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Improvement of visual acuity by spatial cueing: a comparative study in human and non-human primates

Heidrun Golla [a,*], Alla Ignashchenkova [a], Thomas Haarmeier [a,b], Peter Thier [a]

[a] *Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, University of Tübingen, Klinikum Schnarrenberg, Hoppe-Seyler-Strasse 3, 72076 Tübingen, Germany*
[b] *Department of General Neurology, Hertie Institute for Clinical Brain Research, University of Tübingen, Klinikum Schnarrenberg, Hoppe-Seyler-Strasse 3, 72076 Tübingen, Germany*

Abstract

This study investigated the influence of spatial cueing (valid/invalid/no cue) on visual discrimination in human and non-human primates. We employed a spatial resolution task which required the accurate discrimination of the orientation of a Landolt "C" ring. The C appeared as single target in specific retinal locations while subjects maintained fixation of a central fixation point. The minimal discernable size of the "C" (= acuity threshold) was determined as a function of cue condition, retinal eccentricity (3°–15°), and stimulus onset asynchrony (SOA) (200–1100 ms). For both species, we found consistent benefits from spatial cueing with differences in absolute thresholds ranging from 6% to 25%. These differences increased with retinal eccentricity and decreased with longer SOAs. Further experiments performed with humans only, showed that the effect of spatial cueing on visual discrimination is independent of spatial uncertainty, i.e. the number of possible target locations (2 versus 4), but fades with longer target presentation times. From our results we draw the following conclusions. (i) Since sensory noise and spatial uncertainty was small in our tasks, spatial shifts of attention involve signal enhancement in both, human and non-human primates. (ii) The similarity of the results obtained for humans and macaque monkeys indicates that the latter may serve as a suitable model system in studies trying to tackle the neural underpinnings of attentional control. (iii) In order to elicit robust effects on visual discrimination by spatial shifts of attention, a paradigm comprising short SOAs (∼200 ms) and target presentation times (∼150 ms), and retinal eccentricities larger than ∼9° seems most promising.

1. Introduction

At any moment we are confronted with a continuous stream of sensory information of which only a small part is relevant for our behavior. Attention is the neuronal function which enables us to focus our analysis of sensory information onto behaviorally crucial elements of the input thereby optimizing the use of capacity limited resources. The process of assigning priority to a certain sensory stimulation over others is most obvious for the visual system: objects which suddenly appear in the periphery of the visual field usually elicit a saccadic eye movement directed to the object, moving the object image onto the fovea, thereby giving access to the advantages of foveal vision. Saccades are *overt* shifts of spatial attention. However, spatial shifts of attention can also be performed in a *covert* manner, i.e. without concomitant eye movements (Deubel & Schneider, 1996; Helmholtz, 1924). Historically, covert shifts of visual attention have first been addressed experimentally using detection tasks with differences in reaction times as observed for different cue conditions serving as a measure of both costs and benefits of covert shifts of attention (Norman, 1968; Posner, Snyder, & Davidson, 1980). More recently (e.g. Yeshurun & Carrasco, 1999), visual discrimination tasks have been given preference to detection tasks because the effect of attention may be confounded by motor preparation. Specifically, a valid

* Corresponding author. Tel.: +49-7071-2980469; fax: +49-7071-295326.
E-mail address: heidrun.golla@uni-tuebingen.de (H. Golla).

cue (presented at the location of the following target and amounting to the majority of trials) by itself might induce motor preparation of the response (Posner et al., 1980). Such a response bias is prevented by employing visual discrimination tasks in which the cue indicates the location of the object, but does not provide information on object identity.

An improvement in visual discrimination by spatial cueing has been reported regularly for displays adopting multiple targets, post-target masks or crowding elements like lines or other distractors, i.e. for conditions of significant sensory noise. (Henderson, 1991; Henderson & Maquistan, 1993; Lyon, 1990; Mackeben & Nakayama, 1993; Nakayama & Mackeben, 1989; Saarinen, 1993; Shiu & Pashler, 1994, 1995). On the other hand, effects of spatial cueing on visual discrimination have not always been observed for setups with low sensory noise such as given in displays without post-target masks or distractors. Whereas a number of earlier studies failed to demonstrate an influence of spatial cueing on visual discrimination for such low noise conditions (gap resolution: Nazir, 1992; single digit target identification or vernier acuity: Shiu & Pashler, 1994, 1995), more recent work has demonstrated convincingly that visual discrimination (e.g. single digit or letter discrimination, shape or orientation discrimination or spatial resolution) improves as a consequence of valid cueing also under conditions of low sensory noise (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Carrasco, Williams, & Yeshurun, 2002; Egly & Homa, 1991; Henderson, 1996; Luck, Hillyard, Mouloua, & Hawkins, 1996; Saarinen, 1993; Van der Heijden, Wolters, Groep, & Hagenaar, 1987; Yeshurun & Carrasco, 1999). The overall pattern of results obtained so far in human studies addressing the influence of spatial cueing on visual discrimination—regular improvement of discrimination in the presence of sensory noise but weaker, sometimes missing effects of spatial cueing under conditions of low sensory noise—has been taken as evidence for the assumption that the reduction of the confounding influence of non-targets may represent the main mechanism underlying attentional effects ("noise reduction theory"), but that "signal enhancement" also plays a significant role. A more explicit model covering the contribution of signal enhancement on the one hand and noise reduction on the other hand has been put forward by Lu and Dosher (Dosher & Lu, 2000a, 2000b; Lu & Dosher, 1998) who suggested that, in principle, both mechanisms are able to improve visual discrimination but that the specific stimulus configuration may be the decisive factor determining whether stimulus enhancement or noise reduction will be more effective. Specifically, stimulus enhancement may become manifest only in noiseless stimulus environments.

