

Rapid learning in attention shifts: A review

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Many lines of evidence show that the human visual system does not simply passively register whatever appears in the visual field. The visual system seems to preferentially “choose” stimuli according to what is most relevant for the task at hand, a process called attentional selection. Given the large amount of information in any given visual scene, and well-documented capacity limitations for the representation of visual stimuli, such a strategy seems only reasonable. Consistent with this, human observers are surprisingly insensitive to large changes in their visual environment when they attend to something else in the visual scene. Here I argue that attentional selection of pertinent information is heavily influenced by the stimuli most recently viewed that were important for behaviour. I will describe recent evidence for the existence of a powerful memory system, not under any form of voluntary control, which aids observers in orienting quickly and effectively to behaviourally relevant stimuli in the visual environment, in particular the stimuli that have been important in the immediate past. I will also discuss research into the potential neural mechanisms involved in these learning effects. Finally, I will discuss how these putative memory mechanisms may help in maintaining the apparent stability and continuity of the ever-changing visual environment, which is such a crucial component of our everyday visual experience.

It is often said of the goldfish that it has extremely limited memory capacity. That after swimming for a few seconds in its bowl, it will not recognize a visual scene viewed moments before. It will essentially regard the scene as completely novel. This view of complete amnesia for the goldfish is probably too extreme, given demonstrations of its capacity to learn (Flood, Overmier, & Savage, 1976; Portavella, Vargas, Torres, & Salas, 2002), but the interesting point for the present purpose is the implicit comparison with humans, or other animals with more complex nervous systems than the goldfish. It seems to be implied in these accounts that the more complex organisms will easily recognize an old scene as

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one previously viewed, and that their memory for the details of these previously viewed scenes will be quite good.

If this is true of humans, which indeed seems intuitively most often the case, a large amount of information must be stored between successive glimpses of a visual scene; the shape and colour of different parts of the scene, the relative locations of the objects in the scene, and the identity of each object in the scene must be kept track of from one moment to the next. The ratio of all the information in the scene that could be retained against the general capacity of the visual system does, however, probably not favour the visual system in the long run. There is simply too much information that must be retained (see, e.g., Nakayama, 1990; Reeves & Sperling, 1985).

In recent years, a large amount of evidence has indeed accumulated showing that a lot of information in any given visual scene is either not processed, or only represented fleetingly and coarsely by the human visual system (see, e.g., Phillips, 1974, 1983; Sperling, 1960; Wolfe, 1999). In other words, a large amount of visual information is either not seen or forgotten rapidly despite being in full view. For example, Grimes (1996) and McConkie and Zola (1979) showed that if observers view a complex scene followed by an eye movement to a different location in the scene, they are surprisingly insensitive to large changes made to the scene during the eye movement, and their memory for what was seen before the eye movement is often quite poor (Carlson-Radvansky & Irwin, 1995; Irwin, 1992; Irwin & Andrews, 1996). Also, dramatic changes between two otherwise identical pictures of a visual scene take a surprisingly long time to be noticed if a picture of the changed scene is alternatively presented with the original picture at a rapid rate with some visual event between the two views (e.g., a blank field or blotches resembling those from a mudsplash on a windshield appearing on the scene, while the changes take place; O'Regan, Rensink, & Clark, 1999; Rensink, O'Regan, & Clark, 1997; see also Simons, 1996).

In another example of how much less information from the visual environment is often processed than one may think, observers were asked to judge which of the two lines of a briefly presented cross, followed by a mask, was longer. If a salient stimulus was presented at the same time as the cross, even at the locus of fixation, a large number of observers (up to 75%) failed to notice it (Mack & Rock, 1998; Rock, Linnett, Grant, & Mack, 1992). Research using more dynamic scenes has revealed more sustained "inattentional blindness" where, for example, a task that involves keeping track of the positions of a set of moving objects on a computer screen results in surprisingly low rates of noticing of a salient stimulus that moves across the screen (Most et al., 2001). Even more dramatic examples of this have been shown to occur in real-world scenes or in person-to-person interactions (Neisser & Becklen, 1975; Levin, Simons, Angelone, & Chabris, 2002; Simons & Chabris, 1999; Simons & Levin, 1997). Humans, then, often behave as if they are just as amnesic as the goldfish!

It is important to note that the critical variable that determines whether the observers notice changes in scenes, or not, seems often to be whether visual attention is diverted or taxed in some way (by the blank period, the mudsplashes, the line judgement, or an attentional tracking task). Furthermore, the features of the objects that observers attend to dictate what they notice in their visual environment. Observers watching a video of two teams (one dressed in white, the other in black) passing a basketball between them while counting how many passes one of the teams makes, were far more likely to notice a person in a gorilla costume walk unexpectedly onto the scene if they were counting the passes of the team in black (Simons & Chabris, 1999; see also Most et al., 2001). This has led many researchers to propose a key role for attention in visual perception, even going so far as arguing that attention is needed for any meaningful visual perception (Mack & Rock, 1998; Nakayama & Joseph, 1998; Rensink, 2000).

Given these often dramatic examples of how fallible and error prone our visual system tends to be, it is in fact surprising that we can navigate and interact with our visual environment as well as we do. Demonstrations like the ones described above, showing how relatively little information seems actually to be actively processed by the visual system, have led to proposals that the visual system is economic in what is represented in the perceptual process. It has been proposed that the visual system forms only fleeting representations of the visual scene and only as needed for the task at hand (Ballard, Hayhoe, Pook, & Rao, 1997; Dennet & Kinsbourne, 1992; O'Regan, 1992; Rensink, 2000). According to this view only the key features that are actually needed for successful interactions with the environment are retained in most cases. Such views open up the question of how these fleeting representations could be formed, and how the identity of objects would be retained from one moment to the next. What allows us to update visual representations, in particular those that are most relevant to behaviour in each case? My purpose with this review paper is to provide a summary of research pertinent to this question of how the apparent stability of the visual environment is maintained by the visual system, given the apparent gap between what information is present in the visual scene and how much information is actually processed to any great extent by the visual system. I will summarize my own work, and that of others, that has addressed this issue, and will attempt to explain how the research may reveal the operational characteristics of memory mechanisms that serve to maintain a stable representation of the visual environment from one moment to the next. As I mentioned above, many researchers think that visual attention plays a key role in this process, and my thesis here is that the proposed memory mechanisms play a vital role in determining the way attention is allocated in a given visual scene.

OBJECT-CENTRED LEARNING IN THE DEPLOYMENT OF ATTENTION

A substantial experimental literature is devoted to the study of how attention is allocated, or drawn, towards the locus of a suddenly appearing stimulus in the visual scene (Folk & Remington, 1999; Folk, Remington, & Johnston, 1992; Jonides, 1981; Posner, 1980; Theeuwes & Burger, 1998; Yantis & Jonides, 1990, 1999; see Folk & Gibson, 2001, for an overview of some of the issues involved). It has, for example, been found that the processing of stimuli at the location of this abrupt event can be faster (Posner, 1980) and more fine grained or precise than at other locations in the visual scene (e.g., Carrasco, Williams, & Yeshurun, 2002; Nakayama & Mackeben, 1989). This form of attention deployments has been termed exogenous capture of attention (see, e.g., Most & Simons, 2001, for a recent review). The key word in this context is “capture”—this process of attentional allocation has been thought of as an automatic one that takes place irrespective of the observer’s goals in each case. On the other hand, it has also been shown, that the degree to which abruptly appearing stimuli capture attention can be modulated considerably by motivational factors such as the task of the observer in each case (Folk & Remington, 1999; Folk et al., 1992; Gibson & Jiang, 1998; Luck & Thomas, 1999; Pashler, 2001). This has led some researchers to propose that the degree to which a stimulus captures attention is contingent upon the attentional “settings” of the observers in each case—thus if the observers task is to make a discrimination on a green stimulus in a field of red stimuli, green stimuli will be more likely to capture attention than red ones (see, e.g., Folk & Remington, 1999; Folk et al., 1992). Although such an “entry by appointment only” view is probably too extreme (Theeuwes & Burger, 1998; Theeuwes & Godijn, 2001; Yantis & Jonides, 1990) the message remains that if the external event is not behaviourally relevant, its capacity to capture attention may be diminished.

In Kristjánsson, Mackeben, and Nakayama (2001) and Kristjánsson and Nakayama (2003), we investigated whether the allocation of attention to such an external event, away from the current locus of fixation, can be modulated by whether there is a consistent relationship between the properties of that stimulus and the location of an upcoming target stimulus that a discrimination task must be performed upon. Figure 1 shows an example of the general experimental paradigm used in these experiments. A peripheral cue is presented, followed by a target at the cued location. The target on any given trial was equally likely to appear at any of the possible locations around the imaginary ellipse centred on the fixation cross. As shown by Nakayama and Mackeben (1989), attentional orienting under these conditions is not under explicit voluntary control, and, as mentioned above, it has often been argued that attention is summoned automatically to such an external event (e.g., Jonides, 1981; Theeuwes & Godijn, 2001; Yantis & Jonides, 1984). The key question in our experiments was the

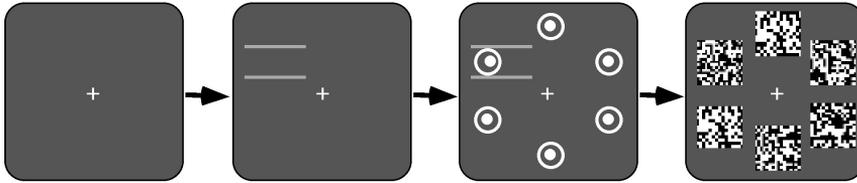


Figure 1. A general outline of the experimental paradigm used in Kristjánsson, Mackeben, and Nakayama (2001) and Kristjánsson and Nakayama (2003). The task was to indicate whether the “eye” target at the cued location was “looking” left, right, up, or down. A trial started with a central fixation cross followed by a brief cue (80–200 ms, depending on the experiment) followed by the “eye” target and distractors presented for 80 ms or less (depending on experiment). The sum of the target and cue times was always less than 200 ms, however. The trial then ended with the presentation of a random dot mask visible until the observer responded. Note that the display items are not drawn to the scale used in the experiments, but are condensed for ease of representation. See the original papers for details about the experimental design in each case.

following: If the process of attentional allocation in this context is a simple reflex, as many have argued, then the benefits of attention should apply equally well everywhere within the cue. There should be no preferred location where the target would be the most discriminable; the task should be equally easy or hard, no matter where the target appears within the cue. Note that the task is performed without eye movements—the total presentation times of the cue and target are too brief (less than 200 ms), to allow an eye movement to the target location before the mask appears.

