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Foraging through multiple target categories reveals the flexibility of visual working memory☆

Tómas Kristjánsson*, Árni Kristjánsson

Department of Psychology, University of Iceland, Iceland

A R T I C L E I N F O

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A B S T R A C T

A key assumption in the literature on visual attention is that templates, actively maintained in visual working memory (VWM), guide visual attention. An important question therefore involves the nature and capacity of VWM. According to load theories, more than one search template can be active at the same time and capacity is determined by the total load rather than a precise number of templates. By an alternative account only one search template can be active within visual working memory at any given time, while other templates are in an accessory state – but do not affect visual selection. We addressed this question by varying the number of targets and distractors in a visual foraging task for 40 targets among 40 distractors in two ways: 1) *Fixed-distractor-number*, involving two distractor types while target categories varied from one to four. 2) *Fixed-color-number* (7), so that if the target types were two, distractors types were five, while if target number increased to three, distractor types were four (etc.). The two accounts make differing predictions. Under the single-template account, we should expect large switch costs as target types increase to two, but switch-costs should not increase much as target types increase beyond two. Load accounts predict an approximately linear increase in switch costs with increased target type number. The results were that switch costs increased roughly linearly in both conditions, in line with load accounts. The results are discussed in light of recent proposals that working memory reflects lingering neural activity at various sites that operate on the stimuli in each case and findings showing neurally silent working memory representations.

1. Introduction

As you search for mustard and ketchup in an unfamiliar super-market, what is the optimal strategy? You do not know which brands this super-market sells, and you cannot think of a defining feature in the shape of mustard or ketchup bottles that distinguishes them from most other condiments except that mustard tends to be yellow and ketchup red. You scan the shelves searching for red and yellow, occasionally pausing as your eyes land on a red or a yellow bottle. But what is actually happening as we search the shelves for the two colors? Do we look for both colors simultaneously, or are we possibly searching for one color at a time, rapidly switching between searching for yellow and red as our eyes scan the shelves? This question touches on many important questions within the scientific literature on vision and attention. How do we search complex scenes? What roles do working memory and attention play in the search process? Do we form search images, or templates to search effectively, and how do they guide our search? Can we maintain more than one search image (or template) at the same time? Can we, in other words, search for ketchup and mustard simultaneously?

To address such questions, several models of attention have been developed. Some of the most influential are two stage models involving a pre-attentive parallel stage followed by an active attentive stage involving serial processing such as Feature-Integration Theory (Treisman & Gelade, 1980) and the Guided Search model (Wolfe, 1994; Wolfe, Cave, & Franzel, 1989). These models are mostly based on findings from single target search tasks and do not as easily account for results from search tasks involving multiple targets, such as visual foraging tasks (Kristjánsson, Jóhannesson, & Thornton, 2014; Wolfe, 2013). Note that the latest version of the guided search model will take data and results from foraging and other multi-target search tasks into account (Wolfe, Cain, Ehinger, & Drew, 2015).

Early models of visual foraging compared human foraging with optimal foraging, that assumes that as the target yield within a particular search environment, decreases below average, foragers will switch to a new foraging patch (Charnov, 1976; Pyke, Pulliam, &

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* Corresponding author at: Department of Psychology, School of Health Sciences, University of Iceland, 101 Reykjavík, Iceland.
E-mail address: tok1@hi.is (T. Kristjánsson).

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Charnov, 1977). But optimal foraging models also apply to foraging patterns, that is, foragers should choose the closest possible target to minimize the total distance travelled while foraging (Pyke et al., 1977). While this account is logically enticing, several studies have shown that humans are not optimal foragers (e.g. Hutchinson, Wilke, & Todd, 2008; Pierce & Ollason, 1987) and that there are biases and flexibilities in foraging behavior, not accounted for by optimal foraging models (Cain, Vul, Clark, & Mitroff, 2011).

1.1. Templates guide foraging

Most researchers agree that during search and foraging observers use *search images* or *templates* whose content reflects the task goals in each case (Bond & Kamil, 2002; Dukas & Kamil, 2001; Jackson & Li, 2004; Nakayama, Maljkovic, & Kristjánsson, 2004). Such templates are assumed to be held in capacity limited working memory (Awh & Jonides, 2001; Bundesen, 1990; Carlisle, Arita, Pardo, & Woodman, 2011; Desimone & Duncan, 1995; Grubert & Eimer, 2013; Vickery, King, & Jiang, 2005; Woodman, Carlisle, & Reinhart, 2013), and these capacity limits may be one reason why participants do not always forage optimally.

There are, however, long standing disagreements over how these templates guide attention. A fundamental question involves the number of templates that can simultaneously guide attention. According to a recent proposal, there can only be one template active in working memory at any given time (van Moorselaar, Theeuwes, & Olivers, 2014; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Ort, Fahrenfort, & Olivers, 2017; see also Oberauer, 2002). Similarly, Huang and Pashler (2007) proposed that observers only have access to one feature value at a given moment. This idea has also been proposed in the literature on animal foraging. For example, birds are bad at dividing their attention, and have trouble searching for two categories of prey simultaneously (Dawkins, 1971; Dukas, 2002). Recent evidence, that mostly involves demonstrations of a cost to switching between templates, is seemingly consistent with this proposal. In Houtkamp and Roelfsema (2009) observers performed an RSVP task where they searched for either one or two targets within a stream of rapidly presented items. They had great difficulty with performance when there were two potential targets within the stream, while when there was only one, performance improved greatly, suggesting that participants could only use a single template for guidance at a given time, and that any additional templates increased the chances of missing targets. In Dombrowe, Donk, and Olivers (2011) observers made saccades from the left to the right between target items of one color or two different colors. Performance was impaired when targets were of two different colors and Dombrowe et al. (2011) concluded that changing or switching between attentional templates takes around 250-300 ms. In van Moorselaar et al. (2014) observers performed visual search while they maintained a variable number of items in visual working memory. van Moorselaar et al. (2014) found only interference from the visual working memory load when a single color was maintained in working memory, not when more colors were maintained.

