

“I know what you did on the last trial” - a selective review of research on priming in visual search

Arni Kristjansson

Department of Psychology, University of Iceland, Oddi V/Sturlugotu, 101 Reykjavik, Iceland

TABLE OF CONTENTS

1. Abstract
2. Introduction
3. A selective summary of the behavioral findings
4. Dimensional weighting
5. Single-cell Neurophysiology in non-human primates
6. Evidence from Neuropsychology
7. Neuroimaging of humans
8. Theoretical accounts of priming
9. Conclusions
10. Acknowledgements
11. References

1. ABSTRACT

One could argue that studies of how we scan our visual environment have been stuck in the eternal present, investigating the properties of a particular search situation without reference to what has occurred before. There is, however, increasing evidence that what we have previously viewed, perhaps only moments before, has a large influence on what we see, what grabs our attention and how we organize the visual scene. A large amount of evidence pertinent to the question of what has been termed *priming* in visual search is reviewed here, evidence from psychophysics, neurophysiology and neuropsychology. Two theoretical accounts of priming are contrasted, the view that priming reflects facilitation of the processing of specific features versus views that priming reflects facilitated object formation and subsequent response selection. Strong versions of either view are rejected as neither can explain all the available evidence on their own. It is concluded that priming in visual search is probably not a unitary phenomenon but can reflect processing changes at various levels of the hierarchy of perceptual processing.

2. INTRODUCTION

When we attend to a red rose among the green leaves of a rosebush this has an effect on how we subsequently orient our visual attention. When we glance away from the rose our attention is more likely to be drawn to another red rose around us, or something that shares properties with it, such as another object of the same color. When we search our visual environment our attention is thus not only drawn towards the salient items, the new items, the items that have a high contrast against the background or those that differ in color from the background as the rose does from the leaves, but also to items that have *recently been important to us* for one reason or another. When what we have recently seen influences what we subsequently see, this is known as *priming* (1-4). Research on such priming effects indicates that our visual system is generally sensitized to things that it has processed recently and that those items are processed faster than otherwise (5).

Searching for the red rose is an example of a visual scanning task (6) or what is now better known as a *visual search* task (7-9). Studies of how we search such a

Priming in visual search

scene for a particular target can tell us much about how our visual system operates and what it considers important. Many have, in fact, argued that evidence from such tasks can tell us what has been important to us in our evolutionary past (10,11). Studies of how we perform visual search and what we attend to are, however, often focused on how the search occurs in the here and now, not on how our recent experiences and goals affect the search.

Recent years have seen a rising interest in how what happens in the immediate past affects what we subsequently see. Kristjánsson and Nakayama (12, see also 5,11) have argued for the existence of a primitive memory system, not under any form of voluntary control, for orienting our visual system, that focuses our attention on what we have recently seen and has been important to us for one reason or another. The evidence for such a memory system comes mainly from studies of how what we perceive and act on in one instant affects how we subsequently process visual stimuli. While the behavioral characteristics of such effects are becoming increasingly well known, such effects at the neural level have, in recent years, also started to receive attention.

The current text is a selective summary of research on these issues, focusing on evidence from psychophysics, neuropsychology and neurophysiological studies of monkey and man as well as some of the most prominent theoretical developments that have surfaced in light of the experimental evidence.

3. A SELECTIVE SUMMARY OF THE BEHAVIORAL FINDINGS

Treisman (13) reported results of experiments studying the influence of what occurred on the last trial on visual searches where a single feature distinguished the target from distractors (a *feature* search) and *conjunction* searches where the observer searches for a target defined by the particular combination of two different features, such as color and shape. Treisman found an intertrial priming benefit in response times of 10% to 15% when the same target appeared in the same location as on the last trial. The benefit was halved when the same target appeared in a different location – but Treisman found no benefit for a new target in the same location as a previous target of a different sort.

The experiments of Maljkovic and Nakayama (14,15) have been very influential in terms of the behavioral effects of priming in visual search. Their observers were instructed to look for the oddly colored diamond among distractors of a different color and judge whether the target diamond had a notch at the right or left, a task introduced by Bravo and Nakayama (16). Maljkovic and Nakayama (14) found that observers were considerably faster to make the discrimination if the color of the target was the same as on the last trial.

Maljkovic and Nakayama (15) also found that repeated position of the target speeded search, even though its color changed, which Treisman (13) did not find. They

also found that effects from repeating target color and target position could be disentangled, with separable effects for the two, but also that the two can build up simultaneously. Position priming has also been found by others since (17-21). The discrepancy between Treisman's finding and Maljkovic and Nakayama (15) might be accounted for in terms of differences in task. Treisman's task involved a present/absent judgment whereas the task used by Maljkovic and Nakayama involved judging whether a diamond target that was present had a notch at the right or left and presumably required the application of covert focal attention towards the target location (5).

Kristjánsson, Wang and Nakayama (22; see also 13,23,24) found priming with feature repetition where a single feature does not designate the target (a *conjunction* search task). Thus search for a red vertical bar among red-horizontal and green-vertical bars is speeded if the orientation of the target is the same as on the previous trial, but not if the target changes from vertical to horizontal. These studies have also indicated that recent history may in fact contribute significantly to effects that have often been attributed to top-down attentional guidance (see also 25, and further discussion in section 8, here).

Priming does not occur under all conditions in visual search. Olivers and Meeter (26) pointed out that priming is much less, or even absent, when the response property is unrelated to the target property (known as a *compound* search task). For example, Kumada (27, experiments 1A and 1B) found that when observers performed singleton search tasks (targets defined by contrast on single features; orientation, color or size) intertrial priming with repetition of a target feature occurred when the response was on the target defining dimension (the task was to respond whether a target was present or absent). However, when the same target had to be localized and a discrimination made on the target itself no repetition priming was seen. This result from Kumada was seemingly at variance with what Maljkovic and Nakayama (14) found since their task was also a discrimination on the target (to locate a notch on a diamond).

