

Covert Orienting of Attention in Macaques

I. Effects of Behavioral Context

ERIC M. BOWMAN, VERITY J. BROWN, CAROLINE KERTZMAN, URS SCHWARZ,
AND DAVID LEE ROBINSON

*Section on Visual Behavior, Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health,
Bethesda, Maryland 20892*

SUMMARY AND CONCLUSIONS

1. A task was used by Posner (1980) to measure shifts of attention that occurred covertly, in the absence of an eye movement or other orienting response. This paradigm was used here to assess the nature of covert attentional orienting in monkeys to develop an animal model for neurophysiological studies. Shifts of attention were measurable in monkeys and were consistent across a variety of experimental conditions.

2. The paradigm required that monkeys fixate and release a bar at the appearance of a target, which was preceded by a cue. Reaction times to targets that followed peripheral cues at the same location (*validly* cued) were significantly faster than those that followed cues in the opposite visual field (*invalidly* cued). This difference was defined as the *validity effect*, which as in humans, is used as the measure of a covert attentional shift.

3. When the proportion of validly to invalidly cued targets was decreased, no change was seen in the validity effect of the monkeys. This is in contrast to humans, for whom the ratio of validly to invalidly cued targets affected the magnitude of the validity effect. When 80% of the targets were preceded by cues at the same location, the validity effect was greatest. The effect was reversed when the proportions were reversed. From this result, it is concluded that cognitive processes can affect covert orienting to peripheral cues in humans, whereas in trained monkeys, performance was automatic.

4. To test whether cognitive influences on attention could be demonstrated in the monkey, an animal was taught to use symbolic, foveal signals to covertly direct attention. The magnitude of this validity effect was greater than that obtained with peripheral cues.

5. The effects of motivational and perceptual processes were tested. Although overall reaction times could be modified, the facilitating effects of the cues persisted. This constancy across motivational and perceptual levels supports the notion that the monkeys were performing the task in an automatic way, under the exogenous control of peripheral cues.

6. Most visual cuing has been tested with visual landmarks at the locations of cues and targets. These monkeys were trained with such landmarks, and when tested without them, the attentional effect of the cues was nearly abolished. These data suggest that local visual features can be important for covert orienting.

7. To determine the spatial extent of the effect of the cue, monkeys and humans were tested with four cue-target distances (0–60°). Reaction times were fastest at a cue-target distance of 0° (validly cued) for the earliest temporal interval for both monkeys and humans. For the monkey, the validity effect peaked at 20° and declined more eccentrically. For humans, the validity effect was qualitatively similar for distances from 20 to 60°.

8. The present studies demonstrate that peripheral visual cues result in attentional shifts in monkeys, similar to those described in humans. This approach provides an animal model for exoge-

nously elicited attentional shifts. The effects of peripheral cues are reliable in trained monkeys and are minimally susceptible to endogenous or experimental influences. However, like humans, monkeys can exert endogenous control over the covert orienting of attention when symbolic cues are used.

INTRODUCTION

Attention is a selection process whereby some stimuli or locations are given priority at the expense of others. In vision, this selection is often indicated by an eye movement, and the direction of attention is therefore the same as the direction of gaze. However, spatial attention may be covertly oriented, in which case it is dissociated from the direction of gaze or a specific motor response. Stimuli that elicit shifts in attention may be from any sensory modality, and this is termed exogenous control of attention. In addition, attention can be directed by various mental processes, in which case it is termed endogenously controlled.

Exogenous control of visuospatial attention has been studied extensively in the laboratory. Salient sensory stimuli are hypothesized to attract attention to, or prime, a location, and the benefit in the utilization of a subsequent target is used as an indicator of attentional facilitation. Enhancement of processing at cued locations occurs for simple reaction time tasks, visual discriminations, temporal order decisions, cross-modality testing, and integration of visual features (Butter et al. 1989; Eriksen and Hoffman 1972; Jonides 1981; Maylor 1985; Nakayama and Mackeben 1989; Posner 1980; Prinzmetal et al. 1986).

Helmholtz (1909) provided the first experimental evidence of endogenous control of attention, and since then, others have also reported that symbolic cues presented at the fovea result in an improvement in performance (Bashinski and Bacharach 1980; Downing 1988; Posner 1980; Stelmach and Herdman 1991). The breadth of characterization of these cuing tasks in normal humans makes them attractive for studying the neural basis of attentional processes.

The neural basis of attention has been investigated in both monkeys and humans. Studies have reported enhanced responses of neurons to stimuli during attentive behavior or reduced responsiveness to unattended stimuli (Haenny et al. 1988; Moran and Desimone 1985; Mountcastle et al. 1981; Petersen et al. 1985; Spitzer and Richmond 1991; Wurtz et al. 1980). Previous reports from this laboratory have demonstrated that monkeys can perform

this cuing task and that the pulvinar plays an important role (Petersen et al. 1987). In addition there have been studies in humans demonstrating performance deficits after cerebral damage and changes in event-related potentials from normal humans during the performance of this cuing task (Anillo-Vento and Harter 1988; Mangun et al. 1987; Petersen et al. 1989; Posner et al. 1984). However, each of these approaches has limitations. For example, the time-course and controlling factors of covert attentional shifts were not investigated in nonhuman primates. Studies of event-related potentials in humans lack precise anatomic localization and there is variation in the extent of human brain lesions.

One approach to resolve these issues would be to study the parameters of this cuing task in the monkey so that direct studies of the neural basis could be conducted. In the present studies, attentional behavior of macaques was measured and factors that control performance were determined. In situations where the performance of the monkey differed from that reported in the literature for humans, a group of naive humans were also tested under identical conditions. The cuing paradigms used have previously been employed with humans, an approach that enables a direct comparison of human and monkey performance. A brief report of these studies has appeared previously (Bowman et al. 1991).

METHODS

Subjects

Three rhesus monkeys (4.0–7.5 kg; 1 female, 2 males) were studied in these experiments. Fourteen humans (7 females, 7 males; mean age, 36 yr) were tested on selected tasks. Each of the humans was studied on only one task and was naive with respect to the purpose of the experiment.

Surgery

After preliminary training and adaptation to the apparatus, each monkey was implanted with a cranial pedestal and a scleral search coil with the use of sterile surgical procedures (Judge et al. 1980). All medications were administered as reported previously (Robinson et al. 1991). Initial anesthesia was produced with ketamine HCl. Subsequently, pentobarbital sodium was given through a catheter in the saphenous vein. Heart rate, respiratory rate, and body temperature were monitored and body temperature was controlled with a heating pad. After the monkey had regained consciousness, it was returned to its home cage and allowed to recover. For 2 days after the surgery, each monkey was administered analgesics to reduce postoperative pain. During their recovery from surgery, the monkeys were given food and water freely and were checked daily. All procedures were conducted under a protocol approved by the Animal Care and Use Committee of the National Eye Institute and complied with Public Health Service Policy on the humane care and use of laboratory animals.

Apparatus

Subjects sat facing a tangent screen onto which the visual stimuli were rear-projected. Video signals for presentation of stimuli were generated on an IBM AT and fed into a video projection system (Electrohome Electronics EDP 58XL). The background illumination of the tangent screen was in the photopic range at 0.3 cd/m² while stimulus patterns (fixation point, visual landmarks, cues, and targets) were 3.0 cd/m² (Fig. 3C). Presentation of stim-

uli, delivery of rewards, and measurement of reaction times were controlled by a real-time UNIX data acquisition system operated on a DEC PDP-11/73 (Hays et al. 1982). Reaction times from monkeys were measured as the period from target onset to the time that the monkey released a touch-sensitive, nonmechanical bar on the front of the primate chair. Reaction times in humans were calculated with respect to the lifting of an index finger from a touch-sensitive pad (Brown et al. 1993).

Behavioral tasks and training

MONKEYS. After full postoperative recovery, the monkeys' intake of water was restricted. Their weight was monitored daily and maintained at ~90% of their preoperative levels. The monkeys were adapted to sitting in a primate chair with their head restrained and trained to fixate a spot of light projected on the tangent screen. Eye position was monitored, and trials were terminated if the eye moved outside of a computer-generated, $2 \times 2^\circ$ area surrounding the fixation point. Successful completion of a trial resulted in the delivery of a water reward of ~0.1 ml.

Subsequently, two monkeys (*M1* and *M2*) were rewarded for initiating each trial by contacting the bar and releasing it on the appearance of a 2° filled square (target) flashed in the periphery. For monkey *M3*, trials were started by the computer, and the animal was rewarded for contacting the bar when the target appeared. Persistent visual landmarks ($2^\circ +$ marks) indicated the locations where the targets would be presented (Fig. 3C). After satisfactory performance on this task, a briefly flashed (83 ms) cue was introduced between the onset of the fixation point and the appearance of the target. The cues were 2° open squares, which replaced the visual landmarks. The number of brightened pixels in the cues was equal to the number in the visual landmarks. Thus the onset of the cue did not result in a sudden increase in local luminance. Schematic tangent screens are illustrated in Fig. 3C and show the fixation point, cues, targets, and landmarks for validly and invalidly cued trials. These screens are shaded to illustrate that the images were luminance increases; however, the experiments were conducted under photopic conditions.

