Attention changes perceived size of moving visual patterns

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Spatial attention shifts receptive fields in monkey extrastriate visual cortex toward the focus of attention (S. Ben Hamed, J. R. Duhamel, F. Bremmer, & W. Graf, 2002; C. E. Connor, J. L. Gallant, D. C. Preddie, & D. C. Van Essen, 1996; C. E. Connor, D. C. Preddie, J. L. Gallant, & D. C. Van Essen, 1997; T. Womelsdorf, K. Anton-Erxleben, F. Pieper, & S. Treue, 2006). This distortion in the retinotopic distribution of receptive fields might cause distortions in spatial perception such as an increase of the perceived size of attended stimuli. Here we test for such an effect in human subjects by measuring the point of subjective equality (PSE) for the perceived size of a neutral and an attended stimulus when drawing automatic attention to one of two spatial locations. We found a significant increase in perceived size of attended stimuli. Depending on the absolute stimulus size, this effect ranged from 4% to 12% and was more pronounced for smaller than for larger stimuli. In our experimental design, an attentional effect on task difficulty or a cue bias might influence the PSE measure. We performed control experiments and indeed found such effects, but they could only account for part of the observed results. Our findings demonstrate that the allocation of transient spatial attention onto a visual stimulus increases its perceived size and additionally biases subjects to select this stimulus for a perceptual judgment.

Keywords: attention, appearance, illusion, psychophysics, receptive field

Citation: Anton-Erxleben, K., Henrich, C., & Treue, S. (2007). Attention changes perceived size of moving visual patterns. *Journal of Vision, 7*(11):5, 1–9, http://journalofvision.org/7/11/5/, doi:10.1167/7.11.5.

Introduction

Attention alters appearance

Perception is not an objective representation of the sensory input, but rather results from an interaction of bottom-up sensory information with top-down influences. Attention is the central top-down mechanism for selecting relevant aspects of the visual scene for preferred processing. This deployment of spatial attention not only results in lowered thresholds, faster reaction times, better spatial resolution, and more accurate performance (for example, see Dobkins & Bosworth, 2001; Posner, 1980; Sperling & Dosher, 1986; Yeshurun & Carrasco, 1998), but also in an altered subjective perception of appearance: Attention has been found to increase apparent contrast (Carrasco, Ling, & Read, 2004), spatial frequency, gap size (Gobell & Carrasco, 2005), motion coherence (Liu, Fuller, & Carrasco, 2006), color saturation (Fuller & Carrasco, 2006), flicker rate (Montagna & Carrasco, 2006), and perceived speed (Turatto, Vescovi, & Valsecchi, 2007). Thus, attention not only enhances perception, it also distorts our representation of the visual scene according to the behavioral relevance of its components.

Perception of space

Striate cortex and many extrastriate cortical areas represent the spatial layout of our visual environment in a retinotopic map of spatially restricted receptive fields. The relative response strength of different neurons that represent different spatial locations enables the visual system to construct a representation of visual space. The extraction of spatial location from such a population activity requires a labeled-line principle; that is, the location of any neuron's receptive field needs to be known to the decoder.

Dynamic receptive fields and functional consequences

Receptive fields are not static, however, as has been demonstrated for several areas throughout the visual

doi: 10.1167/7.11.5 Received April 10, 2007; published August 23, 2007 ISSN 1534-7362 © ARVO

system. In the lateral intraparietal (LIP) area, receptive field size and position change in the context of a saccade (Kusunoki & Goldberg, 2003) and also as a function of behavioral state: Receptive fields measured during attentive fixation are more foveal, consistent with a shift of receptive fields toward the spatial focus of attention (Ben Hamed, Duhamel, Bremmer, & Graf, 2002). In extrastriate area V4, receptive field profiles are shifted toward an attended stimulus (Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997). This has also been documented recently for neurons in the medial temporal area (MT), which is part of the dorsal visual pathway and is essential for processing visual motion: Spatial attention attracts MT receptive fields toward the spatial focus of attention and thereby changes the spatial position most effective in stimulating a given neuron. The shift is most pronounced for receptive fields overlapping the spatial focus of attention and is reduced for receptive fields further away from the attentional focus (Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). This will concentrate neuronal resources in an attended spot for enhanced processing, but in addition receptive field shifts might influence those aspects of spatial perception that depend on an accurate decoding of receptive field locations, such as the sizes of objects or spatial relations between objects.