The task was an acuity task and the target was an “eye” looking either left, right, up, or down among eyes looking straight ahead (see Figure 1). In the experiments discussed here, the target was presented either on the left or right end of the cue, and always within the two parallel lines of the cue. The position of the target varied from trial to trial but in the critical “streak” condition, there were, on average, more repetitions than changes of target location within the cue (with slight tweaking of the probability of the target appearing in either relative target position). Thus there were short “streaks” of random length, where for a number of trials, the target would be, for example, on the left side of the cue, followed by a sequence of trials where the target would be at the right side. Note that the position of the imaginary circle that the targets appeared on was jittered unpredictably from one trial to the next. If we had not done this observers could, in theory, have figured out the location of a target within a cue just by knowing the location of the imaginary circle (see Kristjánsson et al., 2001, and Kristjánsson & Nakayama, 2003, for further details).

If learning of the cue–target relationship takes place in this context, we would expect to see changes in performance within a streak as the position of the target within the cue remains the same. Performance under this streak condition was contrasted with performance under a “switch” condition where the cue–target

relationship was completely predictable: If the target appeared on the left side of the cue on trial $n-1$, it would appear on the right side on trial n , and then on the left side again on trial $n+1$.

Results for two representative observers are shown in Figure 2. Figure 2A shows that as the target location within the cue is repeated within a streak, performance improves dramatically from approximately 50% (equal to chance performance) up to around 80%. From these results, it is clear that consistency in target location aids performance significantly, suggesting that short-term learning of the cue–target relationship has taken place. Note that predictability on its own does not result in similar learning, since performance under the switch condition was very poor (see Figure 2B), even though the target location alternated completely predictably from the right to the left between trials.

This result is evidence for a learning mechanism for rapid directing of focal attention. Attention can be flexibly and rapidly deployed to either end of a larger object, depending on recent history, under conditions that have often been thought to involve simply the reflexive allocation of stimulus driven attention. It is important to note that the learning is object based, as the cue and target can appear in one of the many places around the circle as depicted in Figure 1 (determined randomly for each trial). Furthermore, this learning can have an effect on performance in less than 200 ms. It is doubtful that voluntary shifts of attention can operate on such a timescale (see, e.g., Ward, Duncan, & Shapiro,

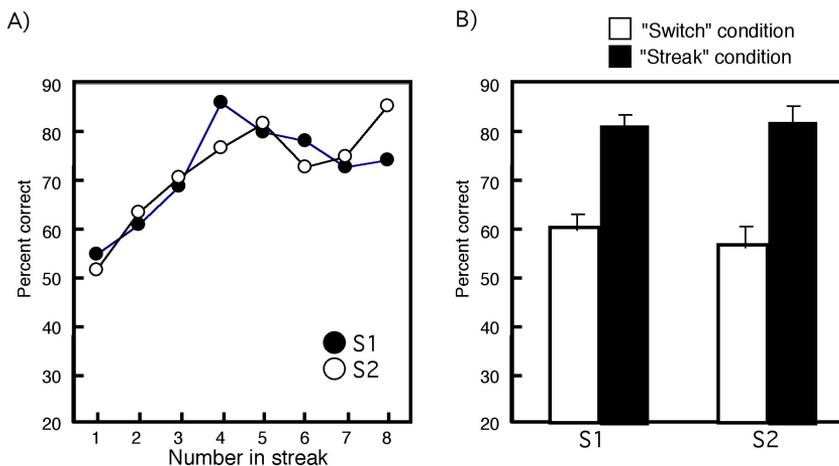


Figure 2. Learning of a position-based cue–target relationship. The figure shows discrimination performance for two observers (S1 and S2) in Kristjánsson, Mackeben, and Nakayama (2001, Exp. 2). (A) Performance as a function of position within a “streak” of trials where the target appeared in the same location relative to the cue for consecutive trials (denoted by “number in streak”). (B) Overall performance for the streak and switch conditions (see text for details). (Data replotted from Kristjánsson et al., 2001.)

1996). So the learning is very unlikely to be under any sort of voluntary control. Another reason for assuming this is that Nakayama and Mackeben (1989) showed that deployments of attention with similar cue-lead and target times as in this experiment were unaffected by prior knowledge of where in the visual field the target appeared. They showed that performance was similar when the target always appeared in the *same* location and when the target appeared randomly in any location on an imaginary circle surrounding the fixation point when the cue lead times were around 100–200 ms and the target appeared for approximately 30–50 ms, similar to the presentation times here. In other words, knowing beforehand where the target would subsequently appear (even before the cue was presented) did not aid performance, while performance was far better at a cued location than an uncued one.

Furthermore, if the observers in our experiment were simply picking up the patterns in the cue–target relationship and using this information to allocate attention, they should logically have done best in the switch condition since the cue–target relationship was completely predictable there, because the target alternated between appearing at the right end or the left end of the cue between trials (see also below, where I describe an experiment that addresses this issue in a more direct way).

FEATURE-BASED LEARNING IN THE DEPLOYMENT OF TRANSIENT ATTENTION

Having observed this selective learning of cue–target relations in object-based coordinates in rapid shifts of attention, we next looked for other relationships that might be learned in a similar manner. Could this putative learning mechanism learn other relationships between objects such as the cue and a subsequent target?

The experiments in Kristjánsson and Nakayama (2003) were designed to address this issue. In that paper we followed the general experimental design of Kristjánsson et al. (2001), while this time asking whether this learning mechanism for attention shifts could learn to selectively allocate attention to a particularly coloured region of an object even if the object changed its orientation, such as when it is flipped horizontally. In order to answer this question we used two kinds of distinctions within the cue: Colour and shape (see Figure 3). In all other respects, the experimental design was similar to the one used in Kristjánsson et al. (2001). For the colour case, the cue was a pair of horizontal lines that were red at one end and green on the other (see Figure 3A). In the streak condition the target appeared at the same coloured end of the cue for long stretches of adjacent trials, while in the switch condition it appeared alternately at the right and left side of the cue from one trial to the next. For the case of shape, the object had a keyhole form, so that one end was round, whereas the other end was angular (as shown in Figure 3C). As with colour, in the streak

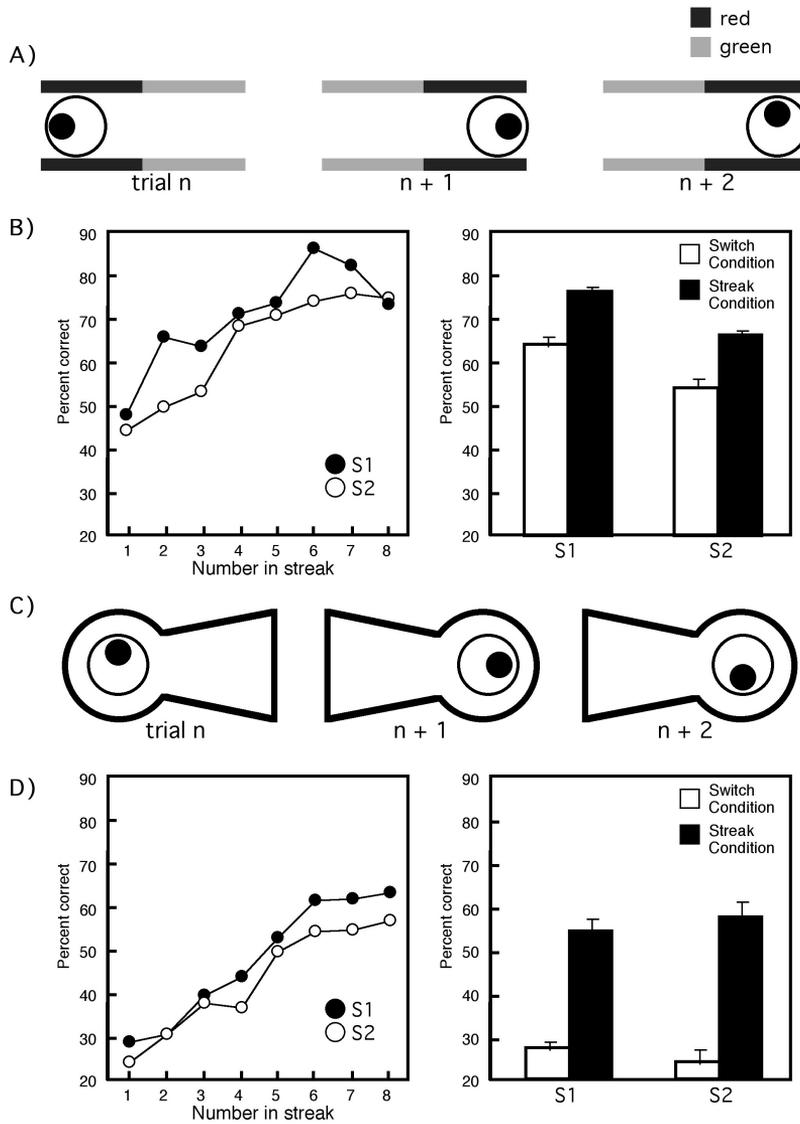


Figure 3. Feature-based learning in rapid shifts of visual attention. (A) The cue-target relationship under the streak condition for the colour cue. The target would appear at the same coloured end of the cue for long streaks of adjacent trials. (B) The panel on the left shows how performance (for two observers) improved within a streak, and the right panel shows overall performance for the streak and switch conditions for the colour cue. (C) The cue-target relationship within a streak for the shape cue. Here the target would appear at the same shaped end of the cue for long streaks of adjacent trials. (D) The panel on the left shows how performance improved within a streak, and the right panel shows overall performance for the streak and switch conditions for the shape cue. (Data replotted from Kristjánsson & Nakayama, 2003.)

