Guidance of Eye Movements during Visual Conjunction Search: Local and Global Contextual Effects on Target Discriminability

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ABSTRACT

The composition of a visual scene influences the ability of humans to select specific details within that scene for discrimination or foveation with saccadic eye movements. With the goal of establishing an animal model to investigate the neural mechanisms underlying the deployment of visual attention and the guidance of saccades during visual search, we studied the visual behavior of three monkeys while they performed a conjunction (color + form) search task similar to those used in human studies. We found that search performance declined when distractors adjacent to the target shared its color, thereby revealing that color was more discriminable than form in these displays and suggesting that monkeys perceptually grouped stimuli by proximity and similarity. Search performance also varied with the overall composition of the display. Most importantly, saccades were biased toward distractors sharing the target color when there were few of them within the display and away from those distractors when they were numerous. Lastly, the monkeys initiated saccades with a fixed latency, suggesting that their responses to the display were automatic and that search strategies did not involve attentional resources beyond those recruited for regulating saccades. We conclude that monkeys adapt their visual strategies, largely via bottom-up processes, to both the local and the global context of the search. These findings suggest that the visual behavior of monkeys is guided by strategies similar to those observed in humans.

INTRODUCTION

The analysis of visual images generally entails the allocation of attentional resources to particular aspects of the images owing to bottom-up and top-down factors (Egeth and Yantis 1997). Such visual strategies exist to circumvent the limited attentional resources available at any point in time and thus reveal the limited capacity of our visual system beyond retinal limitations. One experimental approach that has been particularly valuable to study these strategies is the visual search paradigm, with which we can assess the efficiency of a subject to find a target stimulus within a multi-stimulus display. Our current understanding of how attentional resources are deployed during visual search is related to the variability in the discriminability of the target across tasks (Wolfe and Horowitz 2004). Target discriminability depends greatly on the similarity between the target and its distractors: Finding a target stimulus defined by a single, distinct visual feature (a feature search task) is usually easy and takes little time, whereas search efficiency is difficult and slow when target discriminability is low, especially when the target is defined by a conjunction of features (Treisman and Gelade 1980). In such visual conjunction search tasks, search efficiency also depends on the similarity between distractors: the greater the distractor heterogeneity the more difficult the search (Duncan and Humphreys 1989; Nagy and Sanchez 1990). In the case of feature (easy) search tasks, the visual features appear to be processed simultaneously across the display without much contribution of focal attention and the search target appears to "pop-out", regardless of the number of display items. In the case of conjunction (difficult) search tasks, focal attention seems critical and is deployed sequentially between items or groups of items, increasing the number of items slows down performance.

Search efficiency in conjunction search tasks is, however, not only dictated by the overall difficulty of the task. It can improve substantially when visual attention is guided to a certain feature of the target stimulus present in distractors, thus filtering distractors with other features (Wolfe et al. 1989; Wolfe 1994). This particular visual strategy has been shown with studies in which the stimulus composition of the conjunction search display is manipulated by varying the ratio of different distractor types. Search is most efficient when the display is composed of very few of one type of distractor and least efficient when the composition consists of equal proportions of each distractor type (Bacon and Egeth 1997; Egeth et al. 1984; Kaptein et al. 1995; Poisson and Wilkinson 1992; Sobel and Cave 2002; Zohary and Hochstein 1989). This distractor-ratio effect suggests that attentional guidance may change from trial to trial, possibly because of both bottom-up and top-down factors.

The conclusions reached by the above visual search studies are limited in the sense that these studies did not measure the spatial allocation of attention and thus only provide indirect evidence that attention can be guided. The natural exploration of the visual world involves visual attention being deployed by reorienting the fovea with saccadic eye movements (Yarbus 1967; Keating and Keating 1982; Guo et al. 2003). In fact, a growing body of evidence suggests a functional, practically obligatory coupling between overt and covert shifts of attention (see for review Findlay and Gilchrist 2001), perhaps because these two systems share a common neural circuit (Corbetta et al. 1998). Shifting attention covertly to a spatial location facilitates the processing of saccades directed to that location, whereas planning a saccade to a spatial location facilitates perceptual processing of objects at that location (Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996). Measuring eye movements can thus provide more detailed information about how visual strategies unfold. Several studies have already

demonstrated the value of this approach by revealing that the number of saccades made during a visual search task is highly correlated with the time it takes for subjects to report the presence of a target (Binello et al. 1995; Maioli et al. 2001; Scialfa and Joffe 1998; Williams et al. 1997; Zelinsky and Sheinberg 1997).

With respect to the distractor-ratio effect, Shen and colleagues (Shen et al. 2000, 2003) were the first to relate the deployment of visual attention to the guidance of eye movements. In these studies, the distractors fixated during each trial revealed an adaptive visual strategy. Saccades were directed to specific distractors when these had a feature that was relatively rare in the display, whereas no specific feature dimension was preferentially visited in displays with relatively equal proportions of distractor types. As no specific instructions of search strategy were given in these studies and the stimulus composition was random, one could speculate that the guidance of attention was most strongly influenced by bottom-up processes.

With the goal of elucidating the neural mechanisms underlying the deployment of visual attention and the guidance of saccadic eye movements during visual search, we trained three rhesus monkeys to perform conjunction (color + form) search tasks similar to those used by previous human studies. These experiments did not demand high immediate performance accuracy and thus required little training. The monkeys were required to foveate a target stimulus to receive a liquid reward, but were granted a generous length of time so that they could freely visit whichever stimuli they wished to examine. Here we report on the behavioral performance of these animals as it relates to three specific issues that were not resolved in the previous visual conjunction search studies conducted with monkeys (Bichot and Schall 1999; Bolster and Pribram 1993; Buracas and Albright 1999; Motter and Belky 1998b).

We first asked whether the visual search strategies of monkeys are shaped by the composition of the stimuli within a search display. The original study of Bolster and Pribram (1993) showed that the latency of manual responses during conjunction search increases with the number of distractors sharing a feature with the target, suggesting only indirectly that visual strategies changed with display composition. Since then, the distractor-ratio effect has been examined in only one monkey and with search displays of varying number of stimuli (Buracas and Albright 1999). To answer the question posed above, we monitored the eye movements made by monkeys during conjunction search while the proportion of distractor stimuli within the search display was manipulated from trial to trial. We quantified the performance of the monkeys by measuring the accuracy of the search along with the distribution of errors, the total time taken to find the target, and the initial response latency to the search display presentation.

Generally, both monkeys and humans bias their search by visiting distractors sharing one particular feature with the target (Bichot and Schall 1999; Buracas and Albright 1999; Motter and Belky 1998b; Shen et al. 2003; see also Bolster and Pribram 1993; Zohary and Hochstein 1989) and they rarely fixate distractors that share no feature with the target (Bichot and Schall 1999; Findlay 1997). These studies suggest that different distractors have different values and we wished to determine whether the variability in conjunction search performance could be accounted for by the exact arrangement of the stimuli in a search display. Target discrimination has long been known to depend on the overall organization of a search display (Brown and Monk 1975; Banks and Prinzmetal 1976) and it may be the local surroundings of the target that is the most important determinant (Motter and Holsapple 2000; Poisson and Wilkinson 1992). Using a conjunction search display in which the variability in the proportion of distractors was relatively

constant, we tested the hypothesis that the features of the distractors immediately adjacent to the search target have a differential influence on its discriminability.

