probe requiring a yes/no judgement on whether it was the target colour (see Geng et al., 2017) Probe trials were presented only briefly (300 ms) and backward-masked to render eye-movements ineffective, akin to previous Optimal Tuning studies (e. g. Yu & Geng, 2019).

In Experiment 1, we tested 9 different probe/distractor colours that varied from full yellow to full red (see Fig. 1), with the target colour being intermediate (orange). Distractor/probe colours systematically varied in being progressively redder, and yellower than the target. If our hypothesis is correct, that the Relational studies tapped into a guidance template directing early visual search, and Optimal Tuning studies tapping into perceptual decisions on a target template, we would expect eye-movements in visual search and probe responses to show the same dichotomy in the results as reported in previous literature. That is, the first eye-movements on each trial should show equally high selection rates of all relational matching distractors (e.g., all redder distractors; Becker et al., 2013), reflecting that attention had been biased to the relative colour of the target (e.g., reddest item). Moreover, selection of relational matching distractors should be observed when target is presented among both similar and dissimilar non-targets. Probe trials, on the other hand, should be moderated by non-target similarity in visual search. In the similar blocks, probe trials should show frequent, erroneous selection of an exaggerated target colour that is slightly shifted away from the non-targets, whereas dissimilar blocks should show more accurate selection of the target colour. A corresponding result would reflect that there are two templates involved, a relational attentional template that guides early visual selection towards relational matching features, and a second target template that determines perceptual decisions about which item is the target.

On the other hand, if Optimal Tuning provides an accurate account of attentional guidance and previous discrepant results were due to differences in the stimuli or methods, then both eye-movements in visual search and probe selection should display the same result pattern. That is, both the distractor fixations and probe responses should show most frequent selection of the shifted, exaggerated target colour when the non-targets are similar to the target, and accurate selection of the target when the non-targets are dissimilar from the target. A corresponding result would show that Optimal Tuning accurately describes how attention is biased to the target in visual search.

3. Methods

3.1. Participants

29 volunteers (15 female, mean age: 21.52) from the University of Queensland participated in this study and were reimbursed with $40. Six participants were excluded for having chance performance in the probe conditions (all probe colour had equal selection rates) and two for poor eye-tracking data (< 20% of eye-movements went to the target on no-distractor trials), leaving 21 participants for the final analysis. Study approval was granted by the University of Queensland's Faculty of Psychology Ethics Board.

3.2. Apparatus

Stimuli were presented on a 21-in. CRT monitor (refresh rate: 85 Hz). A chin and head-rest was used to hold the participant's heads in a constant position 600 mm from the screen. Eye-movements were measured with an SR-Research Eyelink-1000 eye tracker at 500 Hz sampling rate. The experiment was controlled by PsychoPy (Peirce, 2007) using Python.

3.3. Stimuli

On *Visual Search* trials, six squares (visual angle of 1.91° x 1.91°) were presented equidistantly on an imaginary circle (8.58° radius) around a black fixation cross (0.76°), against a grey background. Within

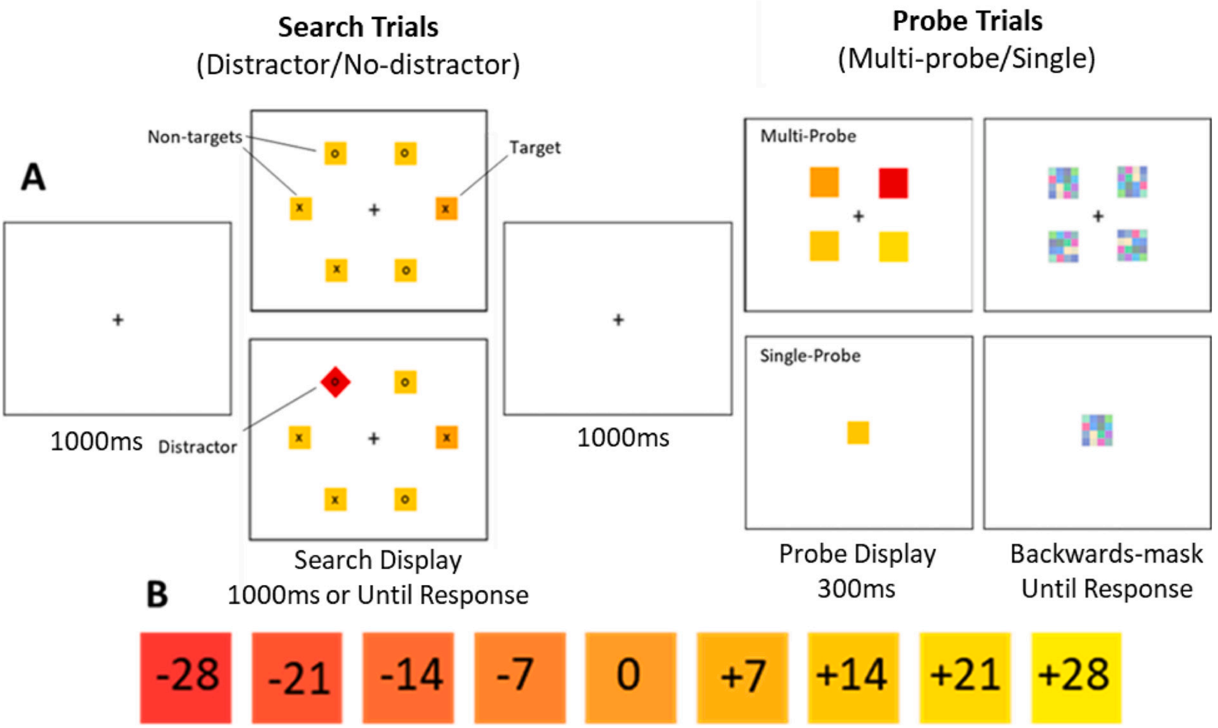

Fig. 1. **A)** Overview of conditions in Experiment 1. On Visual Search trials, a search array was presented, and participants searched for the orange target square (at 0°). Half of all search trials contained a diamond distractor that had one colour ranging from −28° to +28°. On rare trials either a multi-probe was displayed asking which of the four colours matched the search target, or a single probe display, asking whether the single colour presented was the target or not. **B)** Colours used in Experiment 1. Numbers represent the degrees shifted around an RGB colour wheel in reference to the target colour (0°). In the Similar condition the non-targets were ± 7° and in the Dissimilar ±14° (direction depends on whether participants were assigned to searching in a *redder*, or a *yellower* context). Singleton distractors were selected from the remaining values. Colour codes in RGB from left to right: [255, 57, 50], [255, 81, 50], [255, 104, 50], [255, 128, 50], [255, 151, 50], [255, 175, 50], [255, 198, 50], [255, 222, 50], [255, 245, 50].

each of the squares a small black ‘x’ or ‘o’ (0.38°) was present. Participants searched for the same target colour (orange; assigned 0° on the colour wheel) on all trials and responded to the letter within. Each participant completed either a *redder* search (non-targets were more yellow; i.e., positive values on the colour wheel) or a *yellower* search (non-targets were more red; negative values). In the Similar search condition the non-target colours were ± 7° and in the Dissimilar ±14°. Colours are displayed in Fig. 1b. Distractors had had any of the seven unused colours and were rotated by 45° to prevent them from being mistaken for the target stimulus. The distractor was never presented adjacent to the search target and always contained the opposite response letter. On *Probe* trials, displays either contained four probes (*multi-probe trials*), 7.15° away from fixation in a square layout, or a single probe at fixation (*single probe trials*). The probes had a square shape and were the same size as the search items. The multi-probe colours always contained the target colour (0°). The other three colours ranged from −21° to +21° (see Fig. 1). The non-target colours were sorted into three pairs (−7°/+7°, −14°/+14° and − 21°/+21°). Each probe array contained one random colour from each of these three pairs, to control for possible similarity differences across trials. All probes were backward-masked with a coloured checkerboard display of the same size as the probes.

