

## Covert Visual Search: A Comparison of Performance by Humans and Macaques (*Macaca mulatta*)

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The duration of the visual search by human participants for visual features is independent of the number of targets being viewed. In contrast, search for targets formed by conjunction of features is characterized by reaction times that increase as a linear function of the number of items viewed, suggesting that the target detection requires scrutiny of the search array by focal attention. Macaque (*Macaca mulatta*) and human performance on feature and conjunction search tasks was compared by using color or motion, or by conjunctions of color and motion. Like human participants, monkeys exhibited a dichotomy between feature and conjunction search performance. This finding suggests that humans and macaques engage similar brain mechanisms for representation of feature and conjunction targets. This behavioral paradigm can thus be used in neurophysiological experiments directed at the mechanisms of feature integration and target selection.

When viewing multiobject scenes, one rarely becomes aware of the peculiarities of every object. Rather, only those objects that are sufficiently salient or relevant to current intentions enter awareness. This selective processing is commonly termed *visual attention*. The paradigm of visual search has been used extensively to study the characteristics and mechanisms of selective attention in humans. Experiments involving search for specific visual features (*feature search*), such as color or orientation, have found that reaction times (RTs) are independent of the number of objects being viewed. Such results have led to the proposal that simple features are independently encoded in cortical feature maps (Treisman & Gelade, 1980). In contrast, targets formed by conjunctions of features from different visual sensory dimensions (*conjunction search*, e.g., color + orientation, shape + color) elicit RTs that increase as a linear function of the number of objects (*distractors*) viewed. The latter fact spawned the *attentional spotlight* hypothesis, according to which a moveable “searchlight” of focal attention sequentially scans objects in the scene, promoting

integration of features at the spatiotemporal locus of each focus. Treisman and Sato (1990) noted that conjunction search RTs could be influenced by both bottom-up (preattentive) grouping and top-down preactivation of feature maps by stored representation of a target’s features (i.e., *working memory*). This dual control theory of attention was developed further in the *saliency map* notion of Koch and Ullman (1985) and the *guided search* model of Wolfe, Cave, and Franzel (1989) and Wolfe (1994).

The neural structures and events that underlie attentional phenomena have recently become a subject of investigation in nonhuman primates. Most behavioral paradigms used in previous neurophysiological experiments have, however, confounded spatial and feature-specific components of top-down attentional influences, such that the results fail to isolate neuronal correlates of these components (but see Anillo-Vento & Hillyard, 1996). The classic search paradigm offers many degrees of freedom in both feature and spatial dimensions and thus may be instrumental in dissociating these mechanisms. For this reason we have attempted to extend the behavioral paradigm of visual search to nonhuman primates.

In addition to the development of a behavioral paradigm for neurophysiological studies of selective visual attention, our study has enabled us to compare the performance of humans and monkeys on feature and conjunction search tasks involving color and direction of motion and to characterize the effects of extended training on these tasks. The behavioral data obtained provide a foundation for future comparisons between neuronal data and the vast human psychophysical literature on the topic of visual search.

As a point of departure, we drew upon an observation by Nakayama and Silverman (1986), in which targets defined by a unique conjunction of color and motion yield RTs that increase linearly with the total number of items viewed. The

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feature dimensions of color and motion were chosen in anticipation of future physiological studies of cortical visual areas MT and V4, which possess selectivity biases for motion and color, respectively (Maunsell & Newsome, 1987). We first replicated the results of Nakayama and Silverman with humans, using stimuli modified for our planned electrophysiological studies. We then studied task acquisition and performance parameters (RTs and error rates) in macaques. Our results demonstrate that visual search performance by monkeys exhibits the same dichotomy in feature versus conjunction search performance as that of humans. A brief report of these results appeared previously (Buračas & Albright, 1994).

## Method

Nearly identical psychophysical experiments were performed with humans and monkeys. Common features of apparatus, stimulus construction, and behavioral paradigm are described first, followed by a description of features that were specific to humans or monkeys.

### Apparatus

Stimuli were generated with a high-resolution computer video display controller and digital frame buffer (Pepper SGT;  $640 \times 480$  pixels, 8 bits per pixel; Number Nine Computer Corp.; Lexington, MA). The stimuli were displayed on a 14-in. (35.6-cm) Zenith Flat-Screen video monitor for human studies and on a 19-in. (48.3-cm) Phillips video monitor for monkey studies (both monitors ran in a 60-Hz noninterlaced regime). The graphics controller resided in a Pentium-class personal computer, and it permitted color or luminance levels to be selected from a palette of 16 million choices. The voltage-luminance relationship was linearized independently for each of the three guns in the display (Watson et al., 1986). Stimulus movement was achieved by updating the frame buffer in synchrony with the vertical refresh of the video monitor. Different speeds were obtained by varying the number of frame cycles between frame buffer updates. The computer also controlled behavioral data acquisition and monitored eye position in the monkey experiments.

### Visual Stimuli

**General features.** Although the experiments reported herein were strictly psychophysical, the visual stimuli were designed to be compatible with neurophysiological studies. Each trial consisted of a briefly presented sample stimulus followed by a search array. The sample stimulus was always presented at the center of gaze and consisted of a stationary circular aperture ( $1^\circ$  diameter) through which a moving, randomly textured pattern was viewed. The luminance of each texture element was approximately  $10 \text{ cd/m}^2$ , and the background luminance was approximately  $1 \text{ cd/m}^2$ , yielding a local-element-luminance Michelson contrast of 82%. The characteristics of the sample stimulus could vary along only two dimensions: color and direction of motion. Two values of each dimension were allowed, yielding four distinct stimuli (red-left, red-right, green-left, and green-right), which were presented as samples on a pseudorandom schedule. The red and green patterns were generated by modulation of either the red or green phosphor of the video display. The relative luminances of the red and green stimuli were adjusted to be isoluminant (see below). The speed of motion for left and right directions was  $6^\circ/\text{s}$ .

The search array consisted of a set of circular apertures, each constructed in a manner similar to the sample. These apertures appeared in positions selected pseudorandomly from 36 predefined positions ordered in 3 concentric rings, each composed of 12 loci (see Figure 1). Apertures were scaled according to their distance from a centrally placed fixation spot to parallel loss of visual acuity and increasing receptive field (RF) size in areas MT and V4. The choice of scaled apertures had yet another advantage: Objects of mixed scales are known to help focus a test subject's attention (Verghese & Pelli, 1994). This design can better sustain the seriality of search and increase search times, thus allowing more time to record neuronal responses in overtrained subjects. Human participants viewed an array with concentric rings placed at  $2.7^\circ$ ,  $4.6^\circ$ , and  $6^\circ$  of eccentricity and corresponding aperture diameters of  $1^\circ$ ,  $2^\circ$ , and  $3^\circ$  of visual angle. Monkeys viewed similar search stimuli, the sole difference being that they were enlarged by 35% relative to the stimuli used for humans (because of the larger size of the monitor used in monkey experiments). Selected aperture positions (of 36 possible) were randomized across trials to avoid spatial-grouping effects (e.g., proximity or symmetry) that are known to influence search strategies and RTs. Human participants viewed arrays containing 6, 9, 12, or 18 apertures. Four monkeys viewed arrays containing 2, 4, or 8 apertures. A 5th monkey viewed arrays containing 4, 8, or 12 apertures. In all cases, the number of apertures was varied across trials on a pseudorandom schedule. For some monkey experiments (identified below) we used an additional search array containing 2, 4, or 8 apertures positioned concentrically around the fixation spot, in a radially symmetric pattern.

The apertures in the search array could take on any of the four possible combinations of color and direction of motion. Only one aperture could possess the same combination of features as the sample. This aperture was termed the *target* and was present in the search arrays on 50% of trials (target-present trials) and absent on the remaining trials (target-absent trials). All other apertures were termed distractors.