Responses were counted as correct and rewarded if they occurred 200–800 ms after the onset of the target. Anticipatory bar releases, late bar releases, and losses of fixation caused termination of a given trial and the projection of an error signal on the screen. After each error, a variable period (0.5–2.0 s) prevented the monkey from beginning another trial. In the final stages of training of two monkeys (*M1* and *M2*), the reward system was modified so that the number of rewards increased up to a maximum of three per trial for fast reaction times. The criteria for delivering multiple water rewards and the lengths of the error periods were adjusted so that these monkeys responded quickly and accurately. Each monkey was trained until it reached asymptotic performance on the Standard Task (see below). Monkey *M3* was never given multiple rewards for fast performance. Table 1 gives the mean reaction times for each subject on the standard task. The percentage of correct responses is also included; these values include only errors made after the appearance of the target. Data for incorrect trials were not saved for monkey *M3*.

All three monkeys were initially trained with 80% of the targets validly cued (see below). The only time when they were exposed to other cue proportions was during the collection of data for the Cue Probability experiment (Fig. 5). Monkey *M1* was trained and then tested in other physiological experiments 8 mo before the collection of the present data. These training and experimental sessions included $\geq 1,000$ correct trials per day, ~5 days/wk for 8 mo. Monkey *M2* had been trained on a choice reaction time paradigm before learning this task (Brown et al. 1993). It was trained for 3 wk before the present data collection. Monkey *M3* was only trained and tested with high probability valid cues. It was trained

TABLE 1. *Reaction times and accuracy for monkeys and humans*

Subject	Cue	CTI (100 ms)	% Correct	CTI (400 ms)	% Correct	CTI (700 ms)	% Correct
<i>M1</i>	Valid	280	94.4	282	96.0	284	89.5
	Invalid	292	98.5	284	97.3	285	95.9
<i>M2</i>	Valid	349	97.6	375	97.3	360	95.0
	Invalid	367	98.5	374	93.2	350	94.9
<i>H1</i>	Valid	374	100.0	327	100.0	319	100.0
	Invalid	427	100.0	345	100.0	321	100.0
<i>H2</i>	Valid	458	100.0	359	99.0	348	98.9
	Invalid	483	100.0	422	100.0	361	100.0
<i>H3</i>	Valid	394	99.2	326	100.0	304	94.4
	Invalid	386	100.0	309	97.1	339	86.7
<i>H4</i>	Valid	438	100.0	354	99.1	339	100.0
	Invalid	439	100.0	357	96.3	303	100.0
<i>H5</i>	Valid	393	100.0	312	100.0	313	100.0
	Invalid	414	100.0	308	96.6	290	100.0
<i>H6</i>	Valid	507	100.0	349	97.0	347	98.9
	Invalid	525	100.0	370	96.4	330	100.0

Subject	Cue	CTI (50 ms)	CTI (150 ms)	CTI (330 ms)
<i>M3</i>	Valid	<i>ms</i> 389	<i>ms</i> 322	<i>ms</i> 267
	Invalid	397	327	261

Subject	Cue	CTI (100 ms)	CTI (200 ms)	CTI (300 ms)	CTI (500 ms)	CTI (600 ms)
<i>M3</i> (Symbolic)	Valid	375	337	360	348	345
	Invalid	399	367	384	365	355

The data for monkeys *M1* and *M2* and *Humans 1–6* were obtained in the standard task and are also plotted in Fig. 5 for the 80% valid condition. In that situation, 80% of the targets were preceded by visual cues on the same side (see METHODS). The data for *M3* are included at the bottom and are also plotted in Fig. 6. In one situation, cues were flashed peripherally at 3 intervals, whereas the data for *M3* were obtained with the symbolic foveal cuing task (see METHODS). CTI, cue-target interval (in ms); *M*, a trained monkey; *H*, a naive human subject.

and studied in physiological experiments for 26 mo before collection of these data. The cue-target intervals used during actual data collection were the same ones used during all aspects of training. Monkeys *M1* and *M3* were extensively trained on these specific tasks whereas monkey *M2* had considerable experimental experience before 1 mo of training on the present tasks.

NEUTRAL CUES. Many previous studies have analyzed the data in terms of the costs and benefits of cuing by using a neutral cue (Jonides 1980; Posner 1980). It is assumed that all cues (informative and neutral) facilitate performance to some extent by nonspecifically preparing the subject to respond. The inclusion of a neutral cue allows for the calculation of costs and benefits of shifts of attention. The assumption is that neutral cues do not spatially prime a location, whereas informative cues are spatially selective. However, it is essential that neutral and informative cues be identical, except for their information in relation to the target. For example, it is essential that the cues have equivalent effects on the levels of alertness, the amount of processing time required to evaluate each cue, the memory loads, and the duration of the consequences of the cues. In practice, it is difficult to be certain that all of these conditions are met. Even though a neutral cue might produce reaction times that are intermediate to those for valid and invalid cues, it may not be truly neutral. Some have used neutral cues that produced larger benefits than costs when the data were analyzed with reaction times, but greater costs than benefits when the data were evaluated in terms of the percentage of errors (Posner and Snyder 1975). The problems of the cost-and-benefits analysis have been discussed in detail previously, and the present studies were conducted in line with the suggestion to avoid the use

of neutral cues (Jonides and Mack 1984). The present data demonstrate the attentional effect of the cues but have avoided the difficult technical and interpretive issues of cost and benefits.

HUMANS. Subjects were instructed to fixate the central point while responding to the onset of targets. No explicit instructions were given about the cues. In all other respects, the timing and structure of the task were identical to those used with monkeys. Auditory signals were presented at the time of each correct response. Data were collected after the subjects' performance on practice trials indicated that they understood the task.

Task variations

1) *Standard task.* The landmarks, cues, and targets were located 15° eccentric on the horizontal meridian (Fig. 3C). Equal proportions of left and right targets and cues were always presented. For monkeys *M1* and *M2*, the asynchrony between cue onset and target onset was randomly distributed at intervals of 100, 400, and 700 ms. Other cue-target intervals were used for monkey *M3* (Fig. 6). On 80% of the trials the cues were located at the same point as the target (*valid* cue); on the remaining trials the cues were located in the opposite hemifield (*invalid* cue). In all tasks using peripheral cues, the cue offset preceded the onset of the target, and then the target remained illuminated until the subject released the bar.

2) *Cue probability.* In the standard task a cue was considered valid because it was spatially coincident with the target. However, in the standard task, a cue was valid in another sense. On 80% of trials, the cue appeared at the location of the target so that the

occurrence of the cue accurately predicted the target location. In studies of humans, these two factors have been dissociated by changing the proportions of spatially valid cues (Enns and Brodeur 1989; Jonides 1980; Posner et al. 1982). Six humans and two monkeys (*M1* and *M2*) were tested in blocks of trials, and the cues were spatially valid either 80, 50, or 20% of the trials.

3) *Symbolic foveal cues.* Several aspects of the standard task were changed to teach an animal (*M3*) to use foveal, symbolic cues to direct its covert attention. Initially an arrow symbol ($4 \times 4^\circ$) was flashed 18° in the periphery, which pointed at the location of the subsequent target. Next, the target was reduced in size ($0.25 \times 0.25^\circ$) as well as duration (67 ms). As such, the target was barely detectable and the arrow became an important cue. After the animal had reached criterion performance in these conditions, the arrows were moved to the location of the fixation point and reduced in size ($2 \times 2^\circ$). During training the arrow always pointed in the direction of the subsequent target. No visual landmarks were used at the locations of the targets (see below). Five cue-target intervals from 100 to 600 ms were used for these tasks. Only on a limited number of test conditions were the arrow cues invalid; this was done to maintain the credibility of the arrows for the animal. This monkey (*M3*) was trained on this task for 1 mo before data collection.

4) *Motivation.* In the course of daily testing of two monkeys (*M1* and *M2*), the level of performance varied. Unusually high levels of performance resulted in a large number of rewards (15% more than baseline); a post-hoc analysis showed that reaction times on the following day were slow. Conversely, low levels of performance led to few rewards (15% less than baseline) and faster reaction times on the next day. From the changes in reaction times, it was inferred that motivation changed. To determine if motivation level interacts with covert orienting, a post-hoc analysis of data taken from the standard task was performed with respect to these two extremes.

5) *Target detectability.* It is possible that diminished target brightness might increase attentional demands. As a probe for such changes, two monkeys (*M1* and *M2*) were tested on the standard task when the brightness of the targets was halved. This manipulation, as well as the analysis of motivational effects, tested for influences of overall performance on the effects of exogenous cues. Data from blocks of this task were compared with control data on the standard task on the same day.

6) *Visual landmarks.* Most applications of this paradigm have employed visual landmarks, usually boxes surrounding target positions, which provide local spatial references at the cued locations (Mangun et al. 1987; Posner 1980). Such landmarks might reduce the efficacy of cues by reducing the range of dynamic, local luminance changes. Alternatively, such stimuli might enhance the effects of the cues by providing a focus at which attention may be maintained during the temporal gap between the offsets of the cues and the onsets of the targets. To determine whether local spatial landmarks would change the effects of the cues, data from interleaved blocks of trials in which landmarks were absent or present were collected from two monkeys (*M1* and *M2*) trained initially with landmarks.

7) *Cue-target distance.* Two experiments were performed to examine the spatial and temporal effects of the cues. Landmarks, cues, and targets were presented at 10 and 30° laterally on each horizontal meridian and reaction times were analyzed in terms of distance from the cued position. In the first experiment, the cues and targets were predominantly (80%) spatially valid with cues and targets appearing at the same location. In the second experiment, cues and targets were presented at the four locations randomly with respect to each other; thus, for 75% of the trials, the cue and target were not at the same location. Four naive human subjects completed each of these experiments while one monkey (*M1*) was tested in both.