3.4. Design

The experiment contained three intermixed trial types; for one, visual search trials which were either no-distractor trials (the search target being presented among five non- targets) or distractor trials, with the distractor replacing one of the non-targets. Intermixed with the search trials were two types of masked probe trials, either *single probe trials* (“Was this the target?”) or *multi-probe trials* (“Which of these four items was the target?”). Probe types were blocked (and counterbalanced) in each session. Participants completed a total of two sessions; visual search with a Similar or a Dissimilar context, on separate days (counterbalanced). Each session contained 420 visual search trials (140 of which contained a singleton distractor, 20 trials for each distractor colour), 50 multi-probe trials (25 appearances of each probe colour) and 50 single probe trials (20 with the target colour, 5 for each of the 6 remaining colours, including the non-target colour in search). Before each session participants completed 24 no-distractor search trials for practice and to familiarise themselves with the target and non-target colours.

3.5. Procedure

Each trial began with participants maintaining fixation for 700 ms, controlled via an eye-tracker. On Visual Search trials, after another 300 ms had elapsed, a search array was presented for 1000 ms or until a response was made. Participants were required to respond to the letter (x or o) presented within the target square with the corresponding keyboard key. If no response was made in time the trial was terminated. On a subset of no-distractor trials (~18%) a probe trial would be presented 1000 ms after the completion of the search trial. Both the single and the multi-probes were displayed for 300 ms and then backward masked with a coloured checkerboard pattern. In the single probe trials participants indicated with a button response if the colour matched the search target or not. Responses to probe trials were untimed and participants were not given feedback. See Fig. 1(A) for a visual depiction of trials.

4. Results

4.1. Data

13.2% of visual search trials were excluded for invalid eye-movements that either started before the search trial commenced (< 50 ms), or late eye-movements (> 900 ms). For the data analyses, the colour values were recoded so that the target was always set to 0°, the Similar non-targets were at +7° and the Dissimilar non-targets at +14°. With this, the relational matching distractors had negative colour values, ranging from −28° to −7° (−7°, −14°, −21°, and − 28°), and the non-matching distractors all had positive values, ranging from +28° to +7°. The optimal or shifted distractor/probe colour was at −7°, for all participants. Analysed eye- movement data was taken from the first testing session only. Data were analysed with repeated- measures analysis of variance (ANOVA) and *t*-tests. Where appropriate, Greenhouse-Geisser corrected *p*-values and Bonferroni-adjusted *p*-values were reported for ANOVAs and *t*-tests, respectively. For follow-up comparisons, additional Bayesian tests were used to assess the likelihoods of effects. BF_{10} is used to denote the likelihood of the alternate hypothesis being true compared to the null (Quintana & Williams, 2018).

4.2. Eye-movements

To probe into early visual selection, a 2 (Similarity: Similar, Dissimilar) x 6 (Distractor: −28°, −21°, −14°, −7°, +21°, +28°) ANOVA was conducted over the proportion of first eye-movements to the distractor (on distractor trials). The +7° and the +14° distractors were excluded from this analysis, as they were the non-targets in the Similar and Dissimilar condition, respectively (the data, however, are included in Fig. 2). The omnibus ANOVA revealed a significant main effect of Similarity, $F(1,20) = 13.46$, $p = .002$, $\eta^2_p = 0.402$, with a higher proportion of eye-movements directed to distractors in the Similar condition ($M = 46.96\%$) compared to the Dissimilar condition ($M = 37.94\%$). There was a significant effect for Distractor colour, $F(5, 20) = 147.01$, $p < .001$, $\eta^2_p = 0.880$, reflecting that the different distractors attracted the gaze differently. However, the Similarity x Distractor interaction was non- significant $F(5, 20) = 1.44$, $p = .236$, indicating that similarity did not change the pattern of selecting different distractors.

As shown in Fig. 2B and C, all relational matching distractors (e.g., redder distractors) appeared to attract gaze more strongly than the non-matching distractors, in both similarity contexts. To test whether these colours indeed captured the gaze more strongly than the non-matching colours, we first compared selection rates across the paired distractor colours (−28°/+28, −21°/+21°, in both conditions, the −14°/+14° in the Similar condition and − 7°/+7° in the Dissimilar condition). Pairwise comparisons (Bonferroni-corrected) showed that the relational matching distractors attracted gaze significantly more strongly than non-matching distractors, all $ts(20) > 12.14$, $ps < 0.001$ (all $\mathrm{BF}_{10} > 8.45 \times 10^7$, showing extreme support for differences in selection rates).

Next, to assess if the relational matching distractors attracted gaze equally strongly, or if the effect was modulated by target similarity, we compared distractor selection rates (Bonferroni-corrected) across the relational matching distractors in colour order. There were no differences between the −28° and − 21° colours, $t(20) = 0.19$, $p > .999$, $\mathrm{BF}_{10} = 0.23$, the −21° and − 14° colours, $t(20) = 0.74$, $p > .999$, $\mathrm{BF}_{10} = 0.29$, between the −14° and − 7° colours, $t(20) = 1.61$, $p = .368$, $\mathrm{BF}_{10} = 0.69$ (as a BF_{10} less than one indicates that the results are more likely to support the null hypothesis; Quintana & Williams, 2018).

Similarly, the non-matching distractors (21° and 28°) did not differ significantly from each other, $t(20) = 1.59$, $p = .128$, $\mathrm{BF}_{10} = 0.67$, indicating that early visual selection was driven by the relative features of the target, not feature similarity to the target colour value.

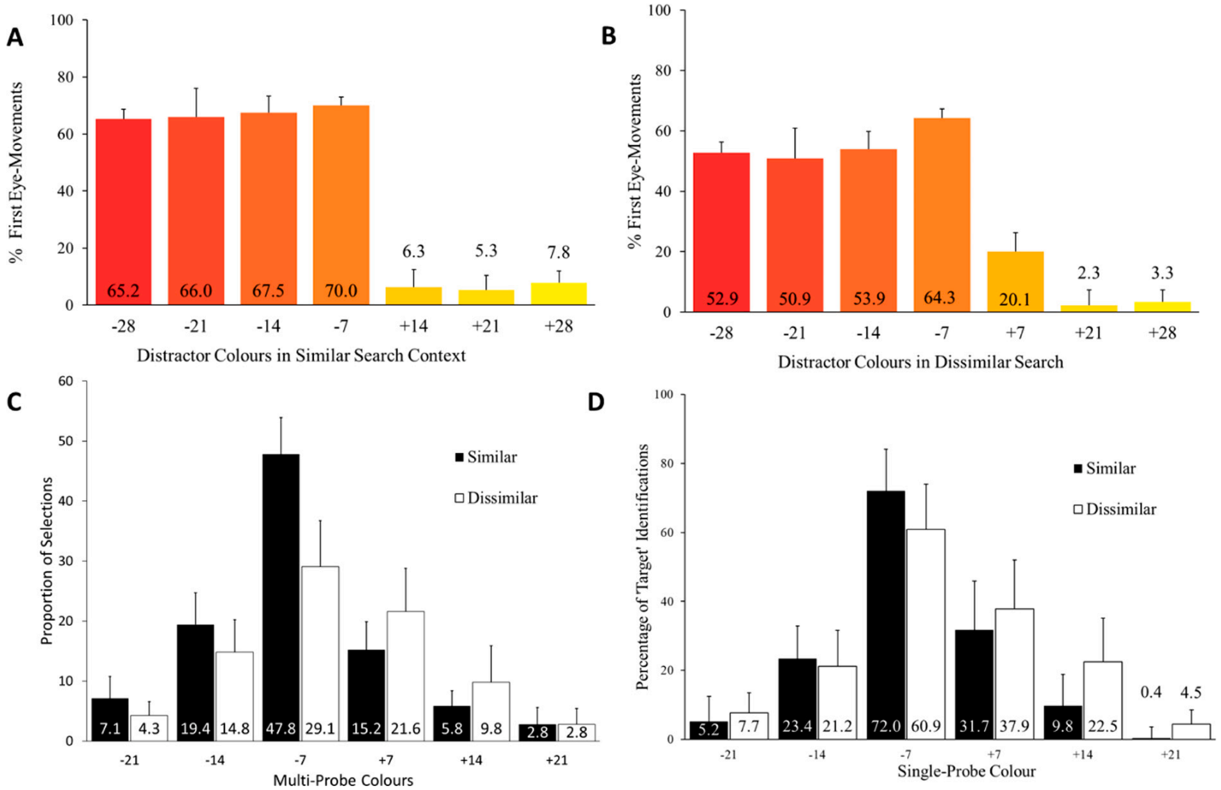

Fig. 2. **A, B)** Results of the Visual Search trials. Data were pooled across colour conditions so that negative values indicate relational matching distractors and positive values indicate non- target similar distractors. In line with a Relational Account, a large proportion of first eye- movements went to all relational matching distractors, both **A)** in the Similar and **B)** the Dissimilar condition. **C, D)** Target identification in probe trials was skewed towards the target- similar −7° probe, both in multi-probe trials **(C)** and in single probe trials **(D)**, reflecting Optimal Tuning Results. Error bars for all graphs represent within-subjects 95% confidence intervals.