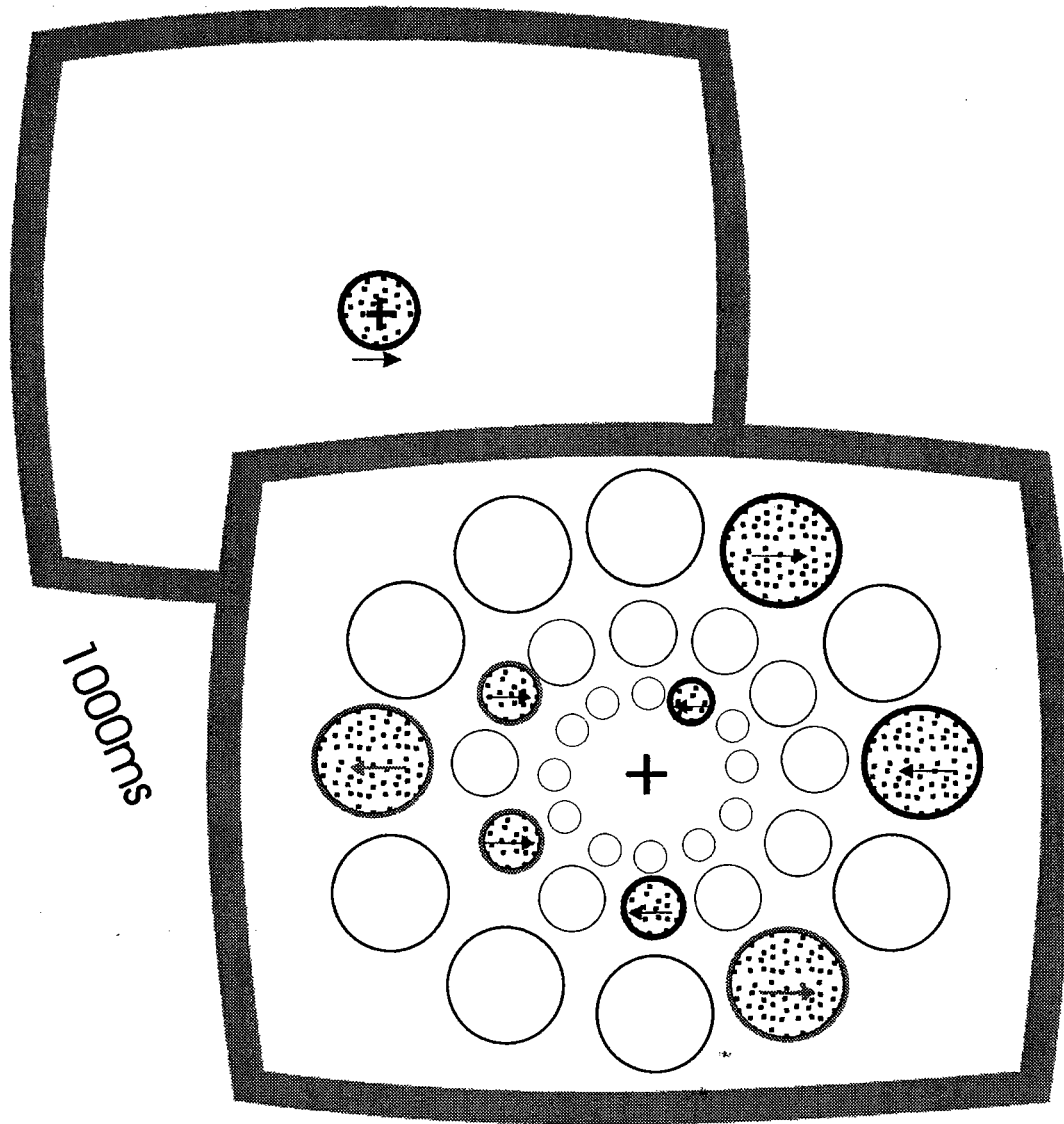
The characteristics of the distractors defined the specific search paradigm, of which there were four types:

1. *Disjunctive feature search: Color.* In disjunctive feature search for color (commonly termed *color popout*), all distractors were assigned the same nontarget color, and their directions of motion were distributed evenly and randomly (50% right and 50% left).

2. *Disjunctive feature search: Motion.* In disjunctive feature search for motion (*motion popout*), all distractors were assigned the same nontarget direction of motion (opposite to target motion). Color was distributed evenly and randomly (50% red and 50% green apertures).

Both feature dimensions were varied in each of these feature search conditions, despite the fact that only one feature dimension was used to define the target in each case. Hence the term *disjunctive*.

3. *Conjunction search: Color and motion.* In the feature conjunction search experiments, all four possible conjunction values were used, which distinguishes our approach from traditional conjunction search experiments (Nakayama & Silverman, 1986; Treisman & Gelade, 1980), in which "antitargets" (objects with both features assuming nontarget values) are usually absent. Color values were distributed evenly and randomly among the distractor apertures. Within the subset of distractors of the nontarget color, the direction of motion was distributed evenly and randomly. Direction of motion within the subset of distractors of the target color was uniformly in the direction opposite to target motion. This design balanced the distribution of color for all set sizes but resulted in fewer apertures moving in the target direction than in the nontarget direction. Our choice of feature distribution in



*Figure 1.* Temporal sequence of stimulus events in each trial. The rear panel illustrates the appearance of the sample stimulus (cue). This stimulus is viewed through a small circular aperture centered on the fixation spot (denoted by the cross) and positioned at the center on the video display. The sample display appears for 1 s, after which the search display appears (front panel). Stationary items in the search display may appear in any of 36 predefined locations (dashed circles; not visible in search array). Each item takes on one of two colors (red or green, indicated by light or dark dots), and the texture inside it moves in one of two directions of motion (left or right, indicated schematically by arrows). Eight search items appear in this example, only one of which (the target) matches the sample (the top aperture). See text for details.

these conjunction experiments was motivated by evidence that color exerts stronger influence over visual search than does direction of motion (e.g., Buračas & Albright, 1996).

**4. Fixed relevant set search: Color and motion.** On the basis of their results, Egeth, Virzi, and Garbart (1984) proposed that humans may selectively constrain attentional scanning to the items in the search array that share a feature with the target. We tested this hypothesis using the *fixed relevant set* task, in which the number of distractors sharing color with the target was fixed (six for human experiments and four for monkey experiments) across trials, and the number of distractors of a different (nontarget) color was varied

(0, 3, 6, and 12 for human experiments; 0, 4, and 8 for monkey experiments) randomly.

### Human Experiments

**Participants.** Seven human participants (2 women and 5 men), ranging in age from 24 to 32 years, participated in these experiments. All but 1 of these participants (one of the authors, Giedrius T. Buračas) were naive regarding the hypotheses being tested. All participants had normal color vision and normal or corrected-to-normal acuity.

**Behavioral paradigm.** A major difference between our paradigm and that used for most previous visual search experiments with humans was the requirement that participants fix their gaze throughout the duration of the search period. Gaze fixation is a mandatory component of our neurophysiological experiments using visual search in monkeys (Buračas & Albright, 1995), the results of which will be reported in a future article. Hence, this requirement was introduced to our human search task for the purpose of making the task more similar to that used with monkeys. We determined the subjective red-green isoluminance point for each participant by using heterochromatic flicker photometry (for details, see Croner & Albright, 1997). Luminance values thus obtained were used to create the textures in the apertures of the search array.

The general procedure for all visual search tasks was as follows: Participants viewed the monitor screen from a distance of 60 cm. Viewing position was maintained and head movements were minimized by the use of a chin and forehead rest. At the beginning of each trial, participants were required to fixate on a small ( $0.1^\circ$  diameter) spot that appeared in the center of the display and to maintain fixation throughout the duration of each trial. Humans are capable of reliable fixation under these conditions (Murphy, Kowler, & Steinman, 1975). One second after the onset of the fixation spot, the sample aperture appeared and remained visible for 1 s (see Figure 2). Coincident with the offset of the sample, a search array appeared. Participants were required to maintain eye fixation and to press a keyboard key when a target was detected. A different keystroke was required to indicate the absence of the target. The response keystroke terminated the search array presentation. On half of the trials, the target was not present in the array (target-absent trials). On the remaining trials, the target was at a position chosen randomly from 36 possible positions (target-present trials). A short beep on error trials provided performance feedback. Although no time limit was imposed, participants were asked to report the presence or absence of the target as quickly as possible without compromising accuracy. All participants were given a block of practice trials, which continued until performance stabilized and subjects expressed confidence and clear understanding of the requirements of the task. Only those trial blocks with 10% or fewer errors were accepted for further analysis. Data were collected over a period of 5 days, two blocks of 480 trials (1 hr) per day.