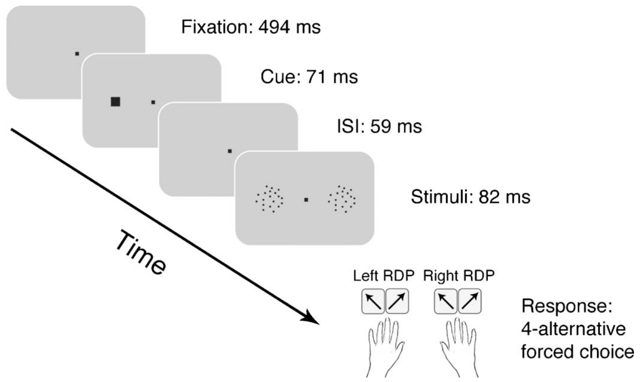

Figure 1. Task design. After a fixation period of 494 ms, a cue was flashed for 71 ms at 4° eccentricity left or right of the fixation point (peripheral cue) or exactly at the fixation point (neutral cue). Then followed a 59-ms interstimulus interval (ISI) and then test and standard RDPs were presented also at 4° eccentricity left or right of the fixation point for 82 ms. In all experiments, test diameter varied from 80% to 120% of the standard diameter in nine equidistant steps. In the main experiment, subjects were instructed to report the horizontal motion component (left or right) of the larger RDP by pressing one of four keys (4-alternative forced choice design).

Hypothesis

If the position label of a neuron is not updated when the receptive field center shifts, the position of a stimulus might be misperceived. Specifically, receptive fields centered outside the edges of an object would, when attracted toward the object's center, report the edge as lying within the receptive field, perceptually enlarging the object.

Adapting a design introduced by Carrasco et al. (2004) for showing attentional modulation of subjective appearance, we tested if drawing automatic attention to a stimulus increases its apparent size.

Methods

General design

The general design was adapted from Carrasco et al. (2004): While subjects had to maintain fixation, a cue was briefly (71 ms) presented either peripherally or at the fixation point to automatically attract attention to the respective location; then two differently sized moving random dot patterns (RDPs) were presented. They were centered left and right of the fixation point at the same eccentricity as the cue (Figure 1). Note that our hypothesis required this alignment of cue and stimulus, whereas in the study of Carrasco et al. the cue was slightly offset from the stimulus location. Subjects were instructed to report if the larger of the two patterns moved with a rightward or leftward tilt from vertical. The timing of cue and target was such that subjects' automatic attention was maximally allocated on the cued RDP at the time they had to perform the size judgment: This design enabled us to measure subjective appearance of the size of the attended and the unattended pattern without equally distributing attention across both of them. The short presentation times also prevent eye movements as the interval between cue onset and stimulus offset is shorter than typical saccadic latency (Bichot, Thompson, Rao, & Schall, 2001; Mayfrank, Kimmig, & Fischer, 1987).

We used moving stimuli in our experiments because receptive field changes with attention have been investigated in area MT in the motion processing system (Womelsdorf et al. 2006). Given that receptive field shifts have also been shown in other cortical areas (Ben Hamed et al., 2002; Connor et al., 1996, 1997), our hypothesis of an increase in perceived size can also be applied to stationary stimuli.

Experimental setup and procedure

Experiments were performed in a dimly lit experimental cabin. Subjects used a chin rest positioned 57 cm from a CRT monitor on which the stimuli were presented (LaCie electron22blue IV 22-in. CRT) with a viewable area of 40° × 30°, a resolution of 40 pixels/deg, and a refresh rate of 85 Hz. Stimuli were presented on a gray background (34.2 cd/m^2). All stimuli were black (0.1 cd/m^2). Stimulus presentation and recording of the subjects' responses were controlled by a custom software developed in-house, which was run on an Apple Macintosh computer.