condition the target appeared at the same shaped end of the cue within a streak, whereas in the switch condition it alternated between the two different shaped ends of the cue from one trial to the next. As before, we tested performance with very brief cue-lead times (140 ms or less) and brief target exposure times (80 ms or less). Most important for the experiments, was the fact that these two features, colour and shape, could vary randomly in position within the cue, left versus right. Thus, the green end of the cue could be on the left or on the right of the object within a streak of the target appearing in the same coloured (or shaped) location on the cue. As in the experiment on position consistency, the cue and target location on each trial varied randomly between the different locations on the imaginary circle.

The results for the colour cue are shown in Figure 3B. On the left we see the same sort of improvement in performance within a streak as with position consistency (Kristjánsson et al., 2001; see Figure 2 here). Thus it is clear that observers can learn a relationship where the target appears consecutively within a streak on, for example, the red side of a two-colour cue, irrespective of where the target is in the visual field on each trial, and whether the red half of the cue was on the right or on the left of the cue. Also, the figure on the right in Figure 3B shows that performance was poor under the switch condition compared with the streak condition, indicating that simple predictability was not sufficient for the learning to take place. If predictability was the feature that was most important for the learning to take place, performance should have been good in the switch condition where the cue–target relationship was always predictable: If the target appeared at the red end of the cue on the last trial it would appear (with 100% certainty) on the green side of the cue on the next trial, and so on. This is clearly not the case here, however.

The results for shape are shown in Figure 3D. As with the colour experiment, the observers could learn a relationship between the cue and target where the target appeared at, for example, the rounded end of the keyhole cue consecutively within a streak. As with colour this learning was independent of the actual location of the target within the array and independent of whether the critical feature of the cue was on the right or left. Note also that the learning cannot be due to predictability alone, since performance was poor under the switch condition where the target appeared alternately at the red or green (or rounded and angular) end of the cue in a completely predictable manner. Thus it is clear that the learning mechanism can learn feature-based relationships as well as relationships based on location consistency within a cue.

In Nakayama, Maljkovic, and Kristjánsson (2004) we further analysed the results from the shape- and colour-consistency experiments in Kristjánsson and Nakayama (2003), showing that shape or colour learning and position learning can take place independently and simultaneously. The results are shown in Figure 4. There was an improvement in performance with position consistency; at the same time there was an improvement in performance that could be

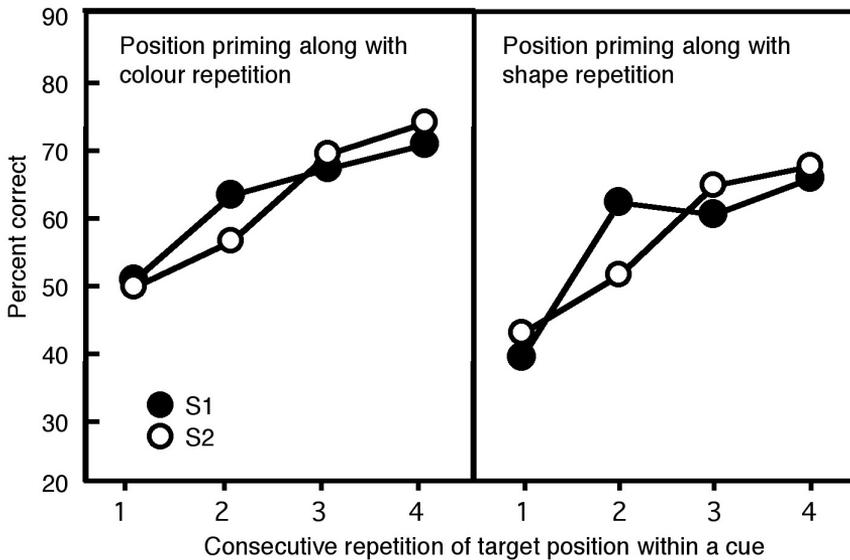


Figure 4. Position based learning can occur simultaneously with learning of feature-based relationships between cue and target. The figure shows discrimination performance for two observers as a function of how often in a row the target was in the same location relative to the cue for the colour consistency experiment (left panel) and the shape consistency experiment (right panel) from Kristjánsson and Nakayama (2003). This position-based learning was taking place at the same time as the learning of feature-based relations between cue and target. The data are from a reanalysis of the results from Experiments 1 (left panel) and 2 (right panel) in Kristjánsson and Nakayama (2003) originally presented in Nakayama et al. (2004).

attributed to a consistent relationship between the colour (see the left panel of Figure 4), or shape (see the right panel of Figure 4) of a part of the cue and the target location. In other words, the two forms of learning were building up independently and simultaneously. This, most probably, means that we have been investigating a relatively primitive learning mechanism that appears not to integrate information from two different modalities (in this case shape, colour, and position) since the two forms of learning are building up independently, and at the same time (see Nakayama et al., 2004, for further discussion).

WHAT ARE THE LIMITS OF THIS LEARNING PROCESS?

Having identified relationships that can be learned in rapid attentional deployments like the present ones, we attempted to identify the limits of this learning process. Are there cue–target relationships that *cannot* be learned in the same manner as we have shown above? From the preceding results, it is clear that the system cannot learn relationships such as in the switch condition where a

relatively complex inference is required. In an attempt to answer this question we investigated whether the system can learn more abstract rules, perhaps to direct attention differentially to two opposite ends of two *different* cues (see Kristjánsson & Nakayama, 2003). Would it, for example, be possible for this learning mechanism to quickly direct attention to the left end of one object and to the right end of a different object depending on the cue–target relationship (within the same block of trials)? We conducted two experiments using the object features colour and shape. There were two conditions in each experiment. For shape, the two conditions were the “consistent” condition, where the target was always on one side of the cue within a block of trials (the right or left) if it was rounded and on the other side, if the cue was rectangular (see Figure 5) and the random condition where there was no consistent relationship between the cue shape and the location of an upcoming target. For colour, the target always appeared on one side of the cue if it was red, and on the other side of it if the cue was green in the consistent condition, but randomly at either end regardless of the cue colour in the random condition (the target locations in the consistent conditions were counterbalanced across blocks but were always the same *within* each block).

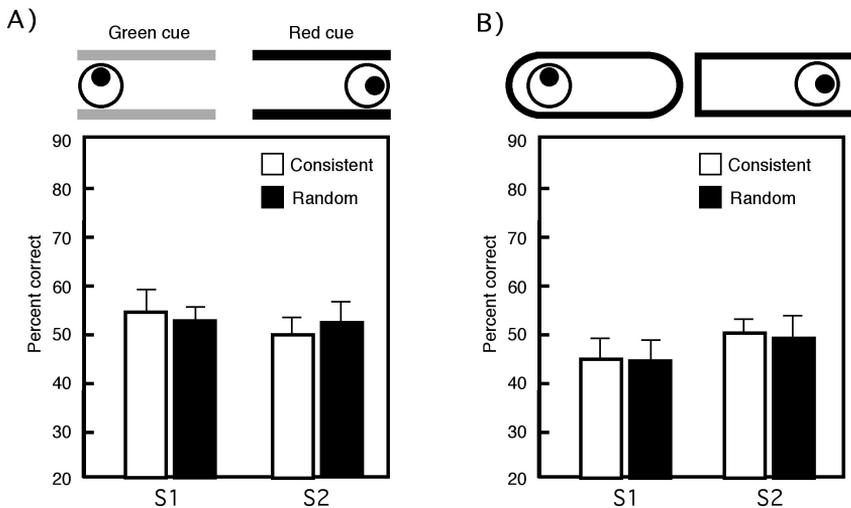


Figure 5. “If-then” relations between cue and target cannot be learned in rapid shifts of attention. (A) Discrimination performance for two observers (S1 and S2) was the same whether the overall colour of a cue predicted the location of an upcoming target or not. (B) Performance remains unchanged whether the overall shape of a cue consistently cues a target location or not. Thus, in the consistent condition the target would appear, for example, always at the left side of the green (or rounded) cue and the right side of the red (or square) cue within a block, while there was no such relationship in the random condition (the data are replotted from Kristjánsson & Nakayama, 2003).

Note that the relationship between the cue and target in the two consistent conditions is particularly challenging, since the inference that is required is a form of an if-then inference: If the cue is red, the target will appear on the left, for example, while in the same session, the target will appear on the right if the cue is green. The results from these two experiments are shown in Figure 5. The results clearly show that such a relationship between the cue and a target clearly *cannot* be learned, since performance was no different from a condition where there was *no* relationship between the cue colour (on the left) or cue shape (on the right), and target location (the “random” condition in Figure 5). The conclusion from these experiments is clear: There are severe restrictions on what can be learned by this learning system in attentional deployments. This is one of the reasons why we call this a *primitive* learning mechanism for attention deployments (see Kristjánsson & Nakayama, 2003; Nakayama et al., 2004).