Olivers and Meeter argued that this apparent discrepancy could be accounted for in terms of the ambiguity inherent in the task. As an example, there is more ambiguity about target identity with few distractors as in the Maljkovic and Nakayama study (their search was for a target among only two distractors) than in the Kumada study where there was a large number of distractors on the screen (see further discussion in section 8). According to Olivers and Meeter ambiguity of this sort is essential if any priming is to occur. Note, however, that Muller and Krummenacher (28) found that the overall magnitude of priming is reduced in compound tasks only when the required response is different than that on the preceding trial.

In addition, quite a bit of evidence has surfaced in recent years showing that priming is not simply bound to the target in each case. Kristjánsson, Wang and Nakayama

Priming in visual search

(22, 23) found that priming occurred on trials where no target was present as well as on trials where a target was present. They did not, however, have experimental power to determine whether this was due to target repetition only facilitating the subsequent decision that no target was present or actual priming from repeated distractor sets. Tasks where target and distractor features are varied independently of one another on consecutive trials have subsequently revealed that such priming of distractor sets (or *context*) is a real and robust phenomenon that can be dissociated from priming due to target repetition (29). Kristjánsson and Driver (30) showed that facilitation of performance with repetition can take place between two adjacent target absent trials. Thus priming can operate on a search array that contains no target to be acted on. The priming effects do not simply operate on the target, or the “object of attention” in each case. Kristjánsson and Driver found that this priming from repeated distractor sets (what might be termed priming of context) applied to *both* feature and conjunction search tasks.

Geyer, Muller and Krummenacher (29) then found, using a conjunctive visual search task, that distractor repetition can even overshadow priming related to the target. They found that when distractor orientation was repeated, additional repetition of the target orientation had almost no additional effect. The findings of Geyer *et al.* were for conjunctive visual search (see also 31) suggesting that such distractor priming effects may not apply in feature search to as large an extent.

It is thus clear that priming between trials in visual search is very strong and applies to various types of task, and aspects of task. The importance of such priming is thus obvious for theories of visual search, an issue that will be further discussed in section 8. A number of other history effects on attentional orienting have been found, such as *probability cueing* (32, 33), *inhibition of return* (34,35) and *contextual cueing* (36) but detailed discussion of those is beyond the scope of the current review (see ref. 11, for discussion).

4. DIMENSIONAL WEIGHTING

It is well known that there are large differences in visual search performance depending on whether the target is the same throughout a block of visual search trials or not (16, 37, 38). Not only does trial to trial priming affect search, as discussed above, but also what has been called *dimensional weighting* within a series of trials (39). A change in the target defining dimension results in a cost in terms of performance, from the change of the dimension defining the target. For instance, if the target changes from being the oddly colored item in the scene to being the oddly shaped item, search times are slowed relative to when the target changes but the target-defining dimension stays constant. Such uncertainty adds a constant factor to the reaction times in a visual search task (see 40, however, for some exceptions to this that may apply under certain conditions). It seems that changes in feature dimension incur a slowing effect upon search that is unrelated to set size, so it probably does not have its major influence on the

search rate, per se, but rather on processes prior to the search or at a stage of response selection (39). Wolfe and colleagues (31) have, for example, argued that increased uncertainty increases response times but does not reduce search efficiency.

According to Muller *et al.* the cost reflects computations operating in parallel across the visual scene at an early level of visual processing. Muller *et al.* argued that target detection is based on feature contrasts that reflect the dimension that our visual system is weighted towards and are thus dimension specific, depending on the particular search type, and search is slowed considerably when the target dimension changes. For fast search to occur the attention system must be weighted towards the feature dimension that defines the target, and a cost is incurred when an attention shift is made to another dimension. The dimension weighting causes intertrial facilitation since the weight pattern persists throughout a block of adjacent trials if the target defining dimension remains constant.

Found and Muller (41, see also 98) argued that a substantial component of intertrial priming effects, the topic of the current review, could be explained by dimensional weighting and that the priming pattern was (largely) *dimensional* rather than *featural*. On the other hand, Kristjánsson (42) found considerable priming from *irrelevant* feature dimensions on the target (see also 30), but the degree to which the feature is attended or unattended is not settled, especially given that the irrelevant feature was nevertheless a feature of the target. It should be noted, though, that the feature priming from the task irrelevant features was variable for different features. Also Maljkovic and Nakayama (15) found that feature priming and position priming had an *additive* effect on response times in a task where position was unrelated to the task (see also 18) which again suggests that the task relevant dimension cannot account for all intertrial priming in visual search¹. Muller and colleagues (43), have then showed that dimensional weighting can in some cases be more potent than cueing of features in producing intertrial facilitation indicating that dimensional weighting can certainly explain components of intertrial facilitation effects, how the large the component is, however, is not currently clear.

Pollmann and colleagues (44) studied dimensional weighting with fMRI and found that frontopolar cortex and pregenual frontomedial cortex bordering the anterior cingulate cortex are strongly activated during dimension switches. The ACC is known to be involved in task monitoring and task conflict (45,46) in conjunction with dorsolateral prefrontal cortex(47). The connection between the switch related activity that Pollmann and colleagues found and control structures such as the ACC is a particularly interesting avenue for further study. Also of interest in their studies (see also ref. 48) was that attentional networks in parietal areas show such activations as well, but not the prefrontal part of the attentional network which is reasonable given that dimension weighting should by definition be non-spatial and the frontal areas most often thought to be involved in attentional orienting, such as the frontal and supplementary

Priming in visual search

eye fields seem to be particularly involved in attention shifts in space as well as saccade programming to change the direction of gaze. Pollmann and colleagues (45), also found some switch related modulations of BOLD signal in brain regions involved in the analysis of specific feature types (such as V4 and V5 for color and motion defined targets). As we will see in section 7, evidence from fMRI indicates that priming may operate at such low levels of the perceptual hierarchy as well, arguing for “lower level” feature-based priming, although we are not suggesting that these effects are necessarily the flipside to those found by Pollmann and colleagues for dimension changes.

5. SINGLE-CELL NEUROPHYSIOLOGY IN NON-HUMAN PRIMATES

Bichot, Schall and Thompson (49) observed that neurons in frontal cortex of macaque monkeys show modulation of activity as a function of experience. Their experiments showed that FEF neurons gradually develop feature selectivity if the monkey performs a search repeatedly for the same sort of target. Bichot and Schall argued that this reflects “experience dependent plasticity that mediates the learning of arbitrary stimulus-response associations.” Olson and colleagues (50,51) have reached similar conclusions using a quite different task (52).