Based on such findings, Olivers et al. (2011) proposed a model of visual working memory where only a single template is active at any given time and capable of influencing ongoing visual tasks (such as visual search or visual foraging). According to their proposal, more templates can be kept in visual working memory, but only one template is *active* and can interact with perception at any given time, and non-active templates are kept in an accessory working memory state and do not affect current visual performance (see also Huang & Pashler, 2007).

Other results seemingly contradict this, however. Predators who divide attention among an increasing number of different prey types decrease their ability to detect any given type (Dukas & Ellner, 1993). This decrease in performance is gradual, but does not involve a collapse in performance as load increases from one to two templates with little, or no difference between two or three templates, as a single-template model predicts, since according to such models, observers must simply switch to one of the items in the accessory state, that are all in a similar state (van Moorselaar et al., 2014). Carlisle et al. (2011) then found ERP evidence for more than one simultaneous attentional template in visual working memory, as did Grubert and Eimer (2015). Strong counter-evidence against the idea of a single active template was provided by Beck, Hollingworth, and Luck (2012), who reported that observers can maintain more than one active visual working memory template. Their observers searched for a target among distractors, attempting to limit attention to objects of two colors, finding that observers switched gaze back and forth between the two colors with no switch costs, in contrast to single-template proposals.

Perhaps the strongest evidence that observers can simultaneously maintain at least two active search templates comes from recent studies on human foraging (e.g. Jóhannesson, Kristjánsson, & Thornton, 2017; Jóhannesson, Thornton, Smith, Chetverikov, & Kristjánsson, 2016; Kristjánsson et al., 2014; Kristjánsson, Thornton, & Kristjánsson, 2016). In Kristjánsson et al. (2014), participants foraged, by tapping on the screen of an iPad, for 40 targets of two types (e.g. red and green disks) among 40 distractors of two different types (e.g. blue and yellow disks). More than 95% of observers switched freely between the two target types during foraging trials, without large costs. Another interesting finding was that when intertarget times (times between successive taps, ITTs) were compared between when the previous target was from the same category, or from a different category, the difference in ITTs ("switch-cost") was only around 50 ms (Kristjánsson et al., 2016). In a recent unpublished study (Ólafsdóttir, Gestsdóttir, & Kristjánsson, 2017), such switch costs were almost non-existent, and are as low as 15 to 20 ms in other studies (Jóhannesson et al., 2016; Ólafsdóttir, Kristjánsson, Gestsdóttir, Jóhannesson, & Kristjánsson, 2016; see Grubert & Eimer, 2015 for related findings). Also, in a study where observers foraged with eye gaze rather than fingers, the switch costs between target-types were essentially zero (Jóhannesson et al., 2016). These results show that people can switch between target categories with seemingly little switch costs, an order of magnitude lower than the 250–300 ms suggested by Dombrowe et al. (2011) and therefore involve a challenge for single-template accounts, since they must then include a mechanism for rapid switching between templates.

Another intriguing question is why participants performing these foraging tasks seemingly do not seem to care whether the next target they choose during foraging is from one target category or the other. The runs during foraging for two colored targets among two distractors are typically close to random (Kristjánsson et al., 2014). If switch costs between templates are around 250–300 ms this would be an extremely inefficient strategy. These findings therefore seem highly discrepant with the idea of a single active template, which takes time to be replaced. They appear to be more consistent with load theories of visual working memory that assume that working memory has limited capacity, but do not place any constraints upon the nature of the WM representations, but simply impose a capacity limit (Alvarez & Cavanagh, 2004; Bays & Husain, 2008). In fact, as load increased in Kristjánsson et al. (2014) and observers had to forage for 2 more complex "conjunction" targets (e.g. red square and green disk targets among green square and red disk targets) they changed their strategy, tending not to switch between targets (Jóhannesson et al., 2017; Kristjánsson et al., 2014). Observers seemed, in other words to maintain two simultaneous templates that involved simple features, but were unable, or unwilling, to maintain two more demanding conjunction templates.