While the mechanisms underlying the perceptual benefits resulting from covert shifts of attention have been thoroughly characterized in humans, there are only few studies testing the influence of spatial shifts of attention on visual performance in non-human primates. This scarcity of studies is unfortunate in view of the fact that non-human primates, widely and successfully used in neurophysiological studies of attention (for review see Treue, 2001), offer a promising model to unravel the neuronal underpinnings of attentional control. In particular, different from functional imaging used in human studies, single cell recordings in the awake behaving monkey allow for direct comparison of neuronal responses with behavioral measures and, in addition, allow also for inspection of those brain regions hardly monitored by imaging techniques such as small subcortical structures like the superior colliculus. To our knowledge only three studies have been reported so far testing the influence of spatial attention on visual performance in both, human and non-human primates. The first two studies (Bowman, Brown, Kertzman, Schwarz, & Robinson, 1993; Witte, Villareal, & Marrocco, 1996) demonstrated that spatial cueing improves reaction times in a visual detection task to a similar extend in both species. In addition, work by Ciaramitaro et al. (Ciaramitaro, Cameron, & Glimcher, 2001), testing luminance discrimination in monkeys and humans as function of the probability that the discriminative stimulus would appear at a particular location in the visual field, showed a clear improvement in visual discrimination for higher location probabilities suggesting that the two species might benefit similarly from attentional orienting.

The present study was performed in order to further our knowledge of the similarities and dissimilarities of the attentional systems of human and non-human primates. Towards this end, we tested whether human observers and rhesus monkeys might benefit from shifts of attention, induced by spatially precise cues, in a concordant manner. In order to avoid the pitfalls of detection tasks such as possible response biases, the influence of spatial cueing was quantified using a visual discrimination paradigm. Specifically, we measured the effect of spatial cueing on visual acuity assessed by single Landolt "C" optotypes, which were presented in one of two (or four) possible positions in the visual field. Furthermore the paradigm used with the stimulus containing only minimal sensory noise would allow us to test whether the attentional effects assumed might involve signal enhancement as the underlying mechanism. The comparative experiments testing shifts of attention in human and non-human primates were supplemented by two further experiments, performed in human subjects only, addressing the question why benefits in visual discrimination have not been observed in some of the former studies using noiseless stimuli (Nazir, 1992; Shiu & Pashler, 1994, 1995). Towards this end, we studied the influence of two parameters, which have not been

systematically addressed so far in studies using noiseless paradigms, but which might be crucial for the demonstration of attentional benefits in visual discrimination under such conditions. In a first experiment, we examined whether the benefits might critically depend on the number of possible target locations of the discriminandum (= "spatial uncertainty") which has been suggested to play a major role (Carrasco et al., 2002; Yeshurun & Carrasco, 1999, 2000). In the second experiment, the influence of target presentation time was tested. The reason to expect a profound influence of presentation time is that the discriminandum itself attracts attention, i.e. that it might serve as its own cue resulting in decreasing attentional effects when the presentation time is increased.

Finally, by testing the influence of spatial cues on visual discrimination as function of a variety of parameters (retinal position, stimulus onset asynchrony (SOA), target presentation time, number of possible target positions (spatial uncertainty)) we are able to define experimental conditions under which the attentional benefits are most robust and which, therefore, would be most promising for future studies addressing the neuronal underpinnings of spatial control of attention.

2. Methods

2.1. General procedure and stimuli

We measured peripheral acuity thresholds in humans and rhesus monkeys based on a paradigm requiring the discrimination of two possible orientations of a conventional Landolt "C" optotype which was scrutinized during controlled, stationary fixation. Attentional effects were defined as the difference in acuity thresholds for two different cueing conditions: In Experiment 1 we compared thresholds obtained for valid and invalid spatial cueing and in Experiments 2–5 the visual performance under conditions of valid cueing was com-

pared with that observed for conditions without cue presentation.

Each single trial (Fig. 1) started with the presentation of a central red fixation point (10 min of arc, 2 cd/m^2) on an otherwise dark background (0.05 cd/m^2). This fixation point remained visible for the total length of each trial. In "cue" trials, the cue, a white dot (20 min of arc, 6.2 cd/m^2, presentation time 100 ms), was presented after a 500 ms period of stationary straight ahead fixation at one of two possible locations along the horizontal or, alternatively, the vertical axis. After an interstimulus interval (= ISI) of variable duration (100–1000 ms), the discriminandum, a white Landolt "C" (6.2 cd/m^2), appeared either at the location of the prior cue (valid cue condition) or at the mirror location, i.e. contralateral to the cue (invalid cue condition), and was present for 50–500 ms. In "no cue" trials, the Landolt "C" presentation started immediately after the 500 ms period of maintained fixation. Trials with different cueing conditions (valid and invalid cueing conditions in Experiment 1; valid and no cueing conditions in Experiments 2–5) were presented randomly interleaved within a block. In order to impede the analysis of afterimages at the end of the "C"-presentation, the "C"-gap was closed for 200 ms, turning the "C" into an "O".