Despite the general observation that both the time it takes to find a target and the number of saccades increases with search difficulty, the initial response to the search display presentation does not necessarily vary. Some studies have reported that the latency of the first saccade augments with increasing search difficulty (McSorley and Findlay 2001; Shen et al. 2000; Zelinsky and Sheinberg 1995), whereas others have reported only negligible differences (Findlay 1997; Maioli et al. 2001; Williams et al. 1997). Differences in both task instructions and subject preference for strategies favoring either speed or accuracy (e.g., Binello et al. 1995) could possibly account for this discrepancy of observations. As such, it is worth noting that most human studies have focused on reporting the presence of the search target with manual responses without requesting target foveation. This should have promoted the visual behavior that humans exhibit naturally. In contrast, previous monkey studies have required their subjects to foveate the target after a single saccade and the latency of the latter indeed varied with search difficulty (Bichot and Schall 1999; Buracas and Albright 1999; see also Sato et al. 2001; Thompson et al. 2005; but see Motter and Belky 1998a). The results of these studies cannot be easily reconciled with the 'free-viewing' human studies. Given that the visual search task that we implemented somewhat mimics this more natural, unconstrained situation, we sought to determine whether the timing of the initial saccade made by our monkeys in response to the search displays was affected by our manipulations of target discriminability.

A preliminary report of these data has been previously presented (Shen et al. 2004).

METHODS

Animal preparation

Three female rhesus monkeys (*Macaca mulatta*, 4.5-6.0 kg) were prepared in a single surgical procedure carried out under anesthetic and aseptic conditions. All animals were cared for under experimental protocols approved by the Queen's University Animal Care Committee and in accordance with the Canadian Council on Animal Care guidelines and the U.S. Public Health Service Policy on the human care and use of laboratory animals.

One day prior to surgery, a 7-10 day prophylactic treatment of antibiotics (25 mg/kg Cefazolin Sodium or 5.0 mg/kg Baytril) was initiated. Anesthesia was induced with Ketamine (6.7 mg/kg IM). A catheter was placed in the saphenous vein to deliver appropriate fluids (Lactated Ringers) at a rate of 10 mg/kg/hr during the surgical procedure. Glycopyrolate (0.013 mg/kg IM) was administered to control bronchial secretions and was re-administered every three hours during surgery. General anesthesia was continued with gaseous isoflurane (1-3%) after an endotracheal tube was inserted under sedation induced by an intravenous bolus of Propofol (5 ml/kg Rapinovet). Heart rate, pulse rate, pulse oximetry saturation (SpO_2), respiration rate, fluid levels and rectal temperature were monitored throughout the surgical procedure.

A stereotaxic apparatus was used to stabilize the animal's head for the implantation of 8-mm long titanium screws (Synthes Canada Ltd, Mississauga, ON). The screws were inserted into holes drilled and tapped manually into the skull. A dental acrylic implant was firmly anchored to the skull via the titanium screws. Sterilized scleral search coils (18-mm diameter, Cooner Wire Co., model AS-631, Chatsworth, CA) were then inserted subconjunctivally into each eye (Judge et al. 1980). The connector leads for the coils were embedded in the dental acrylic implant. A

head-holding device made of medical plastic (ULTEM resin) was also embedded in the implant to restrain the animal's head during the experiments.

The analgesic Buprenorphine (0.01-0.02 mg/kg IM) was administered during surgery to provide adequate pain relief prior to arousal and every 8-12 hours during the recovery period. The non-steroidal anti-inflammatory Anafen (2.0 mg/kg 1st dose and 1.0 mg/kg additional doses) was administered just prior to arousal, the day following the surgery, and once a day thereafter if needed. The antibiotic and analgesic treatment, combined with an extensive recovery period, ensured that the animal was in excellent health prior to the initiation of behavioral training.

Experimental procedures

Using operant conditioning with positive reinforcement in the form of a liquid reward, monkeys were trained to perform behavioral tasks involving fixation and saccadic eye movements. To ensure the animal's motivation, fluid intake was controlled during training and experimental sessions; unrestricted access to monkey chow was complemented with daily allotments of fresh fruits and vegetables. Animal weight, health status, and fluid intake were closely monitored under the supervision of laboratory technicians, animal care staff and University veterinarians.

During each recording session, monkeys were seated in a primate chair with their heads restrained. The stimuli were generated by a display program using Matlab and the Psychophysics Toolbox (Brainard 1997) running on an Apple Power Mac G4 computer. They were presented on a 37-inch computer monitor (Mitsubishi XC-3730C Megaview Pro 37, 60 Hz non-interlaced, 800x600 or 1024x768 resolution, 16-bit or 32-bit color depth) located 57 cm in front of the monkey's eyes. The stimuli were matched for luminance (25 cd/m^2) by a Minolta CS-100

photometer. Green (CIE x=0.20; y=0.75) or red (CIE x=0.61; y=0.38) stimuli were presented on a black background (<0.01 cd/m^2).

The QNX-based Real-Time Experimentation Software (REX) system (Hays et al. 1982) running on a Pentium III PC controlled the behavioral paradigms, visual displays and data acquisition. Positions of the eyes were monitored either with the magnetic search coil technique (Robinson 1963) or with an infrared camera (Eyelink II, SR Research, Osgoode, ON; pupil-only mode, 500-Hz sampling rate) mounted above and in front of the head of the animal and directed to the eyes through a hot mirror. Field coils were placed around the animal to generate opposing horizontal and vertical magnetic fields. This allowed for the recording of voltage proportional to the horizontal and vertical angular eye position generated from the scleral eye coil. The demodulated voltages of the search coil were low-pass filtered to prevent anti-aliasing (8 pole Bessel, fc=241 Hz), digitized to a resolution of 12 bits, and sampled at 1 kHz (A/D converter, Analogic).

Behavioral paradigms

All visual search trials began with the appearance of a stimulus in the center of the screen, the fixation stimulus. The monkey was required to look at the fixation stimulus within 1000 ms of its appearance. Once the animal's gaze entered a computer-defined window (±1.5°) centered around the fixation stimulus, it had to remain on the stimulus for 500-800 ms. If fixation was successful the trial proceeded to the next visual stimulation described below. If fixation was unsuccessful, the trial was aborted. The inter-trial intervals lasted 500-1000 ms, during which the whole monitor screen projected diffuse white light (2.0 cd/m^2) to prevent dark adaptation.

During a block of conjunction search trials, the target was made of a combination of color (isoluminant red or green) and form (circle or square with the same number of pixels subtending

1 deg of visual angle). Our choice of features and display size was inspired by previous studies of distractor-ratio effects in human as well as studies of visual conjunction search in monkeys (see introduction). The fixation stimulus was identical to the target. Within a single day's session, the target remained the same, but the target of each new session shared one feature with the target from the previous session. For example, if in the previous session the target was a red circle, then the next session's target could either be a red square or a green circle. The distractors were also random combinations of color and form and may or may not have shared a feature with the target (see Bichot and Schall 1999). The positions of the target and distractors were randomly generated, equidistant from the fixation stimulus (10° from center) and from each other. The total number of distractor was either kept constant (7 or 11) across a block of trials to examine local and global contextual effects or allowed to vary from 6 to 11 from trial to trial to examine the display size effect (see below). Because there were always three types of distractor, each type was present at least twice in each display.