### Monkey Experiments

**Subjects.** Our subjects were 5 female rhesus monkeys (*Macaca mulatta*) weighing 6.5 to 8.0 kg. Three of these monkeys had not

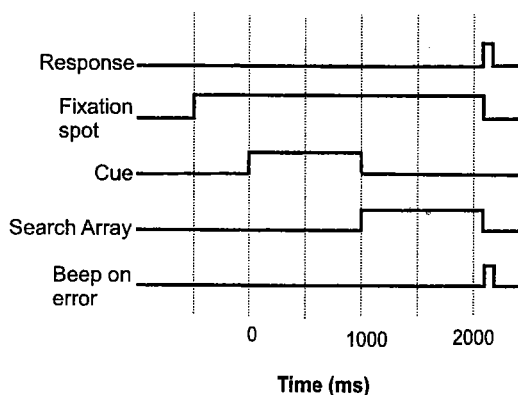


Figure 2. Event timing for human search task. Both target-present and target-absent trials used the same timing structure.

previously participated in behavioral experiments; the other 2 had performed another behavioral task before participating in our visual search experiments. The protocols for these animal experiments were approved by the Salk Institute Animal Care and Use Committee, and they conform to U.S. Department of Agriculture regulations and National Institutes of Health guidelines for humane care and use of laboratory animals.

**Surgical preparation.** After an initial period of adaptation to the primate chair and the behavioral-testing setup, monkeys were surgically prepared for experimentation by conventional techniques (for details, see Dobkins & Albright, 1994; Lemon, 1984). Briefly, a post for head restraint was affixed to the skull with dental acrylic, stainless steel screws were anchored to the skull, and a scleral search coil for measuring eye position was surgically implanted in one eye (Judge, Richmond, & Chu, 1980). The leads of the coil were clamped to a miniconnector and affixed to the cranial implant with dental acrylic.

All surgical procedures were performed under aseptic conditions with halothane anesthesia (0.8% maintenance). Monkeys were given pre- and postsurgical prophylactic antibiotics (presurgery: 30 mg/kg iv Keflin [Cephalothin Sodium, Henry Schein, Port Washington, NY] 3 times at 2-hr intervals; postsurgery: 25–50 mg/kg Keflex [Cephalexin, Henry Schein, orally at 12-hr intervals for 3 days) and analgesics (Buprenex, Henry Schein, 0.03 mg/kg 2×/day for 3 days). The ophthalmic wound was treated by application of an ophthalmic antibiotic (BNP or chloramphenicol, Henry Schein). After healing, the cranial wound was treated weekly by removal of hair, cleansing, and application of a topical antibiotic (Nitrofurazone, Henry Schein, 0.2% in water-soluble powder).

**Behavioral paradigm.** Like human participants, monkeys were required to maintain central fixation of gaze throughout the period of search, that is, search was performed *covertly*. This requirement was imposed because (a) it was deemed essential for subsequent physiological study, as it ensures constant receptive field stimulation during visual search, and (b) it allowed saccadic eye movement to be used as the operant indicator of target location.

The stimulus and behavioral paradigm were similar to those used for humans, the principal exception being that monkeys were required to indicate target presence and location by means of a saccadic eye movement toward the target (see Figures 3 and 4). The monkeys were seated in a standard primate chair and viewed the display from a distance of 60 cm. Head movements were prevented by bolting the implanted head post to the frame of the chair. Eye position was monitored continuously with the scleral-search-coil technique. Each trial began with the appearance of a centrally located fixation spot. After fixation of gaze was achieved, the sample appeared for a duration of 1 s. To reduce the likelihood of a premature response, a short stimulus onset asynchrony (200–300 ms) was inserted between the cue offset and search array onset. A trial was immediately aborted if the subject's eye position deviated from a  $1^\circ$  window centered on the fixation spot at any time before presentation of the search array.

Search arrays were of the target-absent type on half of the trials. On the other half (target-present), the target position was randomly chosen from the 36 possible positions. The monkey could covertly search for the target indefinitely, provided its eyes did not move away from the fixation window. To discourage prolonged fixations, however, a reward was dispensed on target-present trials only if a saccade found the target within 3.5 s of the appearance of the search array. The only allowable eye movement away from the fixation window was a saccade directed toward the target. To ensure this constraint, once a saccade was initiated, target fixation had to occur within 50–150 ms and be maintained for an additional 150 ms. Saccade latencies were registered and recorded for each trial. If successful, the trial was terminated with a juice reward. If the trial

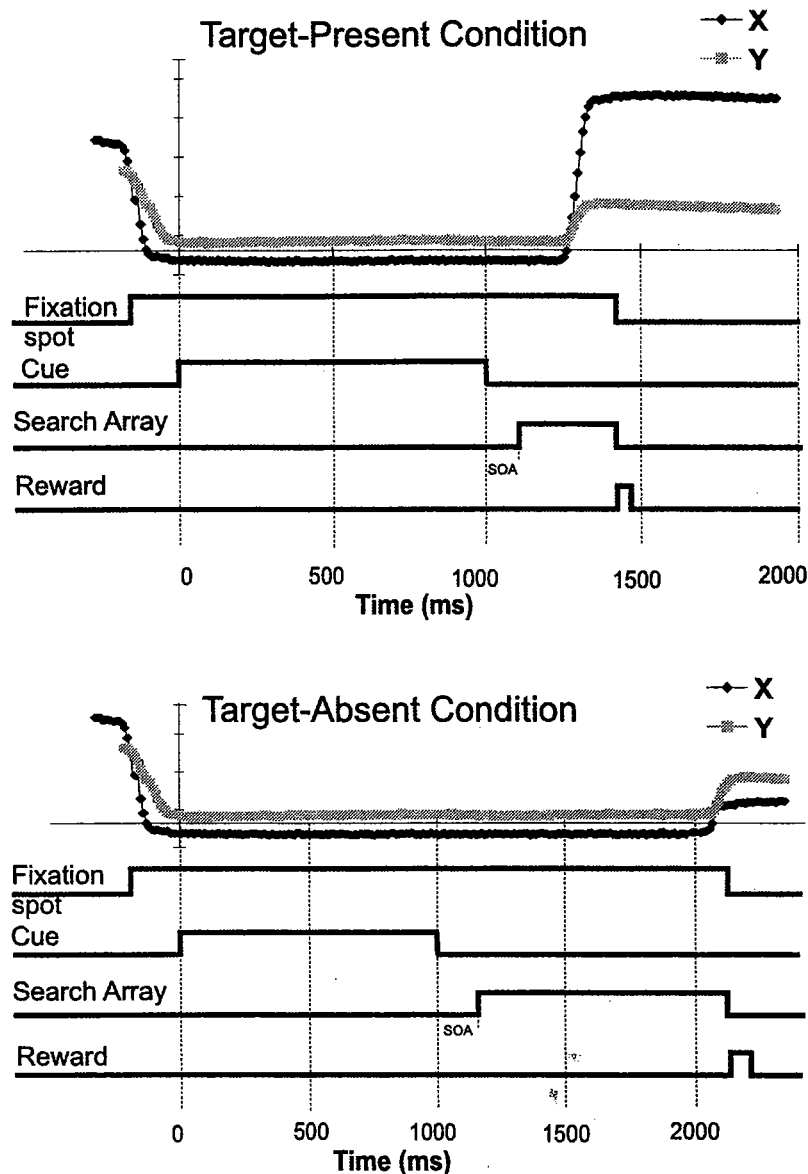


Figure 3. Event timing for monkey search task. Curved thick lines represent sample eye position trace. Top panel shows target-present trials; bottom panel shows target-absent trials. SOA = stimulus onset asynchrony.