4.3. Multi-probe

As shown in Fig. 2, probe responses differed markedly from the eye-movement results, in that the probe responses showed a peak in selecting colours close to the target colour, with a marked decrease in probe responses to more dissimilar colours. A 2 (Similarity: Similar, Dissimilar) x 6 (Probe Colours: −21°, −14°, −7°, +7°, +14°, +21°) ANOVA conducted over the multi-probe data showed a main effect of probe colour, $F(5, 20) = 42.22$, $p < .001$, $\eta^2_p = 0.679$. There was no effect of Similarity, $F(1, 20) = 3.57$, $p = .074$, $\eta^2_p = 0.151$, but a significant interaction, $F(5, 20) = 8.37$, $p < .001$, $\eta^2_p = 0.295$, reflecting that probe responses were modulated by the similarity context (in the search trials).

To assess possible shifts in the probe responses, we first compared the proportion of target identifications within each probe pairing contrasting relational matching probes with relational non-matching probes (−7°/+7°; −14°/+14°, −21°/+21°). Importantly, in the Similar condition, the shifted, −7° probe was misidentified more frequently as the target than the +7° probe, $t(20) = 11.92$, $p < .001$, $BF_{10} = 6.69 \times 10^7$, the same pattern applied for the −14° vs. +14° probes, $t(20) = 5.12$, $p < .001$, $BF_{10} = 489.97$, whereas the −21° and + 21° probes did not differ significantly from each other, $t(20) = 1.78$, $p = .272$, $BF_{10} = 0.87$. By contrast, the Dissimilar condition did not show any differences between any of these probe pairings, $ts(20) < 1.34$, $ps > 0.583$, BF_{10}'s < 0.49, reflecting a more symmetrical distribution of probe responses around the target colour, and an absence of a (strong) bias to report the shifted colour.

To assess whether the result pattern of the multi-probe task was indeed different from the eye-movement results, we subjected the probe responses to the same analyses, comparing target selection rates as colours became more dissimilar from the target colour (pooling over similarity condition). Deviating from the eye-movement results, probe responses to relational matching colours significantly decreased as the colour values became more removed from the target colour: −21° compared to −14°, $t(20) = 5.03$, $p < .001$, $BF_{10} = 407.67$, and − 14° to −7°: $t(20) = 6.24$, $p < .001$, $BF_{10} = 4.7 \times 10^4$. Similarly, probe responses to non-matching colours declined with decreasing target similarity, whereby this effect was significant between the +7° and + 14° colours, $t(20) = 4.49$, $p < .001$, $BF_{10} = 124.71$, but failed to reach significance for the comparison of +14° and + 21° colours at the tail end of the distribution, $t(20) = 2.46$, $p = .093$, $BF_{10} = 2.53$.

4.4. Single probe

The single probe trials showed similar results as the multi-probe trials. A 2 (Similarity: Similar, Dissimilar) x 6 (Probe Colours: −21°, −14°, −7°, +7°, +14°, +21°) ANOVA conducted over the single probe data showed a significant main effect of probe colour, $F(5, 20) = 29.37$, $p < .001$, $\eta^2_p = 0.599$, but no effect of similarity, $F(1, 20) = 0.53$, $p = .473$, $\eta^2_p = 0.026$. The interaction just failed to reach significance, $F(5, 20) = 2.21$, $p = .069$, $\eta^2_p = 0.100$.

To analyse the data for a possible shift, we first compared probe responses across each of the colour pairings. In the Similar condition, the −7° probe was chosen significantly more frequently than the +7° probe colour, $t(20) = 3.98$, $p = .002$, $BF_{10} = 47.27$, indicating that there was a shift towards reporting the exaggerated target colour as the target. However, the other parings did not differ significantly, the −21° compared to +21° colours, $t(20) = 1.31$, $p = .612$, $BF_{10} = 0.48$, or the −14° compared to +14°, $t(20) = 2.12$, $p = .125$, $BF_{10} = 1.58$. These results indicate that while there was a slight shift, it was more limited to the target-similar colours then observed in the multi-probe trials. None of the colour pairings in the Dissimilar condition differed, $ts(20) < 1.91$, $ps > 0.212$, BF_{10}'s < 1.04, reflecting a symmetrical distribution of probe responses around the target.

Comparing responses of the relational matching probe colours to each other (pooled over similarity) revealed that probe responses significantly declined as the colours were more dissimilar from the target, all $ts(20) > 4.39$, $ps < 0.001$, BF_{10}'s $> 1.3 \times 10^4$, and the same effect was also evident in the non-matching colours, all $ts(20) > 2.80$, $ps < 0.044$, BF_{10}'s > 7.46. These results show that selection rates on probe trials decreased the further the colour was away from the target.

5. Discussion

Experiment 1 identified a clear dissociation between the result patterns of eye- movements in visual search and decisions made in masked probe trials, with visual search following the predictions of the Relational Account, and masked probe trials showing results predicted by the Optimal Tuning Account.

In visual search, we observed strong and reliable gaze capture by all distractors that matched the relative target colour. Also to note, this effect was independent of the target/non-target similarity, as both similar and dissimilar search arrays produced the same capture patterns. This capture effect cannot be attributed to a *shifted* target template as there were only small differences in eye- movement rates between the slightly shifted colour (−7°) and the more distinct values (−28°). Instead, these results follow the Relational Account (Becker, 2010) and show that attention is not tuned to a specific feature value but to all items with the target's relative feature (e.g., the *reddest* item on the screen).

Masked probe trials, conversely, displayed the Optimal Tuning effect (e.g. Navalpakkam & Itti, 2007). In the similar search context we observed an asymmetric shift in the probe responses, with the highest proportion of target misidentifications for the exaggerated 'optimal' target colour (−7°). Conversely, this shift was not observed in the dissimilar search context. In both similarity conditions selection rates decreased as the colour values became more extreme, which was not observed in the eye-movement results. This dissociation between probe and search results appears to demonstrate that these two paradigms are measuring different visual processes. Target identification in the masked probe paradigm does not appear to rely on the *guidance template* that directs search behaviour, but instead taps into a process designed to identify the target.

Another interesting finding of Experiment 1 was that neither the eye movement results nor the probe responses seemed to be strongly influenced by bottom-up saliency. Despite the fact that the more extreme distractors (+28,°-28°) had a far higher feature contrast than the intermediate distractors (+7,°-7°), bottom-up saliency did not seem to meaningfully modulate selection rates. These results are in line with previous studies showing little or no effect of bottom-up saliency on eye movements (e.g., Becker, Lewis, & Axtens, 2017; York & Becker, 2020), and bolster the claim that relational search is a top-down, strategic adaptation of the visual system (to cope with naturally occurring variation (e.g., in colours and brightness) in the natural environment).

The eye movement results also strengthen the Relational Account, by showing high selection rates for relational matching distractors that were not confusable with the target. The colours were all perfectly discriminable even when presented alone, as reflected in the responses to the single probe trials (see Fig. 2D). This supports the Relational Account, that attention is tuned to the relative target feature (e.g., redder) when the target can be located in virtue of its relative feature on the majority of trials. The Optimal Tuning account and other feature-based theories propose tuning function with a clearly defined peak (e.g., Navalpakkam & Itti, 2007; Wolfe, 1994), which should have led to stronger capture by a subset of the relational matching distractors, contrary to the present findings. Thus, the results of Experiment 1 support a Relational Account for early processes of visual selection, and an Optimal Tuning Account for later, decision-related processes.

6. Experiment 2

Experiment 1 showed evidence that early visual selection is driven by a ‘relational’ guidance template whereas later probe selection is determined by an ‘optimal’ target template. The processes of target selection and target identification presumably play some role in both visual search and probe selection tasks; targets still must be identified in visual search and probes must be ‘selected’ before they can be identified. However, the results show a dissociation because performance is probed at different points in time – tapping into early attention-guiding processes in visual search (by measuring eye movements to distractors), and later, decision-related processes in probe trials (by measuring accuracy in target identifications). An implication of this view is that relational tuning should occur not only in visual search but also in probe trials (if we could measure early visual selection in probe trials), and that optimal tuning should occur not only in probe trials but also in visual search (if we probe later target identification processes). Experiment 1 does not allow assessing this explanation, as it did not assess early selection in probe trials, or later target identification in visual search.