Each block of conjunction search trials was preceded by a detection task, in which the intended target of the search first appeared in the center of the screen (acting as a fixation stimulus) and then stepped to one of eight positions (10° eccentric). This simple detection task was performed in a single block of 160 trials, allowing the monkey to be familiarized with the correct target for the subsequent test session.

The visual search tasks used to examine local and global contextual factors on target discriminability were run on different days with eight-stimulus (Fig. 1A) and twelve-stimulus (Fig. 1B) displays, respectively. For the former search task, the type of distractor adjacent to the target was varied randomly from trial to trial. For the latter search task, the number of distractors sharing the target color was varied randomly from trial to trial. The possible color-similar to

color-different distractor ratios were 0:11, 2:9, 3:8, 4:7, 5:6, 6:5, 7:4, 8:3, 9:2 and 11:0. The trials in 0:11-ratio displays were thus feature (pop-out) search trials based on color, whereas the trials in 11:0-ratio displays were single feature search trials based on form.

In a subset of sessions, we contrasted the effect of display size on search performance during blocks of conjunction search trials with that obtained in blocks of feature search trials. Unlike the conjunction trials described above, each of the feature search trials began with a central white stimulus as a fixation stimulus and the target and distractors (circles only) within the subsequent display differed only in the color dimension, i.e., the target was either red amongst green distractors, or the converse.

For all behavioral tasks, the monkey was given 500 ms after stimulus presentation to foveate the target for an interval lasting 200-300 ms. If the target fixation was successful, the animal received a maximal liquid reward amount along with a reinforcement tone (333 Hz). If the first saccade was incorrect and landed on a distractor, the monkey was given an additional 2000 ms to foveate the target; a minimal amount of liquid reward was delivered (<0.33 of the maximal amount along with the reinforcement tone) upon eventual fixation of the target stimulus. If the animal failed to either maintain fixation of the fixation stimulus or locate the target stimulus within the allotted time, the trial was aborted, no liquid reward was delivered, and the next inter-trial interval lasted 1000 ms longer.

Data analysis

All experimental data were analyzed off-line with Matlab (The MathWorks, Natick, MA) routines or Visual Basic (Microsoft) routines. Saccades were detected using a velocity threshold criterion (20°/s) from eye velocity traces, which were obtained by differentiating the sampled eye position (Usui and Amidror, 1982). Trials in which the target was successfully foveated after a

single saccade were identified as correct. Trials in which more than one saccade was made before target foveation were identified as incorrect. Trials in which the animal failed to initiate fixation (mistrials) or to make a stimulus-directed saccade were discarded from the analysis. From both correct and incorrect trials, we measured three behavioral parameters: 1) accuracy, the proportion of correct trials within each session; 2) search time, the interval between the onset of the search display and the foveation of the target; and 3) response time, the latency of the first saccade following the search display presentation.

For the experimental sessions examining local contextual effects, trials were grouped into six possible conditions describing the features (or absence thereof, i.e., opposite) shared by the target and its neighboring distractors: opposite/opposite, form/form, form/opposite, color/opposite, color/form, color/color. In the experimental sessions examining global contextual effects, trials were categorized according to number of distractors whose color was identical to that of the target. This ranged from 0 to 11 distractors sharing the color of the target, excluding 1 and 10, in which case a distractor would have appeared only once in the display and could be confused for the target.

All statistical tests were performed using either the Sigma-Stat package (Jandel Scientific, San Raphael, CA) or the SPSS software (Chicago, IL). The significance of each main effect was tested with a one-way ANOVA, followed by a pair-wise multiple comparison procedure (Dunn's test). Statistical significance was accepted at $p<0.05$, and a Bonferonni correction was used when multiple pair-wise comparisons were conducted.

RESULTS

Conjunction search display characteristics

The search for a target stimulus defined by a conjunction of features is typically less efficient than when that target is defined by a single feature and performance is usually impaired by the addition of distractors, as if the display stimuli were being processed serially (Treisman and Gelade 1980). We conducted a series of experimental sessions to test whether this conventional description pertains to the conjunction search display that we used to test our main hypotheses.

Figure 2 contrasts the performance in our conjunction (form and color) search task with that observed in a feature search task, in which the target was defined only by a color difference, and illustrates the effect of manipulating the number of stimuli in the display on search performance in both tasks (see Methods). Data were obtained from a total of 8 conjunction search sessions (30,804 trials) and 3 feature search sessions (10,632 trials) performed by each monkey. Statistical differences within each task (display size effect) were assessed with one-way ANOVA tests, while between-task differences at each display size (task effect) were assessed with pair-wise rank sum tests with a significance level of 0.05 ($p=0.0083$ after correction). Figure 2A shows how accuracy during feature search trials was almost perfect as well as invariant with increasing display size ($p=0.50$), but it was significantly less during conjunction search trials ($p<0.0001$ with the exception of seven-stimulus displays, p=0.013) and gradually fell with increasing display size ($p<0.01$). Figure 2B shows that search time during conjunction search trials was longer than in feature search trials ($p<0.0001$; with the exception of seven-stimulus displays, $p=0.05$) and lengthened with increasing display size ($p<0.0001$), whereas it remained unchanged by display size in feature search ($p=0.71$). The mean (±SD) slope of the relationship

between search time and display size was -0.4 ± 3.1 ms/item in feature search and 12.9 ± 4.1 ms/item in conjunction search. Figure 2C shows that the response time to the display presentation did not vary significantly between tasks (p>0.12) and was invariant with increasing display size (p>0.70). This indicates that even though the conjunction search was more difficult, the monkey did not adopt the strategy of slowing down its response to improve its search accuracy. Furthermore, there was no evidence of a speed/accuracy trade-off in the response time to the display: incorrect first saccades did not have shorter response times than correct ones (not shown). The longer search times observed during the conjunction search task were not due to a delayed response to the search display but to a larger number of saccades.

In summary, both the reduced (though well above chance) search performance and the slowing effect of display size observed during conjunction search trials confirm that the features of the visual stimuli composing our search display elicited behavior predicted by classically-defined conjunction searches. In addition, the absence of longer response times in conjunction search trials relative to feature search trials suggests that the conjunction task did not involve additional visual attention resources beyond that recruited for producing saccades.