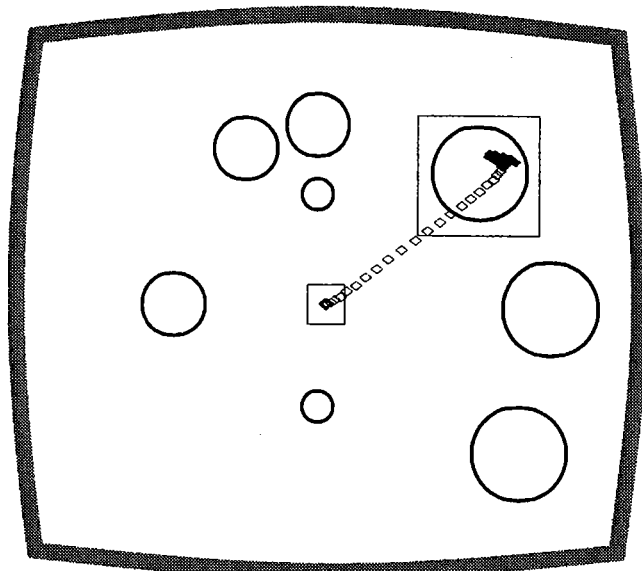
was unsuccessful, the display was darkened and the monkey was penalized by a 5-s period of inaction ("time-out").

On target-absent trials, monkeys were required to maintain fixation on the central spot for 1,000–1,500 ms after the onset of the search array. This procedure did not allow an evaluation of reaction latency for target-absent trials and was introduced solely because it would facilitate acquisition of baseline neuronal responses in subsequent neurophysiological studies. For all but 1 monkey, target-absent trials began with a yellow cue, informing the monkey beforehand about the target's absence.

**Training procedure.** Because the training required for animal subjects may influence search strategies and neuronal representations of target stimuli, we describe it here in some detail. Formal behavioral training began with fixation of gaze. Once monkeys reliably performed this task for 2 s, a search task was introduced. In the first stage of search training, monkeys were presented with a

color popout search array with uniform motion. The time interval allowed for saccadic acquisition of the target (saccade waiting time [SWT] = time from saccade onset until gaze is directed at the target) was initially 2 s, thus allowing multiple fixations. This lengthy SWT permitted monkeys to become familiar with the search array. Once task performance was stable, SWT was gradually reduced to an interval that allowed only one saccade (this time interval varied from 50–150 ms depending on saccade velocity). Monkeys generally learned this task to criterion (80% correct) within 2–4 weeks. At this point, direction of motion was randomized across apertures in the search array. This change had minimal impact on performance.

In the second stage of search training, the motion popout task was introduced with uniform color. This task was generally acquired more slowly than the color popout task (2–10 weeks), presumably because of the lesser saliency of the motion-defined



**Figure 4.** Example of saccadic response to target location indicating covert detection of the target by a monkey. Each diamond represents a single eye-position measurement (sampled every 4 ms). Circles represent positions of items in the search array. The squares in the center of the display and around the target aperture depict electronic eye-windows used to verify initial eye fixation and saccade endpoint. The horizontal "smear" of eye positions at the target location reflects small horizontal tracking eye movements caused by horizontal target motion.

target compared with the color-defined target. In the final stage of search training, the conjunction task was presented. This task represented a qualitative increase in difficulty because it cannot be solved readily without reference to the sample, which was presented at the beginning of each trial. To facilitate the learned association between sample and target, both the sample (at the end of presentation) and the target (after a saccade was made toward it) took on a blue tint. After incorrect saccades, all distractors were dimmed, thus revealing the actual location of the target. This final stage of training was continued until a criterion level of performance (25% above chance) was met (4–9 months).

### Data Analysis

The two independent variables in these experiments were (a) set size (the number of distractors plus target items in the search array) and (b) search type (color, motion, and color-motion conjunction). The principal dependent variable was RT (keystroke for humans, saccade for monkeys). For each search type, data were plotted as RT versus set size. These data were fitted with a linear model, and the slopes and intercepts were used as indices to characterize human and monkey performance. The significance of comparisons of search slopes for group and individual subjects was tested with the *t* test for linear regression slopes (criterion level  $p = .05$ ). Significance of set-size and search-type effects was tested by analysis of variance (ANOVA) on both raw and ranked data (Myers & Well, 1991). Because the outcome of the two tests was identical, we report only the results of the ANOVA on the raw data. Where necessary, the nonparametric Kruskal-Wallis test was used to check for the existence of set size effects. A second dependent variable, error rate, was also evaluated as a function of set size and

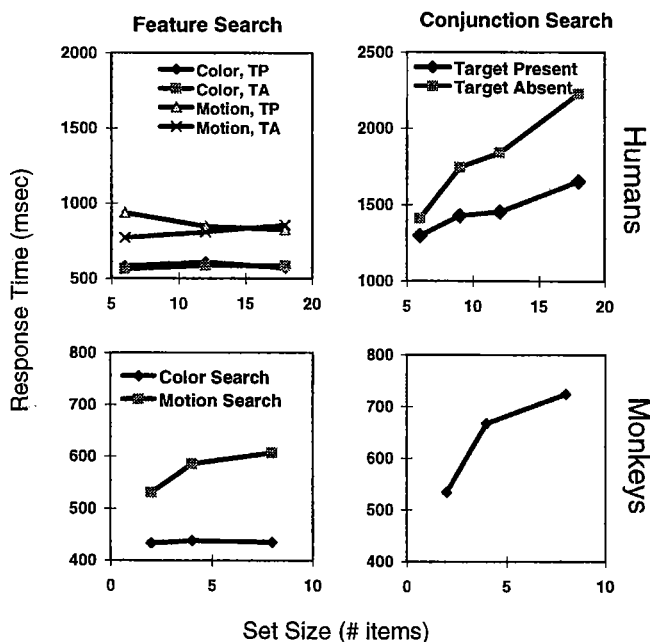
search type. The chi-square test was used for comparisons of error rates.

## Results

### Reaction Time

The traditional account of the dynamics of visual search (Treisman & Gelade, 1980) emphasizes a single parameter: the slope of the function relating visual search RT to set size. This account argues that this parameter is sufficient to discriminate between two modes of visual search: (a) instantaneous, set-size-independent (popout) target detection, driven by low-level feature contrast mechanisms, and (b) scrutiny of the search array driven by attentional top-down mechanisms. The former is defined by RTs that remain constant as set size is increased (slope  $\approx 0$ ), whereas the latter is defined by search times that increase linearly with set size (the traditional criterion is a minimum slope of  $\approx 10$  ms/item; Treisman & Gelade, 1980). Intersubject averaged RT data for both humans and monkeys are plotted in Figure 5.

Feature search, averaged over 3 human participants, yielded  $-1.04$  ms/item for color search (not significantly different from zero),  $t(225) = 0.92$ ,  $p = .36$ , and  $-7.55$  ms/item for motion search,  $t(205) = 2.88$ ,  $p < .005$ . For both color- and motion-defined targets, results conformed to the pattern of popout search (Figure 5, upper left; see top of Table 1 for individual data). The frequently observed tendency toward negative slopes was due to feature contrast



**Figure 5.** Average search functions obtained from 6 humans and 3 monkeys performing disjunctive feature (left column) and feature conjunction (right column) search tasks. Top row shows response times versus set size for human participants from both target-present (TP) and target-absent (TA) trials. Bottom row shows search functions for monkey subjects, target-present trials only.