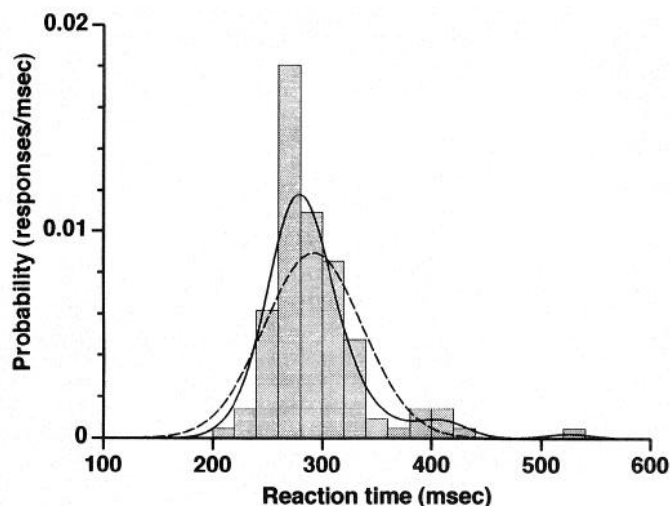


FIG. 1. Three techniques for evaluating reaction time distributions. Shaded bars form a frequency histogram in which reaction times from a single monkey (*M1*) were placed in 20-ms bins. For these data it can be seen that the most frequent reaction times occurred between 260 and 280 ms although some were as fast as 200–220 and as slow as 400–600 ms. These reaction times were obtained for targets with 80% of them validly cued and at a cue-target interval of 100 ms. These data are included in the relevant part of Fig. 5. ---, normal distribution for these same data. This curve was produced by using the mean of this data set and its SD. —, density function of the distribution as derived by methods discussed in the text. Here a Gaussian kernel was substituted for each reaction time, which produced a smoothed curve, resulting in a low-pass filtering of the data. These data are the result of 99 correct responses and represent the minimal sample of data utilized in these studies. The shift in the mean and effect of outliers are evident in this minimal sample, and they are even more prominent in larger samples.

Data analysis

Data were collected in blocks of trials in which 200–400 correct responses were recorded. Figure 1 shows the distribution of reaction times for a typical block. Two to five blocks were collected from each animal during the testing session for a single day. The means, SEs, and ranges were calculated for each individual test condition of each block. Examples of actual reaction times as well as the means in certain conditions can be found in Figs. 1, 2, and 4 and Table 1. In addition, individual trial data from all blocks of a given experiment were pooled into a single database. All of the data analysis was performed using this database and without reference to individual subjects.

Many studies have shown that distributions of simple reaction times are not normally distributed (see Luce 1986). This applies to the data reported here, as shown in Fig. 1, by comparing an empirical distribution (shaded bars) to the normal distribution derived from the mean and SD of the same data (---). The skew of the reaction time distributions made standard parametric tests inappropriate. Instead, the data were ranked. Next, these scores were used in analysis of variance (Conover 1980). This procedure reduced the skew in the reaction time distributions. This type of analysis was an initial exploratory approach to search for interactions among the various experimental manipulations. All analyses of variance reported here were performed on ranked data.

After the analysis of variance suggested a difference between two conditions, a more direct statistical test was used. To confirm that reaction times for two conditions differed statistically, a two-sample version of Watson's U^2 test was performed on the cumulative probability distributions (Fig. 2) (Watson 1962). This test is sensitive to differences between two probability functions. In experiments in which several pair-wise comparisons were made, the critical values of the U^2 statistic were adjusted to control for in-

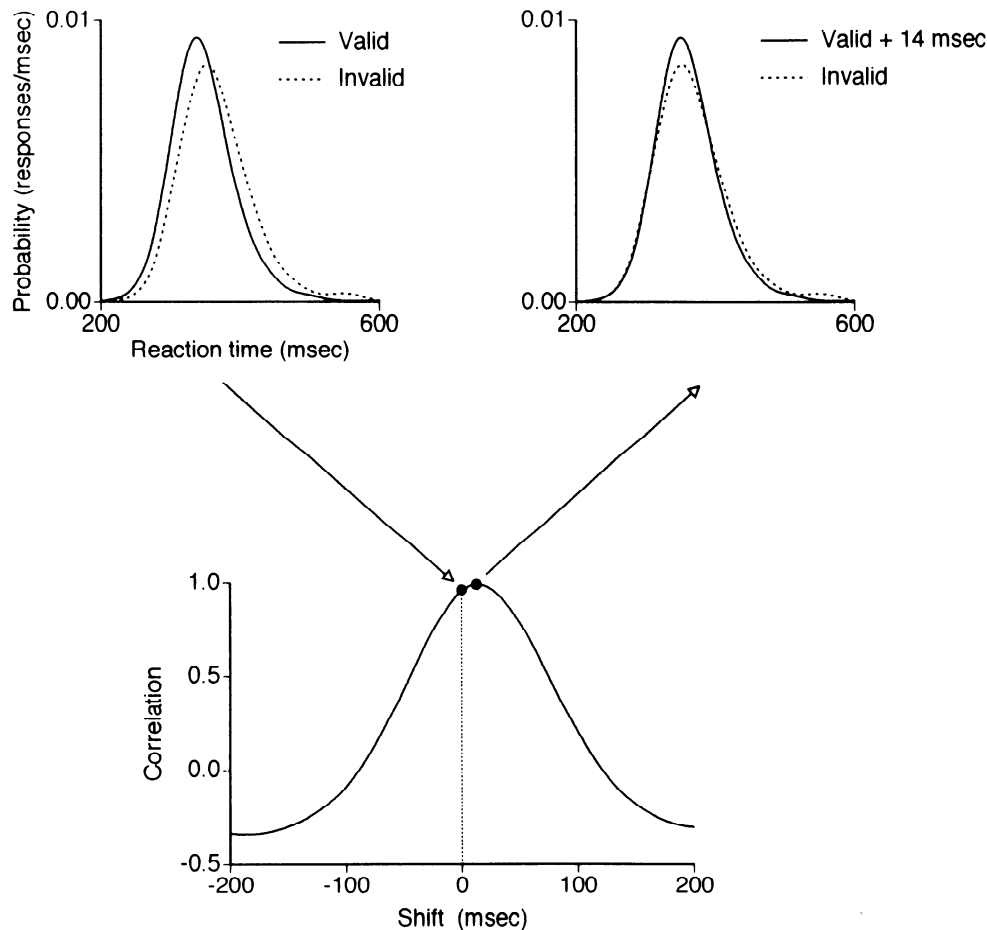


FIG. 2. Quantification of the effects of the cues. *Top left*: 2 density functions of reaction times from a single monkey (*M2*) with the standard task for validly and invalidly cued targets at the earliest cue-target interval (100 ms). Validly cued data represent 939 correct trials, and invalid, 232 trials with 80% of the targets being validly cued. These data are also included in Fig. 5. *Top right*: the same 2 functions, with the curve for validly cued trials shifted 14 ms to the right. This is the time shift for these data that produced the maximal coefficient of correlation (see APPENDIX A). *Bottom*: plot of the cross-correlation functions for these valid and invalid density functions. Vertical axis is the coefficient of correlation; horizontal axis is all the time shifts tested for the set of data. The original, unshifted data are represented by the left dot at time 0. The right dot represents the maximal coefficient of correlation (0.996) obtained from these 2 curves. This point of maximal correlation is 14 ms different from the standard, unshifted plots. Thus the effect of the cue was to shift the curves by 14 ms.

flated statistical error rates associated with multiple tests (Keppel 1987). The U^2 test used in this way is conservative.

Quantification of differences between two conditions

To determine the magnitude of the effects of the cues, a cross-correlation technique was used. APPENDIX A gives a detailed explanation of these techniques and their rationale. This approach shifted the plots of validly cued targets relative to invalidly cued targets until there was the maximal possible correlation between all corresponding points in the two distributions. The shift that produced the maximal point-to-point correlation was determined as the validity effect. This approach minimized the effects of outliers and led to very stable measures of the validity effect (Fig. 3). Thus conclusions derived from this type of analysis can be accepted with greater certainty because the comparisons are made using all data with equal weight. This will be particularly important when comparing conditions that produce small changes. The initial step was to use a density estimation technique to create a smoothed function that characterized the distribution of reaction times in a given condition (Parzen 1962; Silverman 1986). Each estimated probability function was produced by convolving the frequency distribution of the reaction times in a given condition

with a Gaussian function (SD = 20 ms) and normalizing the area beneath the function to one (Silverman 1986).

Once these curves were determined for corresponding valid and invalid conditions, the valid function was cross-correlated with the invalid function. This is illustrated in Fig. 2, where the *top left panel* indicates the probability function for reaction times of one monkey (*M2*) to validly cued (—) and invalidly cued (---) targets at the shortest cue-target interval (100 ms). The *top right panel* shows the same two functions with the valid probability function shifted 14 ms to the right. This shift maximizes the point-to-point similarity between valid and invalid probability functions (Fig. 2, *bottom*). This shift produced the highest coefficient of correlation for these data. The validity effect was defined as this shift in reaction times for validly and invalidly cued targets. Figure 3*A* shows validity effects calculated in this way, and these can be compared with the standard technique of subtracting means, which is illustrated in Fig. 3*B*, for the same set of data. Although both approaches indicate significant validity effects, the stability of the cross-correlation was greater.