Local contextual effects

What aspects of the conjunction search task led to greater proportions of incorrect responses? Because the features and the positions of the stimuli in this search task varied randomly from trial to trial, we asked whether the variability in search performance could be due to a local phenomenon by which the discriminability of the target was a function of how similar the adjacent distractor stimuli were to the target. We examined such local contextual effects on target discriminability in a total of 36,681 trials during 36 experimental sessions (12 sessions in each monkey), in which the animals searched for a target defined by a unique conjunction of

form and color in the eight-stimulus search display (Fig. 1A, see Methods). Figure 3, panel A, illustrates how the visual features of the two distractors flanking the target significantly affected each monkey's search performance, when indexed by the accuracy of the first saccade (one-way ANOVA, $F=25.1$, $df=5$, $p<0.0001$). The highest accuracy (on average, 82.9% correct) was observed when adjacent distractors shared either no feature with the target or only its form; each of these different proportions was significantly higher than all other distractor trials (Dunn's pair-wise comparison tests, $p<0.05$), but not from each other ($p>0.05$). Search accuracy was reduced (on average, 72.1% correct) in trials in which either one of the adjacent distractors shared the target color. Finally, this local contextual effect was maximal when both neighboring distractors shared the target color. In such cases, average search accuracy dropped to 59.3% correct, a proportion significantly lower than all other distractor trials ($p<0.05$). Since the effect of distractor feature on search performance was limited to the color of the distractors, we re-plotted the three parameters we used to quantify search performance according to the number of same-color adjacent distractors (Fig. 3B-D). Figure 3B shows how search accuracy declined significantly when the number of flanking distractors sharing the target color increased from none to two (one-way ANOVA, $F=33.5$, $df=2$, $p<0.0001$). Concurrently, the average search time increased significantly from 236 to 261 ms and to 296 ms (one-way ANOVA, $F=22.4$, $df=2$, $p<0.0001$) (Fig. 3C). In contrast to the preceding two global measures of search performance, the color of the adjacent distractors did not affect the time that the monkeys took to respond to the appearance of the search display (Fig. 3D). The response times of all animals consistently averaged about 167 ms across all conditions (one-way ANOVA, $F=0.07$, $df=2$, $p=0.93$). Thus, the similarity between the color – but not the form – of the target and its neighboring distractors significantly impacted the ease with which each monkey foveated the search target, but it had no

effect on the initial response to the search display. These results parallel those obtained when search difficulty was manipulated by increasing the number of stimuli in the display.

An inspection of the initial saccades that did not land on the target stimulus during this conjunction search task revealed a distinct tendency consistent with the nature of the local contextual effect we just described. Figure 4A shows that the majority of incorrect trials landed on distractors that shared color with the target: on average, 83.4%, a significantly greater proportion than that predicted from a random distribution of errors (t-test, $p<0.0001$). Consequently, the average proportions of saccades incorrectly directed to distractors that had either the target form or opposite features were significantly less than predicted by chance (t-test, $p<0.0001$). Note this behavior was variable and large proportions of incorrect saccades landed on distractors that shared form with the target in some sessions (Fig. 4A, thin gray lines). We also determined whether incorrect saccades were directed to particular landing positions relative to that of the target. Figure 4B showed that these errors were distributed in proportions matching those predicted by chance (t-tests, $p>0.0125$). In addition, very few individual sessions (between 1 and 11 per stimulus position) showed significantly different proportions from expected values (Chi-square tests, $p<0.05$) (Fig. 4B, thin gray lines). Thus, incorrect saccades were generally aimed at distractors that had the same color as the target, regardless of their positions relative to the target. In comparison, the majority ($81.6 \pm 8.4\%$) of erroneous saccades made in the feature search trials examined above landed on distractors adjacent to the target.

The particular distractors targeted by erroneous saccades may compete with the target for attentional resources, which may become most depleted in the proximity of these distractors. This stimulus feature bias also suggests that the grouping of stimuli of identical color could affect search performance. We tested this hypothesis by relating search performance with a

measure of grouping, i.e., how frequently the color of the stimuli differed from their neighbors. Trials were sorted according to the number of color changes in the search display from one stimulus to the next starting from the target; in these 8-stimulus displays there could potentially be 2, 4, or 6 color changes[1]. We found that the number of color changes in the search display had no effect on the average search time (one-way ANOVA, $F=0.24$, $df=2$, $p=0.79$) and the effect on search accuracy failed to reach significance (one-way ANOVA, $F=2.31$, $df=2$, $p=0.10$).

In summary, the ease with which each monkey foveated the search target depended on the proximity of distractors sharing the color of the target, but not simply because such stimuli were grouped within the search display. In addition, these same-color distractors were visited by the largest proportions of incorrect initial responses to the search display, thereby revealing that the target color induced an attentional bias in the animals.

Global contextual effects

Does the attentional bias toward a specific stimulus feature described above depend on the relative uniqueness (salience) of these stimuli within the search display? Is monkey search performance affected by the ratio of distractor types? Further analyses of our data show that search performance for displays with three same-color distractors was significantly less than that for displays with two same-color distractors (accuracy, $p<0.0001$; search time, $p<0.0001$). The proportion of initial erroneous saccades to a same-color distractor for each display type did not, however, vary significantly. Thus, this question could not be answered completely since the distractor features in the conjunction search task used were combined in proportions that did not vary substantially: 28.6% (2/7) or 42.8% (3/7).

We therefore asked whether the search strategy could be shaped by the composition of the search display by varying randomly the proportion of same-color stimuli from trial to trial. We

examined such a global contextual effect on search strategy in a total of 16,217 trials during 12 experimental sessions (4 sessions in each monkey), in which the animals searched for a target defined by a unique conjunction of form and color in a twelve-stimulus search display with variable ratios of distractor types (Fig. 1B, see Methods). Figure 5A shows search accuracy plotted as a function of the number of same-color distractors in the display. With increasing number of same-color distractors, search accuracy diminished to a minimum of 68.6% in displays with 9 same-color distractors; accuracy was highest when the search was based on a single color (0 same-color distractors) or form (11 same-color distractors) difference (98.1% and 83.1%, respectively). This change in accuracy was altogether significant (one-way ANOVA, $F=6.62$, $df=9$, $p<0.0001$). In terms of search time (Fig. 5B), monkeys took the shortest amount of time to foveate the target when there were very few same-color distractors or none at all (minimal average, 187 ms in displays with 0 same-color distractors), but also when they were all of the same color (on average, 270 ms in displays with 11 same-color distractors). The longest search times were observed for most intermediate conditions, reaching a maximum of 331 ms in displays with 8 and 9 same-color distractors. This change in search time was altogether significant (one-way ANOVA, $F=13.4$, $df=9$, $p<0.0001$). While average search time varied by 77% across the different number of same-color distractors, the variation in response time was negligible ($F=1.38$, $df=9$, $p=0.20$), consistently averaging about 180 ms across all display types (Fig. 5C).

The relationship between search time (as well as search accuracy) and the number of same-color distractors in a display appeared asymmetrical. If this was indeed the case, the end conditions (displays with few or many same-color distractors) would tend to differ from each other, but displays with equal numbers of distractor types would tend not to differ from displays

at either end. Examination of the Dunn's pair-wise comparison tests provided quantitative evidence for such an asymmetry. Excluding comparisons with the extreme (pop-out) displays, 50.0% (54 of 108 comparisons) of the trial conditions at either end of the spectrum (2, 3, 4 versus 7, 8, 9 same-color distractors) were significantly different from each other ($p<0.05$). In contrast, these end trial conditions were rarely significantly different from mid-range conditions (5 and 6 same-color distractors) (13.2%, 19 of 144 comparisons). This asymmetrical pattern could have been due to search performance declining monotonically with increasing number of same-color distractors and reversing only with the feature (form) search display (Fig. 5, A and B). To test this possibility, which would be expected if the monkeys guided their search strictly on the target color, we also examined in each session whether the decline in search performance reversed only at the extreme distractor ratio, i.e., 9 same-color displays. We found that search accuracy reversal occurred at 7 and 8 same-color displays in 8.3% and 25% of sessions, respectively. Similarly, search times peaked in the 8 same-color displays in 42% of sessions. Altogether, this asymmetric global contextual effect suggests that, in addition to the proximity of the distractors sharing the color of the target, the presence of same-color distractors within the search display impacted the search performance of each monkey, with the exception of the initial response to the search display.