In subsequent studies Bichot and Schall (53) found that repetition of target features improved performance on a task where the monkeys made saccades towards a target in a pop-out search task. McPeck, Maljkovic and Nakayama (54) have also demonstrated that humans show speeded eye-movements towards targets where color is repeated, in a task similar to the one used by Maljkovic and Nakayama (14,15).

In particular, Bichot and Schall (55) investigated the response properties of single neurons in the frontal eye fields of macaque monkeys as priming in a conjunctive visual search task developed. They found that the neurons discriminated target properties earlier and better when the same features distinguished the target as on the last trial. They also found that these neurons tended to have an enhanced representation of a distractor that had previously been the target. This manifested itself behaviorally as a strong tendency to make errant saccades to a distractor that shared properties with a target on the previous trial. They showed that this pattern also applied to feature search tasks (53).

It is important to note, with regard to the studies of Bichot and Schall, that the monkeys performed saccades towards the targets rather than responding on a keyboard as is the case in the majority of the studies on humans (an exception can be found in ref. 54). Maljkovic and Nakayama (15) found that visual search was speeded when target position was repeated, while the saccade latencies to targets in repeated positions were *longer* than otherwise for the monkeys in Bichot and Schall’s studies. Bichot and Schall (55) pointed out that this could be accounted for by differences in repetition priming patterns for position, as a function of task (17,56 but see 54). Location discrimination

tasks resulted in short lived increases in response times when position was repeated, whereas position repetition in feature discrimination tasks produced a decrease in response times that was longer lasting than the transient increases (17,56, which may in fact be related to what is known as inhibition of return, 34,35). It is thus possible that there is a difference between eye movement tasks and discrimination or simple detection tasks possibly corresponding to the proposed distinct pathways for perception (ventral pathway) and action (the dorsal pathway, 57,58). There is, in fact, some indirect evidence for this view in a study of priming for patients suffering from hemispatial neglect (19) since these patients showed intact color priming but position priming was compromised under certain conditions for the patients with parietal lesions. The parietal cortex is, of course, considered to be part of the dorsal pathway for action.

6. EVIDENCE FROM NEUROPSYCHOLOGY

Kristjánsson and colleagues (19) investigated priming in a singleton search task similar to the task used by Maljkovic and Nakayama (14,15) on neglect patients with lesions of the parietal cortex and the temporoparietal junction following stroke. Part of the goal of the study was to investigate proposals that priming in search affects attention deployments (5,11,12,59) by testing whether the patients with this attention deficit would show intact priming in visual search.

In a reaction time task where the search array was present until response, reliable priming by repeated target location, as well as by repeated target color, was found for the patients. Priming was observed from repeated targets both in the left and right visual hemifields and the priming also *affected* both hemifields. Priming of singleton visual search can thus occur from left-sided targets in the patients to the same extent as at other locations in these search conditions and also improve patients’ performance on their neglected left side. Priming of visual search can also *arise* from their left side, i.e. a target on the left can speed detection of a target in other locations in the visual field.

In experiment 2 (19), the patients performed a secondary task of identifying a small character at display center interleaved between similar successive visual search trials. This was to rule out that location priming could be caused by the lingering of the observers’ gaze at the location of the last target. Both patients showed reliable color and position priming on the right and left further confirming intact priming for these patients, as seen in experiment 1.

It was only when brief displays were used (stimuli presented for 200ms), with the result that the patients missed a large amount of targets in their affected hemifield, that any priming deficit was found. There were now three possible responses: a notch at top or bottom, or *no target* (the target was present on 80% of the trials only). The results revealed an interesting dissociation between color and position priming: Although color priming occurred regardless of whether a preceding left target had

Priming in visual search

been consciously detected or had escaped awareness (i.e. the patients responded that no target was present even though it actually was), location priming depended on *awareness* of that preceding target, with no such priming occurring when the preceding left target escaped awareness.

These results converge rather well with some prior research on patients with neglect (60,61) where “*implicit*” effects on perception from neglected stimuli in the affected left side were found. Imaging studies of neglect patients have then shown that ventral regions of the visual cortex can still be activated *unconsciously* by stimuli on the affected left side that escape awareness (62-65) showing that the influence on perception of those stimuli can be strong even though they go unnoticed perhaps because of ventral stream activity that does not reach awareness.

This result also shows that awareness is not always necessary for priming to occur since color priming could arise from missed left side targets. This fits well with findings that irrelevant and presumably unattended features in pop-out visual search can still result in priming (42). Attending to the target is thus not always necessary for priming to occur.

Saevarsson and colleagues (66) have investigated priming of distractor sets, or context, for neglect patients. Two tasks were tested, a reaction time task as well as an accuracy task with brief masked displays. They found that priming of distractor sets (as described in section 3) could increase detection rates and decrease response times to targets in the affected hemifield of neglect patients. Especially striking was that the rate of noticing of a left visual field target increased from close to zero up to 40 to 50% when the context was repeated. This is a dramatic example of how powerful priming of context can be (22,23,29,30). This is also further evidence for considerable higher level visual processing of stimuli that go unnoticed in hemispatial neglect (61).

Areas in temporal cortices seem important for priming as well (see also discussion in section 7). Walsh *et al.* (67) found that lesions of areas V4 and TEO in (macaque) monkeys led to diminished repetition priming of pop-out search even though performance on the task itself was unimpaired. This result is consistent with what was found for neglect patients in (19) where color priming was intact for the patients who indeed had intact temporal cortices despite their parietal lesions. Similar conclusions for motion sensitive areas (V5/MT) have been seen with neural disruption through transcranial magnetic stimulation of humans (68). The lesioning and TMS studies strongly indicate that studies of patients with damage in ventral stream areas would be of great interest.

A tentative conclusion from neuropsychological studies of priming could be that feature priming is mostly mediated by areas in temporal cortex while parietal areas may be more important for intact position priming. This would fit well with what is traditionally thought to be the respective gross functions of the dorsal and ventral visual

processing streams (57, 58). Evidence from neuroimaging of humans has indicated that this may not be the whole story, however (see section 7). The findings on neglect (18,66) also suggest that considerable processing of stimuli in the affected hemifield occurs that never reaches awareness, which can then influence visual processing of the stimuli on the next trial.