An alternative explanation is that visual search and probe trials genuinely differ in the underlying processes, for instance, because participants used different strategies in response to the different stimulus displays. Of note, visual search and probe displays differed in potentially important respects, including in the number of stimuli, their shape (distractor (*rotated*) vs. probe) and layout, which may have led to different selection processes in visual search vs. probe trials.

Another potential limitation of Experiment 1 is that the results were obtained with only a single colour set (red to yellow) and with colours that differed in luminance, whereas previous studies on the Optimal Tuning account had used equiluminant stimuli that varied between green and blue (e.g., Navalpakkam & Itti, 2007; see also Geng & Witkowski, 2019).

To address these concerns, Experiment 2 used visual search displays and probe displays that were maximally similar to each other, and stimuli and procedures that were more closely aligned with previous Optimal Tuning studies (e.g. Yu & Geng, 2019). In particular, the search arrays in Experiment 2 were identical to the masked probe displays, eliminating superficial differences. In addition to the yellow-red colour set of Experiment 1, Experiment 2 also tested a green-blue colour set, and the colours in both sets were rendered equiluminant, mimicking the stimuli and procedures used in previous Optimal Tuning studies. With this, differences between visual search and probe trials in Experiment 2 cannot be attributed to superficial differences between the stimulus displays, or to the use of particular stimuli or procedures.

To test whether we could find the optimal tuning effect also in the visual search trials, we additionally assessed target identification errors in visual search. As the distractor had the same shape and orientation as the other search items in Experiment 2, it was possible to mistake the shifted (optimal) distractor for the target. Such errors in target identification would result in a wrong response (as the response-defining items were always opposite in target and distractor). Observing more target identification errors in visual search with an optimal (shifted) distractor than other distractors would bolster our view that the same processes occur in visual search and probe trials, with the main difference being in the time-point at which performance is probed.

At the same time, we probed into early selection by measuring the proportion of first eye movements to the different distractors in visual search. If the different results between visual search and probe trials are indeed due to the different time points of the measurements – with eye-movements tapping into early selection and probe trials probing into later, decisional processes – we would expect the proportion of first eye-movements to continue to show an early selection bias for all relational matching items, while target identification should show the same target identification errors as observed on probe trials – with the shifted, ‘optimal’ distractor producing a large proportion of target identification errors that decrease as distractor colours become less similar to the target, and this effect being more pronounced when the non-targets are similar to the target.

7. Methods

7.1. Participants

28 participants (21 female, mean age; 19.43) undergraduate students from the University of Queensland participated in this study for course credit. Two participants were removed for having low target selection rates on no-distractor trials (<30% target selection).

7.2. Apparatus, stimuli and procedure

Experiment 2 employed the same apparatus as Experiment 1. The search displays in visual search trials contained only four search stimuli (3.34° x 3.34°), presented equidistantly (8.10°) from fixation, matching previous work by Yu and Geng (2019). Singleton distractors were no longer rotated, and were thus identical to the other search items except for hue. To avoid uncertainty about which item was the target, feedback was provided for incorrect responses on visual search trials. Probe items were the same size as the search squares and were presented at 6.68° from fixation. Trial timings were the same, however due to the high variability of responses in Experiment 1 probes were now displayed for 400 ms before being masked. Experiment 2 introduced a second set of colours, a “bluer” and a “greener” set in addition to the “redder” and “yellower” set. As participants completed both the dissimilar and similar search in a single session, different target colours were used in each block to prevent long-term memory interference. Participants completed either a “bluer” and “yellower” search, or a “redder” and “greener” search in the Similar vs. Dissimilar condition, with the order of conditions counterbalanced. All colours were now adjusted to be equiluminant (±2 cd/m^2 within a colour set), which rendered adjacent colours less distinct, so the degree interval was adjusted to 8° (from 7°). The ±32° colours (±28° in Experiment 1) were omitted from the experiment, as these colours tended to belong to a different colour category1, resulting in 6 different probe colours that were identical to the distractor and non-target colours (−8°/+8°, −16°/+16°, −24°/+24°) and the target colour (0°). The RGB values for the red-yellow set were – 24°: [251, 101, 85], −16° [246, 107, 75], −8°: [241, 113, 66], 0° (target): [234, 119, 58], 8°: [226, 126, 50], 16°: [217, 132, 44], 24°: [208, 137, 49]. The RGB values for the green-blue set were – 24°: [93, 171, 113], −16°: [80, 171, 126], −8°: [67, 171, 138], 0°: [53, 171, 150], 8°: [37, 171, 162], 16°: [21, 170, 173], and 24°: [8, 168, 184].[1]

7.3. Design

Participants completed the visual search and the multi-probe trials from Experiment 1 in a Similar and Dissimilar search context in two blocks over a single session. In each similarity block participants completed 252 search trials, 70 of which contained a distractor (14 trials with each colour). Intermixed with the search trials were 70 multi-probe trials (35 for each probe colour). Before each block participants completed 28 no-distractor search trials in the respective Similar or Dissimilar condition as practice.

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[1] It is currently unknown whether tuning to the relative features of the target can lead to selection of colours that belong to a different colour category. For instance, in CIE space, tuning to yellower could conceivably lead to selection of green, which is situated beyond yellow (in a straight line from red and yellow). While Ansorge and Becker et al. (2014) and York & Becker, 2020 found some preliminary evidence that different colour categories may operate independently of each other, it is currently unknown whether there are categorical limitations in relational tuning or if relational tuning can transcend into other colour categories.

8. Results

8.1. Eye-movements

Data from 8.3% of trials was excluded for late or premature eye-movements (<50 ms or > 900 ms, as in Exp. 1). To assess the early selection bias, a 2 (Similarity: Similar, Dissimilar) x 4 (Distractor: −24°, −16°, −8°, +24°) repeated measures ANOVA was conducted on the proportion of first eye-movements to the distractors (on all distractor present trials). There was a significant effect of Distractor colour, $F(3, 24) = 93.55$, $p < .001$, $\eta^2_p = 0.796$, no effect of Similarity, $F(1, 24) = 0.93$, $p = .344$, $\eta^2_p = 0.037$, and no interaction, $F(3, 24) = 0.81$, $p = .495$, $\eta^2_p = 0.032$. Bonferroni-corrected pairwise *t*-tests computed over the colour pairs (−28/+28°, −16°/+16° (only Similar condition), −8°/+8° (only Dissimilar condition)) revealed that all relational matching distractors attracted significantly more first eye movements than the paired relational non-matching distractor, all $ts(24) > 10.93$, $ps < 0.001$, BF_{10}'s $> 2.44 \times 10^4$. Critically, there were no differences in selection rates between the adjacent relational matching distractors, −28° compared to −16°: $t(24) = 1.00$, $p = .325$, $BF_{10} = 0.33$ and − 16° to −8°: $t(24) = 0.69$, $p = .498$, $BF_{10} = 0.262$, reflecting that the relational distractors all captured the gaze, including when they were very dissimilar to the target (see Fig. 4). These results mimic the results of Experiment 1 and show that early visual selection was biased to all relational matching distractors.

8.2. Accuracy

To test whether the visual search trials would show a similar shift in target identification responses as predicted for the probe trials (reported below), we analysed target identification accuracy on *visual search trials*. A 2 (Similarity: Similar, Dissimilar) x 4 (Distractor: −24°, −16°, −8°, +24°) repeated measures ANOVA computed over the accuracy of target identification responses showed a significant effect of Distractor colour, $F(3, 24) = 40.81$, $p < .001$, $\eta^2_p = 0.630$, and a significant effect of Similarity, $F(1, 24) = 9.36$, $p = .005$, $\eta^2_p = 0.281$, with more target identification errors in the Similar condition ($M = 40.4\%$) than in the Dissimilar condition ($M = 29.8\%$), but no significant interaction, $F(3, 24) = 0.78$, $p = .507$, $\eta^2_p = 0.032$; hence results were collapsed over the Similarity conditions for subsequent analyses.