Figure 6A shows that the proportions of initial saccades that did not land on the target stimulus also varied significantly with the number of same-color distractors in the display (one-way ANOVA, $F=10.8$, $df=7$, $p<0.0001$). In trials in which the display had only 2 same-color distractors, these distractors attracted 88.5% of incorrect saccades, even though they should have been visited in only 18.2% of the trials according to chance. Overall, the proportion of incorrect saccades that landed on a same-color distractor decreased as the number of such distractors in the

display increased, along with the chance proportion of visiting the latter. In trials in which the display included 9 same-color distractors, only 44.2% of the incorrect saccades landed on these distractors, a proportion significantly much lower than the expected proportion (81.8%). The reversal of this behavioral bias is best appreciated by plotting the difference between the observed proportions of same-color errors and those predicted by chance (Fig. 6B). When the proportions of same-color distractors in the display were low, the incorrect saccades were more likely to land on them. Conversely, monkeys were less likely to make saccades toward those stimuli when their proportions were high, i.e., their incorrect saccades tended to land on stimuli that differed from the rest of the stimuli in the search display only by their colors. This behavior was consistently observed in all three monkeys (Fig. 6B, thin gray lines). It is reasonable to suppose that these distinct, different-color distractors became salient in trials with many same-color distractors and therefore popped out of the display, just like the same-color distractors appeared distinct in the opposite type of trials. Note that a similar variation in saccade bias was also present in the data obtained in the previous conjunction search task: the bias towards same-color distractors in displays with only two such distractors was larger than that observed in displays with three same-color distractors (57.1% vs. 36.8%, $p<0.001$).

In summary, monkeys appeared to respond to conjunction search displays by making saccades to stimuli whose color was particularly rare within the display. This strategy may have facilitated the animal's overall search performance during the conjunction search trials, but it remained less efficient than in the extreme display conditions, in which the target was defined by only one of the features: color or form.

DISCUSSION

Influence of display composition on target discriminability

The influence of display composition on target discriminability, hence search performance, in visual conjunction search was evidenced by the effect of the number of distractors in the display, the presence of same-color distractors near the target, and the proportion of same-color distractors in the display. These results illustrate how the deployment of perceptual resources can be taxed by the local and global distribution of stimuli within a search display.

Our results provide evidence that the visual search performance of monkeys is shaped by the proportion of distractors that share a feature with the target (especially color in this study) in a manner analogous to what has been observed in humans (Bacon and Egeth 1997; Egeth et al. 1984; Kaptein et al. 1995; Poisson and Wilkinson 1992; Shen et al. 2000, 2003; Sobel and Cave 2002; Zohary and Hochstein 1989). This global context effect cannot, however, be entirely related to that observed when the number of distractors was manipulated: Although the number of same-color distractors increased within the fixed-size display in the former task, the proportion of same-color distractors did not vary in the latter task. Moreover, manipulation of the display size only increased the actual number of same-color distractors from two to four, whereas a four-fold increase (two to nine) was induced in the distractor-ratio manipulation. The variation in search performance observed in these two manipulations could therefore be limited neither to the variation in the number of same-color distractors present in the display nor to the variation in the proportion of same-color distractors. Consistent with these results are those of Buracas and Albright (1999), who found that search times of humans (and of one monkey) increased when the number of distractors that shared a target feature was kept constant in a conjunction display of increasing size. Together, these findings argue against the idea that

observers can fully constrain their search to stimuli sharing features with the target and ignore all others (Egeth et al. 1984). Theeuwes (1992) reached a similar conclusion by showing how the bottom-up salience of stimuli with highly discriminable features can exert a negative influence on the search for a stimulus with different features.

The difference in target discriminability and processing between feature and conjunction search tasks can help explain the influences exerted by distractors immediately adjacent to a target. In the conjunction search trials in which the target was flanked by distractors that did not share the target color, we reason that the search within the target vicinity was facilitated because it was reduced to a local feature search based on color difference. This local pop-out hypothesis is in line with the finding of Brown and Monk (1975) that the search for a simple visual target is facilitated by the removal of a noisy local surround. Other local interactions have been observed with the flanker task effect, in which the identification of a stimulus in a non-search task is enhanced by the presentation of flanking distractors with shared features, presumably because less visual processing becomes necessary (Eriksen and Eriksen 1974). Such flanking distractors in our experiments could have, however, deterred the discrimination of the target by masking its identity, as it has been shown in dense visual displays (Cohen and Ivry 1991). The existence of such a stimulus density effect in our experiments is evidenced by the predominance of erroneous saccades landing on distractors adjacent to the target in the feature search task. This masking effect is an expression of the principles of similarity and proximity in Gestalt theory of perception. The general implication of these principles is that target discrimination can be either impeded by the perceptual grouping of the target with distractors or enhanced by the perceptual grouping of the distractors separately from the target (Banks and Prinzmetal 1976). The effective

grouping in our experiments was not the grouping of same-color stimuli but the grouping of the target with its adjacent distractors.

The importance of the local surround on target discriminability is formally articulated by the COntour DEtector (CODE) theory of perceptual grouping by proximity, originally developed by van Oeffelen and Vos (1982, 1983; see also Compton and Logan 1993). This clustering algorithm assumes that the representation of each stimulus is distributed across space and summed into a single surface by bottom-up processes. Whether neighboring stimuli are organized into a group depends on the level of the criterion threshold that is applied to this surface. With respect to our data, the more salient (same as target color) the distractors were immediately adjacent to the search target, the higher the threshold had to be for the target to be correctly discriminated. Logan (1996) incorporated CODE theory within the Theory of Visual Attention of Bundesen (1990) and presented an integrated theory (CTVA) of space-based and object-based attention that successfully accounts for the flanker task effect (Eriksen and Eriksen 1974), the display density effect in conjunction search (Cohen and Ivry 1991), and the grouping effect in visual search (Banks and Prinzmetal 1976). We believe the latest version of CTVA, which incorporates the principle of grouping by similarity, can fully account for the local contextual effect and the attentional bias that the monkeys exhibited for certain distractors, i.e., those sharing the target color in this study.

Visual guidance of saccades

Our finding that saccades were generally biased toward distractors sharing the color of the target in the standard visual conjunction search task indicates that color acted as a predominant visual feature guiding the search for the target. Such a potent color bias has also been observed in a number of visual search studies in both humans and monkeys (Buracas and Albright 1999;

Motter and Belky 1998b; Sobel and Cave 2002; Williams 1967; Zohary and Hochstein 1989). What our study adds to these previous data is the finding that the overt attentional bias toward this specific stimulus feature also depends on the relative uniqueness of these stimuli within the search display when their proportions are manipulated. Saccades were biased toward stimuli that were of the same color as the target when the proportion of these stimuli was relatively low, but the monkeys shifted their attention toward stimuli whose color differed from the target when the display was mostly composed of same-color stimuli. This result is consistent with the studies that examined the guidance of visual attention in humans (Bacon and Egeth 1997; Egeth et al. 1984; Kaptein et al. 1995; Poisson and Wilkinson 1992; Sobel and Cave 2002; Zohary and Hochstein 1989) and it is particularly in line with what Shen et al. (2000, 2003) measured from the gaze behavior of human subjects performing visual conjunction search tasks with variable distractor ratios. This effect on the global measures of search performance in the monkeys was somewhat less pronounced than in these human studies. One salient difference is that, in these studies, subjects reported the presence/absence of a target with manual responses, which have longer latencies than saccades. In addition, the distractor-ratio effect is most reliably demonstrated in target-absent trials, which take the longest to process (e.g., Poisson and Wilkinson 1992; Shen et al. 2000, 2003). The fast responses of the monkeys could have precluded this effect from being fully expressed. Their adaptive gaze behavior thus gave us a more direct measure of their visual strategies, which were analogous to humans.