Subjects were instructed and monkeys trained to maintain fixation of the central red fixation spot and to indicate which of two possible orientations of the Landolt "C" gap had been presented (gap either at the top or at the bottom; two-alternative forced choice). While human observers responded by pressing one of two possible buttons, monkeys were trained to execute a saccade into one of two learned directions after stimulus presentation (see below for details). Positive feedback for correct responses was provided by means of a short tone (humans) or by fluid release (monkeys). Human subjects were instructed and monkeys trained to be as accurate as possible but not necessarily as fast as possible. In the monkey experiments maximal acuity was prompted by the rewarding protocol chosen (see below). The sequence of Landolt "C"s presented during the
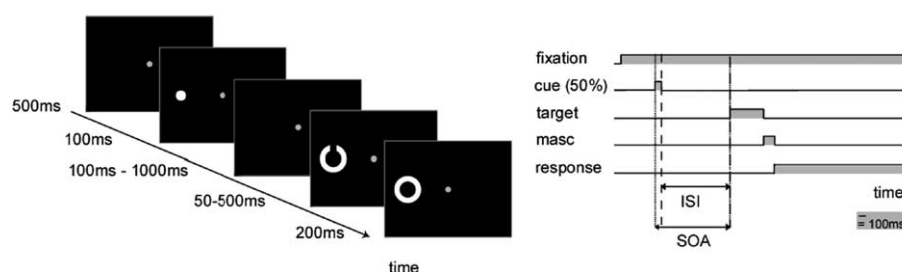

Fig. 1. Stimulus sequence: each single trial started with the presentation of a central red fixation point followed by the Landolt optotype which was announced in cue trials by a white dot located at the same (valid cue; Experiments 1–5) or opposite (invalid cue; Experiment 1) position as the Landolt "C". The Landolt "C" and, thus, also the cue could appear at one of two (Experiments 1–5) or four (Experiment 5) positions. ISI = time interval between cue offset and target onset; SOA = time interval between cue and target onset (SOA).

course of one measurement was controlled by an adaptive staircase procedure (PEST; Liebermann & Pentland, 1982) with separate procedures running interleaved for the different cueing conditions (valid cue versus invalid cue condition (Experiment1), valid cue versus no cue condition (Experiment 2–5)) and the different Landolt positions. Specifically, with two possible target positions and two differing cueing conditions, four independent PEST strategies were implemented in one experiment, all starting with the same Landolt "C" gap size (ranging from 18 to 24 min of arc for the different subjects). The size of the Landolt "C" gap amounted to 20% of the outer Landolt diameter, i.e. the size of the Landolt "C" and its gap was varied congruently. Acuity thresholds for the four conditions, defined as the Landolt "C" gap resulting in 75% correct responses (with the chance performance level being 50%), were derived from probit analyses (McKee, Klein, & Teller, 1985) with subsequent x^2 goodness-of-fit tests which were performed on the responses obtained from at least 30 trials under each condition. The difference between acuity thresholds for the valid cue and the no cue/invalid cue condition served as an estimate of the benefit resulting from spatial cueing and used to quantify the effect of attention.

The general psychophysical procedure and the visual stimuli were the same for human and non-human experiments. Minor differences concerned the computer monitor used to present the stimuli (human subjects: 19-in. computer monitor, Mitsubishi, frame rate 72 Hz, 1280×1024 pixels; monkeys: 21-in. computer monitor, Flexscan F760i-W, frame rate 72 Hz, 1280×1024 pixels) and the viewing distance applied. While monkeys viewed the stimuli at a fixed distance of 43 cm, the viewing distance in experiments on humans was varied depending on the retinal eccentricity of the target (15°: 57 cm; 9°: 80 cm; 3°: 120 cm). Longer viewing distances for smaller eccentricities were necessary in humans in order to guarantee that the pixel resolution of the monitor was sufficient for reliable acuity measurements.

In all experiments eye movements were monitored, using an infrared reflection system in humans (CCD eyetracker, AmTech®, Weinheim, Germany, spatial resolution <0.1° of visual angle, temporal resolution = 200 Hz), and standard search coil techniques in the monkeys (spatial resolution <0.1° of visual angle, temporal resolution = 1000 Hz). Head movements were minimized by means of a bite bar (experiments on humans) and by using chronically implanted head posts for the painless fixation of the monkeys' head. The eye records were analyzed online by the computer which also controlled the stimuli presentation. Deviations of eye position from the fixation point exceeding a defined threshold (a square with 2 or 2.5° side length centered around the fixation point), were fed back acoustically as errors. Trials with insufficient fixation were ignored by

the adaptive staircase procedure and excluded from further analysis.

2.2. Human subjects

In total, 26 human subjects (12 male, 14 female; mean age 26 years; range 23–35 years) participated in the experiments. All observers had normal or corrected to normal acuity. Each subject was trained 2 or 3 times under "standard conditions" (cue presentation time: 100 ms, SOA: 250 ms, target presentation time: 150 ms, target position 9° right or left from the fixation point) in order to become familiar with the experimental paradigm. Subjects' informed consent was obtained according to the declaration of Helsinki (BMJ 1991; 302: 1194) and the study was approved by the ethics committee of the University of Tübingen.

2.3. Specific features of monkey experiments

Two male rhesus monkeys (B. and Z.) participated in the first three series of experiments. All procedures including implantation of search coils and head post followed standard protocols (see e.g. Thier & Erickson, 1992) that complied with the NIH Guide for Care and Use of Laboratory Animals and were approved by the Local Animal Care Committee.

Monkeys were trained via operant-reinforcement techniques: In order to receive a reward—a unit of water or juice released through a tube in front of the monkeys' mouth—they had to identify the orientation of the Landolt "C" correctly while keeping their gaze within the specified eye position window centered around the fixation point. As mentioned before, monkeys had to indicate the orientation of the Landolt "C"-gap by saccadic eye movements directed to one of two possible targets (two green dots, 40 min of arc, 10 cd/m²) which were presented 9° above and below the fixation point, respectively. A gap at the top of the Landolt ring required an upward saccade, correspondingly, a gap at the bottom of the Landolt "C" a downward saccade. Saccades and, thus, perceptual responses were accepted if the eye position after the saccade fell within a square of 4° side length centered around the saccade targets and if the saccade was executed within the first 1200 ms after the Landolt "C" had disappeared. In order to prompt the monkeys to work close to their individual acuity threshold, the following rewarding procedure was employed. First of all, the animals received reward units, twice the standard size, when two trials were successfully completed in sequence, thereby speeding up the convergence of the staircase procedure towards lower Landolt "C" levels. Of course, close at the threshold level, the monkeys would not be able to give correct responses consistently. In order to motivate the monkeys to keep on working reliably also at the threshold,

they received a "mega reward", of three times the amount of a standard reward for each correct answer given in response to Landolt "C" gaps being slightly smaller or larger than the expected threshold. Negative feedback was not used. The animals needed about 4 months of daily training to learn the task. After further 3–5 weeks, in which the performance stabilized psychophysical data were systematically collected for the different experimental conditions.