7. NEUROIMAGING OF HUMANS

Kristjánsson and colleagues (18) used whole brain imaging of humans to study the neural correlates of priming in visual search, again using a modified version of the Maljkovic and Nakayama task (14). Before describing the results in detail it should be noted that all the effects that surfaced in conjunction with the behavioral priming pattern were *repetition suppression* effects where neural activity, as measured with the BOLD signal, was reduced with repetition (69).

Repetition of target location led to suppression of the BOLD signal in bilateral intraparietal sulci, the anterior cingulate, as well as other neural structures often associated with the control of spatial attention, such as the frontal eye fields (FEF) and inferior regions of right parietal cortex. Geng and colleagues (21), using a task where a target sometimes appeared on it's own and sometimes with a distractor, also found repetition suppression in attentional control structures following repeated target location. Interestingly these effects were only seen when a distractor was also present, showing that uncertainty about target location and/or identity may be crucial for repetition priming to occur (26, 70).

Repeating target color instead of target location led to BOLD suppression not only in brain regions that were largely common with those affected by location repetition but also in some distinct regions notably in the left inferior temporal cortex, close to a region previously associated with color cognition (71,72) independently of where in the visual field the target appeared. The repetition effects in FEF are consistent with the findings from single-cell neurophysiology in monkeys explained in section 5 (53,55).

The location-specific effects depended on the current target hemifield in a contralateral manner. For a target in the left visual field, greater location than color repetition effects were found in right inferior parietal cortex, anterior IPS, and inferior frontal gyrus, whereas for a right visual-field target, this applied to left IPS and medial left FEF.

In addition, repetition of both color and location led to repetition suppression in control structures such as the FEF and IPS, but the most distinctive effect was in an anterior part of the left fusiform gyrus. This region showed repetition suppression only when both color and position were repeated together, but not for repetition of color alone or location alone.

To summarize, repetition of target color and position was strongly associated with the operation of

Priming in visual search

attentional networks (73-76), supporting claims that the priming pattern may operate as a memory system for the deployment of attention to recent behaviorally important items, but the findings from neglect reviewed in section 6 indicate that this attentional involvement may not be the whole story and that activity in ventral regions may lead to color priming despite damaged attentional networks.

It should be noted, in this context, that Corbetta and Shulman (75) have argued, largely from evidence from neuroimaging studies, for two processing streams for attention, one involved in bottom-up attentional selection, largely confined anatomically to the right hemisphere involving activity in the temporoparietal junction and lateral frontal areas, and the other, less lateralized, serving top-down selection reflecting activity in intraparietal areas and superior frontal cortex (see also 77, for some related evidence using the visual marking paradigm). The damage in neglect seems sometimes to involve the temporoparietal junction (78,79)² and the involvement of these two types of attention, with regard to priming, might be interesting to explore in future research.

8. THEORETICAL ACCOUNTS OF PRIMING

Various theoretical accounts have been proposed to account for priming in visual search since the pioneering studies of Maljkovic and Nakayama (14) and Treisman (13). The largest difference between these accounts is the level of perceptual processing at which priming is assumed to occur.

Maljkovic and Nakayama thought of the priming pattern as reflecting facilitation of relatively low-level memory traces. They said: “priming of pop-out increases the speed of attention deployments to subsequent targets having the same *feature* characteristic [and this] reflects a functionally beneficial memory system specialized for the rapid and automatic selection of items for focal attention and saccadic eye movements” (59, p. 571).

The *episodic retrieval* account of Huang and colleagues (82) argues, on the other hand, that priming occurs at a late stage in the perceptual process, perhaps an object based stage, or even at the stage of response selection, and that the behavioral pattern following repetition reflects the priming of objects rather than features. Hillstrom (24) argued for a somewhat similar view. Noting that priming is modified by top-down factors Hillstrom proposed a short-term episodic memory account of priming. Such accounts assume that the priming has its critical effect at the level of response selection based on whole objects. As Huang *et al.* (82) put it: “...the priming pattern results from contact with an episodic memory representation of the previous trial” (p. 12). Treisman and colleagues (83) argued that repeated performance of the same task results in improved performance which may depend on the accumulation of separate memory traces for each individual experience of a display. Treisman (13) then went one step further suggesting that the priming reflected the facilitation of object files (84). Treisman argued that the priming pattern she observed (in particular priming in

conjunction search) arose because perceiving an object creates a temporary representation of it in an object file that then influences how we perceive the stimulus set on the next trial and that if the target object is the same as on the last trial perception of that object is facilitated since an object file has already been formed.

There is, however, a lot of evidence, from psychophysics, from neuroimaging, and from neuropsychology, which suggests that priming occurs at an earlier stage of the perceptual process than simple response selection or an object-based stage of processing, evidence that is consistent with the proposal of feature specific facilitation originally proposed by Maljkovic and Nakayama (14). This evidence does not rule out object or response selection accounts, but strongly indicates that there is more to the story than such accounts imply.

For example Sigurdardottir, Kristjánsson and Driver (85) have shown that priming results in genuine changes in sensitivity to repeated targets, rather than simple modulation of response characteristics (see also 31, experiment 6, and 88). Sigurdardottir *et al.* found, using brief masked displays with accuracy as the dependent variable, that sensitivity measured by signal detection methods increased independently of changes in response criteria, both for a conjunction search task and a feature search task, when target features were repeated. This is not consistent with pure response selection accounts of priming. It should be noted that this finding is in seeming contrast to the results of Huang and Pashler (86), who found only a small, non-significant effect of orientation repetition with feature search of brief displays (but note that there actually were hints of this non-significant effect across 4 experiments!). Their task was a coarse localization task, however, (deciding whether a target in a search array was on the left or right of the midline of the array), a task quite different from the acuity judgment task on the color singleton target as required in Sigurdardottir *et al.* (experiment 2), possibly explaining the difference in findings.