While the strong influence of color suggests that the monkeys relied on the target color to find the conjunction target, how their searches were guided by the stimuli that formed the smallest color group within the display suggests that salience was also a significant factor. Such a visual strategy based on both target-feature and stimulus salience was best reflected in the

asymmetrical distractor-ratio effect that we observed. A search strictly based on the color of the target would predict a search performance linearly related to the proportion of same-color distractors in the display, whereas a search limited to stimulus salience would predict a quadratic function; a dual-strategy search would predict the asymmetrical search performance of our monkeys (Bacon and Egeth 1997). While our results differ from the rather symmetrical search performance reported by Shen et al. (2000, 2003), they more closely resemble some of the results obtained by Sobel and Cave (2002; see also Bacon and Egeth 1997), especially when explicit instructions to limit search to a specific feature were given[2]. One could therefore argue that the visual strategies of our monkeys were not simply guided by bottom-up factors. It is, however, questionable whether the target-feature strategy that monkeys exhibited reflects only top-down influences. For instance, a non-negligible proportion of erroneous saccades were directed to distractor stimuli whose color was different from the target. In addition, this strategy cannot fully account for the search performance varying with the total number of stimuli in the display without large variation in the number of target-feature stimuli (see above).

It is also possible that the strong bias for stimuli sharing the target color in our displays was due to our choice of stimuli. Discriminability is a function of the similarity between features (Duncan and Humphreys 1989), and the within-color discriminability in our displays may have been larger than the within-form discriminability. This should have made color a much more salient feature to guide the search for the conjunction target. To test for this possibility, we increased the within-form discriminability in a few experimental sessions by replacing the circles and squares in our conjunction search displays with diametrically opposite forms: crosses (+) and annuli (O) (see Bichot and Schall 1999). This new search display yielded no display size effect in each of the three monkeys, thereby supporting the hypothesis that monkeys used color to

guide their searches not because they were under top-down influences but because color was a highly discriminable feature in the display. The dependence of this non-reciprocal effect of stimulus feature on relative discriminability during conjunction search echoes the results of Theeuwes (1992) obtained in feature search tasks and also explains how a small group of distractors can disrupt more feature search performance when these stimuli share the color of the target instead of its orientation (Motter and Belky 1998b).

In general, the monkeys' searches appear to have been guided primarily by bottom-up processes. Given that we did not put a strong emphasis on accuracy during the training of these animals, they must have viewed the conjunction search displays in terms of its salient features.

Inflexible initial responses

Measurements of both the accuracy and the latency of overt responses have been used to estimate the processes underlying cognitive tasks (Meyer et al. 1988). In this study, however, only response accuracy was found to depend on target discriminability. The timing of the responses to the display presentation did not reflect the differences in information-processing load associated with the type of search tasks (feature and conjunction search tasks), the number of distractors in the display, the presence of same-color distractors near the target, and the proportion of same-color distractors in the display. The monkeys did not adapt their responses to the demands of the tasks and the accuracy of their searches was significantly diminished. Together with the absence of speed/accuracy trade-offs, the unchanging latencies of these initial responses despite the changing load of the different tasks and trials suggest that they resulted from an automatic process (Jonides et al. 1985), i.e., largely independent from voluntary control (see also Findlay 1997 for a similar interpretation). The monkey's decision about when (and where) to make a saccade to a visual stimulus within the search display thus appears to have

been based on limited processing of the visual information available in the display, which explain the uniformly distributed landing positions of erroneous saccades in conjunction search.

The wide variety of observations regarding the timing of responses in previous visual search studies was pointed out in the introduction, in which we also suggested that an emphasis on accuracy could possibly determine whether subjects adapt their response times. In this regard, perhaps the unconstrained nature of our task design (and the limited training associated with it) did not provide the sufficient incentive to optimize the behavior, i.e., satisficing was satisfactory (Simon 1957). We contend that this fast visual behavior is what humans (and primates in general) naturally exhibit during natural vision. Short and invariant fixations during active visual search, regardless of the search difficulty, have also been observed previously in both humans (Maioli et al. 2001) and monkeys (Motter and Belky 1998a,b). These observations also imply that covert attentive scanning beyond that of selecting the next saccade target had limited opportunity to take place during the individual fixations associated with free-viewing search, thereby additionally limiting the visual processing of the display.

FOOTNOTES

[1] The number of trials that counted eight color changes was too small for statistical analysis.

[2] The asymmetrical search performance functions and reversing saccade biases that we observed in our monkeys were also replicated in a pilot study with two human subjects performing the same visual conjunction search task.

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FIGURE CAPTIONS

FIGURE 1. Conjunction search tasks. A: In both tasks, monkeys were required to look at a fixation stimulus that was identical to the target. Once fixated, the fixation stimulus disappeared and the visual array was presented. Monkeys were then required to generate a saccade to a target defined by a conjunction of color and form. If foveation of the target was initially unsuccessful, monkeys were given an additional 2000 ms to foveate the target. This is a sample display for eight-stimulus conjunction task examining local contextual effects. B: Sample displays for twelve-stimulus conjunction task examining global contextual effects. Displays are of 0 same-color (left), 5 same-color (middle), and 9 same-color (right) distractors. The dotted circle and arrow indicate current gaze position and saccade vector, respectively.
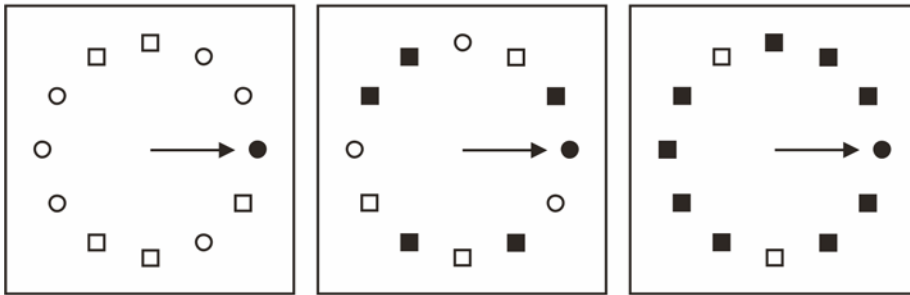
FIGURE 2. Conjunction search task characteristics. Behavioral performance across feature (solid lines) and conjunction search (dashed lines) tasks for all monkeys. Accuracy, measured as average percentage correct, (A), average search time (B), and average response time for correct responses (C) are plotted as a function of display size. Each asterisk (*) indicates a significant task effect while the diesis (‡) indicates a significant display size effect. Error bars, s.e.