Subjects initiated each trial by pressing the space bar on a computer keyboard. Thirteen subjects (six male, seven female) participated in all experiments. All were students between 19 and 26 years, all were naive to the purpose of the experiments and had normal or corrected-to-normal vision. Within one experimental session, subjects first performed 500 trials of a tuning measurement to adjust the difficulty of the task and then one of six different size experiments (1000 trials each) described below. All six experiments were performed by each subject in six sessions in randomized order.

Tuning experiment

Because the allocation of attention is known to vary with task difficulty (Spitzer & Richmond, 1991; Urbach & Spitzer, 1995), we compensated for interindividual performance differences in the direction discrimination task as well as difficulty differences due to the different experimental settings, for example, standard size, or training effects during the course of the whole series of experiments. To ensure that the size perception experiments were performed under comparable conditions, we varied the deviation of motion direction from the vertical. The directions used in each experiment were adjusted for each subject by preceding each experimental run with a "tuning" measurement. Subjects were asked to maintain fixation on the fixation point, a small black square (0.2° × 0.2°). Immediately after the start of the trial, a black arrow (0.4° long and 0.1° wide) pointing either to the left or to the right was presented 0.5° to the left or to the right of the fixation point for 306 ms. Directly after arrow offset, two black RDPs with the same parameters as the standard stimulus of the following experiment were presented left and right of the fixation point. Both were either moving upward or downward with a leftward or rightward deviation ranging from 3° to 15° from vertical in five equidistant steps (with an exception: for the experiment with the largest standard size we used steps of 1°, 2°, 3°, 6°, 9°, and 12° in the tuning measurement). Subjects were instructed to report the sidewise direction component (left or right) of the stimulus indicated by the arrow. For the following experiment, we chose the deviation from vertical for which the subject reached a performance of 75% correct.

Main experiment: task and stimuli

In the main experiment, each trial began with the presentation of the fixation point for 494 ms. Then the cue, a black square (0.25° × 0.25°), was flashed for 71 ms either at 4° to the left or to the right of the fixation point (peripheral cue) or on top of the fixation point (neutral cue). After an interstimulus interval (ISI) of 59 ms, two circular RDPs were shown for 82 ms, centered 4° left and right of the fixation point. Both RDPs moved upward or downward with a leftward or rightward deviation from vertical. The RDP on one side was always the standard stimulus with a size of 2° diameter, whereas the size of the other RDP (the test stimulus) varied from 80% to 120% of the standard diameter (1.6–2.4°) in nine equidistant steps. The positions of the cue, the test, and the standard stimulus as well as the motion direction of both stimuli (up or down with leftward or rightward tilt) were randomized. To determine the effect of absolute stimulus size, we also ran this experiment with standard stimuli of 1° and 4° diameter.

Control experiments

Several control experiments were conducted to investigate potential cue biases. In the first control experiment, the cue appeared after the stimuli (postcue), with the same cue and stimulus presentation durations and the same ISI, an approach also used by Gobell and Carrasco (2005). In the second control experiment, the same settings as in the main experiment were used but subjects were instructed to report the direction of motion of the smaller of the two RDPs (reversed instructions experiment; also used by Carrasco et al., 2004; Fuller & Carrasco, 2006; Montagna & Carrasco, 2006; Turatto et al., 2007). In the third control experiment, subjects were asked to report only which of the stimuli appeared smaller without performing the motion discrimination task (single task experiment, also used by Carrasco et al., 2004).