Table 1  
*Slopes and Intercepts of Search Functions of Human Participants*

Task and participant	Target-present trials		Target-absent trials	
	Slope	Intercept	Slope	Intercept
Motion popout				
R.D.	-3.12	690.95	2.52	627.68
J.B.	-19.18	1,614.50	18.80	992.61
G.B.	-2.00	626.15	3.75	589.24
Color popout				
R.D.	-3.33	551.88	4.35	496.12
J.B.	-0.23	729.41	-2.19	696.19
G.B.	0.70	511.87	3.42	474.70
Conjunction search				
R.D.	13.33	694.74	20.24	687.18
J.B.	39.45	1,541.88	59.81	1,437.78
K.Z.	8.22	877.47	48.08	507.43
J.C.	22.01	1,000.23	50.37	862.44
L.R.	27.20	973.79	53.19	1,225.08
R.C.	11.02	917.39	57.83	800.13

(i.e., contrast between target and distractor features), which improves target detectability as set size increases (e.g., Nothdurft, 1993a, 1993b). Average search times for motion-defined targets were somewhat higher, suggesting that this task was more demanding than the color search task.

Monkeys' feature search for color yielded an average of 1.05 ms/item (5 monkeys; not significantly different from zero),  $t(3148) = 1.1$ ,  $p = .27$ , and 10.12 ms/item for motion search (3 monkeys),  $t(2124) = 4.9$ ,  $p < .000001$  (see Figure 5, lower left). Slopes reflecting the relationship between RT and set size for feature search of individual monkeys are presented at the top of Table 2. Search slopes for color-defined targets were always less than 10 ms/item (linear fits based on means and medians are shown). Search times for motion-defined targets were consistently higher than those for color-defined targets (two-way ANOVA,  $p < .001$ ), paralleling the pattern observed in human participants.

Average performance of both humans and monkeys during the search for color-motion conjunctions (Figure 5, right) met the criterion for the second mode of search:

Conjunction search rate was found to be 19.85 ms/item when averaged over 6 human participants (significantly different from feature search,  $p < .001$ ; see the bottom part of Table 1). The average conjunction search slope for 3 monkeys was 17.39 ms/item (significantly different from feature search,  $p < .002$ ; see the bottom part of Tables 1 and 2). Thus, although the average slope produced by monkeys searching for a motion-defined target approached the criterion value for a serial search, it was nearly two times smaller than the observed average slope produced by monkeys' conjunction search. Moreover, monkeys and humans, as a group, exhibited comparable search slopes, despite the fact that the behavioral response was different: a keystroke indicating target presence for humans and a saccade indicating target location for monkeys (but see subsection *Intersubject Differences* below). Y intercepts of the RT-set-size functions were larger for humans than for monkeys (~1,000 ms vs. ~400 ms), which can be attributed to the different operant responses used.

Another seriality criterion advanced by Treisman and Gelade (1980) is that the search function obtained on target-present trials should be approximately half of that obtained on target-absent trials. Indeed, for most human participants, the target-present slope (average  $\approx 20$  ms/item) was less than half of the slope seen on target-absent trials (average  $\approx 57$  ms/item). Comparable measures were unobtainable from monkeys because of the nature of the task. (Monkeys were required to fixate for an extended period of time [1,000–1,500 ms] to indicate target absence; see *Method* section for details.)

The gross picture of monkey and human performance formed on the basis of the traditional RT measure supports our contention that the two species perform the visual search task in a qualitatively similar way. Moreover, depending on the stimulus, both species exhibit the same two search modes. Because this analysis is restricted to the single parameter of RT, however, it neglects many important features of search performance in humans and monkeys. In particular, another measured parameter—error rate—reveals an important difference between the search strategies used by humans and monkeys.

Table 2  
*Slopes and Intercepts of Monkey Search Functions*

Task and subject	Slope <sup>a</sup>	Slope = 0?	Intercept <sup>a</sup>
Color popout			
Mickey	-12.45 (0.00)	$t(815) = 4.20$ , $p < .0001$	407.65 (317.0)
Rikiki	4.09 (5.93)	$t(560) = 1.20$ , $p = .23$	599.21 (550.5)
Roulette	0.43 (3.93)	$t(606) = 0.48$ , $p = .63$	270.41 (243.0)
Tigger	3.70 (7.11)	$t(1161) = 6.32$ , $p < .000001$	226.93 (200.5)
Motion popout			
Mickey	5.96 (8.25)	$t(299) = 2.10$ , $p = .038$	281.55 (476.0)
Rikiki	9.15 (11.39)	$t(816) = 3.70$ , $p < .001$	607.00 (575.5)
Tigger	11.64 (10.86)	$t(1005) = 15.30$ , $p < .00001$	237.90 (233.0)
Conjunction search			
Mickey	7.92 (8.38)	$t(613) = 4.88$ , $p < .0001$	353.19 (316.33)
Rikiki	38.97 (54.96)	$t(1316) = 165.00$ , $p = .000001$	594.49 (449.5)
Zoey	7.07 (7.75)	$t(236) = 4.19$ , $p < .0001$	171.30 (175.5)

<sup>a</sup>Values in parentheses were calculated by using medians of response distributions for every set size.

### Error Rates

One essential difference between human and monkey performance is that the two species have different objectives in our tasks: Humans are instructed to minimize errors, whereas monkeys are trained to maximize reward. This strategic difference is likely to underlie the marked differences in error rates between the two species (see Figure 6). Even after prolonged training ( $\geq 12$  months) monkey performance remained somewhat variable and occasionally fell below criterion.

Independent of species-specific strategies, error rates are indicative of task difficulty and complement RT performance characteristics. Average human error rates are very low ( $< 6\%$ ) for all three types of search (Figure 6, upper panel). Monkey error rates, in contrast, were moderate ( $\approx 20\text{--}30\%$ ) and independent of set size for the two types of feature search, for error rate dependence on the set size,  $\chi^2(4, N = 3) = 1.59, p = .45$ . Monkey error rates were significantly larger for the conjunction search task (Figure 6, lower panel), and they increased dramatically with set size, for color-conjunction search errors,  $\chi^2(2, N = 3) = 9.23, p < .01$ . This set-size dependence demonstrates that monkeys are willing to sacrifice accuracy for speed. In such circumstances, only the joint consideration of speed and error rates can yield an accurate description of task difficulty and thus the attentional demands of the task. Although the average error rates of monkeys performing the conjunction search task were large ( $\approx 20\%, 50\%$ , and  $60\%$  for 2, 4, and 8

apertures, respectively), performance surpassed chance error rate (50%, 75%, and 87.5%, respectively; see x in lower panel of Figure 6) by an approximately fixed difference of 25–30%.

Because monkeys fell behind humans in their performance level, we explored the distractor-choice probabilities on error trials to better understand monkey search logic. We found that target selection was preferentially guided by color. The probability of hitting a distractor sharing color with the target was significantly higher than chance (saccade to target color|error) =  $p(\text{saccade to target color error}) / p(\text{error})$  was 0.61 and 0.52 for 2 monkeys, whereas chance probability  $p(\text{saccade to target color|error})$ , was 0.41 and 0.40, respectively,  $\chi^2(1, N = 1) = 230.3, p < .00001$ , and  $\chi^2(1, N = 1) = 76.51, p < .00001$ , respectively. In contrast, we did not observe guidance by direction of motion,  $p(\text{saccade to target direction|error})$  was 0.29 and 0.31 for 2 monkeys, and the chance probabilities were 0.29 and 0.38;  $\chi^2(1, N = 1) = 0.0, p = 1.0$ , and  $\chi^2(1, N = 1) = 26.5, p < .00001$ , respectively (probability calculations were based on 1,394 and 1,199 trials. Hence, the color information was a more important factor in determining the target choice than was the direction of motion. This observation is in accord with the recent report by Motter and Belky (1998).