FIGURE 3. Local contextual effects. Behavioral performance in the eight-stimulus conjunction search task. Accuracy (A) as a function of the features of the two adjacent distractors (opp: opposite distractor; form: same-form distractor; color: same-color distractor). Accuracy (B), average search time (C), and average response time for correct responses (D) have been replotted as a function of the number of same-color adjacent distractors. Error bars, s.e.
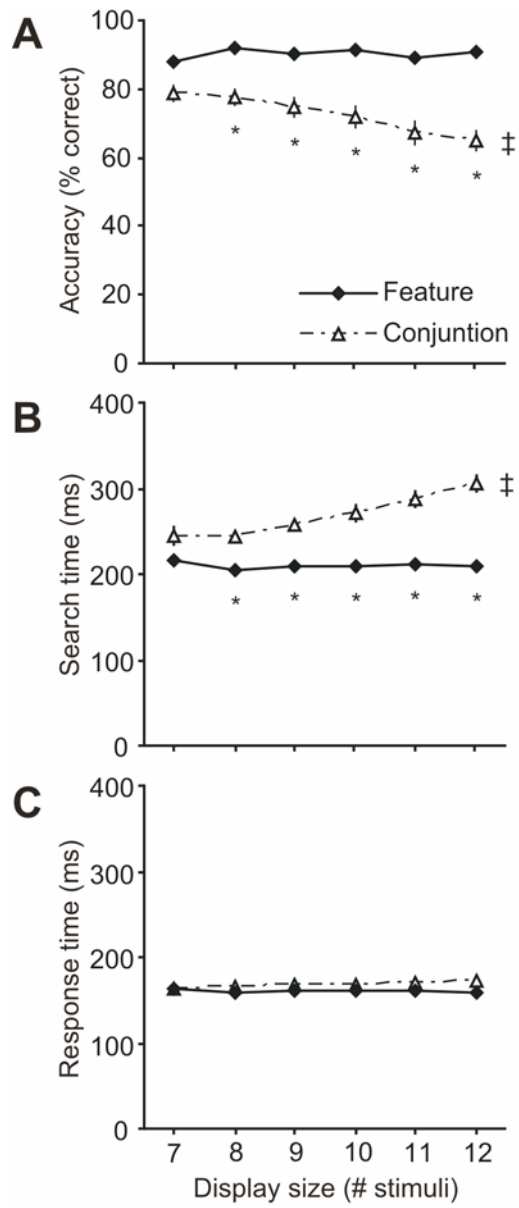
FIGURE 4. Incorrect responses in the eight-stimulus conjunction search task. The average percentage of erroneous saccades as a function of distractor feature (A) and distractor distance from target (B). Thin gray lines indicate the percentages obtained in each individual session. Dashed lines represent expected values as predicted by chance. Error bars, s.e.