Data analysis

For each experiment, we determined the proportion of standard cued, test cued, and neutral cue trials in which subjects chose the test stimulus as the larger stimulus as a function of the test size (normalized to the respective standard size). These values were fitted with a psychometric function by an iterative likelihood maximization procedure, and the point of subjective equality (PSE), where subjects chose test and standard equally often, was determined for each cue condition and each experiment. To estimate the goodness of the fits, a bootstrapping was performed (Wichmann & Hill, 2001): 10,000 runs with 1,000 trials each were simulated for each experimental condition and subject, using the fitted psychometric functions as the basis for the simulated data. For only 1 of the 234 (13 subjects × 6 experiments × 3 conditions) measured psychometric functions, a statistically significant difference between simulated and measured data was found (alpha adjusted for multiple comparisons: .00022; overall significance level: .05), and we therefore did not exclude data on this basis. Two subjects were excluded because they did not reach a size discrimination performance of 84% in the main experiment. The PSE values of the remaining 11 subjects were compared with a repeated measures ANOVA using SPSS software (SPSS Inc., IL): Effects of the different standard sizes were compared with a 3 × 3 repeated measures ANOVA with the factors cue location and standard size, effects of the order of cue and stimulus presentation were compared with a 3 × 2 repeated measures ANOVA with the factors cue location and cue presentation time, and effects of the instruction (report direction of larger RDP, report direction of smaller RDP, only report smaller RDP) were compared with a 3 × 3 repeated measures ANOVA with the factors cue location and instruction. To analyze if the direction task difficulty was affected by the cue or the experimental condition, we compared direction discrimination performance for trials in which the cued stimulus was evaluated with trials in which there was a neutral cue and with trials in which the uncued stimulus was chosen, regardless if the chosen stimulus was test or standard with a 5 × 3 repeated measures ANOVA (experiment × cued/neutral/uncued chosen).

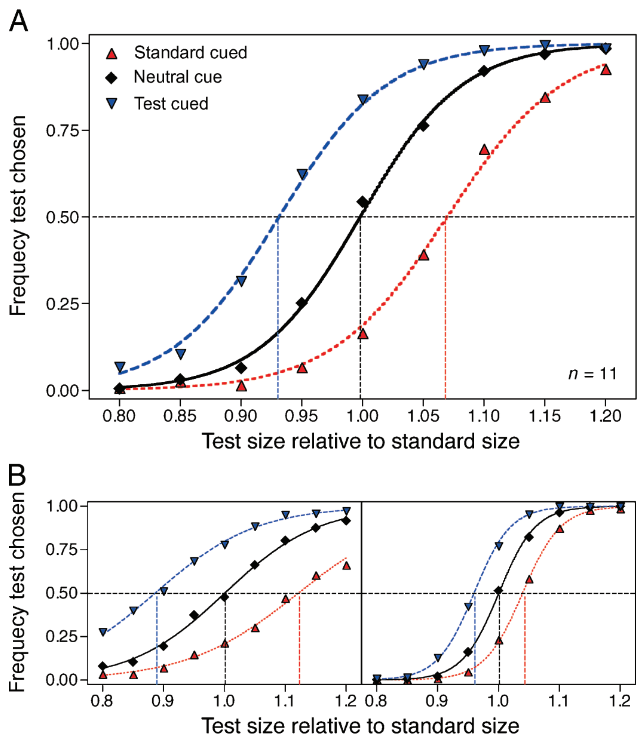

Figure 2. (A) Average results of the main experiment. For test cued, neutral, and standard cued trials, the percentage of trials is plotted in which the test stimulus was chosen as bigger than the standard stimulus of 2° diameter as a function of test size. Data are averaged across 11 subjects and then fitted with a psychometric function using iterative likelihood maximization. (B) Average results of the same experiment using a standard size of 1° diameter (left) and 4° diameter (right).

Results

In each experiment, we determined the PSE, that is, the test stimulus size which appears equal to the standard stimulus size, under different attentional conditions: standard stimulus cued, test stimulus cued, and neutral cue.

Effects of attention on perceived size

In Figure 2A, for each cue condition (standard stimulus cued, test stimulus cued, and neutral cue), the average proportion of trials in which subjects chose the test stimulus as larger than the standard stimulus is plotted as a function of test size relative to standard size. Data points were fitted with a psychometric function. The PSE corresponds to the x value where the psychometric function crosses 50%. In the neutral cue condition, this is a relative test size of almost exactly 1; that is, as expected in this condition the PSE and the point of physical equality (PPE) are equal. When the test stimulus is cued, the PSE is shifted to the left, indicating that a test stimulus which is 7% [±2% standard deviation (*SD*)] smaller than the standard stimulus is perceived to be of equal size as the standard. When the standard stimulus is cued, the PSE is shifted 7% (±2% *SD*) to the right, indicating that in this condition a test stimulus which is 7% (±2% *SD*) larger than the standard stimulus is perceived to be of equal size as the standard. This pattern of results is present in all subjects.