3. Results

3.1. Experiment 1

The first experiment was performed in order to test whether covert shifts of attention might influence visual discrimination in monkeys at all and, if so, whether the effects obtained for the monkeys would be similar to those observed in human subjects. In a first attempt to answer this question, we compared acuity thresholds for validly cued targets (75% of all trials) with those obtained for invalidly cued targets (25%) presented randomly interleaved. 14 human subjects and both monkeys participated in this experiment. One measurement consisted of 320 (humans) and 420 (monkeys) trials, respectively. In each single trial, the cued optotype (with its gap being at the top or at the bottom) appeared at 9° right or left from the fixation point. The presentation time of the cue (100 ms) and of the target (150 ms), and the SOA (250 ms) were kept constant. Data were subjected to a two-way analysis of variance (ANOVA) with the factors cueing condition and position (right versus left).

Both, human subjects and monkeys, showed improved acuity thresholds if the discriminandum was preceded by a valid rather than an invalid cue (Fig. 2).
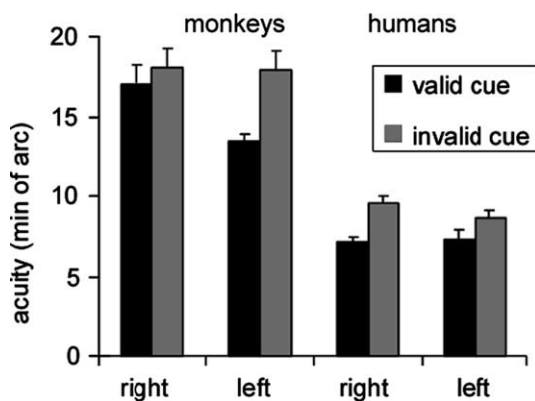

Fig. 2. Means and standard errors of acuity thresholds at 9° horizontal retinal eccentricity for monkeys and humans under the valid (75% of trials) and invalid (25%) cueing conditions. Presentation time of the cue: 100 ms; presentation time of the target: 150 ms; SOA: 250 ms.

This difference between thresholds reflecting the perceptual consequence of spatial shifts of attention averaged 18.9% in the human subjects and 15.2% in the two monkeys and was statistically highly significant for both species (monkeys: $F = 18.66$; $p = 0.0015$, humans: $F = 22.88$; $p < 0.001$). While monkeys and humans showed the same principle pattern of results, their performance differed with respect to two features. As can be derived from Fig. 2, the acuity thresholds in the monkeys were higher than those of the human subjects by a factor of 2. Second, the effect of spatial cueing in the monkeys was more pronounced for the right target location as compared to the left position ($F = 9.06$; $p = 0.002$). This asymmetry in the effect of spatial cueing was absent in the human subjects ($p = 0.1$).

3.2. Experiment 2

In the second experiment and all following experiments only trials with valid or no cues (50% each) were presented, i.e. the spatial cue—if present—always indicated the true position of the following target. Trials with valid trials only were used because monkeys worked most consistently under this condition. As will be demonstrated, the effects of spatial cueing for this paradigm were similar to the previous experiment comparing valid and invalid cueing conditions. Experiment 2 tested whether the attentional effects in monkeys and human subjects might depend on retinal eccentricity, i.e. whether or not spatial attention might have a uniform influence on visual discrimination achieved by an amplification of the visual signal by a constant factor. Towards this end, the horizontal target position was systematically varied in three separate experimental blocks (3°, 9° and 15°), each consisting of 160 (humans) or 240 (monkeys) trials, respectively. Thirteen human subjects and both monkeys contributed to this experiment. The presentation time of the cue (100 ms) and of the target (150 ms), and the SOA (250 ms) were again fixed. Acuity threshold measurements were subjected to a three-way ANOVA with the factors cueing condition, retinal eccentricity and position (left, right).

As shown in Fig. 3, a robust benefit from spatial cueing was again observed for the valid cue condition as compared to the no cue condition. This was indicated by the fact that for all retinal target positions the mean acuity thresholds were lower for cue trials as compared to the neutral trials. An improvement in visual acuity was seen in both, human subjects and monkeys, with the mean difference between thresholds averaged over all positions being 12.9% in the humans and 14.3% in the monkeys. The improvement in visual acuity was statistically highly significant (monkeys: $F = 68.75$; $p < 0.001$; humans: $F = 18.23$; $p = 0.0011$). It depended on horizontal retinal eccentricity (Fig. 3) with stronger differences between acuity thresholds for the no cue and
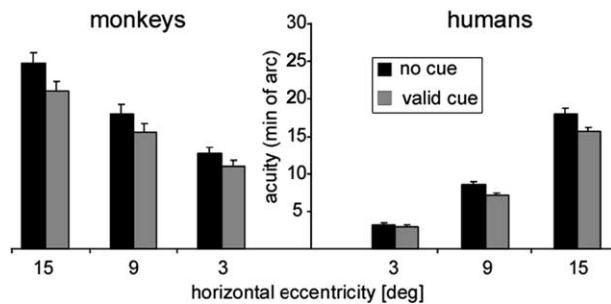
Fig. 3. Influence of spatial cueing on visual acuity as function of retinal eccentricity: Means and standard errors of acuity thresholds for monkeys and humans under the no cue (black bars) and the valid cue conditions (grey bars) obtained from three different positions along the horizontal axis. Thresholds for right and left positions were pooled. Presentation time of the cue (100 ms) and of the target (150 ms), and the SOA (250 ms) were the same as in Experiment 1.