IS THE LEARNING UNDER VOLUNTARY CONTROL?

As I have emphasized before, in all the experiments involving this cueing paradigm, the cue-lead and target presentation times were very brief. The cue-lead times were 200 ms or less and target presentation times were 80 ms or less, and the combined cue-lead and target times never added up to more than 200 ms in any given experiment. The consensus in the literature has been that attention shifts on this timescale are automatic orientation reflexes not under any form of voluntary control (see, e.g., Klein, Kingstone, & Pontefract, 1992; Nakayama & Mackeben, 1989). If this is true, top-down modulation or explicit strategies should not affect the outcome of the experiments. We could not, however, rule out on this basis alone, that observers used some form of top-down strategies to perform the tasks. Is it possible that observers picked up on the cue–target contingencies and explicitly directed their attention to the part of the cue they thought the target would appear? To try to answer this question we made observers perform a cued discrimination task similar to the two-colour cue task mentioned above, first without any knowledge of the cue–target contingencies, followed by a session where they were informed of the cue–target relationship, and were furthermore encouraged to use this knowledge to aid their performance (see Kristjánsson & Nakayama, 2003, Exps. 5 and 6). If observers are able to use explicit knowledge about the cue–target relationship to aid performance, they should do a lot better under the “full-instruction” condition than when no instruction was given. The results, however, were clear: No performance difference was found between the “no-instruction” and “full-instruction” conditions. It seems that observers were not able to use their explicit knowledge of cue–target contingencies to aid their performance. Furthermore, we asked the observers after the experiment whether they felt that they had been able to use the information to aid their performance. All the subjects reported that they had

found that quite impossible. The cue-lead time and the target-presentation times were simply too short. Nevertheless these were the exact same conditions as those where the observers had shown learning of the cue–target relations previously (see Kristjánsson & Nakayama, 2003). Explicit knowledge of the cue–target relations has no effect, either way, on the learning process.

This result is, in fact, perhaps not surprising since it has been shown that *voluntary* attention shifts tend to be slow (Wolfe, Alvarez, & Horowitz, 2000), too slow to operate effectively within the time frame imposed by the task in these experiments. Thus it seems that attention shifts on this timescale are not mediated by a process that is under explicit top-down control, and the same must therefore apply to the learning investigated in the experiments described above if they are to exert their effects in this brief time period.

PROCESSING OF VISUAL SEARCH STIMULI IS FASTER IF TARGET SHARES PROPERTIES WITH PREVIOUS TARGET

In a series of studies Maljkovic and Nakayama (1994, 1996, 2000) have investigated how previous task history can influence subsequent performance in a simple visual search task. Their basic task was an “odd-one-out” search for a single oddly coloured diamond among two diamonds of another colour. When the target was found the observers had to judge whether a corner was cut off on the left or right part of the target diamond. The three items could only be of two colours within any given block of trials (e.g., red and green) so the two distractors were always of the same colour. Under these conditions the target tends to be salient and is found quickly and easily. In the visual search literature this is known as a pop-out task, while the task was different from “standard” visual search tasks in that it involved a discrimination task as well. The goal of their first series of experiments was to compare performance on trials where the *colour* of the target was the same as on the previous trials versus when the target colour was the other one of the pair of colours.

The findings from their experiments were clear. Response times fell systematically as the number of repetitions within a “streak” of same colour targets increased. So just as in the case of attentional cueing experiments where a consistent cue–target relationship leads to improved performance (Figure 2), there is a strong benefit in task performance from repeating the colour of the object of attention. Maljkovic and Nakayama termed this effect the “priming of pop-out” (see also Goolsby & Suzuki, 2001; Hillstrom, 2000; Maljkovic & Nakayama, 1996, 2000).

In Maljkovic and Nakayama (1996) the authors then tested whether a similar consistency—in this case location consistency—also leads to improvements in performance as measured by reaction times. The task was a similar search for a colour singleton as in the experiments testing the priming effects from colour

repetition. The critical thing here was whether response times would be speeded when the target appeared in the same position as on the last trial versus when it appeared in a different position on the last trial. The results showed that as with colour repetition there was a large benefit from repeating the target location from one trial to the next.

Maljkovic and Nakayama (1996, Exp. 2) also showed how the two forms of learning, (of colour and location) can build up independently, which corresponds well with the pattern of learning of cue–target relationships in rapid attentional deployments that I explained earlier, where it was shown that learning of location and feature consistency can build up independently (see Figure 4). The similarity between the two forms of learning suggests that the two may be manifestations of the operation of a similar learning mechanism.

PRIOR KNOWLEDGE OF UPCOMING TARGET COLOUR DOES NOT ALTER THE PRIMING PATTERN IN THE PRIMING OF POP-OUT

Taken together, the experiments reviewed up until now show how important previous task history is in determining performance in the present. It seems that observers have a strong tendency to orient attention to features of a task relevant item presented previously. Two further questions can be asked at this point about this priming effect in visual search. First, is this learning under voluntary control? If the properties of priming of pop-out are similar to the cue–target learning investigated in Kristjánsson et al. (2001) and Kristjánsson and Nakayama (2003), or do indeed reflect the workings of a similar mechanism, we would predict that it *would not* be modified by deliberate cognitive effort. A second, related, question is whether this sort of priming can actually harm performance when the colour of the target item switches from one colour to the other from one trial to the next. If this mechanism is not under voluntary control and simply follows the stimulus features, we would indeed expect that to be the case. Our finding that performance under the switch condition of the experiments in Kristjánsson et al. and Kristjánsson and Nakayama was particularly poor is related to this question.

In an elegant demonstration of how the priming they investigated cannot be modulated by top-down control, Maljkovic and Nakayama (1994) presented the visual search targets in sequences of two greens, two reds, two greens, two reds, and so on. In all other respects the paradigm was a similar pop-out search task to the one used before. Critically, the experiment was run under two sets of instructions. Under one condition, the observers were asked simply to perform the experiment as usual and ignore the sequence of coloured targets. Maljkovic and Nakayama called this the “passive” condition. In the “active” condition, the observers were informed about the sequence of target colours and were encouraged to use this knowledge to help them with the task by anticipating the

target colour on each upcoming trial by subvocalizing the colour of the upcoming target prior to each trial. The result was that no evidence was found that the observers' performance improved with the active attempt to use the knowledge about what the target colour would be, a result very similar to the one where we informed our observers of the cue–target relationship (explained above; see also Kristjánsson & Nakayama, 2003). Also, Maljkovic and Nakayama observed similar priming effects as before in that they found a large difference in response times to the target between the first and second trial of a sequence of like coloured targets. This shows convincingly (as with the learning in the cueing paradigm mentioned above) that performance is uninfluenced by prior knowledge or expectancy. The flipside of this is that this learning cannot be deactivated—the priming harms subsequent performance, since responding to, for example, a green target following two red ones was slow even though the observers knew the upcoming target colour. One could say that the priming “vetoes” top-down guidance in this context.

The findings of Maljkovic and Nakayama are another demonstration of how learning and priming can influence the speed and efficiency of attentional shifts. The similarities between the learning of cue–target relations described in the previous section and the priming of pop-out are undeniable. Neither seem amenable to voluntary control and both operate in object-centred coordinates rather than, for example, retinotopic coordinates (except for the priming of position in the priming of pop-out). In both cases position and feature learning can build up independently of each other. I want to propose here (see also Nakayama et al., 2004) that the two phenomena are manifestations of a unitary learning process not under voluntary control, that allows quick reorientation to recently viewed stimuli. I will have more to say on this in a later section after I review some other forms of learning between trials in attentional deployments.

A more general conclusion seems, however appropriate at this point. It is clear that the visual system does not simply passively register whatever appears in the visual field. The visual system seems to select stimuli according to what is most relevant for the task at hand and this form of attentional biasing (perhaps related to the “biased activation” proposal of Desimone & Duncan, 1995; see also Reynolds, Chelazzi, & Desimone, 1999), is heavily influenced by the stimuli most recently viewed, that were important for behaviour.

PRIMING IN A CONJUNCTIVE VISUAL SEARCH TASK

In Kristjánsson, Wang, and Nakayama (2002) we have further investigated priming in visual search using a more challenging visual search task than the one used by Maljkovic and Nakayama, a task where the target stimulus does not pop out from the distractors to the same degree as in the task used by Maljkovic and Nakayama (in their experiments the target was always the

oddly coloured diamond among two diamonds of a different colour; see also Hillstrom, 2000).

A very popular view of the way visual search proceeds postulates that the search involves the combined operation of bottom-up mechanisms sensitive to local feature contrasts (will, say, easily pick out a black item among a set of white ones) as well as top-down mechanisms that bias the search towards certain types of stimuli. In a search for, for example, a red vertical bar, these top-down mechanisms will bias the search towards red items and vertical items. These are the key processes involved in visual search according to many models of the search process (Duncan & Humphreys, 1989; Treisman & Sato, 1990; Wolfe, 1994; Wolfe, Cave, & Franzel, 1989).

In the so-called “conjunction” search task, no single feature distinguishes the target from the distractors. The target is only defined by a conjunction of features and shares one feature with each of the two distractor sets. An example of this is a search for a red vertical bar among red horizontal bars and green vertical bars (so that each set of distractors shares one feature with the target). According to many theories of visual search, top-down activation of the relevant feature maps is needed for efficient search under these conditions. Experimental results have indeed generally been supportive of this framework (Bacon & Egeth, 1997; Duncan & Humphreys, 1989; Friedman-Hill & Wolfe, 1995; Treisman & Sato, 1990; Wolfe et al., 1993).