1.2. Current goals

Our aim was to directly address the question whether more than one template can be simultaneously actively maintained in visual working memory. We therefore varied the number of targets and distractors in a visual foraging task for 40 targets among 40 distractors. We varied the number of target and distractor types in two ways: 1) Fixed distractor

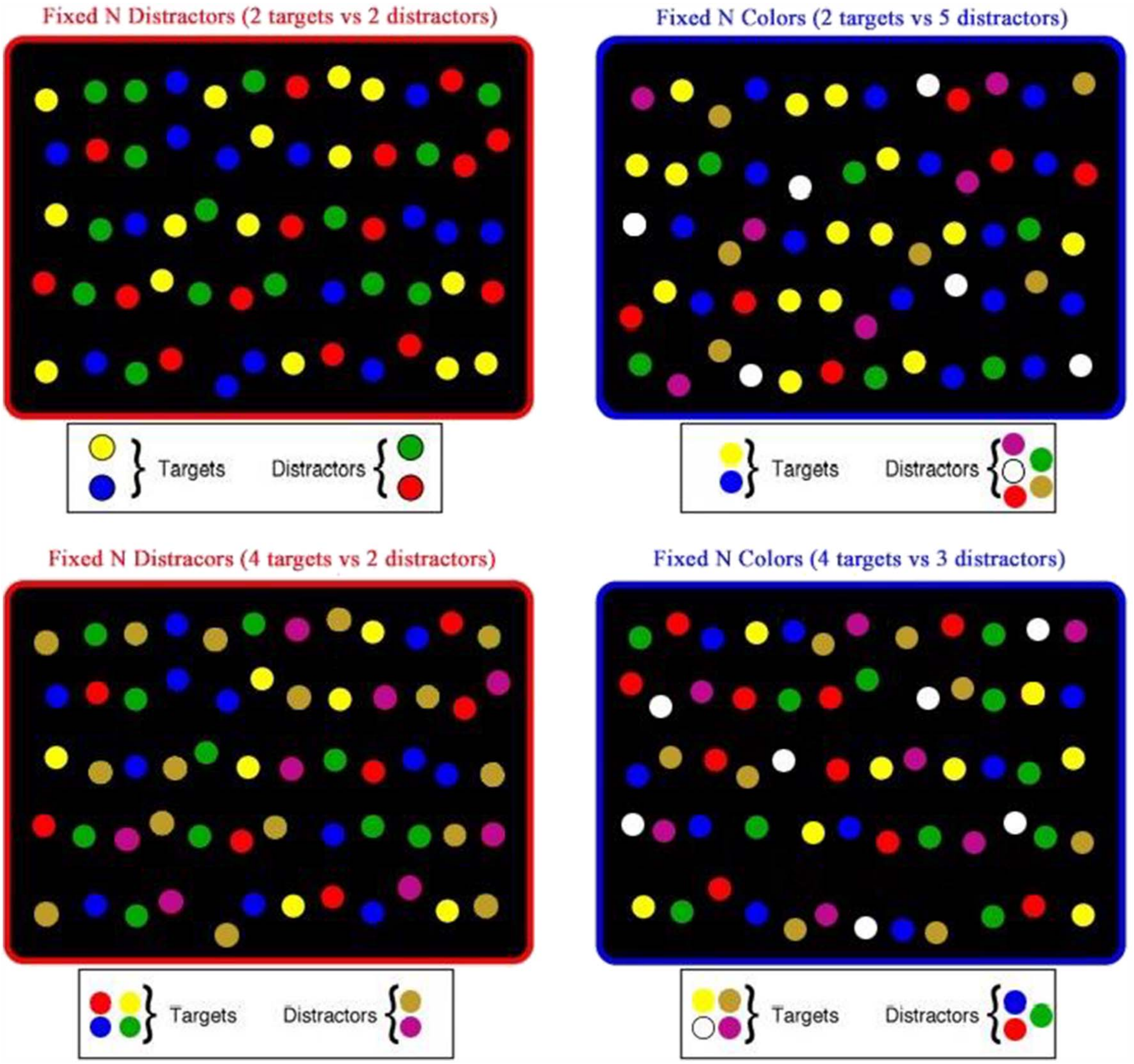

Fig. 1. Examples of the two types of foraging task with the fixed-distractor-number condition on the left (red frames) and the fixed-color-number condition on the right (blue frames). Displays with 60 stimuli are shown for convenience, while 80 stimuli (40 targets and 40 distractors) were presented on each foraging trial. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

number, involving 2 distractor types while target categories varied from 1 to 4. 2) Fixed color number (7), so that if the target types were 2, distractors types were 5, while if target number increased to 3, distractor types were 4 (etc.). We measured how the number of templates affected intertarget times (ITTs), using a modified version of the iPad foraging task from Kristjánsson et al. (2014). If only one template can be active at any one time, a clear prediction is that the ITTs should be low when participants forage for only one target type. When target types increase to two, there should be large switch costs as items must be transferred from the accessory state to an active template and the color previously active, moved to the accessory state. But when target types are increased to 3, ITTs should then not increase as other accessory state items should be equally available. In other words, performance with only one target should be vastly superior to the other conditions with more target types, but those should not differ much among themselves, since the other items should all be in an accessory state. Under a load account, conversely, as more target types are added, presumably requiring more working memory, instead of a sharp slowing of ITTs between one and two target types and then either no difference or only a slight slowing of ITTs between two and four target types, we should simply expect a mostly linear increase in ITTs as load increases (see e.g. Alvarez & Cavanagh, 2004). Another prediction from the single-template account is that observers should strongly prefer to stick to the same target type on consecutive selections during foraging, since if observers need to switch between an active template in working memory and items in the accessory state, this should take time and be effortful. In light of the above, our method involved gradually increasing the load during a visual foraging task. Both the fixed-distractor-number, and fixed-color-number conditions involve the same prediction – from the single-template account we should expect a big difference in performance for 1 vs 2 targets, but not a dramatic difference between 2 vs 3 or 3 vs. 4 targets. A load account predicts, on the other hand, a gradual increase in ITTs as more target types are added to the task, presumably increasing the load.