Another finding that causes potential problems for pure feature based accounts, however, is that intertrial priming can be modified by top-down expectations (24, 87). Muller *et al.* (87) found that when participants had to explicitly encode and retain the target defining dimension in memory, feature priming effects increased compared to when no such encoding was required, an undeniable effect of the goal in each case (in other words a “top-down” effect)³ Note that Maljkovic and Nakayama have conclusively shown that knowledge of what is coming up has little or no effect on the priming pattern – so the “top-down effect” on priming can only be limited and may not apply to all situations (see 24, however, for some evidence of conditions where top-down effects can influence priming in a pop-out search task).

Supporting feature based accounts of priming, Goolsby and Suzuki (88) found that priming did *not* occur on trials when a precue cued the location of an upcoming target so that observers did not have to search for the target.

Priming in visual search

Such cued trials nevertheless *evoked* priming on a subsequent trial. In this task the response requirements are the same, while the search has been eliminated because of the location cue. The priming pattern should be unaffected under response selection accounts, yet no priming was observed on such trials (see 70 for further discussion) which should have been the case if response repetition was essential for priming to be seen. Finally, Maljkovic and Nakayama (59) were able to clearly distinguish between priming in search and more “traditional” explicit memory. Using a post-cued recall procedure embedded in a series of trials where priming of search built up they found that explicit memory is not as selective nor as long lasting as the priming effects.

I have previously mentioned the dimensional weighting account (39,41). Found and Muller (41) argued that dimensional weighting could, at least to a considerable extent, account for repetition priming patterns in visual search so that when the target remains the same within a set of trials, intertrial facilitation from repeated items from that dimension occurs. There seems to be no question that repetition of the target defining dimension accounts for considerable parts of the priming pattern. On the other hand, priming from irrelevant items as well as the piecemeal nature of priming in visual search, as evidenced for example in the aforementioned fMRI and neuropsychology studies, seems to argue against strong versions of this account.

In the aforementioned neuroimaging study (18; see also 89) there was some evidence for object-based priming. Areas in the anterior part of the left fusiform gyrus showed repetition suppression only when both color *and* position were repeated, but the study addressed priming of feature and position, not the priming of two different features as in Huang *et al.* (82). Overall, however, the neuroimaging results suggest that priming can operate at various levels of perceptual processing, on single features as well as a later stage perhaps related to object processing.

It seems that neither object/response-based nor feature based accounts of priming can, on their own, do complete justice to the wealth of data on priming in visual search tasks. In fact the evidence suggests that priming may occur at multiple levels of the perceptual hierarchy. This is, of course, precisely what the fMRI results (18) and the neuropsychological results reviewed in section 6 suggest. Proposals where priming is assumed to be possible at varied stages of a perceptual hierarchy seem the most plausible in the light of this.

The *ambiguity* account of Meeter and Olivers (26,70) argues that intertrial priming occurs only under circumstances of ambiguity. Olivers and Meeter (26) say: “ambiguity refers to the presence of uncertainty, conflict, or competition *at any level* between stimulus and response” (my italics). As an example, they (70) found that intertrial priming *decreased* in a Maljkovic and Nakayama type search task when the number of distractors was increased, thus decreasing uncertainty about distractor identity, which might account for the absence of priming in some

compound search tasks (27, discussed in section 3). Meeter and Olivers also found that priming *increased* when a singleton distractor was added to such a display thus increasing uncertainty about the target identity.

The ambiguity account seems a satisfying descriptive account of the behavioral data available so far. While this concept of ambiguity doesn’t on its own explain the actual mechanisms of priming, it does provide a good framework for determining under what conditions priming does, and does not occur. But there is more to their proposal. Meeter and Olivers (70) suggest that intertrial priming can take place “at any processing step, from attentional selection to response execution.” This seems to fit well with the views presented in this review that priming is not a *unitary* process and can occur at various stages of the perceptual hierarchy. Thus according to their view priming can occur at various steps of processing of visual stimuli provided there is some ambiguity about the task.

Kristjánsson and colleagues (5,11,12) argued that we possess a primitive memory system not under voluntary control which manifests itself in priming in vision and some other related learning effects. Nature has, according to this view, equipped us with a mechanism that allows us to reorient quickly and efficiently to behaviorally pertinent items in our visual environment. Prey tracking the movements of a predator will, as an example, benefit from being able to reorient quickly to features of predator such as its color, as will a parent keeping track of his child running around a playground benefit from being able to reorient quickly and efficiently to the particular color of the child’s coat. This conception receives support from the demonstrated tight link between covert and overt orienting in space (90-93, see e.g. 94, for review).

Kristjánsson, Wang and Nakayama (22) argued that intertrial priming could account for the majority of effects usually attributed to top-down guidance. They found that there were practically no differences in performance when the target identity was always the same within a block of trials and when priming had built up for a few trials. fMRI studies showing how attention systems are influenced by priming (18,21,89) strongly support the claim that priming has an effect on top-down guidance, since top-down guidance is assumed to reflect our attentional set. Wolfe and colleagues (31) chose to term these priming effects *implicit* top-down guidance – they think of priming as reflecting information accrual across a set of trials – and that this should be considered a form of knowledge since implicit information about the task accrues. According to Wolfe *et al.* (95) maximal top-down effects occur when observers are shown an image of what to search before each trial and the item to search for remains constant since this activates explicit and implicit top-down guidance, a view clearly consistent with the dimension weighting account of visual search (39,41). Priming from irrelevant features (42) complicates this conception of priming somewhat, however, since it is hard to argue that the repetition of irrelevant feature increases knowledge about the task.

Priming in visual search

Finally I propose that priming reflects a memory trace of a previously viewed item left in some form of perceptual memory, or something akin to a perceptual representation system as described by Tulving and Schacter, (4) and Magnussen and colleagues (96,97). They argued that some effects of implicit memory might be due to traces of neural activity that persist and influence what occurs consequently. Priming, as seen in visual search, may reflect such traces of neural activity as well as facilitated response selection of assembled objects, and this may vary as a function of the type of stimuli being used (see e.g. ref. 99).