Bonferroni-corrected pairwise *t*-tests computed over the colour pairs (−28/+28°, −16°/+16° (only Similar condition), −8°/+8° (only Dissimilar condition)) revealed that relational distractors led to higher error rates than their non-matching colour pair, all $ts(24) > 6.58$, $ps < 0.001$, BF_{10}'s $> 2.1 \times 10^5$. Among the relational matching distractors each adjacent colour led to a higher rate the closer it was to the target. Corrected t-tests revealed that the −24° distractor had the lowest error rate, compared to the −16° item, $t(24) = 2.50$, $p = .038$, $BF_{10} = 2.74$ and in the turn the −8° produced more errors than the −16° $t(24) = 3.24$, $p = .008$, $BF_{10} = 11.65$. These results reflect a similarity effect, in that erroneous responses to the distractor is more likely the more similar the distractor is to the target (see Fig. 4). Mimicking the results of probe responses in Experiment 1, selection of the distractor with the exaggerated, shifted target colour was especially likely. With this, the results of the target identification responses resemble the findings of the probe task, and are noticeably different from the results of the first eye movements to the distractors.

8.3. Multi-probe

A 2 (Similarity: Similar, Dissimilar) x 6 (Probe Colour: −24°, −16°, −8°, +8°, +16°, +24°) ANOVA conducted over the probe responses showed a significant effect of Probe Colour, $F(5, 24) = 48.77$, $p < .001$, $\eta^2_p = 0.670$, but no effect of Similarity, $F(1, 24) = 1.10$, $p = .304$, $\eta^2_p = 0.044$, and no interaction, $F(5, 24) = 1.04$, $p = .373$, $\eta^2_p = 0.041$. Hence, for the following analyses, the data were pooled over the two similarity conditions.

To identify a possible shift or asymmetric skew in the data, we compared probe responses to relational matching and non-matching colours of equivalent distances with Bonferroni corrected *t*-tests. For all three pairs, pooled over similarity condition, the relational matching probe colours showed a higher proportion of target misidentifications than the relational non-matching colours, −8°/+8°: $t(24) = 5.21$, $p < .001$, $BF_{10} = 956.77$, −16°/+16°: $t(24) = 4.48$, $p < .001$, $BF_{10} = 181.71$, −24°/+24°: $t(24) = 2.59$, $p = .048$, $BF_{10} = 3.21$. This indicated that the distribution of responses was skewed towards the relational matching probe colours. Importantly, selection rates decreased the further the probe colours were away from the target colour, both within the relational matching colours, with −24° compared to −16°, $t(24) = 3.39$, $p = .004$, $BF_{10} = 16.10$, and − 16° compared to −8° $t(24) = 8.76$, $p < .001$, $BF_{10} = 2.04 \times 10^6$. This pattern was observed also in the non-matching colours, +8° to +16° $t(24) = 5.61$, $p < .001$, $BF_{10} = 2.3 \times 10^4$, and + 16° to +24° $t(24) = 3.66$, $p = .002$, $BF_{10} = 28.99$. These results closely resemble the trends observed in target identification responses on visual search trials. Both data sets show selection of an exaggerated, shifted target feature value, consistent with the Optimal Tuning Account.

9. Discussion

Experiment 2 replicated the observed results in Experiment 1, even after the stimuli, methods and procedures were adapted to closely match previous Optimal Tuning studies. The visual search results rendered a perfect depiction of the Relational account. All distractor colours that matched the relative target colour reliably attracted the gaze, without discrimination for similarity differences between target and non-targets, and regardless of how far removed the distractor colour was from the target. These results indicate that attention was biased towards the relative colour of the target, not a particular feature value.

By contrast, probe responses showed an asymmetrical shift to the exaggerated target colour that was shifted away from the non-target colour. Deviating from Experiment 1, the dissimilar condition now also showed an asymmetric skew and shift to the exaggerated target colour, and similar and dissimilar conditions did not differ in the pattern of probe responses. It appears we underestimated the impact of equiluminant colours in Experiment 2, with colours in the dissimilar search context appearing more similar in hue than those from Experiment 1. Thus the dissimilar non-targets were similar enough to the target to produce the asymmetric shift in the probe results.

Within the visual search trials, there was a clear dissociation between early visual selection, as indexed by first eye-movements, and later, target identification processes, as indexed by response accuracy. While the first eye-movements were biased to all relational matching distractors, the responses showed a preference for the shifted, exaggerated target colour, in line with probe trial results and the Optimal Tuning Account. This suggests that the target identification process during visual search is based on the same or similar mechanisms as in the probe trials. Thus, the two distinct patterns of results between eye-movements in visual search and judgments in probe trials are likely due to differences in the timing of the measurements; with the first eye-movements reflecting early visual selection; and target identification judgments in visual search and in probe trials reflecting a later decisional process. These results confirm our initial hypothesis that the probe task used in Optimal Tuning studies measures later processes of perceptual decision-making, not an early attentional bias that drives visual search behaviour.

10. Experiment 3

If Optimal Tuning does not describe an attentional effect, what then is causing the shift in response to the probe? According to the Optimal Tuning account, the shift to an exaggerated target feature value reflects a strategic adaptation of top-down tuning, to achieve better discriminability of the target and facilitate target selection. In Experiment 3 we tested an alternative explanation for Optimal Tuning results: that the shift may be due to a perceptual mechanism that exaggerates *perception* of the target colour, introduced by the search display. Of note, in the search arrays, the target was always presented against a background of monochromatic non-targets. It is possible that the similar non-targets in the search display shifted the perception of the target colour, so that the target colour was perceived, for instance, as slightly more red when it was presented among similarly coloured, slightly yellower non- targets. Such a perceptual shift or bias has been reported to occur in simultaneous contrast effects and visual illusions and is presumably caused by lateral inhibition (e.g. Brewer, 1996; Eagleman, 2001; see also Albright & Stoner, 2002). In typical simultaneous contrast illusions, the test colours are presented against the background of other (inducing) colours or directly adjacent to them, whereas in the present search and probe displays, the colours are separated spatially from each other. Still, simultaneous contrast could theoretically skew the perception of the target to an exaggerated colour if the target is surrounded by stimuli that all have a similar colour to the target and are all identical (similar to the Ponzo illusion; see also Rafiei, Hansmann-Roth, Whitney, Kristjánsson, & Chetverikov, 2020, for a similar effect with orientation).

Importantly, simultaneous contrast effects or a corresponding perceptual bias could explain the shift to an optimal colour: In the probe trials, the presented colours were all different from each other, and thus unable to create a corresponding simultaneous contrast effect. Thus, the exaggerated *optimal* target colour on a probe trial may have produced an equivalent perceptual input as the target on a search trial (which seemed exaggerated due to the simultaneous contrast effect). Importantly, the shift and asymmetric skew would not be due to strategic tuning to an optimal target colour, but to a simultaneous contrast effect that is purely automatic and hard-wired (i.e., caused by lateral inhibition).

Experiment 3 tested the simultaneous contrast explanation by presenting the search target in various non-target contexts and probing the participants' direct perception of the target colour using an un-speeded colour matching task. Specifically, to compare the perceptual input of the target colour among similar and dissimilar non-target colours, participants were presented with a visual search array, and asked to pick the colour corresponding to the target on a colour wheel presented on the opposite side of the screen. As the test colours were continuously present in this task, the experiment tested perception of the target colour or its appearance, rather than a top-down template or mental representation used to guide attention or decision-making. Moreover, to discourage formation of a top-down target template of any kind, the target and non-targets randomly varied in hue on each trial, preventing that prior knowledge of stimulus features could lead to strategic tuning to an optimal colour (Navalpakkam & Itti, 2007),

If perceptual biases akin to the simultaneous contrast effect can explain Optimal Tuning effects then we would expect a similar shift (as in the probe trials in Experiment 1 and 2) in the perception of the target in a similar non-target context and a smaller or no shift in a dissimilar non-target context. A corresponding outcome would imply that the shift to an 'optimal colour' as reported by Optimal Tuning could be due to a non-veridical perception of the target rather than a strategy to optimise target selection and discrimination.

11. Methods

11.1. Participants

31 participants (19 female, mean age; 20.76) from the University of. Queensland participated in this study for course credit.