A resampling procedure was used to estimate the SE of the validity effect (Efron 1982). For this procedure, 200 paired sets of randomly resampled reaction times were taken from the valid and invalid conditions, and the validity effect was calculated from

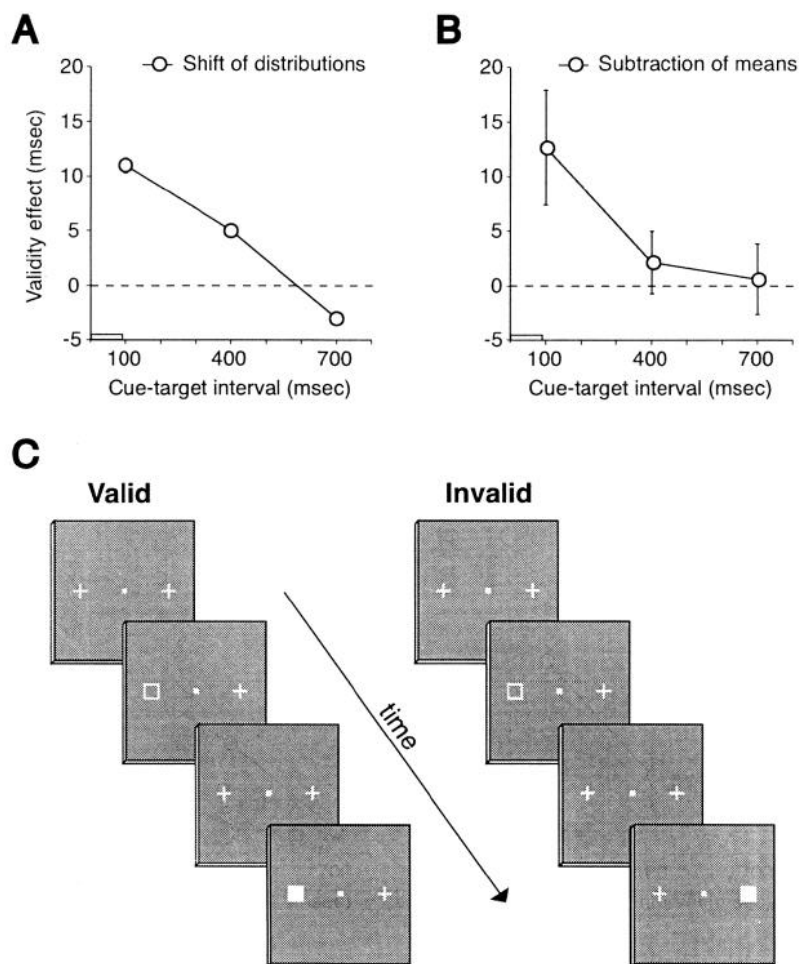


FIG. 3. Example of validity effect in monkey *M1*. *A*: data plot of the magnitude of the validity effect (invalid relative to valid) at 3 cue-target intervals as determined by cross-correlation (APPENDIX A). Each point represents data for ≥ 460 correct trials. Vertical and horizontal lines through the dots represent SE; for many data points, these values are so small that no line is apparent. *B*: data plot of the magnitude of the validity effect for the same data when the means are subtracted (invalid minus valid). Note that the magnitude of the initial validity effect is greater and the estimated variance is much greater. The rectangle at lower left represents the time during which the cue was displayed. *C*: schematic tangent screens illustrating the fixation point, cues, targets, and landmarks for validly and invalidly cued conditions. Cues were open squares whereas targets were filled, luminance-increased squares. Screens are shaded to indicate the luminance increases of the images, but the experiments were conducted in photopic conditions. Targets were presented at varying intervals after the flashed cue (see METHODS).

each paired set. The SD across all 200 paired sets was used as the estimated SE. Because many of these SEs were very small, the illustrations have short horizontal lines to indicate this measure.

The "cue-target distance" experiment was conducted with cues and targets at 10 and 30°. Analysis of data from this type of experiment is complicated by the potentially confounding effects of target eccentricity, which is known to slow reaction times (Osaka 1976), and cue-target distance; the largest cue-target distance (60°) always included the most eccentric target. To remove the effects of target eccentricity from a given trial, the mean reaction time to all targets presented at that same location, regardless of cuing condition, was subtracted from the reaction time for that given trial.

RESULTS

1) Standard task. In the standard task, 80% of the targets were on the same side as the cue (validly cued), left and right targets and cues were equally probable, and cues and targets were separated by intervals of 100, 400, and 700 ms. All monkeys trained on the standard task responded more quickly to validly cued targets than to invalidly cued targets and these differences were significant. Figure 3 illustrates a typical response pattern for one monkey. Beneath the graph are schematic screens showing the cues, targets, and landmarks for valid and invalid trials (Fig. 3C). The data in Figure 3A were derived from the cross-correlation analysis (see METHODS and APPENDIX A) and illustrate a consistent, statistically significant effect of the cue with small variance.

The data in Fig. 3B were derived by subtracting the means of the valid reaction times from the invalid reaction times, which is the conventional approach, and this leads to a larger initial effect but also less reliability (see METHODS for additional details). Subsequent figures will illustrate results using the cross-correlation technique. Data for targets and cues on the left and right sides have been combined. For the shortest cue-target interval (Fig. 3), cues on the same side as the target were associated with significantly faster responses than cues in the opposite visual field from the target [$U^2(387, 99) = 0.298, P < 0.02$]. The validity effect, the difference between invalid and valid reaction times (see METHODS), diminished at longer cue-target intervals (Fig. 3).

The absolute magnitude of the early validity effect and the rate at which it diminished differed for each monkey. Nonetheless, the shift in reaction times to validly and invalidly cued targets at the early interval was observed in all monkeys tested in several variants of the standard task (Table 1) (see below). The accuracy of the subjects' performance was not a reliable indicator of the effects of the cue (Table 1). Reaction times can be displayed as cumulative functions like those in Fig. 4. In such an approach, the number of reaction times accumulates with longer times and eventually 100% of the reaction times are displayed. The distribution of reaction times to validly cued targets at the earliest interval was faster than the remaining distributions

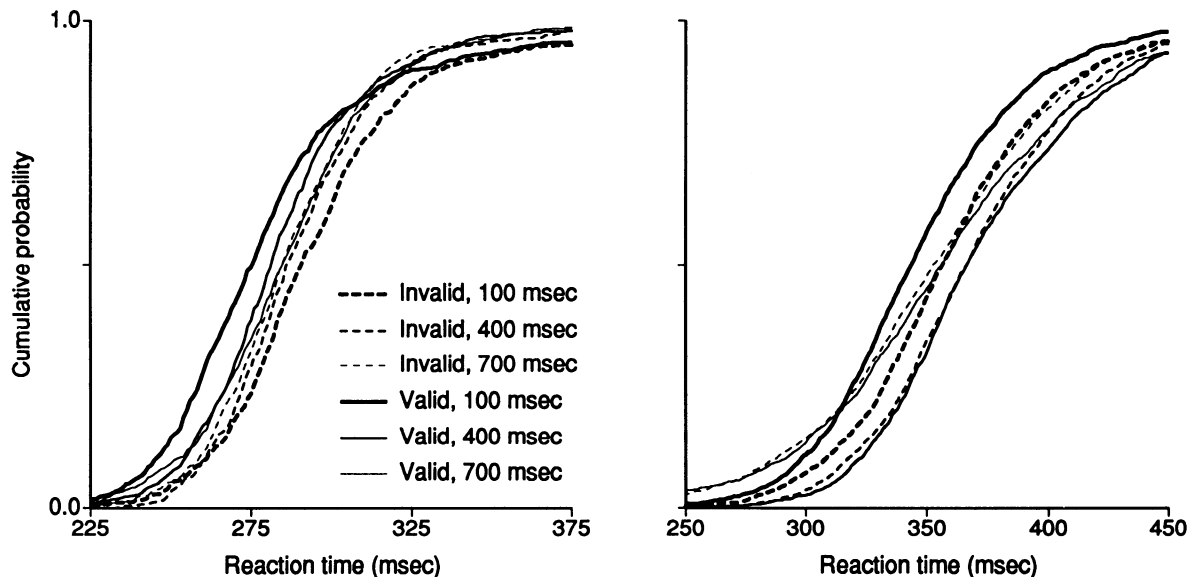


FIG. 4. Cumulative probability functions for all conditions tested for 2 monkeys. For each curve, the vertical height at any point represents the proportion of reaction times that have been made at each point in time (reaction time on the horizontal axis). Note that validly cued targets at the shortest interval (thick solid line) are uniquely fast for both animals. *Left*: data from those used in Fig. 3 (*M1*). *Right*: data derived from 3,326 correct trials of a second monkey (*M2*).

(Fig. 4, thick solid lines). This is shown by a relative shift of this curve to the left. This suggests that the cues enhanced visual processing in their vicinity rather than decremented performance in the contralateral visual hemifield.

2) *Cue probability*. Two monkeys (*M1* and *M2*) were tested with valid cues appearing on 80, 50, or 20% of trials, and they exhibited similar patterns of performance regardless of cue proportions (Fig. 5, *top*). The mean reaction times for the 80% valid cues are included in Table 1. Each set of lines in the figure represents the pattern of results from a given ratio of valid to invalid cues. There was a significant interaction between cue type and cue-target interval [$F(2, 12862) = 19.967, P \ll 0.001$] such that the monkeys always responded more quickly to validly cued targets at the earliest interval [$U^2(2258, 2751) = 0.828, P \ll 0.001$]. The initial validity effect diminished when valid cues were presented on only 50 or 20% of the trials but never reversed. The monkeys always shifted their attention (i.e., had a significant validity effect) to the cued position even when cues were predominantly invalid.