9. CONCLUSIONS

The most satisfying account of the data on priming in visual search that is reviewed above seems to be that priming reflects facilitation of perception, attending and responding. Given the variety of tasks used it is perhaps not surprising that this varied pattern is seen in the available evidence. In addition, there are, most likely, various functional benefits to priming (11,12). Priming may function as an adaptive mechanism that reorients our gaze or attention to items that have recently been important to us.

10. ACKNOWLEDGEMENTS

AK is supported by a long-term fellowship from the Human Frontiers Science Program and the research fund of the University of Iceland.

11. REFERENCES

1. Bartram D. J.: The role of visual and semantic codes in object naming. *Cognit Psychol* 6, 325-356 (1974)
2. Biederman, I. and Cooper E.: Priming contour deleted images: evidence for intermediate representations in visual object recognition. *Cognit Psychol* 23, 393-419 (1991)
3. Schacter D.L. and Buckner R.L.: Priming and the brain. *Neuron* 20, 185-195 (1998)
4. Tulving E. and Schacter D.L.: Priming and human memory systems. *Science* 247, 301-306 (1990)
5. Nakayama K., Maljkovic V. and Kristjánsson A.: Short-term memory for the rapid deployment of visual attention. In M. Gazzaniga (ed.), *Cognitive Neurosciences III* (pp 397-408). The MIT Press. (2004)
6. Neisser U.: Decision time without reaction time: Experiments in visual scanning. *Am J Psychol* 76, 376-383 (1963)
7. Egeth H., Jonides J. and Wall S.: Parallel processing of multielement displays. *Cognit Psychol* 3, 674-698 (1972)
8. Treisman A. and Gelade G.: A feature-integration theory of attention. *Cognit Psychol* 12, 97-136 (1980)
9. Wolfe J. Visual Search. In: Pashler H., (Editor) *Attention*. (pp. 13-73). University College London Press (1998)
10. Johnston W.A. and Stayer D.L.: A dynamic, evolutionary perspective on attention capture. In C. Folk and B. Gibson (Eds.), *Attraction, distraction and action: Multiple perspectives on attentional capture* (pp. 375-397). Elsevier. (2001)

11. Kristjánsson A.: Rapid learning in attention shifts - A review. *Vis Cognit*, 13, 324-362 (2006)
12. Kristjánsson A. and Nakayama K.: A primitive memory system for the deployment of transient attention. *Percept Psychophys* 65, 711-724 (2003)
13. Treisman, A.: Perceiving and re-perceiving objects. *Am Psychol* 47, 862-875 (1992)
14. Maljkovic V. and Nakayama K.: Priming of pop-out: I. Role of features. *Mem Cognit* 22, 657-672 (1994)
15. Maljkovic V. and Nakayama K.: Priming of pop-out: II. Role of position. *Percept Psychophys* 58, 977-991 (1996)
16. Bravo M. and Nakayama K.: The role of attention in different visual search tasks. *Percept Psychophys* 51, 465-472 (1992)
17. Tanaka, Y. and Shimojo, S.: Repetition priming reveals sustained facilitation and transient inhibition in reaction time. *J Exp Psychol Hum Percept Perform* 26, 1421-1435 (2000)
18. Kristjánsson A., Vuilleumier P., Schwartz S., Macaluso E. and Driver, J.: Neural basis for priming of pop-out revealed with fMRI. *Cereb Cortex* 17, 1612-1624 (2007)
19. Kristjánsson A., Vuilleumier P., Malhotra P., Husain M. and Driver, J.: Priming of color and position during visual search in unilateral spatial neglect. *J Cogn Neurosci* 17, 859-873 (2005)
20. Geyer T., Muller H.J. and Krummenacher J.: Cross-trial priming of element positions in pop-out visual search: Limited in capacity and dependent on stimulus arrangement. In the press in *J Exp Psychol Hum Percept Perform*
21. Geng J.J., Eger E., Ruff C., Kristjánsson A., Rothstein P. and Driver, J.: On-line attentional selection from competing stimuli in opposite visual fields: Effects on human visual cortex and control processes. *J Neurophysiol* 96, 2601-2612 (2006)
22. Kristjánsson A., Wang D. and Nakayama K.: The role of priming in conjunctive visual search. *Cognition* 85, 37-52 (2002)
23. Wang D., Kristjánsson A and Nakayama, K.: Efficient visual search without top-down or bottom-up guidance. *Percept Psychophys* 67, 239-253. (2005)
24. Hillstrom, A. P. Repetition effects in visual search. *Percept Psychophys* 62, 800-817 (2000)
25. Theeuwes J., Reimann B. and Mortier, K : Visual search for featural singletons: No top-down modulation, only bottom-up priming. *Vis Cognit* 14, 466-489 (2006)
26. Olivers C.N.L. and Meeter M.: On the dissociation between compound and present/absent tasks in visual search: Intertrial priming is ambiguity-driven. *Vis Cognit* 13, 202-222 (2006)
27. Kumada, T.: Feature-based control of attention: Evidence for two forms of dimension weighting. *Percept Psychophys* 63, 698-708 (2001)
28. Muller H.J. and Krummenacher J.: Locus of dimension weighting: Preattentive or postselective? *Vis Cognit*, 14, 490-513 (2006)
29. Geyer T., Muller H.J. and Krummenacher J.: Cross-trial priming in visual search for singleton conjunction targets: role of repeated target and distractor features. *Percept Psychophys* 68, 736-749 (2006)