2. Method

2.1. Participants

21 students at the University of Iceland (16 female; aged between 21 and 37 years old, M = 24.6) participated voluntarily, but received partial course credits for participation. All reported normal or corrected-to-normal vision, were right-handed and gave written, informed consent. All aspects of the experiment were reviewed and approved by the appropriate ethics committee and conformed to the ethical guidelines set out by the Declaration of Helsinki for testing human

participants.

2.2. Equipment

The stimuli were displayed on an iPad 2 with screen dimensions of 20 × 15 cm and an effective resolution of 1024 × 768 pixels. The iPad was placed on a table in front of participants in landscape mode, so that viewing distance was approximately 60 cm. Stimulus presentation and response collection were carried out with a custom iPad application written in Swift using Xcode.

2.3. Design

Participants completed 16 foraging trials with 40 targets in each of the eight conditions of the experiment, 128 trials in total. In the fixed-distractor-number condition, the number of target categories varied so that there were one, two, three or four target categories (TCs) among two distractor categories (DCs). In the fixed-color-number condition, the total number of colors on the screen was constant (at seven) but the number of distractor categories varied as a function of the number of target categories: If there was 1 target category, there were 6 possible distractor colors, while if there were 4 target categories, there were 3 distractor color categories. So, in the fixed-distractor-number condition there were 4 variations: 1 TC among 2 DCs, 2 TCs among 2 DCs, 3 TCs among 2 DCs, and 4 TCs among 2 DCs. In the fixed-color-number case there were also four variations: 1 TC among 6 DCs, 2 TCs among 5 DCs, 3 TCs among 4 DCs and 4 TCs among 3 DCs.

2.4. Stimuli

Eighty disks appeared on a black background on each trial, 40 targets and 40 distractors (see Fig. 1). There were seven possible colors: red, green, blue, yellow, white, orange and pink. The diameter of targets and distractors was 20 pixels, (approximately 0.46°, at the typical viewing distance of 50 cm). The items were randomly distributed across a non-visible 10 × 8 grid that was offset from the screen edge by 150 × 100 pixels. The whole viewing area therefore occupied 15 × 12 cm (approximately 14.3 × 11.4°). The exact position of individual items within the grid was jittered by adding a random horizontal and vertical offset to create less uniform appearance. Gaps between rows and columns ensured that items never occluded one another. The overall spatial layout and location of targets and distractors was generated independently on every trial.

2.5. Procedure

The experiment was run in a quiet, dark room. On each trial, participants were instructed to tap all targets as quickly as possible using the index finger of their dominant hand. A counter at the bottom of the screen indicated the number of completed trials. Participants were instructed to finish 16 trials and let the experimenter know when they had finished. They were told that after two practice trials, they would complete eight blocks of 16 trials for each condition and that they could take a break between any of the blocks. One trial refers to a completed sequence where all 40 targets were tapped. After initial set up, the experimenter told the participant twice, what colors they should tap, and then left the room. Participants pressed a "play" button on the screen when ready and the stimuli appeared. Targets disappeared immediately after they were tapped. If participants tapped a distractor, the trial ended, an error message was given, and they could start a new trial by pressing the play button. When all targets had been tapped, a smiley face appeared, along with feedback about total trial time. Participants started the next trial by tapping anywhere on the feedback screen. Whether participants started with fixed distractor number or fixed color number was counterbalanced. All observers finished 16 foraging trials in each condition. If they made an error they had to perform another foraging trial until they had completed 16 successful trials.

2.6. Data analysis

We had two main measures of interest. Firstly, the intertarget times (ITTs), reflecting the time between each tap on a target. Secondly, we also assessed switch costs, that is, the difference in ITTs when observers select the same target type as on the preceding selection, and when they select a different target type from the last selection. Before analyses, taps on empty areas of the iPad screen and all taps on incomplete trials were filtered out. For each of the dependent variables, averages were calculated for each participant for each condition (4 × 2) and all outliers (> 3 SDs away from the mean for each participant in each condition) were removed. We also measured the total run number on each trial, which can range from the number of target categories (TCs), for example in the conditions where there are 3 TCs, the minimum number of runs is 3, where all targets of one color are tapped before moving to the next color, to the total number of targets (where participants *always* switch between target categories). The total number of targets was always 40, when there was 1 TC, all 40 targets came from that category. When there were 2 TCs 20 targets came from each category. For 3 TCs, there were 13 targets from two of the categories but 14 from one category (determined randomly). When there were 4 TCs, there were 10 targets from each category. If observers forage randomly (pick targets regardless of type) we should expect this run number to be approximately $(\text{TCs} - 1)/\text{TCs} * 40$. In addition, the distance between the targets tapped was recorded, in order to assess the efficiency of the foraging path. Finally, we measured the number of error trials (where observers tapped a distractor) for each condition. For all analyses, other than error rate analyses, error trials were excluded from the analyses.