11.2. Apparatus, stimuli and design

Stimuli were presented on 17-in. CRT monitor against a grey background. Four squares (2.67° x 2.67°) were presented on the left hand side of the screen (2.87° from a central point). On each trial the target square was uniquely coloured using the base target colours from Experiment 2 (bluish-green or orange). The target colour varied over a 20° range to prevent habituation or the use of long term-memory strategies in responding. The non-target squares all had the same colour: In the Similar condition, the non- target colours were ± 8° from the target colour, instantiating the same conditions as in Experiment 2. As the Dissimilar condition in Experiment 2 also showed a significant shift in response distributions, the distance of the non-target colours in Experiment 3 was increased, from ±16° to ±24° away from the target colour. In addition, we included a Baseline condition in which the non-target colours were + 180° away from the target colour, i.e. a completely unrelated colour.

The right hand side of the display contained a colour wheel representing the equiluminant colours in RGB space used in Experiment 2 (see Fig. 3.). Within the wheel a circle was presented that would change colour to correspond to the colour at the mouse cursor position, and the participants' task was to select the colour on the colour wheel to match the target on the left side of the display. Prior to each trial the orientation of the colour wheel was randomly rotated to prevent response biases. In total there were 180 experimental trials, 60 for each similarity context (Similar, Dissimilar, Baseline). Participants completed 20 practice trials prior to the experiment to familiarise themselves with the procedures.

11.3. Procedure

On each trial four coloured squares were presented, one of which was the target colour. To simulate the speeded nature of visual search and prevent adaptation to the different colours, the squares continuously flashed on (450 ms) and off (450 ms) until a response was made. Participants were required to select the matching colour of the unique target square as precisely as possible on the colour wheel. There was 500 ms break between trials. In the practice trials only a single square was presented and participants received feedback on their response precision. A visual depiction of the test screen is displayed in Fig. 5.

12. Results

Two participants were excluded for high response variability (*SD*s > 10°). Colour conditions were collapsed and re-coded so that all negative values represented shifts to relational matching colours, and all positive values represented the relational non-matching colours (as in Experiments 1 and 2).

12.1. Raw scores

Outlier responses (> 30° from the target colour) were excluded from the analysis (< 1% of trials). A one-way repeated-measures ANOVA comparing the similarity conditions (Similar, Dissimilar and Baseline) was performed on the raw colour responses, measured as the deviation (in degrees) from the veridical target colour. As predicted by the perceptual bias explanation, there was a significant effect of similarity, $F(1, 28) = 42.41, p < .001, \eta^2_p = 0.602$. Linear contrasts revealed a larger bias towards the exaggerated target colour in the Similar context ($M = -3.41°$) compared to the Dissimilar context ($M = -2.67°$), $t(28) = 2.34$, $p = .027$, $BF_{10} = 2.02$ and the Baseline condition ($M = 0.45°$), $t(28) = 8.35$, $p < .001$, $BF_{10} = 2.78 \times 10^6$. The Dissimilar condition also showed a significantly larger shift than the Baseline condition, $t(28) = 6.69$, $p < .001$, $BF_{10} = 5.50 \times 10^4$.

12.2. Binned conditions

To render the results more comparable with Experiment 2, the raw response scores were sorted into categorical bins matching the distractor/probe colours used in Experiment 2. To that aim, raw responses were sorted into the closest colour category, i.e. -11° to - 5° were

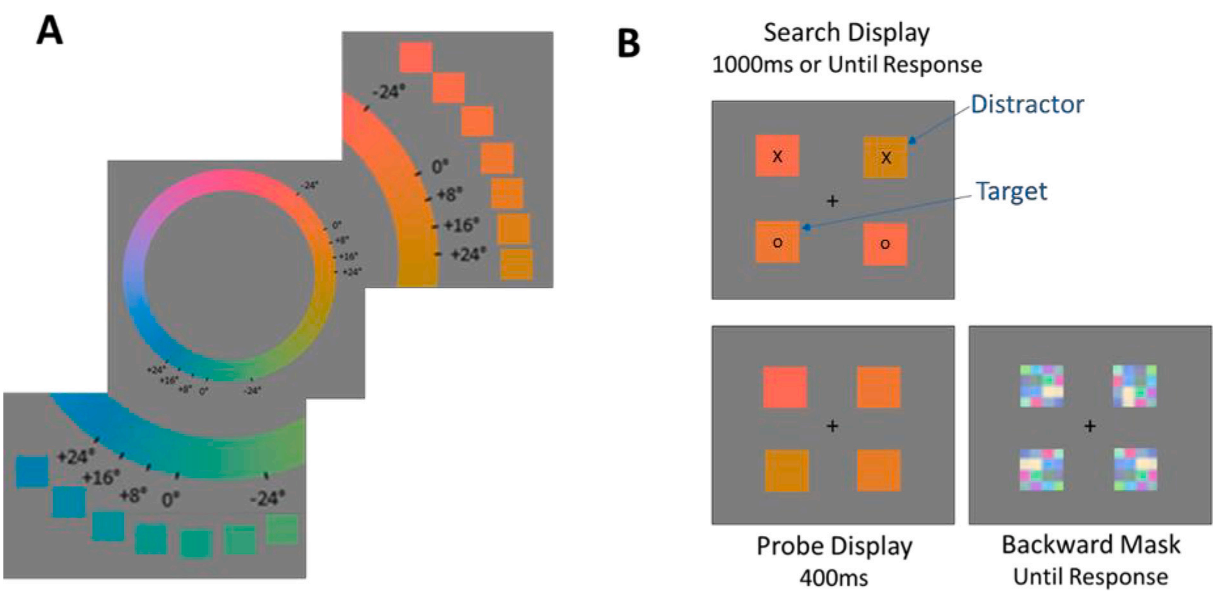

Fig. 3. (A) Equiluminant colour space used in Experiments 2 and 3 (created in RGB). 0° represents the target both in the red/yellow set and in the blue/green set. (B) Example of the 4- item search display and probe / mask display used in Experiment 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