Priming in visual search

30. Kristjánsson A, and Driver J.: Priming in vision: Target repetition effects, context effects and role reversal effects. *Perception* 34 (Suppl.), 40c (2005)
31. Wolfe J.M., Butcher S.J., Lee, C. and Hyle, M.: Changing your mind: On the contributions of top-down and bottom-up guidance in visual search for feature singletons. 29, 483-502 (2003)
32. Miller, J.: Components of the location probability effect in a visual search task. *J Exp Psychol Hum Percept Perform*, 14, 453-471 (1988)
33. Geng, J.J. and Behrmann, M.: Spatial probability as an attentional cue in visual search. *Percept Psychophys* 67, 1252-1268 (2005)
34. Posner M.I. and Cohen Y. Components of attention. In H. Bouma and D. Bowhuis (Eds.), *Attention and performance X. Control of language processes*. Erlbaum (1984)
35. Klein, R.M.: Inhibition of return. *Trends Cognit Sci* 4, 138-147 (2000)
36. Chun M. M. and Jiang Y.: Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology* 36, 28-71 (1998)
37. Treisman A.: Features and objects: The 14th Bartlett memorial lecture. *Quarterly Journal of Experimental Psychology* 40A, 201-237 (1988)
38. Schneider, W. and R. M. Shiffrin.: Controlled and automatic human information processing: 1. Detection, search, and attention. *Psychol Rev* 84, 1-66 (1988)
39. Muller H.J. Heller, D. and Ziegler, J.: Visual search for singleton feature targets within and across feature dimensions. *Percept Psychophys* 57, 1-17 (1995)
40. Cohen A. and Magen H.: Intra- and cross-dimensional visual search for single-feature targets. *Percept Psychophys* 61, 291-307 (1999)
41. Found A. and Muller H.J.: Searching for unknown feature targets on more than one dimension: investigating a "dimension-weighting" account. *Percept Psychophys* 58, 88-101 (1996)
42. Kristjánsson, A.: Simultaneous priming along multiple dimensions in visual search task. *Vision Res* 46, 2554-2570 (2006)
43. Muller H.J., Reimann B. and Krummenacher J.: Visual search for singleton feature targets across dimensions: Stimulus- and expectancy-driven effects in dimensional weighting. *J Exp Psychol Hum Percept Perform* 29, 1021-1035 (2003)
44. Pollmann S., Weidner R., Muller H.J., and von Cramon D.Y.: A fronto-posterior network involved in visual dimension changes. *J Cogn Neurosci* 12, 480-494 (2000)
45. Pollmann S., Weidner R., Muller H.J. and von Cramon D.Y.: Neural correlates of visual dimension weighting. *Vis Cognit* 14, 877-897 (2001)
46. Weissman D.H., Giesbrecht B., Song A.W., Mangun G.R. and Woldorff M.G.: Conflict monitoring in the human anterior cingulate cortex during selective attention to global and local object features. *Neuroimage* 19, 1361-1368 (2003)
47. Egnér T. and Hirsch J.: Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nat Neurosci* 8, 1784-1790 (2005)
48. Pollmann S., Weidner R., Muller H.J., Maertens M. and von Cramon D.Y.: Selective and interactive neural correlates of visual dimension changes and response changes. *Neuroimage* 30, 254-265 (2006)
49. Bichot N.P., Schall J.D. and Thompson K.G.: Visual feature selectivity in frontal eye fields induced by experience in mature macaques. *Nature* 381, 697-699 (1996)
50. Olson C.R. and Gettner S.N.: Object-centered direction selectivity in the macaque supplementary eye field. *Science* 269, 985-988 (1995)
51. Tremblay L., Gettner S.N. and Olson C.R.: Neurons With Object-Centered Spatial Selectivity in Macaque SEF: Do They Represent Locations or Rules? *J Neurophys* 87, 333-350 (2002)
52. Kristjánsson A., Mackeben M. and Nakayama K.: Rapid, object-based learning in the deployment of transient attention. *Perception* 30, 1375-1387 (2001)
53. Bichot N.P. and Schall J.D.: Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. *J Neurosci* 22, 4675-4685 (2002)
54. McPeck R. M., Maljkovic V. and Nakayama K.: Saccades require focal attention and are facilitated by a short-term memory system. *Vision Res* 39, 1555-1566 (1999)
55. Bichot N.P. and Schall J.D.: Effects of similarity and history on neural mechanisms of visual selection. *Nat Neurosci* 2, 549-554 (1999)
56. Tanaka Y. and Shimojo S.: Location vs feature: reaction time reveals dissociation between two visual functions. *Vision Res* 36, 2125-2140 (1996)
57. Goodale M.A. and Milner A.D.: Separate visual pathways for perception and action. *Trends Neurosci* 15, 20-25 (1992)
58. Ungerleider L.G. and Mishkin M.: Two cortical visual systems. In D.J. Ingle, M.A. Goodale and R.J.W. Mansfield, eds. *Analysis of visual behavior*. MIT Press (1982)
59. Maljkovic V. and Nakayama K.: Priming of pop-out: III. A short term implicit memory system beneficial for rapid target selection. *Vis Cognit* 7, 571-595 (2000)
60. Cohen A., Ivry R., Rafal, R. and Kohn, C.: Response code activation by stimuli in the neglected visual field. *Neuropsychology* 9, 165-173 (1995)
61. Driver J., and Vuilleumier P.: Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition* 79, 39-88 (2001)
62. Vuilleumier P., Armony J. L., Clarke K., Husain M., Driver J., and Dolan R. J.: Neural response to emotional faces with and without awareness: Event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia* 40, 2156-2166 (2002)
63. Vuilleumier P., Sagiv N., Hazeltine E., Poldrack R. A., Swick D., Rafal R. D. and Gabrieli J. D. E.: Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proc Natl Acad Sci USA* 98, 3495-3500 (2001)
64. Rees G., Wojciulik E., Clarke K., Husain M., Frith C. and Driver J.: Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain* 123, 1624-1633 (2000)
65. Rees G., Wojciulik E., Clarke K., Husain M., Frith, C. and Driver J.: Neural correlates of conscious and