3. Results

3.1. Intertarget times (ITTs)

ITTs for the different number of target categories for the fixed-distractor-number and the fixed-color-number conditions are shown in Fig. 2. A 4 × 2 (number of target categories × conditions) univariate

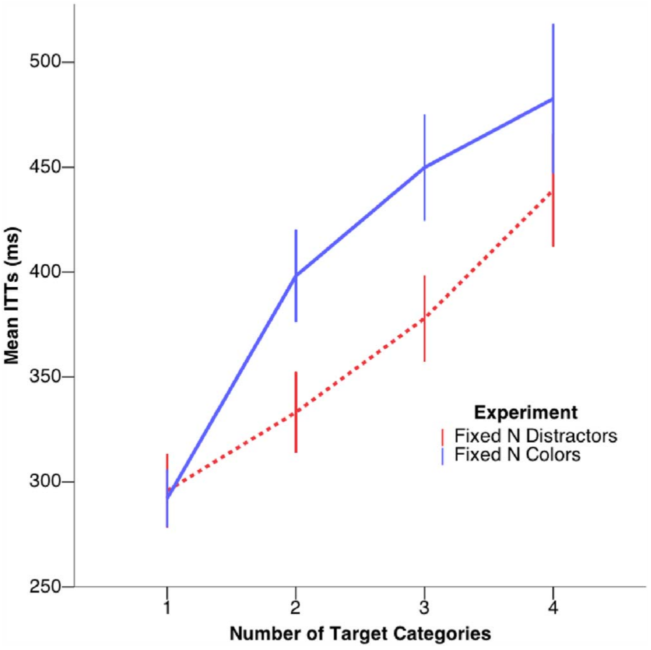

Fig. 2. The intertarget time as a function of condition and the number of target categories. The lines represent the mean ITTs for each condition.

ANOVA showed that both main effects were significant (F(3168) = 8.45; $p < 0.001$; $\eta_p^2 = 0.601$ for the number of target categories and F(1168) = 30.95; $p < 0.001$; $\eta_p^2 = 0.162$ for condition) and the interaction between number of target categories and condition was also significant (F(3168) = 4.60; $p = 0.004$; $\eta_p^2 = 0.079$).

The interaction is visible in Fig. 2 as the two conditions have very similar mean ITTs with one target category, but as target categories are added, the mean ITTs are affected more in the fixed-color-number condition than the fixed-distractor-number one. The single-template account and the load account, yield different predictions as explained above. The single-template account predicts that there should be a large difference in ITT's between 1 and 2 targets while the difference between 2 and 3 and 3 and 4 TCs should be small as in all these cases observers must use the single active template and items in the accessory state. It could be argued that there should be an upward slope between two and four target categories as changing between three templates rather than two in the accessory state could lead to priming effects. However, this upwards slope should not be large, and notably, no such slopes were visible in the interference task tested by van Moorselaar et al. (2014). At the very least we should expect a change in the slope between two and three target categories, so that the slope should be steeper between one and two target categories than between two, three and four target categories. This is a clear prediction from the single-template model. Load models make a different prediction: the larger the number of templates, the larger the ITTs should be, but this increase in difficulty should be additive with increased load. Curve estimation for each condition shows that for both conditions a linear model accounts well for the results (Fixed-distractor-number: F(1,82) = 108.36 $p < 0.001$ $R^2 = 0.569$; Fixed-color-number: F(1,82) = 120.32 $p < 0.001$ $R^2 = 0.595$). Overall, this pattern of results must be considered to better fit load models of visual working memory (see General Discussion).

3.2. Switch costs

According to single-template accounts, there should be a substantial switch-cost when there are two target categories, but there should be little or no increase in that switch-cost when more target categories than that are added. van Moorselaar et al. (2014) found interference effects for two items in working memory, but these interference effects did not increase as the number of items to be memorized increased, and this should also be the case for switch-costs under single-template accounts. Fig. 3 shows the mean switch-costs for the different numbers of target categories in the two experiments. The first thing to note, is that the switch-costs are in all cases lower than predicted by the single-template account (250–300 ms; Dombrowe et al., 2011; see also Vickery et al., 2005). They are as low as 25 ms for 2 targets among distractors in the fixed-distractor-number condition. Interestingly, there was no difference in switch-cost between three and four target categories when the total number of colors on the screen was kept constant. However, a 3 × 2 (number of target categories × experiment) univariate ANOVA confirms what Fig. 3 suggests, that there is a significant difference in switch-costs depending on the number of target categories (F(2126) = 24.64; $p < 0.001$; $\eta_p^2 = 0.291$). The effect of condition was also significant (F(1126) = 31.55; $p < 0.001$; $\eta_p^2 = 0.208$) as was the interaction between the two (F(2126) = 7.14; $p = 0.001$; $\eta_p^2 = 0.106$). The slopes, however, are not linear in either condition.

3.3. Intertarget distance

Fig. 4 shows mean distance between taps as a function of the two conditions. There was an approximately linear increase in mean target distance for both the fixed-distractor-number condition and the fixed-color-number condition. A 4 × 2 (number of target categories × condition) ANOVA on the average distance in pixels showed that the effect of number of target categories is significant (F(3168) = 58.67; $p < 0.001$; $\eta_p^2 = 0.524$), but neither the main effect of condition nor the interaction between number of target categories and experiment was significant ($p = 0.168$ and $p = 0.187$ respectively). The distractors do not seem to affect mean distance like they affect the ITTs. It is important to note, that mean intertarget distance could also influence the ITTs seen in Fig. 2 as the time required to rapidly move to a target area is a function of the ratio between the distance to the target and the width of the target, which is known as Fitts's law (Fitts, 1954; MacKenzie, 1992). As the average distance between tapped targets increases with the number of target categories, so should the average