### Fixed Relevant Set Search

The preferential selection of items possessing the target color is consistent with the hypothesis that subjects constrain visual search to items that share at least one feature with the target and ignore the remaining distractors (Egeth et al., 1984). According to this hypothesis, the steep search-function slopes observed were due only to variation in the number of items that possessed a target feature (*relevant set*). Specifically, search times should be constant when relevant set size was fixed and only the number of irrelevant distractors varied. We tested this hypothesis in the fixed relevant set search experiment. When the number of items sharing color with the target was constant (6 items), but the number of the “irrelevantly” colored items was varied (0, 2, 6, and 12), the slope of the search function exhibited by human participants ( $n = 3$ ) was 23.9 ms/item (error rate  $< 5\%$ ), which is very similar to that of a standard conjunction search. One monkey (Mickey) was tested on stimuli in which the relevant set was fixed to 4 items and the number of irrelevant items varied between 0, 4, and 8. The slope of the search function was 10.0 ms/item, and error rates were 32% for 0 irrelevant items, 43% for 4, and 57% for 8; cf. Figure 6. Contrary to the findings of Egeth et al. (1984), both species performed the fixed relevant set search with RTs and error rates that matched those of the standard search. Thus, though our error rate analysis indicated that target selection is preferentially guided by color, this is not an exclusive bias for either humans or monkeys.

### Intersubject Differences

Although the results presented thus far present a picture of typical performance of humans and monkeys on the different

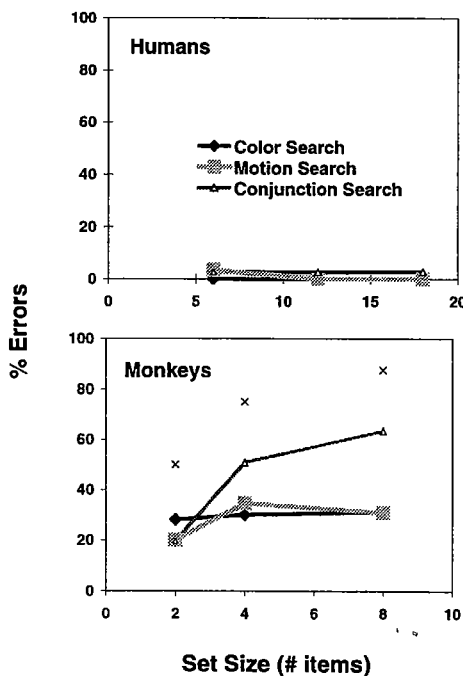


Figure 6. Average error rates during visual search by humans and monkeys. Top panel shows errors incurred by humans, averaged over target-present and target-absent trials. Bottom panel shows average errors incurred by monkeys on target-present trials. The points above data plots (marked by x) indicate errors associated with chance performance.



search tasks, a number of individual differences in performance were noted. These differences are highlighted in the following section, in which we present results of a closer examination of performance data.

*Set-size and search-type effects.* Slopes reflecting the relationship between RT and set size for feature conjunction search are presented at the bottom of Tables 1 and 2 for humans and monkeys, respectively. Human conjunction search slopes ranged from 8.2 to 39.4 ms/item, whereas monkey search slopes ranged from 7.1 to 39.0 ms/item.

Slopes reflecting the relationship between RT and set size for color and motion feature search are also presented in Tables 1 and 2. A single major deviation from the mean slope ( $-12.45$  ms/item; significantly different from zero),  $t(815) = 4.19$ ,  $p < .0001$  for the color feature search was exhibited by 1 monkey (Mickey) during the color search task. This monkey viewed feature search arrays of larger set sizes (4, 8, or 12 items) than did the remaining monkeys. The correspondingly larger color contrast in these displays may have accounted for the decrease in search times with increasing set size.

For 1 monkey (Rikiki), the conjunction search slope was substantially larger than the slopes obtained for either motion- or color-defined targets, conjunction-color slope comparison:  $t(1878) = 5.33$ ,  $p < .000001$ ; conjunction-motion slope comparison:  $t(2134) = 6.09$ ,  $p < .000001$ . The other monkey (Mickey) for which we were able to collect data on both feature and conjunction search performance exhibited conjunction search slopes that were only slightly larger than those for motion feature,  $t(914) = 0.44$ ,  $p = .66$  (see Table 2). Nevertheless, the model-free comparison of conjunction and motion search performance of this monkey showed a significant effect of both set size,  $F(2, 906) = 9.82$ ,  $p = .002$ , and search type,  $F(1, 906) = 10.53$ ,  $p < .001$ . The Set Size  $\times$  Search Type interaction only approached significance,  $p = .082$ , for errors:  $\chi^2(2, N = 1) = 0.72$ ,  $p = .7$ . As discussed above, this small difference in slopes might be due to the propensity of monkeys to trade accuracy for speed. The difference between color and conjunction search slopes, however, was significant for this monkey,  $t(1428) = 6.2$ ,  $p < .000001$ . The error rate difference approached significance,  $\chi^2(2, N = 1) = 5.05$ ,  $p = .08$ , supporting the notion that the conjunction search task was indeed more demanding than the color search task.

### Comparing RT Distributions

The conventional approach to understanding visual search performance involves characterization of the dependence of mean (or median) RTs on set size. However, search models also place constraints on the dependence of variance on set size. In particular, a serial search model that assumes random sampling of the search array and no noise sources predicts that standard deviation should be proportional to the set size (e.g., given the search function slope of 40 ms, in the absence of additional noise sources the standard deviation for 6, 9, and 18 apertures should be 75, 109, and 213 ms, respectively). In practice, however, set size accounts for

only a small fraction of RT variance. Trial-by-trial variability of RTs for a fixed set size may be very large (for participant J.B., whose search slope was 39.45 ms/item, RT standard deviations were 775.8, 728.6, and 681.0 for set sizes 6, 9, and 18, respectively) and not correlated with the set size because of internal (e.g., decision, motor) noise and spurious spatial interactions between distractor representations in the randomized search arrays. We believe that the trial-by-trial variability in RTs caused by random generation of search array spatial distributions effectively masked the dependence of variance on set size. Interestingly, a casual inspection of RT distributions (see Figure 7) suggests that the effect of set size is to shift the whole distribution by a certain time step without changing the underlying probability-density function (inset of Figure 7). Thus, the residual variability, unaccounted for by a linear dependency on set size, seems to be independent of set size (the correlation between standard deviations and set size across all monkeys was .22 for the target-present case). We have addressed the sources of this residual variability by means of a model (Buračas, Albright, & Sejnowski, 1996) that learns to perform the visual search task. This study suggests that the set-size-independent variability may be accounted for by two kinds of factors: (a) noise in the cognitive processing and motor command generation, and (b) the interaction of these processes with the variable distribution of stimulus values in the search array.

The most remarkable observation in the present study is that RT distributions for different set sizes are similar in shape for both humans and monkeys, despite the difference in behavioral response type (saccade vs. manual keystroke). Furthermore, the degree of overlap of RT distributions for different set sizes is also qualitatively comparable. This observation corroborates our hypothesis that human and monkey visual search is affected by the sources of variability listed above in essentially analogous fashion, thus potentially involving similar brain mechanisms.

### Learning Effects

We have also observed that extensive practice can reduce set-size effects (see also Sireteanu & Rettenbach, 1995). Figure 8 (top) displays the dramatic, three-fold reduction of slopes for 1 human participant that occurred over 1 week of practice (over 2,000 trials). The slope for target-present trials declined from 37.1 to 15.3 ms/item, and the slope for target-absent trials declined from 143.9 to 63.9 ms/item. Intercepts decreased as well (from 1,865.4 to 832.1 ms), reflecting improvement at the motor and decision-making stages. Even after extended training on the conjunction search, however, the dependency of search times on set size remained significant for all human participants.