Effects of stimulus size

The physiological data on receptive field shifts in area MT show an inverse relationship of the shift magnitude and the distance between attentional focus and original receptive field center (Womelsdorf et al., 2006). Assuming that the cue draws attention to the stimulus center, the distance of the attentional focus to the “critical” receptive fields overlapping the border of the stimulus depends on the stimulus size. The larger the stimulus, the less the critical receptive fields should shift and thus the smaller the effect of attention on size perception should be. In line with this argument, we performed the same experiment with two additional standard sizes. Figure 2B shows the results from the experiments with 1° standard diameter and

4° standard diameter. In both experiments, the test cued curve is shifted to the left while the standard cued curve is shifted to the right, in line with the hypothesis that the allocation of attention onto the cued stimulus makes it appear larger. Consistent with the physiological data, this effect is negatively correlated with stimulus size: The average shift is 4% between neutral and cued trials for the larger standard size of 4° (1% *SD*), 7% for the medium standard size of 2°, and 12% for the smaller standard size of 1° (6% *SD*). The shift magnitudes were compared for the three different standard sizes using a 3 × 3 repeated measures ANOVA. The main effect of cue location on the PSE but not on the slope of the psychometric function (which represents the size discrimination threshold) is significant. Although there is no main effect of standard size on PSE, there is a significant interaction between standard size and cue location; that is, the difference in the magnitude of the PSE shift between the different standard sizes is significant. There is a main effect of standard size on the slope of the psychometric function, indicating that the size comparison is harder for smaller stimulus sizes. The interaction between cue location and standard size is not significant for the slope.

Postcue control experiment

The shifts of the PSE found in the main experiment are consistent with an increase of perceived size of the attended stimulus but could also result from a simple bias to select the cued over the uncued stimulus. To test for such a cue bias, we performed the postcue control experiment in which the order of cue and stimulus presentation was reversed: With the cue presented after the stimuli, a cue bias effect should remain while any attentional effect on the stimulus should disappear (see Gobell & Carrasco, 2005). Figure 3 shows the average results of the postcue control experiment. As in the main experiment, the neutral cue condition yields a psychometric function with a PSE near 1, but the psychometric curves in the test cued and standard cued conditions are

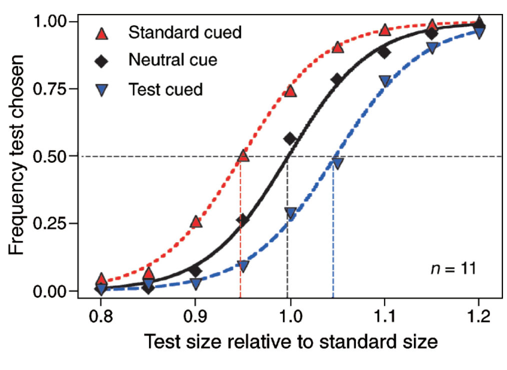

Figure 3. Average results with the cue presented after the RDPs.

shifted in the opposite direction. The average shift of the PSE is 5% (±2% *SD*). This means that while in the main experiment the cued stimulus is preferentially chosen as larger, in the postcue experiment the cued stimulus is chosen less frequently than the uncued stimulus. The 3 × 2 repeated measures ANOVA comparing the main experiment with the postcue control experiment yields a significant main effect of cue location on the PSE but not on the slope and no main effect of cue presentation time on PSE or slope. The interaction between cue location and cue presentation time is significant for the PSE but not for the slope. Altogether, this indicates a shift of comparable magnitude but in opposite directions in the postcue and main experiments.

Effects of instruction

Although the results in the main experiment are not likely caused by a simple cue bias, we have not yet excluded a more complex kind of cue bias in which the cue has some influence on the stimulus that biases subjects to select it without increasing its apparent size. Therefore, we performed the reversed instructions control experiment, in which subjects had to evaluate the smaller stimulus: Here, an increase in perceived size would be reflected in a tendency to choose the cued stimulus less often than the uncued stimulus (see Carrasco et al., 2004; Fuller & Carrasco, 2006; Montagna & Carrasco, 2006; Turatto et al., 2007). Because an increase in perceived size and any cue bias would compensate each other in this design, the effect of attention might be underestimated or even occluded. A difference in the absolute size of the PSE shift between the main experiment and the reversed instructions experiment would indicate the presence of a bias effect.