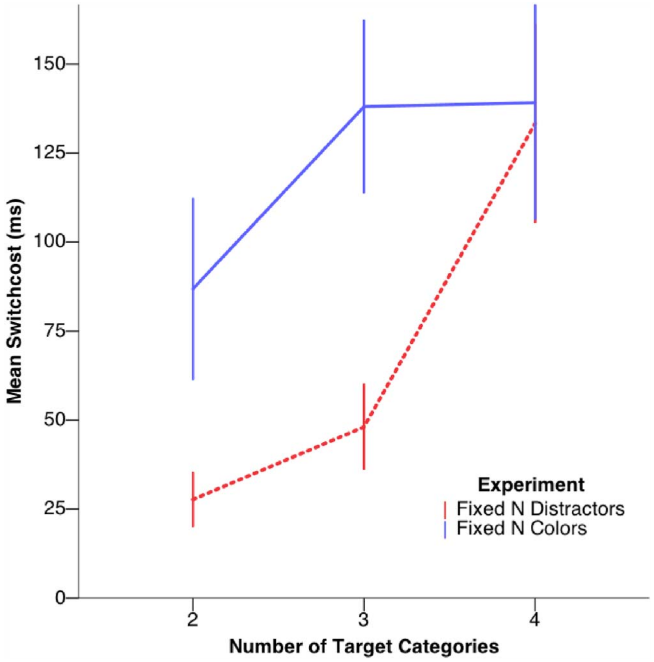

Fig. 3. The mean switch-cost in milliseconds, measured as the difference between the average ITT when the previous tap was on a target from the same target category and the average ITT when a previous tap was on a target from the same target category, for each participant in each condition.

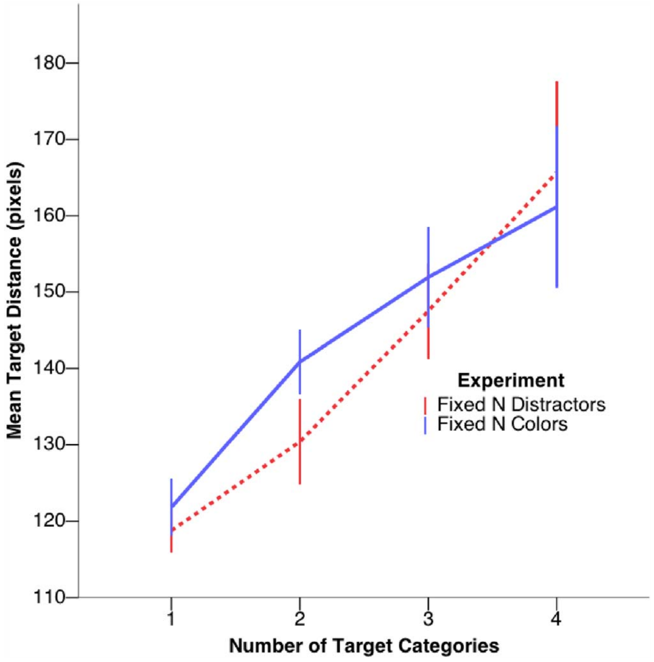

Fig. 4. Mean intertarget distance in pixels between each tap on targets for the different number of target categories in the two different experiments.

ITTs, but this should be constant across conditions.

3.4. *Number of runs*

To assess whether the number of runs was random or not, we calculated a score that indicates how participants' foraging deviated from random target selection. The expected number of runs if foraging were random would be $(TCs - 1)/TC * 40$. For each trial, the expected number of runs was subtracted from the actual number of runs made on that trial. A univariate ANOVA with TCs and condition as the independent variables, participants as a random factor and the deviance score as the dependent variable revealed significant main effects of TC and condition (Condition: $F(1,20) = 4.73$ $p = 0.042$ $\eta_p{}^2 = 0.191$; TC: $F(2,40) = 26.50$ $p < 0.001$ $\eta_p{}^2 = 0.570$) and an interaction between condition and TC ($F(2,40) = 4.36$ $p = 0.019$ $\eta_p{}^2 = 0.179$). As we have shown in many studies, participants typically forage randomly if the targets can be distinguished on one feature. Our results here show that although the foraging is slightly less than random, observers still use 14 to 16 runs in the two-target conditions, which means that they switch quite often between target types, which is inconsistent with single-template accounts. The deviation from random then increases with target type number, consistent with load accounts.

3.5. *Error rates*

Before excluding all trials that ended in a tap on a distractor, we analysed those errors to see how the fixed-distractor-number and the fixed-color-number conditions affected error rates (Table 1). As expected, errors increased as the number of target categories increased. This reflects the added difficulty of searching for targets from many categories compared with from only a few categories. There were also slightly more errors in the fixed-distractor-number condition than in the fixed-color-number condition. This may reflect the number of stimuli of each color. In the fixed-distractor-number condition, there were always two distractor categories, each consisting of 20 stimuli. In the fixed-color-number condition, the number of stimuli from each distractor category varied between 6 and 13. The presence of 20 homogeneous stimuli of a single color may have attracted attention to a larger extent than distractor categories with fewer stimuli. There was, however, a larger effect of the number of target categories on error rates, suggesting that this manipulation increases the attentional load more.