Monkeys showed a qualitatively different pattern of progress. As stated above, the optimization strategy used by monkeys (maximizing reward instead of minimizing errors) elicited very short search times for all set sizes. This bias was evident from the first exposure of the monkeys to the task (Figure 8, bottom row, left panel). In contrast to human performance, learning progress was marked not by a reduc-

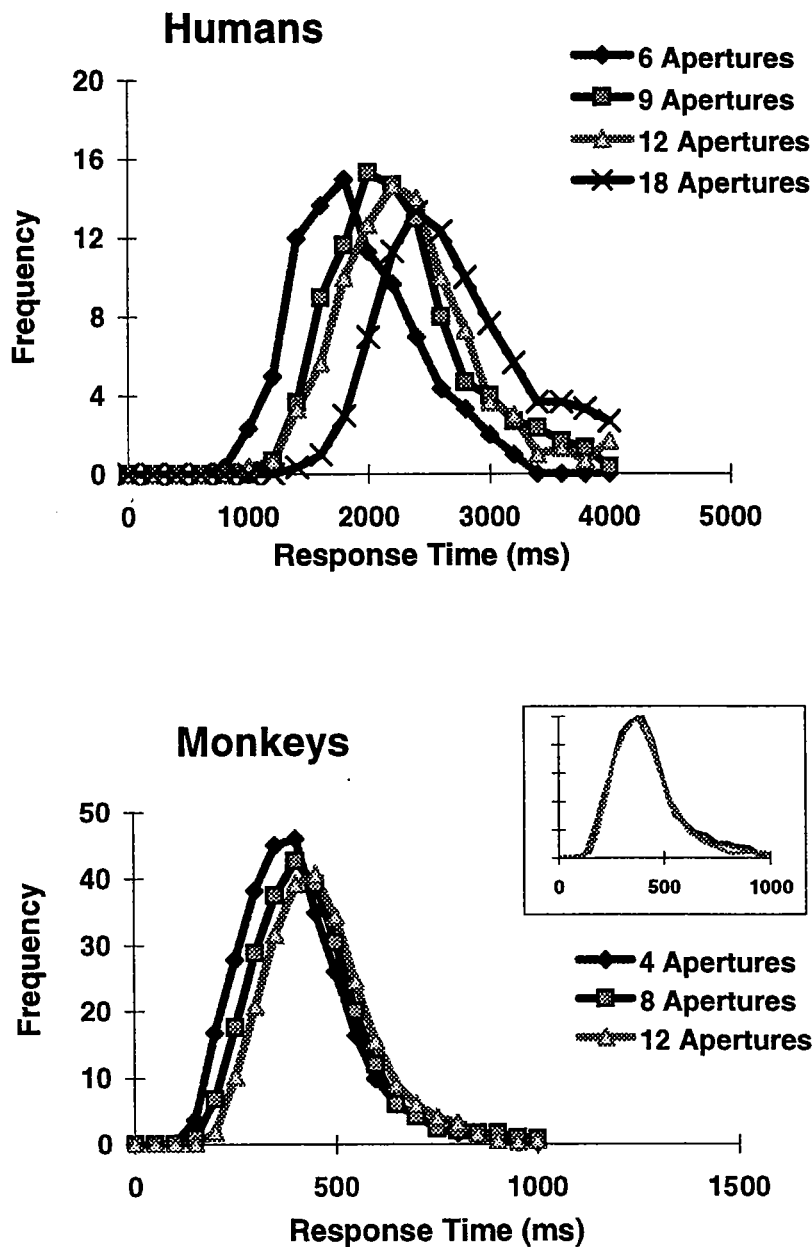


Figure 7. Response time (RT) distributions for humans and monkeys. The principal effect of set-size variation is to shift the whole distribution by a fixed RT interval. RT variance is independent of the set size. Inset in monkey RT distribution graph shows overlap of normalized and shifted (by 25 and 75 ms) RT distributions.

tion in search slopes but rather by a systematic (set-size independent) decline in error rates, suggesting that, with practice, monkeys gradually shifted from guessing to covert scanning of the search array. (The progress over 4 months of practice is shown in Figure 8, top row.) This interpretation is supported by our observation that in some cases, contrary to human learning, the average search times increased even after prolonged training, which is consistent with learning to serially scan the search array. Thus, the different course of learning in humans and monkeys might be the source of the

differences between monkey and human performance emphasized in the above *Error Rates* section.

### Discussion

In the present study, we explored the possibility of extending the classic visual search paradigm to nonhuman primates, with the goal of subsequently using this paradigm to investigate neuronal correlates of feature conjunction, target selection, and visual awareness. We presented evi-

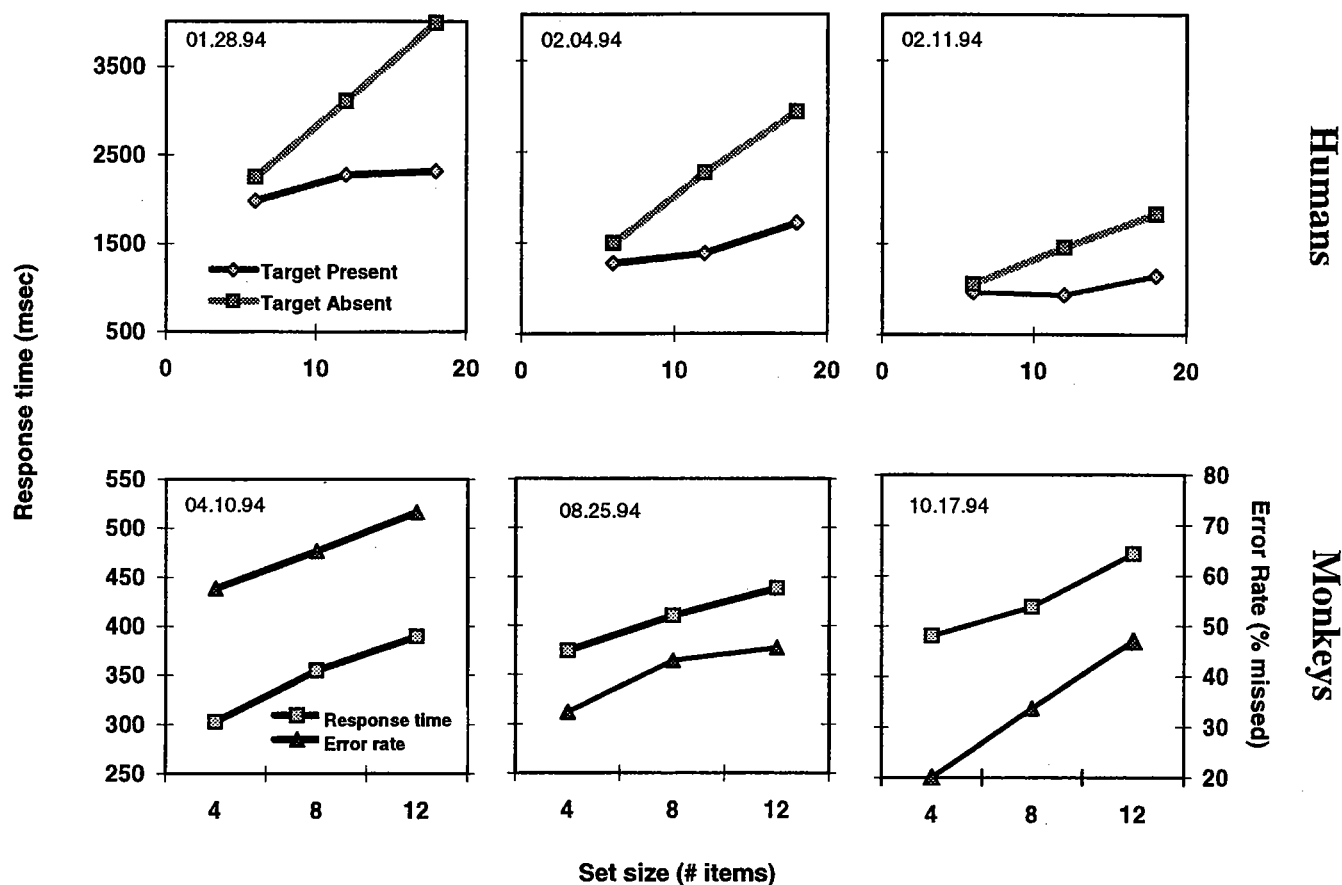


Figure 8. Learning effects for humans and monkeys. Top row shows the evolution of response times (RTs) for both target-present and target-absent trials of 1 human participant (R.C.) over a period of 1 week. Bottom row shows the evolution of RTs and error rates of 1 monkey (Mickey) over a period of 6 months (left: after 6 weeks of training on the conjunction task; center: 6 months; right: 10 months). The main effect is a set-size-independent decline in error rate. RTs also increased somewhat with training, but RT slopes remained unchanged. This combination of changes reflects a transition from very high rates of guessing on the part of the monkey to a genuine target-search strategy.