FIGURE 5. Global contextual effects. Behavioral performance of all three monkeys in the twelve-stimulus conjunction search task. Accuracy (A), average search time (B), and average response time for correct responses (C) are plotted as a function of the number of same-color distractors in the display. Error bars, s.e.
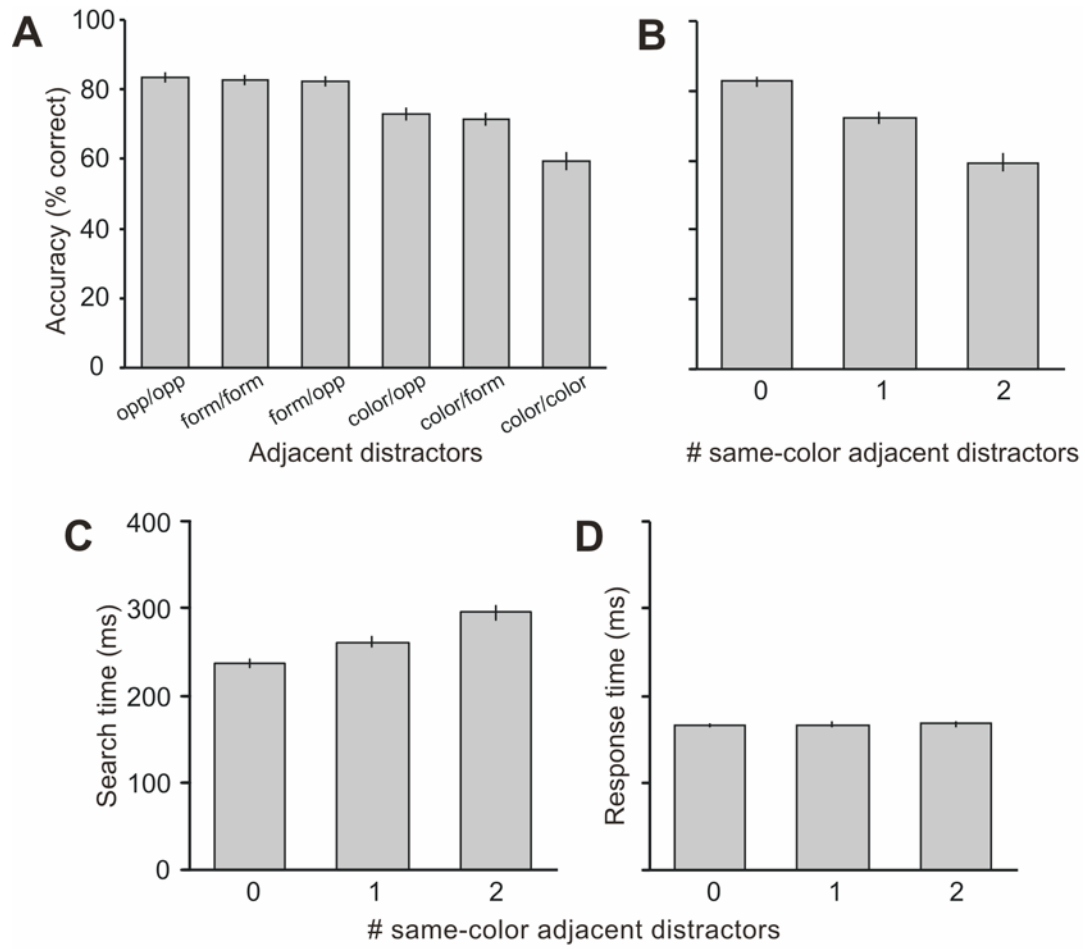
FIGURE 6. Incorrect responses in the twelve-stimulus conjunction search task. The average percentage of erroneous saccades directed to a same-color distractor as a function of the number of same-color distractors within the display (A). Dashed lines indicate expected values as predicted by chance. Saccade bias (observed – expected) is plotted as a function of the number of same-color distractors within the display (B). A positive bias indicates a preference for the target color while a negative bias indicates an aversion to the target color. Thin gray lines indicate the mean saccade biases obtained from each monkey. Asterisks indicate statistical significance ($p<0.01$). Error bars, s.e.
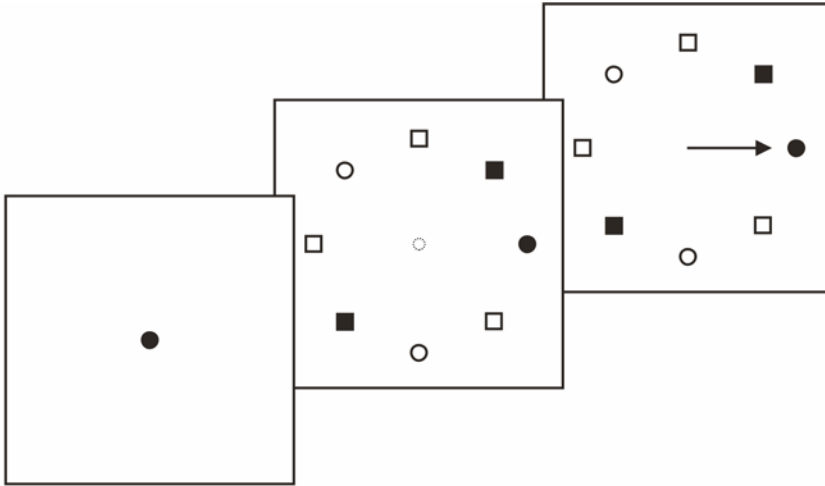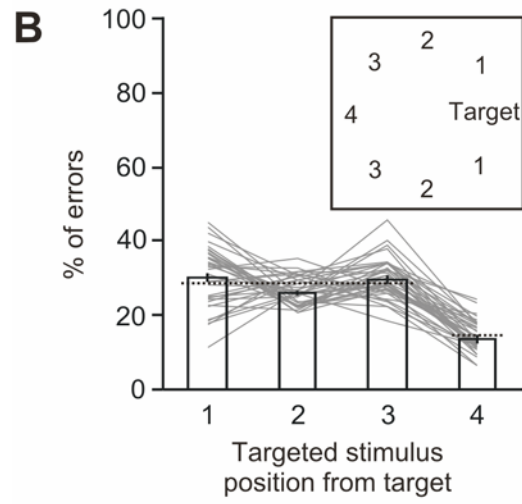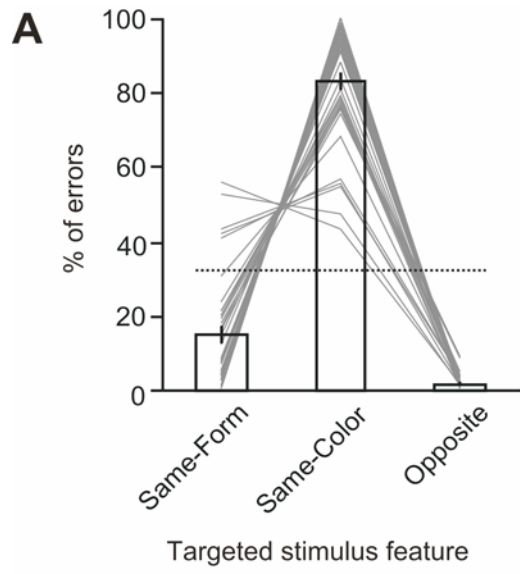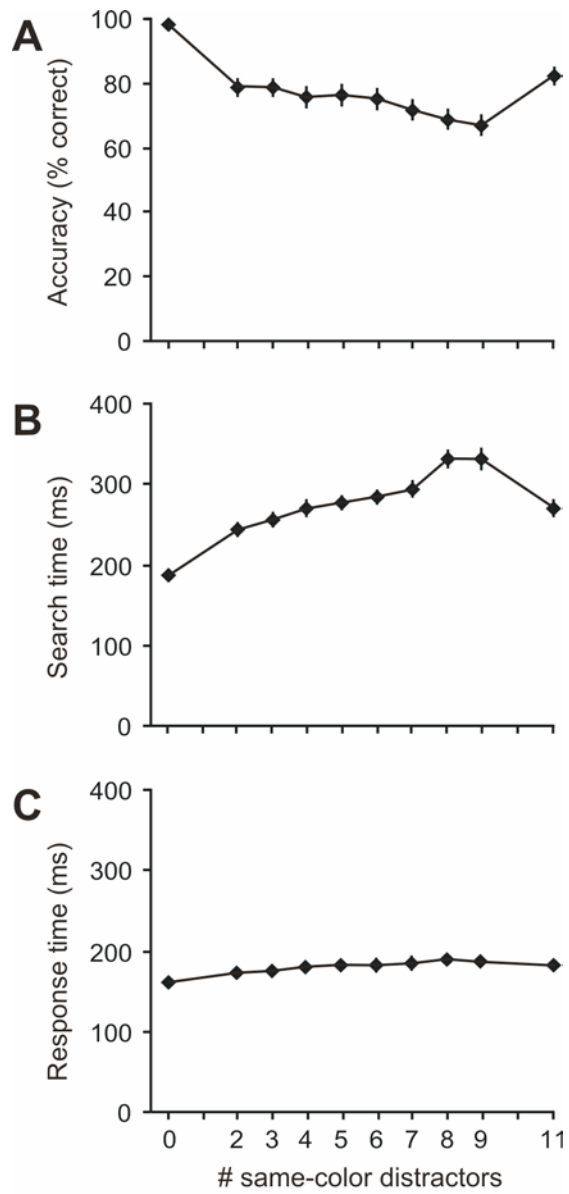
Shen and Paré
Figure 1

Shen and Paré
Figure 2

A Accuracy (% correct) vs Adjacent distractors (opp/opp, form/form, form/opp, color/opp, color/form, color/color)

B # same-color adjacent distractors (0, 1, 2)

C Search time (ms) vs # same-color adjacent distractors (0, 1, 2)

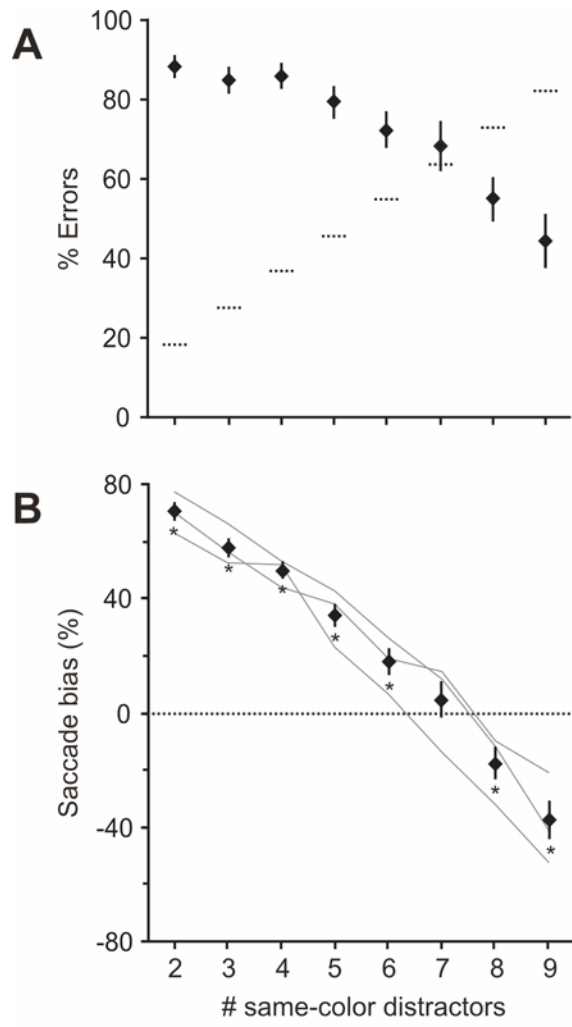**D** Response time (ms) vs # same-color adjacent distractors (0, 1, 2)

Shen and Paré
Figure 3

Shen and Paré
Figure 4

Shen and Paré
Figure 5

Shen and Paré
Figure 6