In Kristjánsson et al. (2002) we showed how between trial priming (in this case of the orientation of the target) could account for a large component of the effects normally attributed to top-down guidance in conjunction search tasks. Two examples of the task that was used are shown in Figure 6A. We contrasted performance under a standard conjunction condition where the search task was the same (to find a red vertical bar among green vertical and red horizontal bars) on *all* trials, with a “random” condition where the search task alternated unpredictably between trials from being a search for a red horizontal bar among green horizontal and red vertical bars and a search for a red vertical bar among red horizontal and green vertical bars. The important point to note is that the information available for top-down guidance is much less in the random condition than the conjunction condition, since in the random condition, the target on each trial can be either horizontal or vertical, and the target identity always depends on the identity of the distractors, whereas in the conjunction condition the target was always vertical. Thus, theories of visual search that rely on top-down guidance and bottom-up feature contrasts should predict that the search would be much slower in the random condition than in the conjunction condition. The observers were instructed to search for the red vertical item under the conjunction condition while in the random condition they were simply instructed to search for the oddly oriented red target.

Overall, the performance was faster under the conjunction condition than random condition. However, when the target to be found was the same for a few

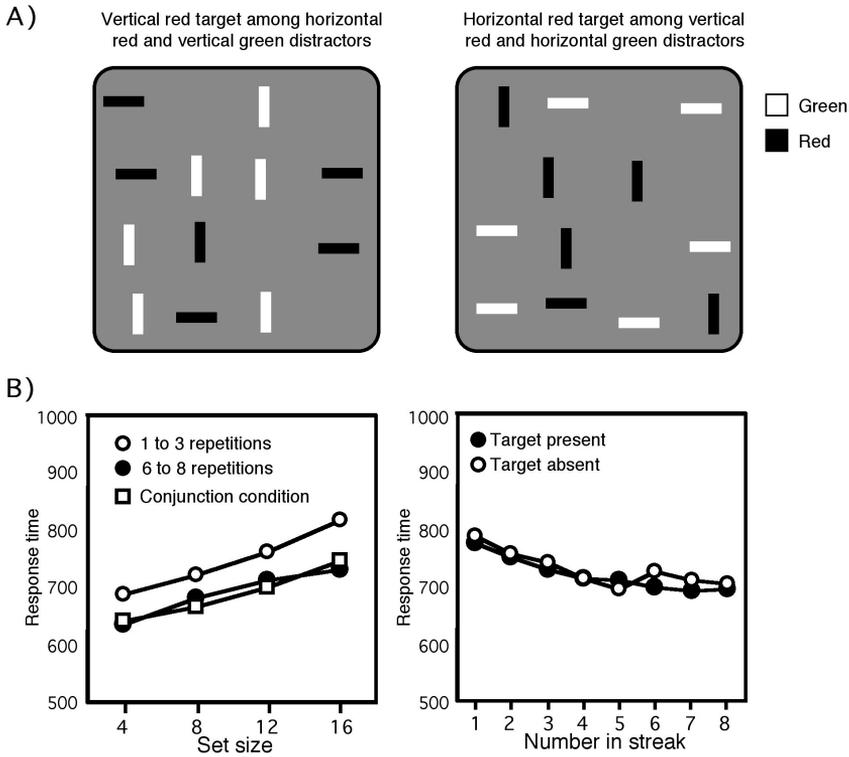


Figure 6. The role of priming in conjunctive visual search. (A) The two possible display types in the “random” condition of Kristjánsson et al. (2002). In the “conjunction” condition the target was always the same (the vertical red item). (B) The left part shows the results for the conjunction condition (open squares) and the random condition (the circles). The open circles show performance for the first three trials within a streak of trials of the same orientation, and the filled circles show performance for the 6th to 8th trials within such a streak. The right part then shows how response times decrease within a streak for the target-present trials (filled circles) and the target-absent trials (open circles). The data are replotted from Kristjánsson et al. (2002).

trials in a row in the random condition, search performance became similar to when the potential target was the same on *all* trials (see Figure 6B, left panel). In other words performance in the random condition became similar to performance under the conjunction condition when the same target had appeared for a few trials in a row (no more than 6–8 repetitions). On the other hand, performance was a lot slower under the random condition right after the target identity switched from being the vertical red bar to the horizontal red bar or vice versa. This result shows that priming plays a critical role in determining response times in visual search. Even though the amount of available top-down guidance was very different between the two different conditions, performance became

equivalent. In Wolfe, Butcher, Lee, and Hyle (2003), the authors presented results supporting our general conclusions, using a different search paradigm where the target could be distinguished from a distractor on the basis of a single feature alone (generally called a “pop-out” task).¹ It is noteworthy that the priming effects in the conjunction search task seem to have an effect on overall search times, rather than the search *rates* since the priming does not change the response times as a function of the set size, but only has an effect on the overall search times (see also Wolfe et al., 2003). Effects that influence overall search times rather than search rates have traditionally been thought to mean that the effect exerts its influence at a stage of different from the search itself (e.g., Horowitz & Wolfe, 1998). The possibility that our conclusions raise, however, is that top-down guidance in visual search studies has different effects from what has often been thought.

The right panel of Figure 6B then shows how response times decreased as the target orientation was repeated in the random condition for the target-present and target-absent trials. The figure shows that a similar pattern was found for both the target-present and target-absent trials, suggesting that priming may be based on the whole search array rather than just the target in each case, since there is a strong priming benefit on search performance even though there is no target present. It is likely that the observers find it easier to decide that no target is present in the search array when the two distractor sets are the same between trials. Consequently, we have gone on to show that the priming attributable to the target-absent, or “blank” trials is indeed completely independent of target identity (Kristjánsson & Driver, 2005) and can take place between two adjacent trials where no target was presented on *either* trial (see Figure 7C below). I have more to say on that issue below.

The results in Figure 6 (from Kristjánsson et al., 2002) show that priming can account for a large chunk of effects usually attributed to top-down guidance, since performance under the “random” condition became similar to performance under the “conjunction” condition with only a few repetitions of the same target. Clearly this repetition benefit cannot be attributed solely to top-down guidance since there is uncertainty about the target identity on each trial. It is important, however, to keep in mind that this applies only to the current paradigm so other paradigms may be found where explicit top-down guidance plays a more significant role. The findings clearly show, nevertheless, how the short-term learning under investigation here can have critical effects in a well investigated experimental paradigm, where the leading theories do not account for these priming effects in any explicit way.

¹ Wolfe et al. (2003) termed these effects examples of *implicit* top-down guidance as opposed to explicit top-down guidance. Whether these priming effects can actually be construed as such remains to be seen, however. What is clear, however, is that the priming effects are impervious to any influence from explicit top-down control (see, e.g., Maljkovic & Nakayama, 1994).

PRIMING OF PERCEPTUAL GROUPS

I mentioned earlier that some authors have argued that attention is necessary for conscious perception (Mack & Rock, 1998; Nakayama & Joseph, 1998; Rensink, 2000). A number of experiments have shown, however, that processes of perceptual organization such as grouping by colour or luminance are operative under conditions of seeming inattention blindness, indicating that the “blindness” is not quite complete. Thus, for example, Russell and Driver (2005; see also Driver, Davis, Russell, Turatto, & Freeman, 2001) found that grouping of like colour was operational even when observers were engaged in a difficult task at the centre of gaze. In a similar vein, Moore and Egeth (1997) presented a pair of horizontal lines with a background of black and white discs that were either randomly placed, or systematically placed such that they formed the inducing elements of either the Ponzo, or Müller–Lyer illusions. The observers’ task was to report which of the two lines was the longer. The result was that when the discs formed the inducing elements of the aforementioned illusions they robustly influenced the line-length judgement even though observers were unable to subsequently report anything about these inducing patterns and seemed unaware of the fact that they had been presented.

Grouping processes also seem to operate in visual search tasks where a specific target stimulus must be found against a background made up of a set of distractors (Duncan & Humphreys, 1989; Treisman, 1982). The distractor items can, in this case, be considered to form a background that must be ignored once it is clear what the identity of the target is. In a set of experiments my colleagues and I have investigated the fate of the distracting items in a visual search display in terms of how, and to what extent they are processed. From the aforementioned results from the “inattention blindness” paradigm (Moore & Egeth, 1997; Russell & Driver, 2005), one can assume that grouping processes are still operative, presumably meaning that at least some rudimentary processing of unattended or ignored stimuli takes place, at the very least to the extent that they are perceptually grouped.

As mentioned before, the most popular view of the way visual search proceeds postulates that search proceeds through the combined operation of bottom-up mechanisms, sensitive to local feature contrasts, and top-down mechanisms that bias the search towards certain types of stimuli by selectively activating the relevant feature maps. If search is to be efficient (typically defined as taking equally long no matter how many distractors accompany the target in the display) either or both of these processes must be able to operate effectively.

In Wang, Kristjánsson, and Nakayama (2005; see also Kristjánsson, Wang, & Nakayama, 1999; Nakayama, Kristjánsson, & Wang, 2000) we showed that the combined effect of top-down and bottom-up mechanisms cannot, however, account for all occurrences of efficient search from visual search experiments,

since we found that search could be very efficient, even in cases where targets could not be distinguished from distractors either by bottom-up guidance or top-down guidance. Using a paradigm that we termed “multiconjunction search” where the target can be any of four different display items on any given trial, we found very efficient search with many different sets of stimuli (see Figure 7A). The instructions to the observers were to simply search for an odd-one-out target on each trial and indicate whether it was present or not. The two distractor sets on each trial were picked from the three remaining item types and always shared one feature (colour or shape) with the target. Aforementioned theories of visual search would predict that search would be inefficient under these conditions, since the target cannot be distinguished from the distractors by bottom-up contrasts of simple features and top-down selection cannot allow efficient search, since any of the set of possible display items can be the target on any given trial. To put this another way, there is no preferential information that helps to find any of the four potential targets for each trial, except that the target on each trial will be the odd-one-out.