Changing the proportion of validly to invalidly cued trials produced dramatic effects on the human subjects' performance (Fig. 5, *bottom*; Table 1), as previously reported (Enns and Brodeur 1989; Jonides 1980; Posner et al. 1982). The top, solid line corresponds to the standard condition with 80% validly cued targets, and it illustrates a large initial validity effect that reverses with increasing cue-target intervals. The mean reaction times for the individual subjects are included in Table 1. When valid and invalid cues were equiprobable (50%), there was no initial validity effect. At longer intervals, reaction times to invalidly cued targets were faster than to validly cued targets (negative validity effect). When the proportion of spatially valid trials decreased to 20%, reaction times to invalidly cued targets were faster, even at the earliest interval tested (100 ms). Moreover, this negative validity effect became more pronounced at longer cue-target intervals. This interaction

between cue type, cue-target interval, and cue-type proportion was significant [$F(4, 3580) = 4.724, P < .001$].

3) *Symbolic foveal cues*. A possible interpretation of the results described above is that monkeys are unable to endogenously (i.e., cognitively) guide their covert visuospatial attention. Numerous studies have demonstrated endogenous control of attention in normal humans (Helmholtz 1909; Muller and Findlay 1987; Muller and Rabbitt 1989; Posner 1980; Warner et al. 1990). A monkey (*M3*) was trained on the "symbolic foveal cue" task in which an arrow presented at the center of the screen indicated the side on which the target most probably would appear (see METHODS for additional details). In this situation the animal exhibited significant and strong effects of symbolic cuing at even the earliest interval tested [$U^2(2122, 630) = 2.21, P \ll 0.001$] (Fig. 6; Table 1). These effects were larger than the standard significant effects when peripheral cues were used with the same animal (Table 1).

4) *Motivation*. To ascertain if different levels of motivation changed attentional behavior, two monkeys (*M1* and *M2*) were tested at extremes of their performance. On 5 days when the monkeys had worked on the previous day for <85% of their normal fluid intake, the animals were 30 ms faster overall in responding relative to the 4 days when they worked the previous day for $\geq 15\%$ more than their normal fluid [$U^2(1622, 1604) = 4.434, P \ll 0.001$]. There was no significant interaction between level of motivation, cue type, and cue-target interval [$F(2, 3208) = 0.542, \text{NS}$], but there was a typical interaction between cue type and cue-target interval [$F(2, 3208) = 5.508, P < 0.005$]. There was a reduction in the magnitude of the validity effect at the 100-ms interval when the monkeys were highly motivated (Fig. 7, *bottom*). This suggests that the validity effect may diminish as reaction times approach a minimum, but that no qualitative change in performance was induced by the high levels of motivation. A significant validity effect was still present.

5) *Target detectability.* To determine the effects of slow responding and decreased target detectability, the monkeys were tested with two levels of target brightness (see METHODS). Reducing the brightness of the targets produced a 9-ms overall delay in reaction times [$U^2(1523, 1538) = 1.437, P \leq 0.001$]. No significant interaction between target intensity, cue type, and cue-target interval was detected (Fig. 7, *top*). These data indicate that there was no attentional modification as a result of changes in luminance that were sufficient to slow significantly reaction times.

6) *Visual landmarks.* Two monkeys were tested on the standard task with and without landmarks to determine the effects of visual references. The landmarks were plus signs (+) at the two loci where the cues and targets appeared (see METHODS and Fig. 3C). Figure 8 shows the normal pattern of reaction times when spatial landmarks were employed (—) and the validity effect obtained on separate days when the landmarks were not used (---). The early validity effect did not reach significance in the absence of the landmarks [$U^2(666, 155) = 0.172, NS$]. Previous studies of humans have also demonstrated that performance is better with visual landmarks (Mangun et al. 1987).

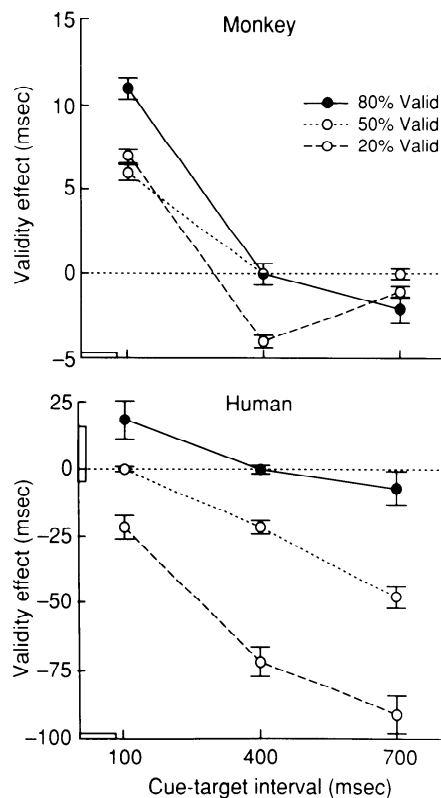


FIG. 5. Effects of varying proportions of valid cues. *Top*: —●—, data from standard task, in which 80% of the targets were validly cued and 20% of the targets were invalidly cued; ---○---, data from tests with equal probabilities; - - -○- - -, data for blocks with only 20% valid cues. These are the data combined from 2 trained monkeys (*M1* and *M2*) and represent over 1,705 trials for each point. The mean reaction times for the condition with 80% validly cued targets are included in Table 1. *Bottom*: data from the same experimental conditions using 6 naive human subjects. Each data point was calculated from ≥ 800 trials. The mean reaction times in the 80% validly cued trials are included in Table 1. The bracket on the y-axis indicates the range of values obtained for the same experiment on monkeys, as illustrated at *top*. Conventions as in Fig. 3.

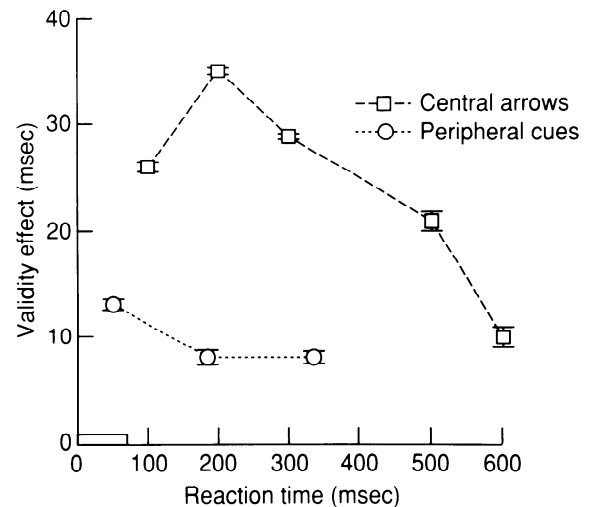


FIG. 6. Comparison of symbolic and peripheral cues. Validity effects plotted on the *top* (---□---) come from trials in which the animal (*M3*) had learned that an arrow presented directly ahead would signal the side on which the target would be flashed. Each point was plotted from an average of 2,155 correct trials. Data points on the *bottom* (---○---) come from tests of the same animal with the flashed peripheral cue. Values are derived from 218 trials on average. Conventions as in Fig. 3.

7) *Cue-target distance.* When targets were presented at one of four possible cued locations, with 80% of the trials validly cued, there was a significant validity effect at all distances at the 100-ms cue-target interval. The monkey responded more quickly to validly cued targets than to all invalidly cued targets (Fig. 9, *top left*). At the later temporal intervals this pattern was not present. The interaction between cue-target distance and cue-target interval was significant [$F(6, 8290) = 8.485, P \leq 0.001$].

Results from four human subjects are shown in Fig. 9 (*bottom left*). The interaction between the cue-target distance and the cue-target temporal interval was significant [$F(6, 7111) = 8.250, P \leq 0.001$]. However, the patterns at each cue-target interval resembled each other closely; human subjects responded significantly more quickly to all targets that were validly cued (0° cue-target distance). For the remaining invalidly cued targets, there was no relationship between the spatial distance of the target from the cue and the relative speed of responding. The cue produced a facilitation at its locus and not at any distance $>20^\circ$.

When the position of the cues and targets varied randomly with respect to each other, for the monkey, the initial validity effect was substantially reduced, and the validity effects at later intervals were negative (Fig. 9, *top right*). Four humans showed a validity effect at the early temporal interval, which was reduced and reversed at later intervals (Fig. 9, *bottom right*).