We aimed at measuring the pure attentional effect in the single task control experiment, in which subjects had to indicate the smaller stimulus without reporting its motion direction. In this control experiment, there is no second task and therefore no cue bias related to it (see Carrasco et al., 2004). Therefore, although the magnitude of attentional modulation might be underestimated if subjects distribute their attention between the two stimuli, any effect that is observed reflects a pure attentional influence, providing a lower bound for the attentional effect magnitude. Figure 4 shows the average results of the reversed instructions control experiment and the single task control experiment. Because the *Y*-axis now plots the proportion of trials in which the test stimulus was chosen as smaller, the psychometric curves have an inverted shape. In both experiments, the PSE of the neutral cue condition matches the PPE and the test cued curve is shifted to the left while the standard cued curve is shifted to the right. This is consistent with the hypothesis that the cued stimulus is perceptually enlarged by attention and not consistent with a bias to select the cued stimulus more

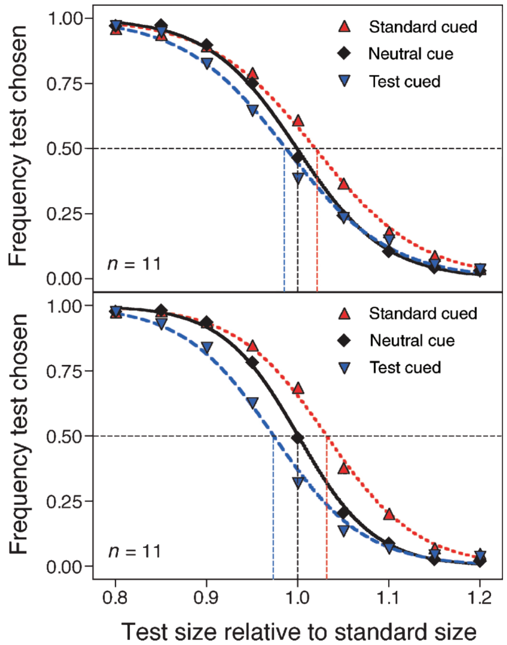

Figure 4. Average results of the reverse instructions and single task control experiments. Subjects were instructed to report the motion direction of the smaller stimulus (top) or to choose the smaller stimulus directly (bottom).

frequently. In comparison to the main experiment, average shift magnitudes are smaller in both control experiments (2% ± 3% *SD* when the motion direction of the smaller stimulus had to be reported, 3% ± 2% *SD* when the smaller stimulus had to be chosen directly without an evaluation of its motion direction). Two of the 11 subjects show a shift in the opposite direction when they had to report the motion direction of the smaller stimulus and no shift when the motion direction was not reported; the data from all other subjects qualitatively correspond to the average data. The main experiment and the two control experiments in which subjects had to choose the smaller stimulus were compared with a 3 × 3 repeated measures ANOVA. Again there is a main effect of cue location on PSE and size discrimination threshold (i.e., the absolute slopes of the psychometric function), and there is no main effect of instruction on PSE but on the slope. The interaction between cue location and instruction is significant for the PSE but not for the slope: The change in size perception is less when subjects choose the smaller instead of the larger stimulus.

Direction discrimination performance

To test for a facilitatory effect of attention in the second task, we compared the direction discrimination performance when subjects had chosen the cued or the uncued stimulus or when none of the stimuli were cued, disregarding if the choice of the larger or the smaller stimulus was correct or if test or standard stimulus was chosen. The 5 × 3 repeated measures ANOVA (5 experiments × cued chosen/neutral/uncued chosen) shows a main effect of the chosen stimulus. Pairwise comparisons of the estimated marginal means reveal that subjects were better at evaluating the direction of motion when they evaluated the cued stimulus or when there was a neutral cue than when they evaluated the uncued stimulus (Figure 5, $p = .037$ and $p = .006$, respectively), although there is no performance difference between the "cued chosen" and the neutral trials. The performance in the direction discrimination task averaged over all cue conditions and all experiments is 75% (±11% *SD*), indicating that subjects followed the instruction and paid attention to the direction task.