To tie these findings to the present topic of how previous task history, in the short run, influences deployments of visual attention, we argued that the efficient search we observed, where explicit guidance from bottom-up, and top-down mechanisms is eliminated, could be explained by perceptual grouping. Then we went on to show how priming of perceptual groups occurs in the absence of any target-related priming effects. In one of the experiments in Wang et al. (2005, Exp. 6) we showed that priming can have a major effect on the results in this search task. Figure 7C shows how search becomes faster as the same search is repeated for a number of consecutive trials. More importantly, in Kristjánsson and Driver (2005) where we used a similar search paradigm, we have showed that the priming, or facilitation of performance, can take place between two adjacent target-absent trials (see Figure 7B). The importance of this finding in the present context is that priming can operate on a whole search array that does not contain a target to be acted on. This strongly suggests that priming can operate on grouped sets of items that must be ignored. The task of ignoring the distractor sets can, in other words, be facilitated by previous exposure to the same set of items even when no target is present. These priming effects from blank trials are important in that they show that the history effects that are the topic of this review are not only found for the “object of attention” in each case; they are also found for tasks where *all* display items are to be rejected as distractors. Whether or not these more “global” priming effects are manifestations of a similar sort of (or the same) mechanism to the ones that operate on the target in each case remains to be seen, however, but what is clear is that priming of rejected or ignored items can play a role in maintaining the stability of our visual environment, just the same as such effects connected with the target in each case.

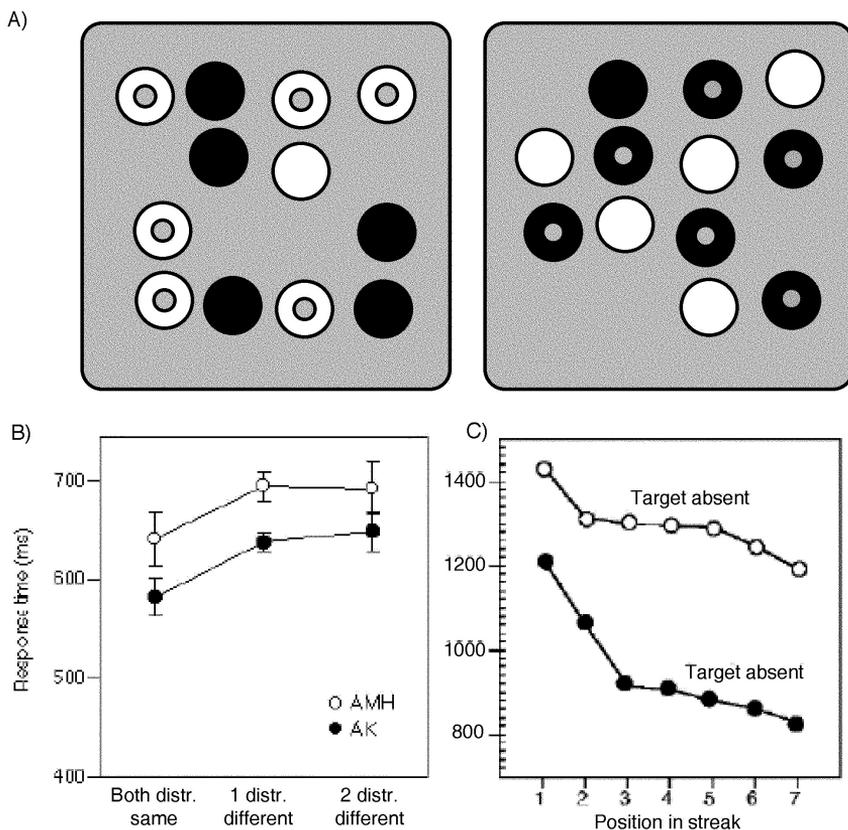


Figure 7. (A) Two examples of the experimental display in Wang et al. (2005; a comparable task was used in Kristjánsson & Driver, 2005). The target could, on any given trial be one of four different display items (a white disc, black disc, white donut, and black donut). In Wang et al. (2005) the target could only be distinguished from the distractors by a conjunction of features, meaning that the target always shared one feature with each of the two distractor sets on any given trial, while in Kristjánsson and Driver (2005) no such restrictions were in place; any of the four possible display items could be the target among distractor sets from any two of the remaining three possible display items. So in the sample display the target is the white disc, sharing the feature of whiteness with the white-donut distractors, and being a disc with the black-disc distractor set. (B) The response times for two observers between two adjacent target-absent trials depending on whether both distractor sets are the same as on the previous trial, one set is changed, or both sets are changed (from Kristjánsson & Driver, 2005). (C) Changes in performance as a function of the repetition of the same type of search for target-present and target-absent trials separately (from Wang et al., 2005).

WHAT ARE THE NEURAL MECHANISMS INVOLVED?

Using studies of patients with neurological disorders and functional neuroimaging, my colleagues and I (Kristjánsson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Kristjánsson, Vuilleumier, Husain, Macaluso, & Driver, 2004b) have investigated the neural correlates of priming effects in a visual search task where observers search for an oddly coloured item among distractors of a different colour (using a task similar to the one used by Maljkovic & Nakayama, 1994, 1996).

In the neuroimaging study, our observers performed the pop-out visual search task while their brains were scanned with functional MRI in an attempt to measure changes in blood flow as priming develops. We found suppression of BOLD (Blood Oxygenation Level Dependent) activity,² correlated with both colour and position priming in many diverse brain regions, but in particular with regions connected with mechanisms traditionally thought to be involved in attentional orienting (see, e.g., Awh & Jonides, 2001; Corbetta & Shulman, 2002; Culham, Cavanagh, & Kanwisher, 2001; Hopfinger, Buonocore, & Mangun, 2000; Jovicich et al., 2001; LaBar, Gitelman, Parrish, & Mesulam, 1999; Yantis & Serences, 2003), such as the intraparietal sulcus in the parietal cortex, and the frontal eye fields in the frontal lobes, suggesting that the priming may involve enhanced attentional processing of the features of a primed stimulus (see also Yoshida et al., 2003, for partly overlapping findings with a similar task, although in their study they did not find any repetition suppressions in regions such as the frontal eye fields as was the case in our study). Consistent with a role for the frontal eye fields in the priming effects, Bichot and Scholl (1999, 2002), using single cell neurophysiology on monkeys performing a comparable visual search task to the one that we used, found that FEF neurons showed enhanced responding to the target and decreased responding to the distractors as more and more trials of the same type were repeated. These cells, then, seem to discriminate target from distractors earlier and better with repetition.

In our imaging study, modality specific priming effects for colour priming only, were found in the lateral occipital complex/fusiform gyrus, possibly corresponding to area V4, an area most often associated with colour processing (Bartels & Zeki, 2000; but see Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998). Priming effects specific to position priming were found in areas in the inferior parietal lobe and lateral inferior frontal cortex that have been proposed to be part of a network connected with reflexive attentional orienting to stimuli that capture attention (Corbetta & Shulman, 2002).

² Suppression of BOLD activity following the repetition of a particular stimulus is indeed a common finding in the fMRI literature; usually termed “repetition suppression” (see, e.g., Grill-Spector & Malach, 2001; Kourtzi & Kanwisher, 2001; Yoshida, Tsubomi, Osaka, & Osaka, 2003).

Using a similar sort of experimental task³ we also tested performance on this task on patients with defective attentional mechanisms following brain damage (Kristjánsson et al., 2005). Their lesions were centred on the inferior parietal lobes and they exhibited behavioural patterns consistent with the clinical diagnosis of hemispatial neglect (Halligan, Fink, Marshall, & Vallar, 2003; Karnath, Ferber, & Himmelbach, 2001; Karnath, Milner, & Vallar, 2002; Mort et al., 2003; Vallar, 1998). The results from those experiments show that these priming effects are relatively intact in these patients, which indicates that the attentional network that is disrupted in neglect cannot be the sole locus of these priming effects, even though the imaging results mentioned above show strong correlation between repetition suppression effects of attentional mechanisms and priming measured behaviourally. An important difference was, however, observed between colour and position priming for the neglect patients. As mentioned before, we used a task similar to the one used by Maljkovic and Nakayama (1994, 1996) where the target was the oddly coloured diamond, and the observers had to judge whether the target diamond had a notch cut off at the top or at the bottom. In one version tested in Kristjánsson et al. (2005), we only presented the stimuli for 200 ms followed by a blank screen. For the neglect patients this meant that on a large number of trials they missed a target if it was presented on the left. This behavioural pattern is normally thought to reflect the neuropsychological disorder of extinction, which is very often seen concurrently with neglect in the same patients. Measuring the priming patterns for those trials where a preceding target had been missed we found strong priming effects for colour from missed targets, but no priming at all for position from the missed targets. This, most likely, means that the attentional network that is disrupted in neglect patients plays a vital role in the position priming, but not (at least not to the same extent) in the colour priming. It is also important to note that the imaging results revealed the strongest repetition suppression as a function of priming in the intraparietal sulcus (along with the frontal eye fields; see Kristjánsson et al., 2004b), while the patients we tested had damage that was more ventral in the parietal cortex. In other words, the critical regions in the parietal cortex may have been intact in our patients. On the other hand the inferior parietal regions that showed the position-priming specific effects in the imaging study may indeed have been the same regions that were lesioned in our patients.