DISCUSSION

The primary finding of these studies is that trained monkeys have a consistent shift of attention as an initial response to peripheral cues, even in spite of many manipulations of task parameters. These monkeys differ from humans in the degree to which cognitive processes impact covert orienting of attention. While visuospatial orienting to exogenous cues (i.e., simple sensory events) is easily mod-

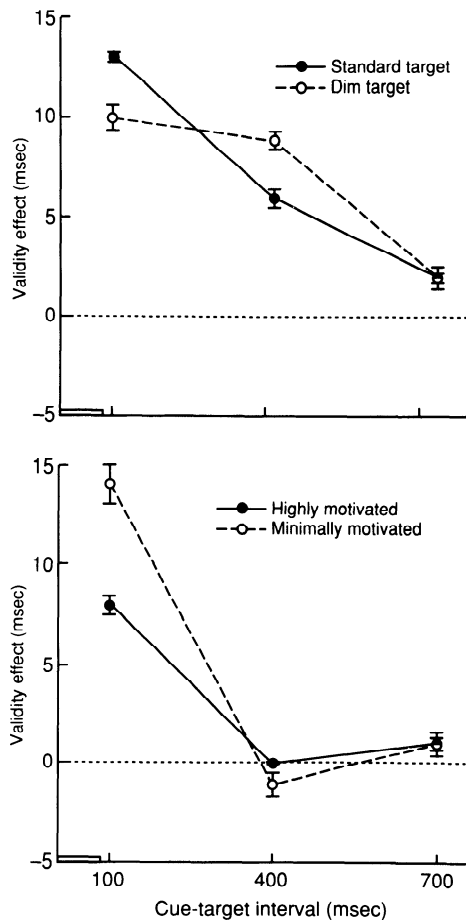


FIG. 7. Effects of target detectability and motivation in monkeys. *Top*: overall reaction times to the dim target were lengthened by reducing its luminance by 50%. This did not significantly change the magnitude of the effects of the cues. These data are combined from two monkeys (*M1* and *M2*); 510 trials were used for each point. *Bottom*: although overall reaction times were speeded when the monkeys were tested under conditions of high motivation, the pattern of the validity effect did not differ significantly. Data are combined from tests of 2 monkeys (*M1* and *M2*), and each point comes from 537 correct trials. Conventions as in Fig. 3.

ifiable in naive humans, in the present highly trained, monkeys they appear to be more stereotyped. However, in certain circumstances, monkeys can endogenously (i.e., cognitively) guide covert orienting (Fig. 6) (Bushnell et al. 1981; Wurtz and Mohler 1976). These observations, and the data suggesting that monkeys consistently shift attention toward peripheral cues, establish the macaque as an animal model for exogenous and endogenous covert orienting of attention. The monkey is useful for studies of the neural basis of exogenously triggered, covert orienting, because the effects of the peripheral visual cues are significant and stable.

Stability of the validity effect

The present data show, for monkeys, that valid cues enhance responding to subsequent visual targets. This effect persists with a variety of experimental manipulations. 1) Speed of responding was manipulated by changing target luminance and level of motivation. Under both conditions, the validity effect was reliable. This is similar to previous studies in which humans were instructed to respond fast or when bright targets were used to speed responses, and here

too the validity effect was the same as the standard control (Kertzman et al. 1990; Robinson and Kertzman 1990). 2) Unlike reports for humans (Berlucchi et al. 1989; Enns and Brodeur 1989; Jonides 1980; Posner et al. 1982), and contrary to the effects reported here for humans, the validity effect for monkeys was stable even with changes in the percentage of valid cues (Fig. 5, *top*). 3) When cues and targets were separated by varying distances, the validity effect in monkeys was consistently present (Fig. 9, *top left*). These observations suggest that in highly trained monkeys the effect of the cue is reliable and that this paradigm is useful for neurophysiological studies.

The only manipulation which eliminated the initial validity effect was the removal of spatial landmarks in monkeys trained with them (Fig. 8). These data suggest that the efficacy of the cue is under the control of the local visual environment (Hughes and Zimba 1987). The landmarks may enhance the effectiveness of the cue and thereby make it difficult to disengage from invalid cues (Mangun et al. 1987). However, we have previously trained monkeys without landmarks, and an early validity effect was observed (Petersen et al. 1987). In a structured field there are greater demands on the control of fixation, and this requirement may enhance the effectiveness of the cue and thereby facilitate the validity effect (Engel 1971).

Comparison of covert orienting in monkeys and humans

For some features, monkeys and humans resemble each other in the performance of this task; in other respects they differ. Both species can shift their attention to exogenous cues as well as endogenous cues (Fig. 6) (Muller and Findlay 1987; Muller and Rabbitt 1989; Posner 1980; Warner et al. 1990). Both species maintain the validity effect even when the speed of responding changes (Fig. 7) (Kertzman et al. 1990; Robinson and Kertzman 1990). Finally, both species respond similarly to invalidly cued targets when tested for the spatial extent of the cue (Fig. 9, *top* and *bottom left*). The two species differ most clearly when the pro-

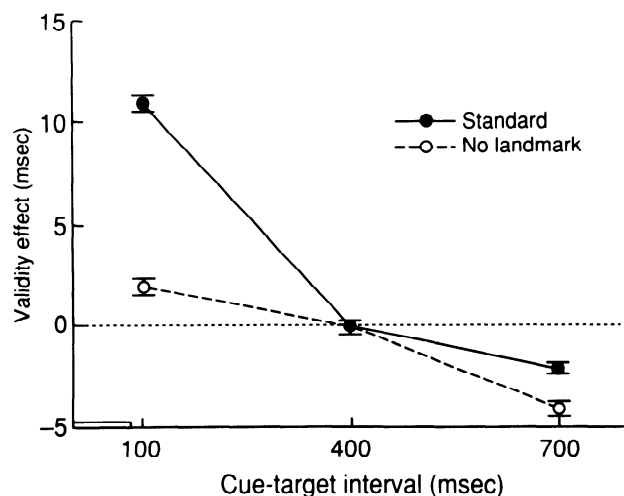


FIG. 8. Effects of spatial reference. The 2 monkeys (*M1* and *M2*) were tested on blocks of trials in which the plus marks (+) at the cue and target locations were present (—; 1,570 trials per point) or absent (---; 779 trials per point). The absence of the landmarks disrupted the monkeys' performance. Conventions as in Fig. 3.

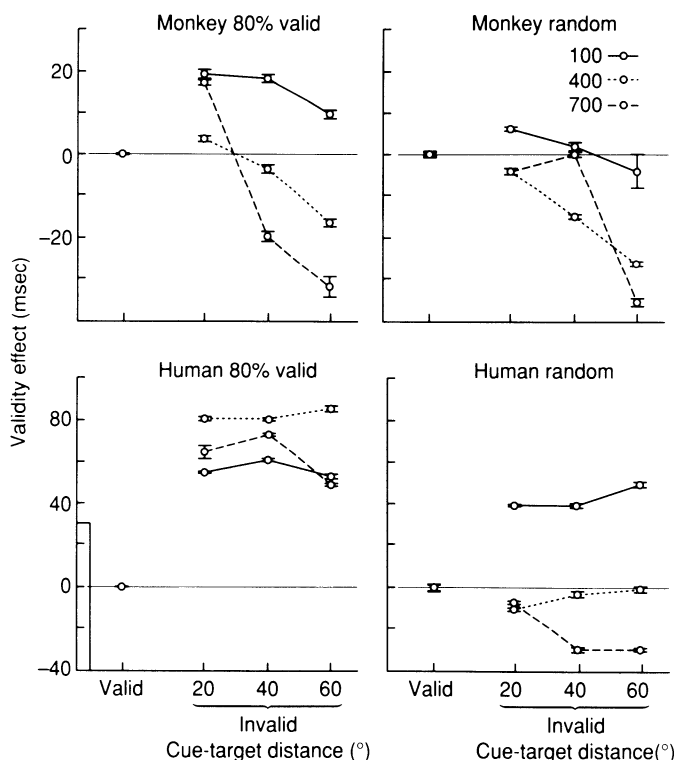


FIG. 9. Interaction between cue-target spatial distance and cue-target temporal interval for monkey (*M1*) (*top*) and humans (*bottom*). Data in each condition were corrected for the effects of target eccentricity (see METHODS). Cues, targets, and landmarks were presented 10 and 30° eccentrically along the horizontal meridian. Conditions with the same cue-target temporal interval are connected. For the data on *left*, 80% of the trials were validly cued; the most frequent cue-target distance was 0° (80% of trials). For the graph at *top left*, data come from 1 monkey (*M1*), and each point was calculated from 680 correct trials. For the data on *right*, the stimulus conditions were identical to those on *left*, except that cues and targets were presented at random locations with respect to each other. Thus most targets were invalidly cued. The probability that the cue and target would be presented at the same location (valid trial) was 25%. Results from 1 monkey are illustrated, and 170 trials comprise each data point. *Bottom*: 4 naive human subjects were tested, and each point represents ≥ 590 correct trials. *Bottom left*: the bracket on the vertical axis indicates the range of values obtained for the same experiment on the monkey.

portions of valid cues change (Fig. 5). They also differ in their response to cues at several locations when the positions are randomly determined (Fig. 9, *top* and *bottom right*).

The absolute magnitude of the early validity effect in humans was twice as large as that in monkeys (Fig. 5; Table 1). There are two interpretations of this difference. First, the monkeys' long periods of training (see METHODS), and the technique of rewarding them for fast responses, may have resulted in a "floor effect," which diminished the potential magnitude of the validity effect. Support for this interpretation is the observation that the validity effect was diminished when reaction times were faster, as in the analysis of the effects of motivation (Fig. 7, *bottom*). Furthermore, the monkeys' reaction times were faster than the humans' (Table 1). Second, humans may have employed cognitive strategies that augmented covert orienting, while the monkeys may not, because of their over-training. Previous studies have shown, and we have confirmed here, that naive humans are sensitive to changes in the probabilities of cues

and targets (Fig. 5, *top*; Fig. 9, *bottom*) (Berlucchi et al. 1989; Enns and Brodeur 1989; Jonides 1980; Posner et al. 1982). Trained monkeys always oriented toward the cues without regard for their veracity (Fig. 5, *top*; Fig. 9, *top right*). Comparable results in a monkey have been obtained using training with different proportions than used here (Davidson et al. 1992). Previous training is necessary for animal studies, and all these monkeys may have been so accustomed to the task that cognitive strategies might not have been employed. Such processes might be effortful and therefore not cost effective. This notion is supported by the fact that when a monkey was forced to use information conveyed by symbolic cues, the magnitude of the validity effect doubled in comparison to the effect obtained from exogenous cuing (Fig. 6). For these reasons, a comparison between naive humans and trained monkeys for the absolute magnitude of the validity effect elicited by exogenous cues may be misleading. Instead, the overall pattern of the validity effects and the degree to which they change under different experimental contexts for each species should be considered. Even though the validity effect in the present animals is smaller than in humans and may have reached a floor effect, it is still a reliable and consistent effect. Thus this approach generates a good animal model of these specific aspects of covert orienting. However, this effect is a baseline that can be modulated by other mechanisms.