Discussion

In the main experiment, subjects reported the motion direction of the larger of two stimuli (test and standard), using a standard size of 2° diameter. Attention on the test stimulus makes a smaller test stimulus appear equal to the standard stimulus, whereas attention on the standard stimulus makes a larger test stimulus appear equal to the standard stimulus. We found the same results with a standard size of 1° and 4° diameter, although the magnitude of the effect inversely varies with the size of

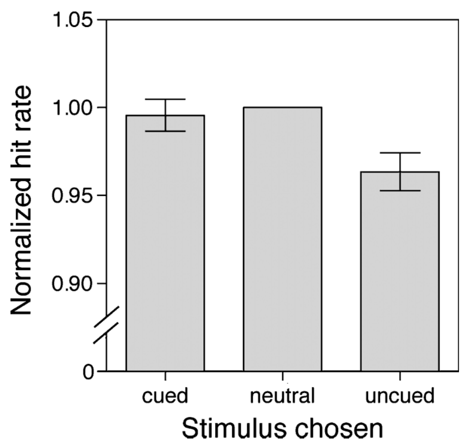

Figure 5. Direction discrimination performance. Average performance in the direction task independent of the size comparison task for trials in which the cued stimulus was evaluated, for neutral cue trials and for trials in which the uncued stimulus was evaluated. Hit rates were normalized to the neutral trial hit rate for each subject and then averaged. Error bars indicate the standard error of the mean.

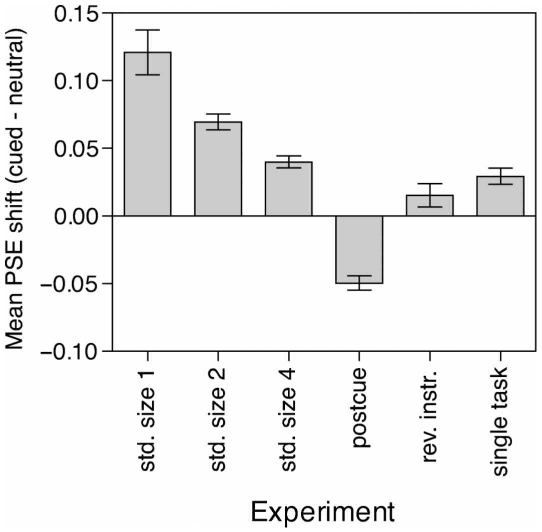

Figure 6. Overview of effect sizes. Shifts of the point of subjective equality (PSE) in cued trials relative to neutral trials were computed for each subject and then averaged across the 11 subjects. Error bars indicate the standard error of the mean.

the standard stimulus. Figure 6 summarizes the effect sizes for all experiments.

These PSE shifts show that subjects selected the cued stimulus more often than the uncued stimulus. This is in agreement with the hypothesis that the allocation of automatic attention to a stimulus increases its apparent size. Alternatively, a simple cue bias might lead subjects to respond to the cued stimulus preferentially. This kind of cue bias should persist when the cue is presented after the stimulus, whereas any attentional effect on stimulus selection should disappear. In the postcue experiment, there was no bias to choose the cued stimulus more often, supporting the interpretation of the PSE shifts as an attentional effect (Figure 6, postcue). Instead, the cued stimulus was chosen less frequently than the uncued stimulus. This might be explained with a masking effect: The postcue might mask the cued stimulus so that subjects tended to select the uncued stimulus simply because they were able to judge its motion direction more easily.