Overall, the findings from fMRI and neuropsychology indicate that the priming effects are reflected in activity in an extended network of regions in the brain. Clearly, well-known neurological structures often associated with attentional mechanisms are involved. Areas responsive to colour seem to reflect

³ To rule out lateralized effects in the imaging studies and object-based attentional confounds in the patient study, connected with the left versus right discrimination in the task used by Maljkovic and Nakayama, we used a similar task to them, except that the diamonds had a cutoff at the top or at the bottom and the task was an up versus down judgement on the target.

colour priming, while the attentional mechanisms damaged in hemispatial neglect may be the ones that show the strongest priming related effects for position repetition. Further research is, however, quite clearly necessary to provide conclusive answers about the neural mechanisms underlying the behavioural effects and the precise involvement of the attentional mechanisms.

GENERAL DISCUSSION

The general conclusion that I want to draw here, is that with each attentional allocation to a certain feature or location, processing for that feature (or location) is subsequently facilitated. This can build up over a few trials if the critical property remains constant, resulting in strong facilitation for this property after a few trials. This facilitation allows faster and more accurate analysis of the locus of that property, be it a feature or a location. This can take place in object-based coordinates, for a feature or a given location on an object, but is also evident for absolute positions in the visual field as shown by Maljkovic and Nakayama (1996; see also Kristjánsson et al., 2005; Kristjánsson et al., 2004b). There are, of course, many examples from the experimental literature of how previous history influences perception directly. Various aftereffects are prime examples, such as the motion aftereffect (see Anstis, Verstraten, & Mather, 1998; and Mather, Verstraten, & Anstis, 1998, for a thorough overview). One of the most interesting features of these aftereffects is that they seem to modulate sensitivity in some cases. For example, adaptation to a stimulus drifting at a certain velocity increases sensitivity to speed changes around the adapting velocity (Bex, Beddingham, & Hammet, 1999; Clifford & Langley, 1996; Kristjánsson, 2001; see also Gibson, 1937). Even though the evidence here doesn't have the same phenomenological quality as the motion aftereffect, there is little doubt that that the effects of previous history discussed here have a strong influence on perception through the modulatory influence of attention.

The learning mechanisms investigated in the research that I have reviewed here induce a short-lived influence on performance—the effects only last for a limited number of trials (see, e.g., Maljkovic & Nakayama, 1994, 1996). A clear conclusion from this is that the learning is probably not related to mechanisms involved in longer lasting memory traces, nor is it likely to be directly related to working memory functions given that working memory functions are conscious and explicit in nature (Baddeley, 1986; Baddeley & Lieberman, 1980). The learning investigated here is, in contrast, automatic and does not seem to require much cognitive effort, except for that required to perform the basic task in each case. And indeed, as mentioned before, explicit knowledge about the cue–target relationship or the upcoming critical trial cannot be used in this context (Kristjánsson & Nakayama, 2003; Maljkovic & Nakayama, 1994). The learning is also bound to simple features; it cannot integrate over different properties (location or feature), while learning of two different patterns can occur

simultaneously and independently (Nakayama et al., 2004). Priming is generally thought of as an altered representational state for a feature or an object, resulting in facilitated processing for that feature. Our results may reflect such a process that results in some form of biased activation (see, e.g., Desimone & Duncan, 1995; Everling, Tinsley, Gaffan, & Duncan, 2002; Reynolds et al., 1999) of specific features or objects, in object-centred coordinates. It is likely that the learning proceeds through temporary changes of activity in neural mechanisms that have been activated recently, as shown in our neuroimaging results summarized above (Kristjánsson et al., 2004b).

Why do these findings matter?

What are the potential benefits of such a learning system? As I mentioned in the introduction, many lines of evidence suggest that human observers do not maintain a detailed representation of their visual environment from one moment to the next—the findings from change blindness, and inattention blindness studies clearly indicate this. Many have in fact hypothesized that we do not keep a detailed representation of our environment from one moment to the next, but that representations are formed as they are needed (Ballard et al., 1997; O'Regan, 1992; Rensink, 2000; see also Dennet & Kinsbourne, 1992).⁴ What I want to propose here is that these learning mechanisms allow us to quickly reform representations of previously viewed stimuli. To take an example, a predator (or prey) in the visual field of an animal is unlikely to be in the same location in retinotopic coordinates from one moment to the next. Self-motion of the viewer or movement of the predator sees to that. A memory system that keeps track of critical features of that predator would seemingly be of immense importance in this context, allowing quick reorientation to those critical features, and thus faster responding to the danger.

Why would there be this facilitation of like items while at the same time there seems to be equal inhibition of other items that are not task relevant as shown for example by Maljkovic and Nakayama (1994), where observers were particularly slow to respond to display items that served as distractors on the previous trial? The answer must be that this is beneficial since the targets in the visual field seem to be relatively stable over time. The important stimuli in our environment do not normally change rapidly from one moment to the next. Keeping track of the location of one's child as she runs around a playground involves keeping track of the same colour combination of hat and coat over time. At the same time, the pertinent features of the other children in the playground that must be

⁴Note, however, that there is certainly evidence that the visual system seems in some cases to actively create representations that do *not* seem to be needed for immediate behaviour. *Active* filling in at the blind-spot is probably a good example of that (see, e.g., Ramachandran, 1992; see also Ramachandran & Gregory, 1991).

rejected quickly, as “nontargets” are likely to remain relatively stable as well. Similarly, the features of a predator that is being monitored by anxious prey normally stay constant. Other visual features may occur regularly in the same context as the predator, but these must be ignored if attention is to remain focused on the predator. Another example from experimental psychology of such inhibition of items that should be ignored, or are irrelevant, is the *negative priming* effect (Tipper, 1985, 1992), where orienting is particularly slow to stimuli that have been actively ignored in the recent past.

Related phenomena

At this point it seems appropriate to mention some other phenomena in the literature that might be relevant to the learning under investigation here. Chun and Jiang (1998) had their observers perform a relatively difficult visual search task repeatedly. What their observers did not know was that some of the trials had a repeated *context* where all the display items were in the same locations as on previous trials (although they randomly changed colour). Even though this consistency went unnoticed by the observers, the effects on performance were quite large. Observers responded faster for the repeated contexts than novel contexts, and the benefits were specific to the trials where the target was in the same location as before within a given previously presented context, not when it appeared in a novel location within that context. Chun and Jiang (1999) then went on to show that “contextual cueing” of this sort can also occur based on the semantic context of the items rather than their absolute locations within that scene. This is evidence for a relatively long-lasting implicit memory for context, perhaps allowing observers to quickly establish reference points of importance for a previously viewed visual scene (see also Chun & Jiang, 2003). The learning phenomena under investigation here, seem, on the face of it, not to be as long-lived as contextual cueing, but note, however, that they do seem to build up over the course of a number of consecutive trials.

Geng and Behrmann (2002, in press; see also Miller, 1988) have investigated how manipulating the probability of a target appearing in a particular location of a set of possible ones affects response times to visual targets. They have shown that increasing the probability that a target will appear in a particular location within a given block of trials in a visual search task increases the efficiency of attentional allocation to that location. Importantly, Geng and Behrmann showed that this facilitation was not simply due to position-repetition priming similar to what Maljkovic and Nakayama investigated. They called this “probability cueing” and have also showed that this putative mechanism can be distinguished from what is traditionally known as exogenous and endogenous attentional orienting. Probability cueing of this sort may very well be related to the findings discussed in this paper where location consistency within a cue

resulted in learning of cue–target relations, and may allow similar benefits in attentional orienting based on consistency.

A hotly debated topic in the recent literature on visual attention is the putative role of memory processes in visual search tasks. Opinions vary as to whether there is any evidence for memory in visual search or not (Horowitz & Wolfe, 1998, 2003; Kristjánsson, 2000; Shore & Klein, 2000; von Mühlenen, Müller, & Müller, 2003).⁵ If such a memory mechanism does exist however, it would certainly be of relevance in the current context, since it would allow orientation to items of interest and the tagging of already checked items as irrelevant within the same search trial. While the issue is certainly undecided, there is strong evidence that indicates that following the sudden appearance of an object in the visual field (such as a peripheral cue indicating the location of an upcoming target), performance of some sort of a visual task at that site is greatly facilitated temporarily, but then followed by a period during which the allocation of attention to that location takes longer than otherwise (Posner & Cohen, 1984). Some have claimed that this effect, often called “inhibition of return” might be a manifestation of a mechanism that allows visual search to proceed in an effective manner; i.e., making it less likely that a previously inspected item in a search array is revisited (Klein, 1988; Klein & Macinnes, 1999; Takeda & Yagi, 2000; but see Wolfe & Pokorny, 1990, and Klein, 2000). Whether inhibition of return allows the tagging of already inspected items in a visual search task is doubtful, however, since the times scales involved in visual search tasks and inhibition of return are hardly compatible (Ward, Duncan, & Shapiro, 1996).

Another finding, potentially related to the research discussed here, is the so-called “implicit peripheral cueing” investigated by Lambert and colleagues (Lambert, Naikar, McLachlan, & Aitken, 1999; Lambert, Norris, Naikar, & Aitken, 2000). They found that visual orienting was influenced by peripheral letter cues that were reliably connected with particular target locations, even though observers were completely unaware of the validity of the cues. In other words the cues exerted their effect irrespective of whether or not the observers were aware that they were in fact valid cues. This may very well be another example of the workings of a memory system similar (or the same) to the one that I am discussing here.