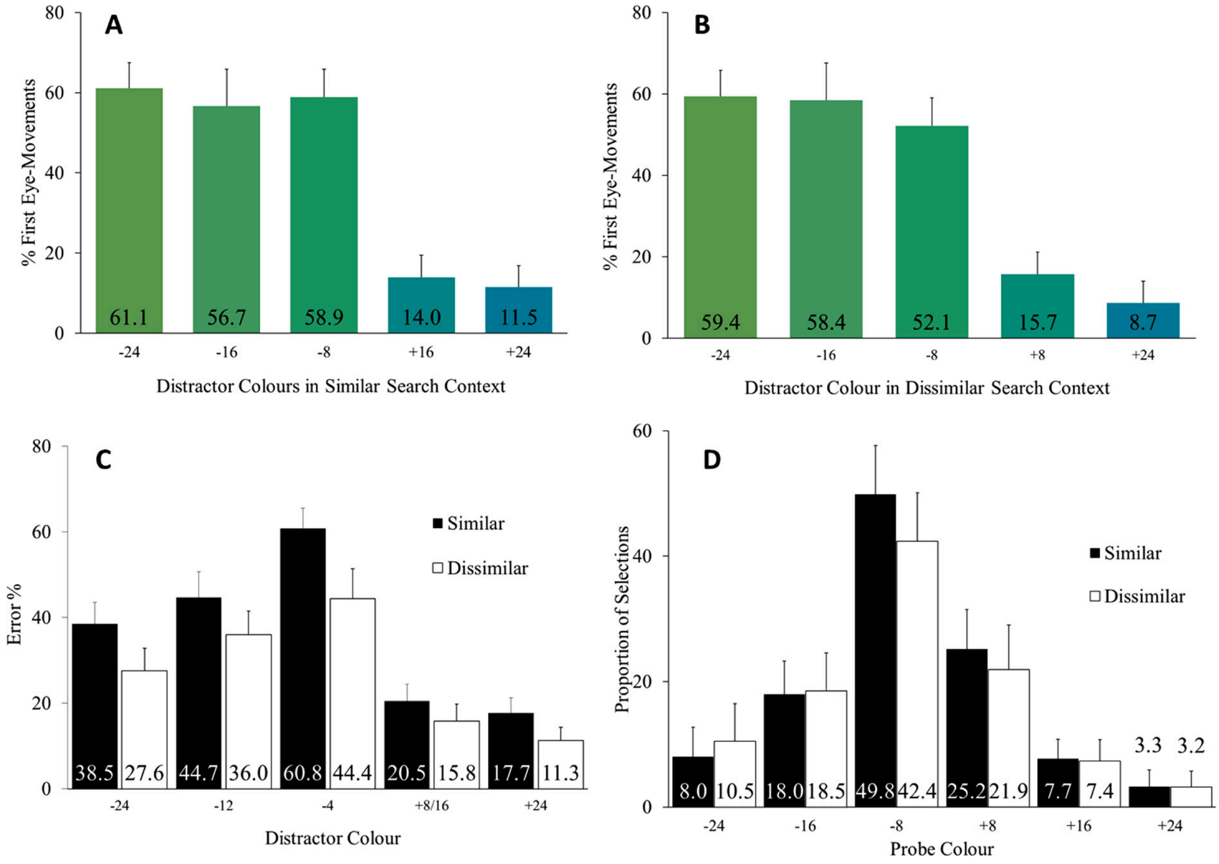

Fig. 4. **A, B)** Proportions of eye-movements directed to distractors in the Similar (**A**) and Dissimilar Context (**B**), pooled across all colour variations so the relational matching colours are represented by negative values. Results show robust gaze capture of all relational matching colours. **C)** Target identification errors on visual search trials show a markedly different result pattern, more akin to the probe responses. **D)** Proportions of colour selections in the probe trials for both similarity conditions, showing a shift towards the exaggerated target colour. Error bars represent within-subjects 95% Confidence Intervals (Loftus & Masson, 1994).

collapsed into −8°. Responses directly in-between two colour categories were apportioned to both by evenly dividing these scores between the two categories.

To assess the comparability of the measured shift in Experiment 2 to the previously observed shift, we computed a 3 (Similarity: Similar, Dissimilar and Baseline) x 5 (Response Category: −16°, −8°, 0°,+8°,

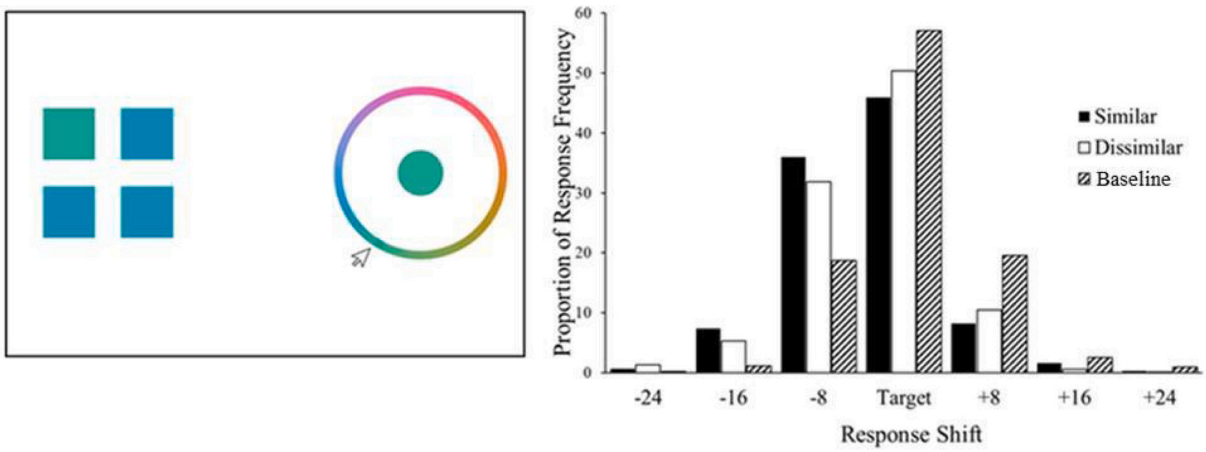

Fig. 5. Left: Illustration of a sample trial in the colour matching task. Participants were required to select the colour of the unique square as precisely as possible. Right: Response bias observed in the results. Negative values indicates a shift to relational matching, target-side colours, away from the non-targets. For better comparability with the results of Experiment 2 the measured shift in the response bias (shift on the colour wheel) was averaged into the same colour categories used by the distractor/probe colours of Experiment 2. Responses halfway between two bins (e.g., +4°, halfway between the 0° target and + 8°) were evenly divided.

+16°) repeated measures ANOVA over the proportion of responses in the binned categories. The ±24° colour category was excluded for having too few responses (< 1% of responses). The results revealed a main effect of Response Category, $F(4, 28) = 225.88$, $p < .001$, $\eta^2_p = 0.890$, as well as a Similarity x Response Category Interaction $F(12, 28) = 18.86$, $p < .001$, $\eta^2_p = 0.402$.

To investigate a possible skew in the distribution of responses, Bonferroni-corrected *t*-tests were computed over the negative and positive colour pairings (−8°/+8°, −16°/+16°), separately for each similarity condition. In both the Similar and Dissimilar contexts, the −8° and − 16° exaggerated target colours attracted significantly more responses than the respective non- matching colours (+8°, +16°), both *ts* (28) > 4.36, *ps* < 0.001, $BF_{10} > 154.25$, indicating a bias towards perceiving the target colour as exaggerated and shifted away from the non-target colour. No such shift or skew in the distribution was evident in the Baseline condition, in which the target was embedded among opposite non-target items (180°), $ts(28) < 1.91$, $p > .132$, $BF_{10} < 0.82$. These results provide evidence that similar non-targets can skew perception of a target colour to render it more distinct from the non-target colour, indicating that the Optimal Tuning Effect may not be due to strategic factors, but to an autonomous, hard-wired perceptual mechanism akin to simultaneous contrast effects.

13. Discussion

Experiment 3 assessed the possibility that similar non-target colours can change the perceived colour of the target. Classically this simultaneous contrast illusion is evoked by a stimulus presented on a contrasting background (Ekroll, Faul, & Niederée, 2004) or directly side-by-side. In the current design, however, we show that a visual search display with spatially separate search items can also create perceptual changes. When the target was embedded in a context of three similar non-target colours, perception of the target was shifted towards an *exaggerated* target colour, as evidenced by the fact that the chosen colour (on the other side of the display) systematically deviated away from the non-target colour. This shift in the perceived target colour was stronger the more similar the targets and non-targets were in hue. Conversely, when the non-targets were on the opposite side of colour space to the target, participants did not show any bias in colour selection. These results show that the perception of a search target can be skewed due to an automatic, passive mechanism that increases the perceptual contrast between the non-target colours and the target colour.

With this, the results pattern is akin to that of previous Optimal Tuning studies (Geng et al., 2017), which showed a larger shift in probe responses in the Similar search context than the Dissimilar. When analysed as categorical responses the perceptual results closely mimicked those from the probe trials of Experiment 2, with a large shift towards the optimal target colour value. These results suggest that the perceptual influences of a high similarity search display can create an effect akin to simultaneous contrast that biases the perception of a target-object to make it appear more distinct. As simultaneous contrast effects are caused by lateral inhibitory connections between neurons that is hard-wired and automatic, this finding provides an alternate explanation to Optimal Tuning's claim that the shift reflects a strategic adaptation of sensory neurons (e.g., to increase the discriminability of the target; Navalpakkam & Itti, 2007).

In contrast the Relational Account remains unaffected by these perceptual biases. As we saw in Experiments 1 and 2, attention is directed to all relational matching colours, ranging from very similar hues to extreme colours that are very different from the target colour. Simultaneous contrast effects cannot explain attention capture by these extreme colour values.

14. General discussion

A key concept throughout the visual attention literature has been that of the *attentional template*, which describes the top-down processes that determine visual selection and guide search behaviour. There have, however, been varying definitions of what this template entails. Originally the attentional template was referred to as the top-down bias towards target properties that increased sensitivity towards features during search (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). However, the target template has recently been used to describe the conscious mental representations of the target item that are stored in visual short-term memory possibly with assistance of long-term memory processes (Geng & Witkowski, 2019; Hout & Goldinger, 2014; Malcolm & Henderson, 2009: Wolfe, 2021). These two concepts have been used interchangeably to describe and explain visual search behaviour. Yet, the concepts do not necessarily describe the same underlying construct. While there is some evidence for an overlap between short-term memory functions and attention (e.g. Hamblin-Frohman & Becker, 2019; Olivers, Meijer, & Theeuwes, 2006), the higher-level mental representations of a stimulus are not necessarily the driving force that determines early attentional selection and/or perceptual sensitivity. In fact, the present study provides clear support for positions which argue for a distinction between target representation templates and attentional guidance templates (Becker, Martin, & Hamblin-Frohman, 2019; see also Becker, Atalla, & Folk, 2020; Hansmann-

Roth, Kristjansson, Whitney, & Chetverikov, 2020; Wolfe, 2020).