valid cue condition for higher eccentricities (humans: $F = 4.52$; $p = 0.022$). For instance, the absolute difference between thresholds for the target position being 3° averaged 0.25 min of arc in the human subjects, while this difference was 2.29 min of arc for the highest eccentricity tested (15°). This dependency was further supported by post hoc comparisons (Newman–Keuls test) which, in humans, revealed statistically significant differences between acuity thresholds for the two outermost eccentricities only (9° ($p = 0.006$), 15° ($p < 0.001$)). As shown in Fig. 3, the performance of the monkeys was qualitatively almost the same, one difference being that a significant improvement in acuity by spatial cueing was present also for the smallest retinal eccentricity tested (3°). As can be derived from Table 1, showing a summary of the standard deviations observed for the different conditions, this difference between species was a consequence of the much smaller standard deviation of the acuity measurements for this specific eccentricity in monkeys as compared to humans. Humans showed a comparable tendency towards a better acuity by spatial cueing at 3° (Fig. 3) which was, however, prevented from becoming significant because of the much larger data variability.

While the *absolute* change in acuity increased in both species with increasing eccentricity, the *relative* improvement as given by the ratio of acuity with valid spatial cueing and acuity without cueing was independent of retinal eccentricity (one way-ANOVA with the

factor eccentricity; humans: $p = 0.36$; monkeys: $p = 0.77$). For each of the three retinal eccentricities and for both species we observed a clear tendency in the direction of a relative improvement of acuity by valid spatial cueing. However, similar to the analysis of absolute thresholds, this tendency was statistically significant only for the two outer target positions (9° and 15°) (non-parametric sign tests; humans: 9° $p < 0.01$, 15° $p = 0.05$; monkeys: 9° and 15° $p < 0.01$).

As already noticed in Experiment 1, the acuity thresholds of monkeys were considerably higher than those of human subjects. This difference was most prominent for smaller eccentricities (with a thresholds' ratio averaging 3.9 for the 3° condition) and decreased with larger eccentricities (thresholds' ratio for the 15° condition: 1.4). The difference in acuity thresholds between species fading with increasing eccentricities reflected a stronger decrease in visual acuity for larger eccentricities in the humans.

Although subjects were not instructed and monkeys not trained to answer as fast as possible, we here also analyzed—in addition to the visual discrimination performance—the reaction times in both species for one exemplary condition (target and cue presentation at 9° horizontally, cue presentation time 100 ms, target presentation time 150 ms, SOA 250 ms). Both species showed significantly shorter reaction times for the cue condition as compared to the no cue condition (monkey: $p < 0.001$; human subjects: $p = 0.029$) with the main difference between monkeys and humans being that the responses of the monkeys (given by saccades) were much faster than the responses of the human subjects (given by pressing a button). Specifically, the mean reaction times obtained from the monkeys were 230 and 198 ms for the no cue and valid cue condition, respectively, while being 793 and 751 ms in the humans, thus demonstrating that the differences in acuity thresholds were not resulting from speed-accuracy trade-offs.

3.3. Experiment 3

Experiment 3 was performed in order to study the time course of covert shifts of attention in both species. Towards this end, the influence of spatial cueing on visual discrimination was measured here as function of the SOA which was varied from 200 to 1100 ms by changing the length of ISI and keeping the time for cue presentation constant. The range of ISIs tested in our experiments (100–1100 ms) was chosen such as to avoid afterimages induced by the cue but to cover a period of time long enough to enroll sustained attention. Number of trials, cueing conditions, and presentation time of the cue and of the target were the same as in Experiment 2. The target was presented at 9° left or right from the fixation point. Eighteen human subjects and both monkeys participated in this experiment. The influence

Table 1
Summary of the means of standard deviations of acuity (min of arc) observed for the different conditions and species

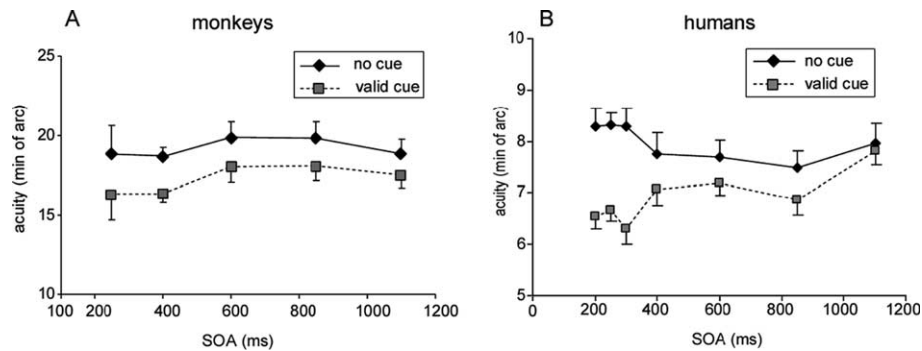| Species	Cue condition	Std 3°	Std 9°	Std 15°
Monkey	No cue	1.14	4.17	5.02
Monkey	Valid cue	1.51	4.59	5.55
Human	No cue	3.86	5.24	5.57
Human	Valid cue	3.13	4.56	5.68

Fig. 4. Means and standard errors of acuity thresholds at 9° horizontal retinal eccentricity for monkeys (A) and humans (B) under no cue (50% of trials) and valid cue (50%) condition as function of SOA. The presentation time of the cue (100 ms) and the target (150 ms) were fixed. Thresholds for right and left positions were pooled.

of spatial cueing on visual discrimination and the dependency of acuity thresholds obtained for the valid cue condition on the SOA was tested by two one-way ANOVAs with the factors cueing condition and SOA, respectively.