Priming in visual search

- unconscious vision in parietal extinction. *Neurocase* 8, 387–393 (2002)
66. Saevarsson S., Joelsdottir S., Hjaltason H. and Kristjánsson A.: Repetition of context in visual search ameliorates neglect symptoms in patients with parietal neglect. (Manuscript submitted for publication)
67. Walsh V., le Mare C., Blaimire A. and Cowey A.: Normal discrimination performance is accompanied by priming deficits in monkeys with V4 or TEO lesions. *Neuroreport* 11, 1459-1462 (2000)
68. Campana G., Cowey A. and Walsh V.: Priming of motion direction and area V5/MT: a test of perceptual memory. *Cereb Cortex* 12, 663-669 (2002)
69. Malach R., Reppas J.B., Benson R.R., Kwong K.K., Jiang H., Kennedy W.A., Ledden P.J., Brady T.J., Rosen B.R. and Tootell R.B. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA* 92, 8135-8139 (1995)
70. Meeter M and Olivers CNL.: Intertrial priming stemming from ambiguity: A new account of priming in visual search. *Vis Cognit* 13, 1-28 (2006)
71. Hadjikhani, N., Liu, A.K., Dale, A.M., Cavanagh, P. and Tootell, R.B.: Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience*, 1, 235-241 (1998)
72. Bartels A. and Zeki S.: The architecture of the color centre in the human visual brain: new results and a review. *Eur J Neurosci* 12, 172-193 (2000)
73. Mesulam M. M.: Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philos Trans R Soc Lond B Biol Sci* 354, 1325–1346 (1999)
74. Kastner, S. and Ungerleider, L.G.: The neural basis of biased competition in human visual cortex. *Neuropsychologia*, 39, 1263-1276 (2001)
75. Corbetta M. and Shulman G.L.: Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3, 201-215 (2002)
76. Yantis S. and Serences J.T.: Cortical mechanisms of space-based and object-based attentional control. *Curr Opin Neurobiol* 13, 187-193 (2003)
77. Pollmann S., Weidner R., Humphreys G.W., Olivers C.N., Muller K., Lohmann G., Wiggins C.J. and Watson D.G.: Separating distractor rejection and target detection in posterior parietal cortex-an event-related fMRI study of visual marking. *Neuroimage*, 18, 310-323 (2003)
78. Karnath H-O., Ferber S. and Himmelbach M.: Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* 411, 950-953 (2001)
79. Karnath H-O., Berger M.F., Kuker W. and Rorden, C.: The anatomy of spatial neglect based on voxelwise statistical analysis: a study of 140 patients. *Cereb Cortex* 14, 1164-1172 (2004)
80. Vallar G. and Perani D.: The anatomy of unilateral neglect after right-hemisphere stroke lesions. A clinical/CT-scan correlation study in man. *Neuropsychologia*, 24 609-622 (1986).
81. Mort J.M., Malhotra P., Mannan S.K., Rorden C., Pambakian A., Kennard C. and Husain M. The anatomy of visual neglect. *Brain* 126, 1986-1997 (2003)
82. Huang L., Holcombe A.O. and Pashler H.: Repetition priming in visual search: episodic retrieval, not feature priming. *Mem Cognit* 32, 12-20 (2004)
83. Treisman A., Vieira A. and Hayes A.: Automaticity and preattentive processing. *Am J Psychol* 105, 341-362 (1992)
84. Kahneman, D., Treisman, A. and Gibbs B.J.: The reviewing of object files: object-specific integration of information. *Cognit Psychol* 24, 175-219 (1992)
85. Sigurdardottir H.M., Kristjánsson A. and Driver J.: Repetition streaks increase perceptual sensitivity in brief visual search displays. In press in *Vis Cognit*
86. Huang, L. and Pashler H.: Expectation and repetition effects in searching for featural singletons in very brief displays. *Percept Psychophys* 67, 150-157 (2005)
87. Muller H.J., Krummenacher, J. and Heller, D.: Dimension-specific intertribal facilitation in visual search for pop-out targets: Evidence for a top-down modulable visual short-term memory effect. *Vis Cognit* 11, 577-602 (2004)
88. Goolsby B.A. and Suzuki S.: Understanding priming of color-singleton search: Roles of attention at encoding and “retrieval”. *Percept Psychophys* 63, 929-944 (2001)
89. Yoshida T., Tsubomi H., Osaka M. and Osaka, N.: Priming of pop-out—an fMRI study. *Perception* 32 (Suppl.), 93c (2003)
90. Deubel H. and Schneider W. X.: Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Res* 36, 1827–1837 (1996)
91. Edelman J., Kristjánsson A. and Nakayama, K.: The influence of object-relative visuomotor set on express saccades. *J Vision* 7(6):12, 1–13 (2007)
92. Kowler E., Anderson E., Doshier B. and Blaser E.: The role of attention in the programming of saccades. *Vision Res* 35, 1897–1916 (1995)
93. Kristjánsson A., Vandenbroucke M. and Driver J.: When pros become cons for anti versus prosaccades. *Exp Brain Res* 155, 231-244 (2004)
94. Kristjánsson A.: Saccade landing point selection and the competition account of pro- and antisaccade generation: The involvement of visual attention – A review. *Scand J Psychol* 48, 97-113 (2007)
95. Wolfe J.M., Horowitz T.S., Kenner N., Hyle M., and Vasan N.: How fast can you change your mind? The speed of top-down guidance in visual search. *Vision Res* 44, 1411-1426 (2004)
96. Magnussen S. and Greenlee MW.: The psychophysics of perceptual memory. *Psychol Res* 62, 81-92 (1999)
97. Magnussen S., Greenlee M.W, Asplund R. and Dyrnes S.: Stimulus-specific mechanisms of visual short-term memory. *Vision Res* 31, 1213-1219 (1991)
98. Olivers C.N.L., Meeter M.: Feature priming in visual search does not depend upon the dimensional context. In press in *Vis Cognit*
99. Kristjánsson A., Ingvarsdottir A., Teitsdottir U.D.: Object- and feature-based priming in visual search. *Perception* In press (2007)

Footnotes: ¹ It is, of course, debatable whether position should be considered a “dimension” – and perhaps not in terms of the dimension weighting account. ² It should be noted that the debate on a critical locus for neglect to occur is far from settled (80,81). A critical locus may in fact not

Priming in visual search

even exist but that neglect may occur following damage to a few different areas, the critical point being that the operation of a network of activity is disrupted.³ It seems that this could also be interpreted as an effect of enhanced feature processing, in other words that the increased requirements for the processing of a particular dimension causes stronger feature processing, and priming in consequence, than otherwise, but there was some indication that the priming was not wholly feature specific but also applied over feature dimensions in the study.

Key Words: Priming; Visual Search; Visual Attention; Visual Neuroscience, Review

Send correspondence to: Dr Arni Kristjansson, Department of Psychology, University of Iceland, Oddi V/Sturlugotu, 101 Reykjavik, Iceland, Tel: 354-5255198, Fax: 354-5526806, E-mail: ak@hi.is

<http://www.bioscience.org/current/vol13.htm>