4. Discussion

Visual working memory is assumed to guide our interactions with the visual environment (Bundesen, 1990; Carlisle et al., 2011; Desimone & Duncan, 1995; Olivers et al., 2011; Vickery et al., 2005; Wolfe, 1994), such as in multiple target foraging tasks like we test here. While there is general agreement on this, the precise nature of VWM is debated. Here we test two important issues regarding VWM: How many active templates can observers maintain in working memory at any given moment and what is the effect is of increasing the working memory load upon visual orientation?

We found a linear slowing of intertarget times with increased target category number, which fits well with load accounts that assume that working memory capacity is limited and that increased numbers of target types will lead to gradually decreasing performance, but that capacity is not determined by a single number. Furthermore, the linear increase in mean tapped target distance with higher target category number and the difference in switch-costs depending on the number of target categories, all argue against models assuming that only a single template at a time can be active in VWM. Additionally, the fact that observers tend to switch mostly randomly between target categories in such a feature foraging task with only two target categories (similar to Kristjánsson et al., 2014) strongly indicates that observers find it easy to switch between templates, against the predictions of the single-template account. The results are, on the other hand a better match to the predictions of load theories. We emphasize that while we argue that our results are more consistent with load accounts, we also think that increased target number will reduce memory quality for individual items (see e.g., Bays & Husain, 2008; Beck et al., 2012) which is indeed consistent with our results.

Table 1
Error trials by condition and number of target categories.

Condition	Number of target categories				Total
	1	2	3	4	
Fixed distractor number	12	24	68	131	235
Fixed color number	8	35	87	71	201
Total	20	59	155	202	436

The single-template account has previously come under criticism. Beck et al. (2012) found that observers could easily switch gaze between two target types with no switch costs. Recently however, Ort et al. (2017) reported switch costs in a related paradigm where free choice was eliminated. They argued that results from Beck et al. (2012) could be explained by differences between proactive vs reactive processing, arguing that when proactive processes are available, switch-costs should be low, but the true test of the number of active VWM templates comes from tasks where participants must rely on reactive processes (as when there is no free choice between targets) and that this reflects that observers can only set up one template that may, or may not, match the target. We speculate, however, that the results of Ort et al. (2017) can be explained with priming effects (Brascamp, Blake, & Kristjánsson, 2011; Maljkovic & Nakayama, 1994). The search task in the no-choice condition was harder for observers (an RT difference of ~20%), and the alleged switch cost may actually reflect a priming *benefit*, not a switch cost per se, and importantly such priming can occur even for choice trials, not only search trials (Brascamp et al., 2011), showing that priming can even account for the pattern in experiment 3 in Ort et al., where the proactive and reactive conditions were interleaved. Note that priming has in some cases been reported to be stronger for more difficult tasks (Olivers & Meeter, 2006) which may partly explain why there were no priming effects present in the proactive condition. But note that priming has been found to require *selection* between task relevant items (Ásgeirsson, Kristjánsson, & Bundesen, 2015; Goolsby & Suzuki, 2001). We also note that priming has been found to interact with working memory storage (Kristjánsson, Saevarsson, & Driver, 2013) which may further complicate this. Secondly, it may be easier to maintain two templates when both types are available in the display (which was not the case in Ort et al., 2017) since template generation and working memory maintenance may interact with the stimuli in the environment.

4.1. *Why do foraging tasks matter for understanding visual working memory?*

It is important to reiterate the relevance of studies of visual foraging to the question of the nature of visual working memory templates and their potential capacity. One question in foraging studies involves under what conditions do participants switch freely between target categories in many short *runs*, (a 'run' is the repeated selection from a target category) and, when do they forage in long non-random runs where they rarely switch between target categories? Tasks such as foraging should, in fact, be *fundamental* to theories regarding WM as guidance during such tasks is assumed to be the main purpose of working memory as is clear from the literature: Working memory "enables us to retain and manipulate relevant information for the near future" (Olivers et al., 2011; p. 327); and "Storing an item in VWM makes it possible to match the template to the visual scene […] and thus helps to guide attention in visual space" (van Moorselaar et al., 2014; p. 1). This is echoed on several other studies and discussions of working memory (Awh & Jonides, 2001; Carlisle et al., 2011; Woodman et al., 2013), and the influence of working memory on attention has often been found to be automatic (Soto, Hodsoll, Rotshtein, & Humphreys, 2008).

Might long-term memory representations partly explain our results, since participants knew what target categories they were searching for and this was constant throughout each block of 16 trials? We cannot rule out that there are interactions between long-term and working memory in our paradigm, nor in other recent WM studies where target identity stays constant between trials. But as explained in the previous paragraph, VWM plays a critical role in guiding visual attention and matching a search template to a visual scene. VWM is also unlikely to hold only active search templates of unexpected non-repeating stimuli, so interactions with long-term memory are probably unavoidable in the operation of visual working memory.

We note that visual working memory has predominantly been studied with change-detection tasks (e.g. Alvarez & Cavanagh, 2004; Kristjánsson, 2006; Kyllingsbæk & Bundesen, 2009; Luck & Vogel, 1997; Xu & Nakayama, 2007). One might, however, argue that change detection involves non-ecological conditions with changes to stimuli, that are, overall, relatively constant from one moment to the next in the real world. The merit of such tasks presumably lies in attempts to *isolate* WM from other processes – but essential functionality of WM may be lost in change detection tasks. Foraging tasks are arguably closer to what WM is used for in visual orienting.