As shown in Fig. 4, the acuity thresholds for the cue condition were again lower than those for the no cue condition, confirming the main effect of spatial cueing (monkeys: $F = 50.21$; $p < 0.001$, humans: $F = 87.86$; $p < 0.001$). Furthermore, Fig. 4 reveals that the perceptual consequences of spatial shifts of attention were most pronounced for comparatively short SOAs, with the strongest differences between thresholds for SOAs from 200 to 300 ms in humans and 250 to 400 ms in monkeys. This dependency of the improvement in visual discrimination induced by spatial cueing on the SOA was statistically significant for the human subjects as confirmed by a one-way ANOVA testing the influence of the factor SOA on acuity thresholds observed for the valid cueing condition ($F = 5.23$; $p < 0.01$), but was not statistically significant in the monkeys ($p = 0.36$). Despite a clear tendency for smaller differences in acuity thresholds between cue conditions with longer SOAs, the acuity thresholds for the valid cue condition were still lower than those obtained from the control condition for the longest SOA tested. Inverse effects of spatial cueing were not observed in either of the two species.

3.4. Experiment 4

Experiments 4 and 5, based on human subjects ($n = 13$) only, were performed in order to contribute to the question why benefits resulting from spatial cueing have not always been observed in the absence of noise. Two parameters, which might influence the strength of cueing effects under such conditions but which have not been systematically addressed so far, were studied here, the first being target presentation time (Experiment 4), and the second being the number of possible target locations (spatial uncertainty; Experiment 5).

Benefits in visual discrimination resulting from spatial cueing are likely to depend on the presentation time of the target. Specifically, one would expect that the attentional effects might disappear with increasing presentation times. The reason is that the target itself attracts attention and, in this sense, might serve as its own cue. This possibility was tested in Experiment 4 by measuring the influence of spatial cueing on visual acuity as function of target presentation time varied from 50 to 500 ms while keeping the SOA constant (250 ms). The cueing conditions, target positions and number of trials were the same as stated for Experiment 3. Only human subjects ($n = 13$) were tested. Acuity thresholds were subjected to a three-way ANOVA with the factors cueing condition, target presentation time and position.

Fig. 5 shows acuity thresholds for the no cue and the valid cue condition as function of target presentation time. As can be derived from this figure, the acuity thresholds for both cueing conditions showed the expected dependency on target presentation time with
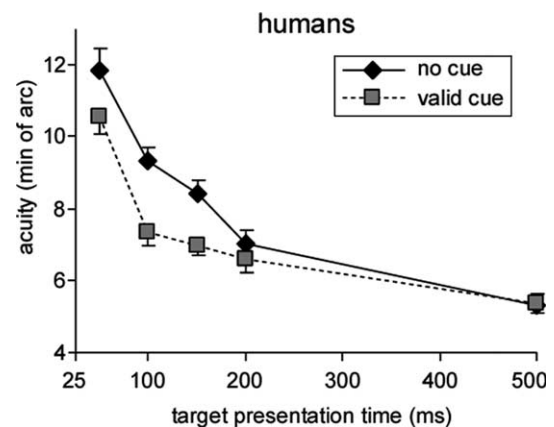

Fig. 5. Means and standard errors of acuity thresholds at 9° horizontal retinal eccentricity for humans under the no cue (50%) and the valid cue (50%) condition as function of target presentation time. The presentation time of the cue (100 ms) and the SOA (250 ms) were fixed. Thresholds for right and left positions were pooled.

lower thresholds for longer presentation times ($F = 54.52$, $p < 0.001$). Evident from Fig. 5 is also the improvement of acuity thresholds as a consequence of spatial cueing as observed in Experiments 2 and 3 ($F = 31.80$, $p < 0.001$). Most important here, this perceptual benefit from spatial cueing depended significantly on target presentation time as indicated by a statistically significant interaction of the factors cue condition and target presentation time ($F = 4.96$, $p = 0.002$). Specifically, the difference between thresholds for the two cue conditions was strongest for shorter presentation times, decreased for longer presentations, and finally disappeared for the longest presentation time of 500 ms.

3.5. Experiment 5

As indicated above, the amount of facilitation of visual discrimination resulting from spatial cueing might also depend on spatial uncertainty, i.e. the number of possible target locations. This possibility, put forward by Yeshurun and Carrasco (1999, 2000), is supported by the observation that attentional benefits have been reported for large numbers of possible target locations (16 locations, Yeshurun & Carrasco, 1999; up to 23 locations, Yeshurun & Carrasco, 2000; 8 locations, Cameron, Tai, & Carrasco, 2002 and Carrasco et al., 2000) while being absent for conditions involving less spatial uncertainty (9 locations, Nazir, 1992; 4 locations, Shiu & Pashler, 1994, 1995). The possibility for attentional effects depending on spatial uncertainty was tested here experimentally by comparing the perceptual benefits induced by spatial cueing for two conditions differing with respect to the number of possible target locations. Under the first condition, the optotype could appear at any of four possible locations (9° left, right, up or down), while under the second condition—consisting of two separate measurements—the Landolt "C" was presented either along the horizontal or the vertical axis with only two positions possible. 14 human subjects participated in Experiment 5. The SOA was set 250 ms and the target presentation time was 150 ms. Acuity thresholds were analyzed by a three-way ANOVA (cueing condition, number of possible target positions, target position).