Finally, it is worth mentioning that Shomstein and Yantis (2002, 2004) found that attentional selection, which has often been shown to be at least partly object based, need not be so in all cases. They argued that the so-called object-based

⁵ Furthermore, a considerable amount of research results shows that when observers move their eyes around a visual scene searching for a particular target, memory is good for previously fixated locations (Dickinson, Chen, & Zelinsky, 2003; Gilchrist & Harvey, 2000; Peterson, Kramer, Wang, Irwin, & McCarley, 2001). My own view, however, is that these studies cannot address the question of memory for attended locations at all, since it is quite clear that we can change the focus of our attention without moving our eyes.

attentional effects might manifest themselves because of an “object-specific prioritization process” that operates only when there is uncertainty about the upcoming target location. What they found, specifically, was that there was no “flanker effect” from irrelevant items (see Eriksen & Eriksen, 1974) within objects when the target always appeared in the same place, as there was when the location of the target on each trial was uncertain. In other words statistical properties determine the way attention is allocated—meaning that object-based selection is in some sense strategic and sensitive to prior probabilities of the target location. The potential overlap of these findings with the learning mechanisms in this paper remains to be seen, however. For example it is not quite clear at what timescale this selection process operates since perceptual processing of the stimuli was not terminated with a mask as in our studies, but Shomstein and Yantis speculated that when the stimuli were masked with short target/mask SOAs, as in the cueing studies documented here, this probability-sensitive selection mechanism would not be operative. In any case, the relation between the findings of Shomstein and Yantis and the effects under discussion here remains an open question.

Neural mechanisms

Many things remain unclear at present about the potential neural mechanisms responsible for the learning effects that are the topic of this review. On the one hand the nonintegrative aspects of the learning argue against the crucial involvement of integrative neural mechanisms such as the parietal cortex. Some have argued that one part of the function of the parietal cortex may be integration of simple visual features into objects (Robertson, 2003; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). As mentioned before, our experiments on hemispatial neglect patients with parietal damage performing a pop-out visual search task did indeed show that the parietal cortex cannot be the sole locus of these effects, since the priming effects there were more or less intact, albeit with the important caveat that the *position* priming effect seemed to require awareness of the preceding priming stimulus, whereas *colour* priming seemed to operate without awareness (Kristjánsson et al., 2003).

On the other hand, the fMRI results from Kristjánsson et al. (2004b) did show considerable correlation of priming with repetition suppression in parietal areas, both for colour and position priming, but these effects were centred on the intraparietal sulcus, more superior to the loci of the lesions of our patients, which could mean that the intraparietal sulcus is indeed a crucial site for these priming effects (see also Yoshida et al., 2003). As in many other studies the neural correlates of priming were found to involve suppression or reduction of neural activity as similar properties are repeated (Grill-Spector et al., 1999; Grill-Spector & Malach, 2001; Kourtzi, Erb, Grodd, & Bühlhoff, 2003; Kourtzi & Kanwisher, 2001; Koutstaal et al., 2001).

The results of single unit studies in the frontal cortex of monkeys performing a visual search task have also pointed to an important role for mechanisms of the frontal cortex. Bichot and Schall (1999; see also Bichot & Schall, 2002) showed how single cells in the frontal eye fields discriminate target from distractors earlier and better with repetition. These FEF neurons showed enhanced responding to the target and decreased responding to the distractors as more and more trials of the same type were repeated. This is indeed in line with our fMRI results mentioned before where we showed significant reductions of BOLD activity in the frontal eye fields with repetition of target colour or location (Kristjánsson et al., 2004b). It seems, then, that the so-called frontoparietal attention network is strongly involved in the priming of pop-out effects. What this may reflect is that the attentional system may have “made up its mind” based on previous task history, which results in decreases in activity in the areas critical for attentional orienting. In other words, one may speculate that the attentional selection has already taken place; the system is already biased towards a particular colour or location resulting in lessened activity since less effort is required for the selection process.

Some strong hints regarding the possible neural locus of learning of cue–target relations, reviewed in the first section of this paper, comes from the work of Olson and Gettner (1995, 1996, 1999; see also Tremblay, Gettner, & Olson, 2002). Their single cell studies in monkeys point to the involvement of the supplementary eye fields (SEF) in the prefrontal cortex in the learning that we observed. In particular, they have found SEF neurons that showed the highest firing rates when the animals were preparing saccadic eye movements to particular locations on a stimulus irrespective of its absolute position. The importance of this in the present context is that the SEF show activity patterns concerned with spatial relations between two stimuli, in object-centred rather than position-centred coordinates. This object-based activity has considerable resonance with what we have found in Kristjánsson et al. (2001) and Kristjánsson and Nakayama (2003). Chen and Wise (1995) have proposed that the SEF play a role in eye movements, and in object-based coordinates rather than in coordinates based on absolute position. Their proposal was that the SEF are part of a neural system that is capable of *learning* flexible, nonspatial stimulus relations between stimuli and the responses to those stimuli.

Since many lines of evidence have shown a tight link between attentional orienting and eye movements both at the neural level (Kustov & Robinson, 1996) and behaviourally (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Kristjánsson, Chen, & Nakayama, 2001; Kristjánsson, Vandenbroucke, & Driver, 2004a), the SEF are ideal candidates for the learning of cue–target relations I have reviewed above given their known role in eye movement generation (Schall, 1991), which seems to operate in object-based rather than absolute coordinates as described above (Chen & Wise, 1995, 1996). Indeed, in a preliminary investigation of whether

this learning can influence eye-movement generation, we found that consistencies of this sort can indeed result in faster and more accurate saccades (Edelman, Kristjánsson, & Nakayama, 2001). Related to this, the priming of pop-out in a visual search paradigm has also been shown to facilitate eye movements (McPeck, Maljkovic, & Nakayama, 1999). Future neuroimaging, neurophysiological, and neuropsychology research will hopefully cast further light on that issue, and perhaps on the involvement of the SEF in the learning processes that I have reviewed in this paper.

Some outstanding questions

Where in the perceptual process do these learning phenomena exert their influence? Even though the evidence in this paper clearly indicates that the learning affects attention deployments and that neural mechanisms connected with attentional control are involved, it cannot be ruled out that these learning phenomena exert their influence at other levels of the perceptual process. It would, for example, be interesting to know whether these effects can have an effect upon surface assignment (Nakayama, He, & Shimojo, 1995; see also Driver & Baylis, 1996; Marr, 1982), a process that has often been thought to occur before any attentional effects (Driver & Vuilleumier, 2001; He & Nakayama, 1994). It is, however, an open question whether attentional deployments are the sole locus of influence of these learning effects. For example, our fMRI study revealed modulations of activity in visual cortex connected with priming, an “early” part of the perceptual process, but the possibility that this reflects feedback modulation of activity rather than something directly connected with the learning effects remains to be seen (see, e.g., Noesselt et al., 2002).

Another potential “puzzle” about the results concerns the fact that the behavioural results from the experiments show little, if any, top-down modulation. In light of this, it seems counterintuitive that the key brain regions involved in the priming from the results of the imaging study are the “prime suspects” of the top-down attentional network (the “frontoparietal” attention network; see discussion of neural mechanisms above). These regions show lessened BOLD activity as the priming builds up. I think that the answer may be that the attentional system has “made up its mind” when the same position or feature has been repeated. The system is already biased towards seeking out a green target if the target has been green for a number of trials in a row, which results in lessened activity in the attention networks with priming. A conclusive answer to this remains unknown, however.

Another interesting question arises from the results above clearly indicating that learning of cue–target relations of position and colour can build up simultaneously and priming of pop-out of colour and position builds up simultaneously. It would be interesting to know how many dimensions can show

such “parallel priming”. Do the primed properties that build up simultaneously need to belong to different modalities? Could priming connected with two colours of a single object build up simultaneously, for example? In other words, can priming of dimensions that share the same neural machinery show such parallel priming? Experiments are currently under way in my laboratory to address some of these issues. It is clear from the results of Krümmenacher, Müller, and Heller (2001) that there is considerable processing of redundant features in visual search tasks, but the “dimension weighting account” of visual search (Müller, Heller, & Ziegler, 1995) also argues that dimensions are weighted according to their behavioural relevance at any given time, so an interesting question concerns whether irrelevant features will result in priming effects, given that the irrelevant dimensions seem to be processed but their weighting in terms of attentional processing is attenuated in line with their behavioural relevance.

CONCLUSIONS

I have summarized an extensive set of results, that show varied manifestations of task history effects on attention deployments. First, I have demonstrated the existence of a relatively primitive learning mechanism that allows attention to be selectively directed to a certain position within an abruptly onset cue depending on the nature of the previous relationship between the cue and the target. This phenomenon seems to share important properties with the priming of pop-out in visual search in that the learning takes place in object-centred, rather than absolute retinal coordinates and the learning is not amenable to voluntary control. Furthermore, learning of two independent relationships can take place simultaneously, which shows that this learning cannot integrate two different statistical patterns (see Nakayama et al., 2004). Related to this is the finding that the learning cannot occur for relations such as an “if-then” contingency (Kristjánsson & Nakayama, 2003), which may be another manifestation of the nonintegrative nature of this learning process. Another important feature of the learning is that it builds up over a number of trials in a cumulative fashion, which is also the case for the priming of pop-out.

I have also documented how similar priming of target identity operates in a relatively difficult visual search task, while also showing how ignored items, more specifically distractor sets in a visual search task, can be primed from one trial to the next, and how this priming of background items occurs independently of any priming bound specifically to the target. I have also discussed how our experimental findings have led us to believe that priming can occur over sets of distractor items, or more generally of perceptual groups. Finally, I have presented preliminary results from ongoing investigations into the possible neural mechanisms responsible for these learning phenomena. While we are beginning to understand the neural mechanisms involved in these effects, much work is

still to be done to obtain a thorough understanding of this issue. What seems clear, however, is that the networks involved in attentional orienting play a key role in the effects. This seems appropriate since the behavioural evidence here has clearly indicated how the learning affects how attention is allocated in a given visual scene.

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