The question of working memory templates has been addressed in the literature on animal foraging (typically called "search images" in this literature; Nakayama et al., 2004), There, it has been assumed that with high discriminability (or low crypticity) runs are shorter and animals freely switch between target categories (e.g. Dawkins, 1971) but when discriminability is low (or crypticity high) animals forage in long, non-random runs where they repeatedly select targets from the same target categories and switch much less than would be expected if selection was random (e.g. Tinbergen, 1960). In a more recent study, Vreven and Blough (1998) found that foraging pigeons show attentional constraints and a performance advantage from practice, exhibiting performance flexibility. This has also been seen for human foraging, where, in a sorting task with beads, non-random runs were observed, with both high and low discriminability (Bond, 1982). There were however important differences in foraging performance between discriminability conditions that led Bond (1982) to conclude that discriminability did indeed affect human foraging performance. Kristjánsson et al. (2014) suggested that this difference in run behavior may not be due to discriminability per se, but rather attentional load. Their participants foraged for two target categories among two distractor categories on an iPad, where in one condition targets and distractors were only differentiated by color (feature foraging), but in the other, target and distractor categories were differentiated by a conjunction of features, shape and color (conjunction foraging). In both conditions discriminability was high, crypticity was low, yet, during feature foraging, participants foraged mostly randomly, freely switching between target categories. During conjunction foraging, participants rarely switched at all, resulting in two long runs (exhausting one target category in a single run, before switching to the other target category). This applied to most participants, although a subset of participants seemed to be able to switch freely during conjunction foraging, and the authors speculated whether this subset of participants had higher working memory capacity. Later work, using the same task has cast doubt on whether super-foragers are qualitatively different from other foragers (Jóhannesson et al., 2017). This has raised the question whether long runs during conjunction foraging reflect difficulties with keeping the two conjunction templates in working memory or whether they represent a strategic choice not to switch (e.g. Ólafsdóttir et al., 2016). Whether this represents an inability to switch or a strategic decision not to switch has also been discussed within the animal literature, Bond (1983) postulated that pigeons optimize their foraging by choosing not to switch, and only switch when it is not optimal anymore to repeat selections.

What all this boils down to is that working memory allocation may be flexible and different measures will yield different capacity estimates. In a recent study, participants had limited time to forage, and in this case they adapted their strategy, and switched far more often during conjunction foraging than when they had unlimited foraging time. Their working memory capacity seemingly depended on task demands, in this case, time limits (Kristjánsson et al., 2016). It is unlikely that the capacity of visual working memory is changed by external factors such as the time limits of the task. The changes observed are much better explained by assuming flexibility in VWM (Eimer & Grubert, 2014).

It is important to emphasize that our claim is by no means that adding targets to the working memory set does not entail a cost. We think that this is clearly unreasonable and our current results in fact argue against this since adding targets increased foraging time and switch costs. In Ólafsdóttir et al. (2016), young children hardly switched at all during a feature foraging task (and had trouble with performance if they did). The young children may therefore not have the required capacity for maintenance of two templates. What we mean to argue is that the capacity is not as categorical as the single-template model predicts.

4.2. Working memory models from a neurophysiological perspective

Let us note finally that it is useful to consider what neural activity visual working memory seemingly involves. In a recent review Christophel, Klink, Spitzer, Roelfsema, and Haynes (2017) discuss how working memory representations appear to be distributed, reflecting persistence of activity in various neural networks, in particular those that are involved in the processing of each feature dimension (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). It my therefore be most useful to think of working memory as a limited resource applied flexibly to memorized items (Ma, Husain, & Bays, 2014). If working memory is a distributed network of lingering activity of neural sites perhaps devoted to another function, it becomes apparent that imposing numerical capacity limits may be a mistake. Additionally, any interference effects may even be specific to these tasks. The most likely key to understanding WM involves understanding it's flexibility (Grubert & Eimer, 2013) in relation to stimulus specific lingering neural activity (Christophel et al., 2017; Ma et al., 2014).

But other findings are more in line with the proposal of multiple states in working memory. Lewis-Peacock, Drysdale, Oberauer, and Postle (2012) had their observers keep multiple items in working memory, finding that only the item that was within the focus of attention could be successfully decoded through voxel activity patterns, but such signals for irrelevant items dropped to baseline, but were activated once they were cued to become task-relevant again. Also, Wolff, Jochim, Akyürek, and Stokes (2017) recently showed that memorized items can be kept in an "activity-silent" neural state, in contrast to the lingering neural-activity proposal. Furthermore, Rose et al. (2016) showed that recently remembered items can be quickly reactivated with TMS. Our proposed explanation for the results here is not inconsistent with recently used items being neurally silent and then quickly reactivated – since our proposal is simply that two (or perhaps even more items), can be active simultaneously, but that this also increases working memory load. What all this highlights is that a satisfactory theory of working memory should probably not be too restrictive, and should emphasize flexibility of working memory.

4.3. Conclusions

Our results suggest that observers can keep more than one template simultaneously in working memory, but also that this entails a cost. We find no evidence of a preferential bias for a single feature value but rather that as more templates are added to the target set, this incurs an increasing cost as load accounts of WM would predict. Additionally, the switch costs when different targets from the last one are selected are at least an order of magnitude lower than previous estimates of the time needed for switching templates (Dombrowe et al., 2011; Wolfe, Butcher, Lee, & Hyle, 2003), casting further doubt upon single-template proposals.

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