Cognitive factors

Several previous studies of humans, using discrimination and localization tasks, have compared attentional shifts evoked by exogenous cues with endogenous attentional shifts elicited by instructions (Muller and Findlay 1987; Muller and Rabbitt 1989; Warner et al. 1990). A conclusion has been reached that endogenous processes are slower in shifting attention. However, the present data show that some cognitive processes can act rapidly. When humans were tested with only 20% of the targets validly cued, these individuals responded fastest to targets that followed cues in the opposite visual field (Fig. 5, *bottom*). Most importantly, the effect was clear at the earliest cue-target interval tested, 100 ms. These data show that naive human subjects can shift attention rapidly using cognitive processes that are not directly localized to the peripheral cue. It should be emphasized that the subjects were not instructed about any of the conditions of the experiment, and most were unaware that anything had changed between testing blocks. The present studies differ from previous experiments because here there was no need to translate the meaning of the cue, only its location. This may explain why there was a fast endogenous switching of the direction of attention in the present studies. For humans with 20% valid cues, the rapid response to invalidly cued targets becomes enhanced at longer cue-target intervals, and it appears that the endogenous effect is present at 100 ms but reaches its maximal strength after longer intervals. At the early intervals, there may be opposing effects between the reflexive response to the cue and endogenously driven orienting. At the later intervals, the exogenous effects may have dissipated and only the cognitive effects persist.

Monkeys can also rapidly shift their attention in response

to endogenous processes (Fig. 6). The effect of foveal cues was present at 100 ms. This is much faster than reported for humans (Muller and Findlay 1987; Muller and Rabbitt 1989; Warner et al. 1990). The speed with which this shift was accomplished may be due to the high motivation and overtraining of the animal or to an extremely rapid decoding of the cue.

Inhibition of covert orienting

Both saccadic eye movements and covert orienting of attention in humans are suppressed toward recently attended loci. This phenomenon has been termed inhibition of return (Posner et al. 1985). The decay and eventual negativity of the validity effects observed here in monkeys and humans are similar to inhibition of return (Fig. 5; Table 1). For the monkey, negative validity effects were observed only rarely. It is possible that inhibition of return would be observed directly in monkeys at longer cue-target intervals. It is also plausible that monkeys may differ from humans only in the absolute magnitude of their validity effect. It also suggests that inhibition of return may be related to the rate of decline of the validity effect rather than its absolute value at a given cue-target interval.

In both monkeys and humans, the cues induced an early validity effect that diminished rapidly and then became negative at the last cue-target interval, 700 ms (Fig. 5, solid line). The pattern observed for humans and monkeys suggests that a compensatory mechanism biases attention away from the cues. In humans, the negative validity effect was very pronounced in the "cue probability" experiment when cues and targets were randomly or rarely paired (Fig. 5, 50% valid, dotted line; 20% valid, dashed line) and in the cue-target distance experiment when probabilities were random (Fig. 9, bottom right, dashed line). For monkeys, although the decay of the early validity effect was present in all variants of the standard task (Figs. 3 and 5–8), a negative validity effect appeared clearly only in the cue-target distance experiment at the longer cue-target intervals (Fig. 9, top). It should be noted that in conditions where there is a negative validity effect, it continues to become more negative with later cue-target intervals (Fig. 5). This effect is more prominent in humans than monkeys.

In summary, trained monkeys provide a model for the basic processes of exogenous control of attention. They also appear to be suitable for the study of covert orienting based on cognitive control through symbolic stimuli. To the extent that monkeys differ from humans in these types of tasks, the differences may provide insights into the neural mechanisms of covert attentional shifts.

APPENDIX A

One approach to comparing the central tendencies of reaction times from these types of studies is to subtract the mean of the valid condition from the mean of the invalid condition. A shortcoming of this technique is that it characterizes each distribution with only a single number. Subtraction of means also produces highly variable estimates of attentional shifts, because the means of sampled reaction times are sensitive to outliers (Figs. 1 and 3). Comparing the differences between means is not always reliable. A more stable estimate can be computed by comparing the distributions of reaction times directly by using cross-correlation (Fig.

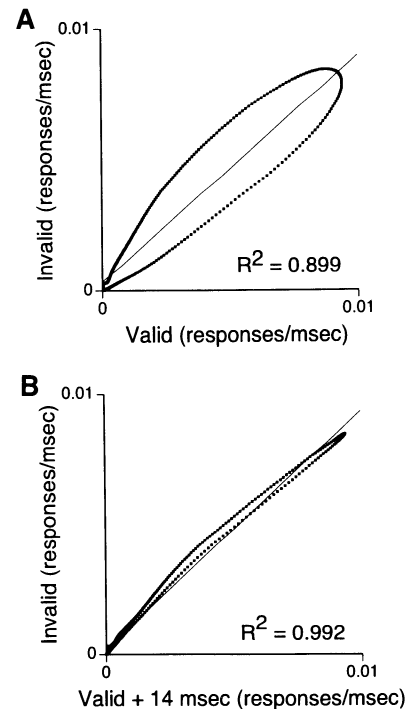


FIG. A1. Scatter plots of reaction time data from the standard task. These plots were generated from the data in Fig. 2 for monkey M2. At the top in A, the probability of responses for validly cued targets at each time interval are plotted against the probability of responses for invalidly cued targets at the same time interval. The thin diagonal line is the simple linear regression. A: the data were plotted from the original data values. B: the responses to validly cued targets had 14 ms added to their time. After this addition of time, there was the maximal correspondence between the 2 data sets, the maximal coefficient of correlation, and this time interval (14 ms) was selected as the validity effect.

2). The rationale of this approach is to find the time shift between the two distributions, which results in the maximal point-to-point correlation among corresponding data points in the valid and invalid distributions. Thus this approach utilizes every data point, not just the mean or some other single measure of central tendency.

The steps utilized here to perform this analysis are the following. First, smoothed histograms of reaction times from corresponding valid and invalid conditions were computed (Fig. 2, top left). This smoothing was done to make the reaction time function a continuous distribution so that values were present at every temporal interval (Richmond et al. 1987). This was accomplished by substituting a Gaussian kernel for each reaction time. The result of this process was to low-pass filter the original data. Second, the amplitudes (responses/ms) of the valid and invalid distributions were plotted against each other for each time interval from 200 to 1,000 ms. This time interval was that period during which acceptable reaction times were collected. An example of such a plot is in Fig. A1. To accomplish this analysis, the first time period was selected (e.g., 200 ms), and the valid and invalid responses for that time interval were plotted against each other. Then the next time interval was selected (e.g., 201 ms), and again the valid and invalid responses were plotted against each other. After all time intervals were tested, a scatter plot was computed and a coefficient of correlation for that scatter plot was determined (Fig. A1). Next the latencies of all the invalid data points were shifted by -1 ms, and again the valid and invalid data points for each time interval were plotted against each other. After this second computation was completed, a second scatter plot resulted and a second coefficient of correlation calculated for that shift. Next the latency of the

invalid data points were again shifted by another -1 ms and the whole process repeated. This process was continued until the coefficients of correlation from all shifts, ± 200 ms, were determined. At this point there was a coefficient of correlation available for each scatter plot for each time shift. Finally, the coefficients of correlation were plotted as function of the shift (Fig. 2, *bottom*), and the shift resulting in the highest correlation was used as the estimate of the validity effect. Figure A1 shows the scatter plot yielding the maximal coefficient of correlation for the data in Fig. 2. In practice, this technique leads to very stable estimates of the validity effect across testing sessions for a given monkey and across monkeys for a given experiment (Fig. 3A).

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Present addresses: E. M. Bowman and V. J. Brown: Dept. of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9JU, Scotland; C. Kertzman and U. Schwarz: Dept. of Neurology, University Hospital Zurich, Frauenklinikstr. 26, CH-8092 Zurich, Switzerland.

Address for reprint requests: D. L. Robinson, Sect. on Visual Behavior, Laboratory of Sensorimotor Research, National Eye Institute, Bldg. 49, Rm. 2A50, Bethesda, MD 20892.