As shown in Fig. 6, the cue effect, i.e. the difference between thresholds for the cue and the no cue condition, was independent of the number of spatial locations, i.e. independent of spatial uncertainty. The irrelevance of spatial uncertainty for the effect of cueing was reflected by an ANOVA which revealed a statistically highly significant influence of the factor cue condition ($F = 30.47$; $p < 0.001$), but no significant differences between thresholds observed for the two- and four-position conditions ($p = 0.91$). Fig. 6 further reveals that the human subjects showed slightly, albeit significantly
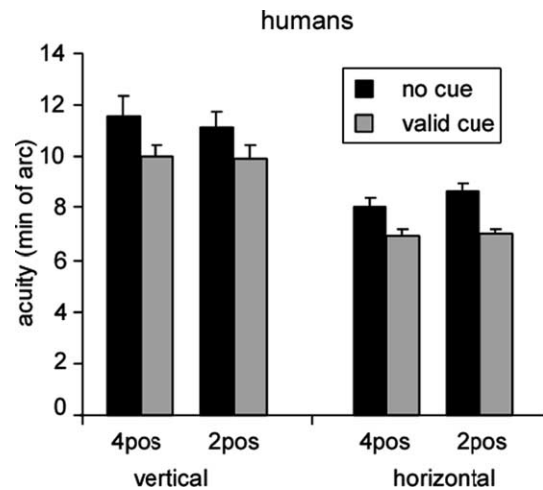
Fig. 6. Means and standard errors of acuity thresholds at 9° horizontal retinal eccentricity for humans under the no cue (50%) and valid cue (50%) condition as function of the number of possible target positions being two (2 pos) or, alternatively, four (4 pos). Thresholds for right/left and up/down positions were pooled.

lower acuity thresholds along the horizontal axis as compared to the vertical cardinal axis ($F = 26.25$; $p < 0.001$).

4. Discussion

4.1. Comparison of monkey and human data: effects of spatial cueing on visual discrimination

Comparative studies assessing the effects of spatial cueing and/or visual discrimination in monkeys and humans are rare but in general show that both species behave similarly supporting the view that they share the same visual and attentional systems. For instance, the two species have been found to show a similar performance in the discrimination of line orientation (Vasquez, Cano, & Acuna, 2000), in covert visual search (Buracas & Albright, 1999) or in a cued brightness discrimination task (Ito, Westheimer, & Gilbert, 1998). Bowman and coworkers (Bowman et al., 1993), using a cued visual *detection* task similar to the paradigm originally introduced by Posner (1980) were among the first to compare the ability to covertly shift attention in monkeys and human subjects. A similar study, varying in addition the temporal sequence of trials and employing different types of cue conditions, was performed by Witte et al. (1996). For both species, the two studies report shorter reaction times for validly cued targets, which has been taken as evidence for a similar attentional system in monkeys and humans.

The major goal of the present study was to confirm this conclusion by adopting a discrimination task which—different to detection tasks—is not prone to

potential response biases. As a main result, in each experiment carried out we indeed observed a clear improvement of visual acuity under conditions of valid spatial cueing as compared to conditions of absent (Experiment 2 + 3) and invalid (Experiment 1) spatial cueing, respectively. Most important, these benefits were quantitatively quite similar for human and non-human primates with the decrease in acuity thresholds induced by spatial cueing ranging from 7% to 17% in the human subjects and 8% to 21% in the monkeys. The demonstration of clear benefits in visual discrimination under conditions of minimal sensory noise, moreover, shows that in both species facilitation of vision by spatial attention involves signal enhancement. This conclusion is concordant with experiments performed by Ciaramitaro et al. (Ciaramitaro et al., 2001) showing that monkeys and human subjects are able to improve luminance discrimination the more the location at which a stimulus would appear can be predicted reliably.

Not only was the main effect of spatial cueing similar for both species, but also its dependency on the parameters varied (cue condition (valid–invalid cue conditions in Experiment 1; valid–no cue condition in Experiments 2 and 3), retinal position, SOA). In both, monkeys and human observers, the differences in acuity thresholds for the conditions compared were larger in Experiment 1 (comparing thresholds for valid versus invalid cue conditions) than in Experiment 2 (comparing thresholds for valid versus no cue conditions). This observation is in agreement with previous studies (see e.g. Luck et al., 1996; Posner et al., 1980), which have shown that differences between valid cue and invalid cue conditions reflect the sum of benefits and costs, respectively, whereas the comparison of valid cue and neutral cue conditions provides an estimate of the benefits only.

The dependency of the attentional benefits on retinal position (Experiment 2) was also very similar in monkeys and humans albeit disclosing minor differences as well. Specifically, the influence of spatial cueing on visual acuity tended to be small (monkeys) or even absent (humans) for an eccentricity of 3° and largest for the largest eccentricity of 15° tested, thus corresponding with a similar pattern observed in earlier studies on humans (Carrasco et al., 2002; Carrasco & Yeshurun, 1998; Yeshurun & Carrasco, 1999). The small effect of spatial cueing in monkeys became significant in our study because of the comparatively small data variability for this particular eccentricity. The much larger variability in humans, on the other hand, prevented the demonstration of a significant effect of cueing in our study. Our interpretation that effects of spatial shifts of attention might be present also in the more central part of the visual field but masked by data variability is supported by previous work showing that attentional benefits, in principle, can also be observed for the foveal/

parafoveal region (e.g. Nakayama & Mackeben, 1989). While the *absolute* change in visual acuity induced by spatial cueing depended on eccentricity, the *relative* change in thresholds did not differ for the retinal positions in the two species. This invariance of the relative change measure supports the notion originally put forward by Posner (1980) that the perceptual benefits induced by valid cueing may be the same ("equipotent") for the whole visual field. Such a uniform influence of spatial attention on visual discrimination could, in principle, result from an amplification of the visual signal by a constant factor.