dence supporting the conclusion that the average characteristics of color-motion conjunction search performance by rhesus monkeys are comparable to those of humans. For both species, the conjunction search task proved to be more difficult than the feature search task, as evidenced by reaction latencies and error rates. In addition, search times and errors were similarly affected by irrelevant colored distractors. The major difference between human and monkey performance was in error rates, which were generally higher for monkeys than for humans; this difference is attributable to different optimization strategies adopted by the two species. Joint consideration of reaction latencies and error rates, however, revealed the same ranking of task difficulty for humans and monkeys. The disjunctive color search task proved to be the least demanding, the disjunctive motion search was intermediate, and the conjunction search was the most demanding of the three tasks. This pattern of search performance is consistent with the notion that feature-defined targets are readily detected because of popout, which is mediated by low-level feature contrast mechanisms. In

contrast, targets defined by conjunctions of features are masked by surrounding distractors and require attentive scrutiny, which is guided by top-down mechanisms. Relatively low conjunction search slopes for 2 monkeys (7–8 ms/item, see Table 2) can be explained in terms of a speed-versus-accuracy trade-off. In contrast to humans, who maintained maximal accuracy, monkeys favored speed over accuracy, effectively reducing conjunction search slopes and increasing error rate.

In the following discussion, we compare our results to those of previous studies and discuss competing hypotheses about the mechanisms of feature conjunction search. In closing, we discuss the feasibility and utility of adopting this behavioral paradigm for neurophysiological experiments.

#### Comparison to Previous Work

Previous attempts to train monkeys on a feature conjunction search task led to somewhat unexpected, and hence controversial, results. Von der Heydt and Dursteler (1993)

reported that overtrained monkeys can perform a color-orientation conjunction search as quickly as a feature search, with the RT-set-size slope approaching zero for both tasks. Humans trained by a comparable number of trials on the same task always exhibited longer search times for conjunction than for feature search. This result suggested that overtrained monkeys, in contrast to humans, adopt a different search strategy or mechanism—perhaps mediated by the development of task-specific, neuronal feature conjunction detectors. In contrast to this earlier study, our results reveal many common characteristics of human and monkey search performance: (a) The RT distributions for both species' cases were of the gamma probability-density-function shape, and the set-size effects assumed a form that shifted these distributions in time, and (b) RTs and error rates considered together revealed that even for overtrained monkeys (12–14 months of practice), conjunction search tasks were always much harder than both types of disjunctive feature search tasks. These observations do not support the claim that humans and monkeys rely on different brain mechanisms for visual search.

The discordance between the report of von der Heydt and Dursteler (1993) and the results of the present study might be explained by the fact that the two studies used different features to form conjunctive targets—color and orientation (von der Heydt & Dursteler, 1993) versus color and motion (present study). Furthermore, it is likely that our task demanded more attentional resources than that of von der Heydt and Dursteler because of eccentrically scaled apertures, which resulted in weaker and spatially nonhomogeneous feature contrast. Indeed, most of our monkeys performed the motion-popout task with slopes approaching Treisman's criterion value for the serial search, suggesting that the motion-defined targets were not as salient as color-defined targets and that their detection demanded some serial scanning.

Although our results do not rule out the possibility that both humans and monkeys might eventually develop feature conjunction detectors after prolonged training, it seems unlikely that such detectors could mediate target popout by contrast mechanisms similar to those thought to mediate feature popout. There exists evidence (e.g., Nothdurft, 1993a, 1993b) that feature popout is mediated by feature contrast mechanisms within cortical feature maps (e.g., Allman, Miezin, & McGuinness, 1985; Desimone, Schein, & Albright, 1985; Knierim & Van Essen, 1992). Thus, feature conjunction popout would require developing a new feature conjunction map to support feature conjunction contrast mechanisms. We deem this implausible because of a combinatorial explosion problem and because it demands extensive rewiring of visual circuitry. A more likely mechanism underlying the plasticity induced by training on a visual search task could be related to the feature-specific gating in feature maps (Buračas, et al., 1996; Treisman & Sato, 1990; Wolfe, 1994; Wolf et al., 1989), which is thought to be driven by top-down influences. The development of such feature-specific gain mechanism would result in the decline of slopes for conjunction search, which indeed has been observed in humans (Buračas & Albright, 1996).

### *Is Search for Feature Conjunctions Serial?*

Treisman and Gelade (1980) originally proposed that the set-size effects observed in feature conjunction search were due to a shifting attentional spotlight, which samples individual items in the search array for further processing. Unfortunately, because the movements of the hypothesized spotlight are covert and unmeasurable, the results of visual search experiments cannot readily distinguish between serial search and alternative models, such as probability summation and integrated competition (Desimone & Duncan, 1995). Thus, arguments bearing on the seriality of attentional allocation in visual search are commonly indirect. One such line of argumentation comes from research that conceptualizes attention as the selection of sensory information for action (e.g., Allport, 1993; Rao & Ballard, 1995). From this point of view, the seriality of attention can be understood as a derivative of a serial decision-action process that samples visual information from restricted loci on demand. For example, Rao, Zelinsky, Hayhoe, and Ballard (1996) have argued that sequential eye fixations by subjects viewing (naturalistic) search arrays provide good evidence for serial visual processing during this task. The argument for feature conjunction search seriality has gained additional support from the evidence that the posterior parietal areas in humans are activated in both an explicitly serial task and a search for conjunctions of features, whereas feature search (disjunctive search) causes no such activation in the posterior parietal areas (Corbetta, Shulman, Miezin, & Petersen, 1995). The results of our electrophysiological study of neuronal responses in a monkey performing a conjunction search task are also consistent with serial search (Buračas & Albright, 1995). Nevertheless, the results of the present study only indicate that feature targets are more salient than conjunction targets for both humans and monkeys.

### *Feature Conjunction Search as a Neurophysiological Paradigm*

For over 3 decades, the visual search paradigm has been used in human behavioral experiments with the hope of better understanding the following issues: (a) the dynamics of attentional scanning (e.g., Neisser, 1967), (b) the role of attention in feature binding and perception of complex objects (e.g., Treisman & Gelade, 1980), and (c) the role of search in visual perception (e.g., Rao & Ballard, 1995). It has nonetheless proved difficult to decide between competing theories, given only behavioral data. Single-unit recording from cortical areas implicated by behavioral experiments could shed light on the unresolved aspects of the issues listed above. Indeed, recent applications of search tasks in the context of electrophysiological recordings have proved very successful; these experiments have led to exciting new discoveries of neuronal correlates of target selection in the frontal eye fields (Schall & Hanes, 1993) and inferior temporal cortex (Chelazzi, Miller, Duncan, & Desimone, 1993). Pursuing this line of discovery further, we reasoned that use of the feature conjunction search paradigm in

electrophysiological experiments might shed light on the nature of attentional dynamics (e.g., serial vs. parallel-competitive dynamics). Among other possibilities, the conjunction search task would allow one to test the controversial proposal that attentional feature integration is mediated by synchronizing neuronal discharges in different cortical maps (e.g., Crick & Koch, 1990; Singer & Gray, 1995).

The results of the present study demonstrate that the feature conjunction search paradigm can be extended to monkeys. Like humans, monkeys exhibit pronounced differences between search for conjunctions and search for disjunctions of color and direction of motion. However, that difference may be reflected in error rates rather than in RTs. The close match in average performance and RT distributions of humans and monkeys supports the idea that feature and conjunction search targets are represented in a similar fashion in humans and monkeys and that those representations are likely to involve similar brain mechanisms. Monkeys trained in this manner thus offer an appropriate animal model for studies of the neuronal mechanisms of feature conjunction search and feature binding.

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