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REFERENCES

- ANLLO-VENTO, L. AND HARTER, M. R. Shifts of attention and event-related potentials (ERPs) in humans: effects of valid and invalid cuing. *Soc. Neurosci. Abstr.* 14: 1014, 1988.
- BASHINSKI, H. S. AND BACHARACH, V. R. Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Percept. Psychophys.* 28: 241–248, 1980.
- BERLUCCHI, G., TASSINARI, G., MARZI, C. A., AND DiSTEFANO, M. Spatial distribution of the inhibitory effect of peripheral non-informative cues on simple reaction time to non-fixated visual targets. *Neuropsychologia* 27: 201–221, 1989.
- BOWMAN, E. M., BROWN, V. J., SCHWARZ, U., AND ROBINSON, D. L. Covert orienting of attention in macaque. I. Behavioral parameters. *Soc. Neurosci. Abstr.* 17: 442, 1991.
- BROWN, V. J., SCHWARZ, U., BOWMAN, E. M., FUHR, P., ROBINSON, D. L., AND HALLETT, M. Dopamine dependent reaction time deficits in patients with Parkinson's disease are task specific. *Neuropsychologia* In press.
- BUSHNELL, M. C., GOLDBERG, M. E., AND ROBINSON, D. L. Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J. Neurophysiol.* 46: 755–772, 1981.
- BUTTER, C. M., BUCHTEL, H. A., AND SANTUCCI, R. Spatial attentional shifts: further evidence for the role of polysensory mechanisms using visual and tactile stimuli. *Neuropsychologia* 27: 1231–1240, 1989.
- CONOVER, W. J. *Practical Nonparametric Statistics*. New York: Wiley, 1980.
- DAVIDSON, M., THOMAS-THRAPP, L. J., WITTE, E. A., POSNER, M. I., AND COLLAZO, C. R. Time course of covert orientation in a rhesus monkey. *Soc. Neurosci. Abstr.* 18: 1398, 1992.
- DOWNING, C. J. Expectancy and visual-spatial attention effects on vision. *J. Exp. Psychol. Hum. Percept. Perform.* 14: 188–197, 1988.
- EFRON, B. *The Jackknife, the Bootstrap and Other Resampling Plans*. SIAM monograph. Philadelphia: SIAM, CBMS-NSF, 1982, vol. 38.
- ENGEL, F. L. Visual conspicuity, directed attention and retinal locus. *Vision Res.* 11: 563–576, 1971.
- ENNS, J. T. AND BRODEUR, D. A. A developmental study of covert orienting to peripheral visual cues. *J. Exp. Child Psychol.* 48: 171–189, 1989.
- ERIKSEN, C. W. AND HOFFMAN, J. E. Temporal and spatial characteristics of selective encoding from visual displays. *Percept. Psychophys.* 12: 201–204, 1972.
- HAENNY, P. E., MAUNSELL, J. H. R., AND SCHILLER, P. H. State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. *Exp. Brain Res.* 69: 245–259, 1988.
- HAYS, A. V., RICHMOND, B. J., AND OPTICAN, L. M. A UNIX-based multiple process system for real-time data acquisition and control. *WESCON Conf. Proc.* 2: 1–10, 1982.
- VON HELMHOLTZ, H. *Handbuch der Physiologischen Optik* (3rd ed.). In: *Helmholtz's Treatise on Physiological Optics*, edited by J. P. C. Southall (1924 translation). New York: Dover, 1909.
- HUGHES, H. C. AND ZIMBA, L. D. Natural boundaries for the spatial spread of directed visual attention. *Neuropsychologia* 25: 5–18, 1987.
- JONIDES, J. Towards a model of the mind's eye's movement. *Can. J. Psychol.* 34: 103–112, 1980.
- JONIDES, J. Voluntary versus automatic control over the mind's eye's movement. In: *Attention and Performance IX*, edited by J. Long and A. Baddeley. Hillsdale, NJ: Erlbaum, 1981, p. 187–203.
- JONIDES, J. AND MACK, R. On the cost and benefit of cost and benefit. *Psychol. Bull.* 96: 29–44, 1984.
- JUDGE, S. J., RICHMOND, B. J., AND CHU, F. C. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res.* 20: 535–538, 1980.
- KEPPEL, G. *Design and Analysis. A researcher's handbook* (2nd ed.). Englewood Cliffs, NJ: Prentice-Hall, 1987.
- KERTZMAN, C., ROBINSON, D. L., SHERINS, R. J., SCHWANKHAUS, J. D., AND McCLURKIN, J. W. Abnormalities in visual spatial attention in men with mirror movements associated with isolated hypogonadotropic hypogonadism. *Neurology* 40: 1057–1063, 1990.
- LUCE, R. D. *Response Times: Their Role in Inferring Elementary Mental Organization*. New York: Oxford Univ. Press, 1986.
- MANGUN, G. R., HANSEN, J. C., AND HILLYARD, S. A. The spatial orienting of attention: sensory facilitation or response bias. In: *Current Trends in Event-Related Potential Research (EEG Suppl. 40)*, edited by R. Johnson, Jr., J. W. Rohrbaugh, and R. Parasuraman. Amsterdam: Elsevier, 1987, p. 118–124.
- MAYLOR, E. A. Facilitory and inhibitory components of orienting in visual space. In: *Attention and Performance XI*, edited by M. I. Posner and O. S. M. Martin. Hillsdale, NJ: Erlbaum, 1985, p. 184–204.
- MORAN, J. AND DESIMONE, R. Selective attention gates visual processing in the extrastriate cortex. *Science Wash. DC* 229: 782–784, 1985.
- MOUNTCASTLE, V. B., ANDERSEN, R. A., AND MOTTER, B. C. The influence of attentive fixation upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 1: 1218–1235, 1981.
- MULLER, H. J. AND FINDLAY, J. M. Sensitivity and criterion effects in the spatial cuing of visual attention. *Percept. Psychophys.* 42: 383–399, 1987.
- MULLER, H. J. AND RABBITT, P. M. A. Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *J. Exp. Psychol. Hum. Percept. Perform.* 15: 315–330, 1989.
- NAKAYAMA, K. AND MACKEBEN, M. Sustained and transient components of focal visual attention. *Vision Res.* 29: 1631–1647, 1989.
- OSAKA, N. Reaction time as a function of peripheral retinal locus around fovea: effect of stimulus size. *Percept. Mot. Skills* 43: 603–606, 1976.
- PARZEN, E. On estimation of a probability density function and mode. *Ann. Math. Statist.* 33: 1065–1076, 1962.
- PETERSEN, S. E., ROBINSON, D. L., AND CURRIE, J. N. Influences of lesions of parietal cortex on visual spatial attention in humans. *Exp. Brain Res.* 76: 267–280, 1989.
- PETERSEN, S. E., ROBINSON, D. L., AND KEYS, W. Pulvinar nuclei of the behaving rhesus monkey: visual responses and their modulations. *J. Neurophysiol.* 54: 867–886, 1985.
- PETERSEN, S. E., ROBINSON, D. L., AND MORRIS, J. D. The contribution of the pulvinar to visual spatial attention. *Neuropsychologia* 25: 97–105, 1987.
- POSNER, M. I. Orienting of attention. *Q. J. Exp. Psychol.* 32: 3–25, 1980.
- POSNER, M. I., COHEN, Y., AND RAFAL, R. D. Neural systems control of spatial orienting. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 298: 187–198, 1982.
- POSNER, M. I., RAFAL, R. D., CHOATE, L. S., AND VAUGHAN, J. Inhibition of return: neural basis and function. *Cognit. Neuropsychol.* 2: 211–228, 1985.
- POSNER, M. I. AND SNYDER, C. Attention and cognitive control. In: *Information Processing and Cognition: The Loyola Symposium*, edited by R. L. Solso. Hillsdale, NJ: Erlbaum, 1975, p. 55–86.
- POSNER, M. I., WALKER, J. A., FRIEDRICH, F. J., AND RAFAL, R. D. Effects

- of parietal injury on covert orienting of visual attention. *J. Neurosci.* 4: 1863-1874, 1984.
- PRINZMETAL, W., PRESTI, D. E., AND POSNER, M. I. Does attention affect visual feature integration? *J. Exper. Psychol. Hum. Percept. Perform.* 12: 361-369, 1986.
- RICHMOND, B. J., OPTICAN, L. M., PODELL, M., AND SPITZER, H. Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. I. Response characteristics. *J. Neurophysiol.* 57: 132-146, 1987.
- ROBINSON, D. L. AND KERTZMAN, C. Visuospatial attention: effects of age, gender, and spatial reference. *Neuropsychologia* 28: 291-301, 1990.
- ROBINSON, D. L., MCCLURKIN, J. W., KERTZMAN, C., AND PETERSEN, S. E. Visual responses of pulvinar and collicular neurons during eye movements of awake, trained macaques. *J. Neurophysiol.* 66: 485-496, 1991.
- SILVERMAN, B. W. *Density Estimation for Statistics and Data Analysis*. London: Chapman and Hall, 1986.
- SPITZER, H. AND RICHMOND, B. J. Task difficulty: ignoring, attending to, and discriminating a visual stimulus yield progressively more activity in inferior temporal neurons. *Exp. Brain Res.* 83: 340-348, 1991.
- STELMACH, L. B. AND HERDMAN, C. M. Directed attention and perception of temporal order. *J. Exp. Psychol. Hum. Percept. Perform.* 17: 539-550, 1991.
- WARNER, C. B., JUOLA, J. F., AND KOSHINO, H. Voluntary allocation versus automatic capture of visual attention. *Percept. Psychophys.* 48: 243-251, 1990.
- WATSON, G. S. Goodness-of-fit tests on a circle. II. *Biometrika* 49: 57-63, 1962.
- WURTZ, R. H., GOLDBERG, M. E., AND ROBINSON, D. L. Behavioral modulation of visual responses in the monkey: stimulus selection for attention and movement. In: *Progress in Psychobiology and Physiological Psychology*, edited by J. M. Sprague, A. N. Epstein. New York: Plenum, 1980, vol. 9, p. 43-83.
- WURTZ, R. H. AND MOHLER, C. W. Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. *J. Neurophysiol.* 39: 745-765, 1976.