The last dependency tested also revealed concordant results in both species. In monkeys and in humans as well the perceptual benefits induced by spatial cueing gradually diminished with increasing SOAs, but were present for SOAs as long as 1 s, the main difference being that this dependency was statistically significant in the human subjects only. In both species clear benefits were observed already for the shortest SOA tested (Fig. 4), suggesting that spatial orienting necessitates less than 200 ms and that the minimum time needed to successfully shift attention seemed to be similar in monkeys and human observers. Similar benefits in human studies have been reported by others for SOAs ranging from 100 to 200 ms, including work testing the effect of spatial cueing on visual discrimination in noiseless paradigms (Carrasco et al., 2002; Egly & Homa, 1991; Henderson, 1996; Luck et al., 1996; Saarinen, 1993; Van der Heijden et al., 1987; Yeshurun & Carrasco, 1999). Even shorter SOAs (50–100 ms, Nakayama & Mackeben, 1989) have been demonstrated to be sufficient for multiple element displays.

4.2. Comparison of monkey and human data: differences in acuity

Whereas the influence of spatial attention turned out to be strikingly similar in monkeys and in humans, our measurements also revealed one major difference between the two species, namely a strong difference in absolute visual acuity. Specifically, the absolute visual acuity in rhesus monkeys was considerably smaller than in humans, more so in the central parts of the visual field as compared to more peripheral eccentricities. Poorer acuity thresholds in monkeys have been observed in earlier studies measuring visual acuity as defined by gap resolution (Cavonius & Robbins, 1973) with the difference in acuity thresholds between monkeys and humans accounting for up to 40%. Such differences, however, have not been seen in a study measuring grating acuity (Merigan & Katz, 1990). The reasons underlying this discrepancy—differences in acuity between species for gap resolution but similar thresholds for grating acuity—and the reasons for the observation that there are differences between species at all under some conditions

are unknown. One possible factor contributing to the differences in acuity between humans and monkeys is the smaller eye of the monkey (diameter of 19 mm [monkey] versus 24–25 mm [human] Polyak, 1953; Kiorpes et al., 1987). The reason is that the smaller eye of the monkey results in a retinal image size smaller by a factor of roughly 2 sampled by retinal cells whose densities are comparable in both species (Curcio & Kimberley, 1990; Østerberg, 1935; Perry & Cowey, 1985; Williams & Boothe, 1981). An alternative explanation of the differences in acuity between monkeys and humans is offered by the possibility that the psychophysical procedure used in the monkeys may have overestimated thresholds. Specifically, in order to reap rewards with a minimum of effort, the monkeys might have tried to keep the size of the "Cs" offered by the staircase procedure comfortably high by ignoring discriminanda with a size in the range of the true threshold. Such a strategy seems to be unlikely, though, because the rewarding regime chosen (see Section 2) emphasized maximal performance. Furthermore, if the monkeys had outwitted the staircase strategy, they should have done so independent of eccentricity. However, this was not the case, since differences in acuity thresholds between the two species clearly depended on eccentricity, being large in the central, but smaller in the more peripheral visual field. Of course, also the "optical" hypothesis is not able to account for the dependency of threshold differences on eccentricity, unless we assume that there are corresponding differences in retinal cone density between humans and monkeys. Since the literature available does not provide any support for this assumption (Curcio & Kimberley, 1990; Curcio, Sloan, Packer, Hendrikson, & Kalina, 1987; Østerberg, 1935; Perry & Cowey, 1985), we can only speculate that the dependency of the differences in acuity thresholds between the two species on eccentricity might reflect different dependencies of cortical magnification.

Irrespective of the differences in acuity and their specific reasons, however, the principal similarity of the attentional benefits in both species shows that the rhesus monkey visual system holds great promise for studies trying to reveal the neuronal mechanisms underlying covert shifts of attention in both, the monkey and the human brain.

4.3. Concluding remarks on the robustness of benefits in visual discrimination resulting from spatial cues in the absence of sensory noise

As indicated in Section 1, two experiments were performed in human subjects only, addressing the question why benefits in visual discrimination have not always been reported in literature for stimuli lacking significant sensory noise (e.g. Nazir, 1992; Shiu & Pashler, 1994, 1995). In order to come up with an answer to this question, Yeshurun and Carrasco (1999) suggested that perceptual benefits induced by spatial cueing (i) might possibly be cancelled by a spatial masking effect, the idea being that the cue might mask the ensuing target if presented in exactly the same location (Nazir, 1992) or, in addition, (ii) might be missed if spatial uncertainty were too low (Shiu & Pashler, 1994, 1995). In view of the results presented here, both explanations must be discarded. The reason is that robust effects were observed here, both, for the target presented at the same location of the cue and for conditions of low spatial uncertainty, i.e. for the target presented at one of only two possible locations. Moreover, the perceptual benefits induced by spatial cueing did not depend on the number of possible target locations (Experiment 5). The need for an alternative explanation becomes apparent also from the fact that the improvement in acuity thresholds induced by spatial cueing observed in the present study was quantitatively the same as the one reported by Yeshurun and Carrasco (1999, compare their Fig. 3) and Carrasco et al. (2002, compare their Fig. 3) adopting 16 possible target locations. From our point of view, two other factors may be crucial, instead in order not to miss attentional effects on visual discrimination in the absence of sensory noise, the first being target presentation time and the second being retinal position. Specifically, effects of spatial cueing turned out to diminish and finally disappear for longer target presentation times (Experiment 4) suggesting that the cue offers no further advantage if target presentation time is long enough to allow for both, orienting of attentional resources and sensory discrimination. In the light of comparatively short target presentation times but small retinal eccentricities (around 5°) applied in those studies missing attentional effects on visual discrimination (Nazir, 1992; Shiu & Pashler, 1994, 1995) we suggest that retinal eccentricity might be the more decisive variable, explaining the discrepancies between previous studies, the reason being the strong dependency of the absolute attentional effects on retinal eccentricity (see above). In summary, in order to elicit robust effects on visual discrimination by spatial cues such as aspired by future studies tackling the neuronal mechanisms underlying the control of spatial attention, a paradigm comprising short SOAs (∼200 ms) and target presentation times (∼150 ms), and retinal eccentricities larger than ∼9° seems most promising.

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