In two experiments the attentional template was assessed via two different paradigms: visual search and masked probe trials. Our results depict two different result patterns for the tasks, reflecting that they cannot be measuring the same construct. In the visual search paradigm eye movements allow the most direct behavioural measurement of attentional selection (e.g. Becker, 2010, 2018; Becker, Harris, et al., 2017; Deubel & Schneider, 1996; Posner, 1980; Zelinsky & Sheinberg, 1997) with eye movement parameters (e.g., proportion of first fixations) allowing direct inferences for the way attention is biased to the stimuli at the start of the trial. The results of two experiments revealed that gaze was strongly attracted to all distractors that matched the relative colour of the target stimulus, in line with previous studies on the Relational Account (Becker, 2010; York & Becker, 2020). By contrast, target identification accuracy followed the Optimal Tuning Account, showing mostly accurate target identifications, with a shift towards an exaggerated target colour when the non-targets were similar to the target. This result pattern was observed both in masked probe trials, and also in search trials (Experiment 2). Even when the gaze was initially attracted to all relational matching distractors, judgments were skewed towards the Optimal Tuning response pattern. This distinguishes two parts of search behaviour; the first eye movements that reflect early visual selection versus the accuracy results that reflect decision-making processes about the selected item, providing a measure of later processes in visual search. We argue that gaze capture provides the most reliable measure of attentional templates or an early *sensory* (aka attentional / pre-attentive) bias. This sensory bias is in line with the definition of attentional templates by Desimone and Duncan (1995) or Wolfe's (2020, 2021) description of *Guidance* templates, in which the template a sensory bias towards stimulus features to produce strong competitive signals. This in turn guides visual attention and eye movements. This *Guidance* template is thus most likely not consciously accessible or reportable but represents the tuning state of the visual system (i.e., the way attention is top-down tuned to the stimuli in the display; see also Becker et al., 2019). The key factor separating this *Guidance* template from a *Target Representation* template in terms of data is the time course in which a behavioural results were recorded.

Like the accuracy results in visual search (Experiment 2), responses to probe trials do not seem to represent sensory attentional biases in the visual system. In both experiments an asymmetric shift was observed that favoured the exaggerated target colour in probe trials. In contrast to visual search trials there was no evidence for a relational bias, as target misidentifications did not occur at an equal rate for relational matching target-side colours that were further removed from the target. This exemplifies the distinction between attention and target identification. While attention was captured by the most extreme, relational matching colours, a second-stage process was able to disregard these stimuli as they failed to match the target template. Thus, it is apparent that conscious representations of the target feature used to make comparisons in target identification are not used to direct attention in visual search.

Previous studies had already shown that implicit knowledge of a visual array can guide behaviour in a way that is not fully correlated with the information reported explicitly (e.g., Hansmann-Roth et al., 2020), and proposed that attention-guiding mechanisms are distinct from the consciously accessible target representations or target templates (e.g., Becker et al., 2019; Becker et al., submitted). The present study provides more direct evidence for this notion, by demonstrating that attention is guided by different, relational principles while later, target identification processes rely on a narrower, more feature-specific target definition. The fact that these different behaviours could be observed in the same trials and within the same participants (see Exp. 2) in the early vs. later responses (eye movements vs. target identification) shows that the different responses are not driven by differences in visual search vs. probe displays, but are due to the different time points at which behaviour is probed. These results show that we need to exercise caution in drawing conclusions about early visual attention from probe detection tasks or perceptual decision tasks in general, as these do not necessarily reflect the factors driving early visual attention (e.g. Becker et al., 2013; Yu & Geng, 2019).

One may ask if a modified Optimal Tuning account could provide an account for early attentional effects, as well as later target identification processes. For instance, by assuming that early selection processes were noise-corrupted, or that there was an imprecise target template one could explain the capture of the more removed, non-optimal colours. However, this seems rather implausible: First, noise is usually equally distributed and thus, would increase selection of all stimuli rather than the limited, observed, capture increase by relationally matching stimuli. Second, Navalpakkam and Itti are proponents of narrow tuning functions and fine-grained selection (e.g., Navalpakkam & Itti, 2006), so that proposing an imprecise/broad target template or noisy selection processes would directly contradict their theory. Third, previous studies on the Relational Account have shown that attention is genuinely tuned to relative features (in Relational Search), and cannot be explained by broad, categorical tuning or other feature-specific accounts (e.g., Becker, 2010; Becker et al., 2013, 2014; Becker, Lewis, & Axtens, 2017; Schönhammer, Grubert, Kerzel, & Becker, 2016; York & Becker, 2020). Finally, the results of Experiment 3 sheds doubt on the claim that later post-attentive or perceptual processes are actively tuned to optimal features.

In Experiment 3, we critically tested whether the Optimal Tuning results could be due to a different, passive perceptual mechanism. The Optimal Tuning account claims that the observed shift in the target template is a strategic adaption to maximise the signal-to-noise ratio and optimise selection. As Experiments 1 and 2 showed that visual selection operates on different (relational) principles, Experiment 3 tested this strategic explanation against an alternative that the observed shift is due to passive, hard-wired processes that causes an effect akin to simultaneous contrast. The simultaneous contrast effect has long been known to influence perception (e.g. Heinemann, 1955). Specifically, when colours are presented in close proximity to each other, they are perceived to be more distinct from each other (i.e., appear to have exaggerated colour values compared to when presented alone; Eagleman, 2001). Our study reveals a perceptual bias or simultaneous contrast effect in visual search for colour. Experiment 3 revealed that the perception of a colour target among three similar non-targets was indeed skewed towards a more extreme colour, indicating that the asymmetric shifts in target identification could be due to the shift in the perceived colour of the target. Importantly, this perceptual bias also followed one of the central tenets of the Optimal Tuning Account, that the shift was more pronounced the more similar the target was to the non-targets. Thus, it is possible that the effects observed in previous Optimal Tuning studies do not reflect a strategic tuning of perceptual and/or decisional processes, but instead a hard-wired, automatic simultaneous contrast effect that alters the perception of the target (e.g., towards slightly redder).

In sum, the present results could be accounted for by an early, relational Guidance template that directs attention to all relational matching items, and a later, feature-specific Target template that guides decision-making about whether the selected item is the target. The results do not determine whether the two templates are based on two separate, distinct mechanisms, or whether they are both components of one overarching template that performs different functions at different temporal points of visual search. In fact, we have argued elsewhere that the notion of a target template or a mental representation may not be the best construct to explain attentional tuning or visual processing (Becker et al., 2019). Given the present findings, the challenge for the future is to formulate possible hypotheses for how initial relational processing could become more narrowly focussed on the specific target feature, and critically test this 'one mechanism' hypothesis against the alternative possibility that early attentional guidance and later perceptual decision-making are based on different and independent processes (see Becker, 2013, for an overview of possible mechanisms, and Becker, Qiu &

Martin, submitted, for the latest progress).

While the possible implementation of Guidance templates and Target templates require further research, the key point of the present study is that early attentional selection and later perceptual decision-making show different result patterns when probed in more detail and with more suitable methods to measure performance on these two tasks. When describing effects in visual search and other attentional paradigms it is important to consider the possible attentional, perceptual and decisional processes involved in each measure. When describing the *attentional* template as the mechanism that biases how attention is directed during search, reverse inferences from later stage, conscious decision making tasks to earlier, attentional processes do not appear to be reliable, and may not provide an adequate measure of top-down bias. Even though there has been a long-standing tradition of using masked probe tasks to make inferences about early attentional processes (e.g. Ansorge, Becker, & Breitmeyer, 2009; Prinzmetal, McCool, & Park, 2005), the present results indicate that this may be problematic. Conversely, early search behaviour should not be used to make inferences about target identification processes in the final stages of target selection.

Authors.

Zachary Hamblin-Frohman: Methodology, Software, Formal Analysis, Investigation, Writing Original, Review.

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Appendix B. Supplementary data

Data for this study, including raw trial information and participant means. Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2021.104732.

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