In the reverse instruction experiment, we tested whether attention has some other effect on the cued stimulus which causes a bias toward selecting it. Asking for the smaller instead of the larger stimulus allows to distinguish an effect on apparent size from a cue bias: A cue bias would still make subjects select the cued stimulus more often, whereas an attentional increase in perceived size of the cued stimulus would lead subjects to select it less often than the uncued stimulus. The observed PSE shift is consistent with an increase in perceived size by attention, although the effect is smaller than in the main experiment (Figure 6, reversed instructions). As indicated above, it is possible that two effects, a small cue bias and a large change in apparent size, partially compensate each other when subjects have to report the direction of the smaller RDP. The cue bias might result from a strategy of reporting the motion direction of the pattern which was easier to see: Attention might have a facilitatory effect and make direction discrimination easier for the cued pattern and so bias subjects to select it more often. In the main experiment, this "easiness" effect and an attentional increase in perceived size would add up, whereas in the reversed instructions experiment they act in opposite directions. The direction discrimination performance analysis shows that subjects are indeed better when they evaluate the cued than when they evaluate the uncued stimulus.

An effect of attentional facilitation of the direction discrimination is not expected in the single task experiment when subjects are asked to report the smaller stimulus without evaluating its direction of motion. Therefore, this experiment should measure the pure attentional modulation of perceived size, although the single task design likely underestimates the magnitude of attentional modulation: Because the single task asks for a direct comparison between the two stimuli, attention might be allocated more evenly between them. Consistent with this interpretation, we found a significant increase in perceived size that is intermediate between the effect observed in the main experiment and that in the reversed instruction experiment (Figure 6, single task).

Although we interpret our observations as a change in the perception of the stimulus, it should be noted that two studies have proposed alternative interpretations (Schneider, 2006, but see Ling & Carrasco, in press; Turatto et al., 2007).

In several previous studies of attentional modulation of appearance, the effect was reduced when instructions were reversed meaning that subjects had to report on the stimulus containing the lesser quantity of a certain feature, for example, the stimulus of lower contrast, spatial frequency, saturation, and flicker (Carrasco et al., 2004; Fuller & Carrasco, 2006; Gobell & Carrasco, 2005; Montagna & Carrasco, 2006; but for an exception, see Turatto et al., 2007). Subjects stated that it feels "more natural" for them to report the more of something than the less of something (Carrasco, personal communication). Thus, an inherent asymmetry favoring the selection of the stimulus containing the higher quantity of a certain feature might explain the smaller effect size with reversed instructions. This asymmetry might be an attentional asymmetry due to an automatic capture of attention by the stimulus of higher saliency.

Our study shows that when attention is drawn transiently to one of two stimuli, attention makes this stimulus appear larger. The magnitude of this effect correlates inversely with stimulus size. This is consistent with physiological data: Receptive field shift magnitudes in area MT vary inversely with the distance of the original receptive field center from the spatial focus of attention (Womelsdorf et al., 2006). If receptive field shifts are the physiological basis of attentional modulation of perceived size, the critical receptive fields for this effect would be those that overlap the stimulus borders. So the larger the stimulus, the larger is the distance between stimulus border and attentional focus, the smaller is the receptive field shift, and consequently the perceptual enlargement of the attended stimulus. Assuming that receptive field shifts are also a correlate of attentional facilitation of visual processing, this observation supports models of attention that assume a decay of attentional facilitation around the spatial focus of attention (Eriksen & St. James, 1986). It is important to note though that this does not necessarily contradict models of attention that postulate a suppressive annulus around the facilitatory center of the attentional focus (Cutzu & Tsotsos, 2003; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005) in which the facilitatory effects of attention are reversed because the spatial extent of the facilitatory attentional focus and such a suppressive surround, given the particular settings employed in this experiment, is not tested. Because receptive field shifts with attention have not only been found in area MT but also in other cortical areas, the effect on perceived size reported here should not be restricted to moving stimuli.

Gobell and Carrasco (2005) have demonstrated that attention also modulates perceived spatial frequency and gap size in a Landolt stimulus. The shrinkage of receptive fields observed physiologically (Womelsdorf et al., 2006) could account for a shift of spatial frequency preferences to higher frequencies.

Gap size estimation depends on the precise localization of the end of the line segments forming the gap. If attention was drawn to the center of the Landolt stimulus, the gap should appear larger just like the overall stimulus. In Gobell and Carrasco's (2005) experiment, however, the cue was always on one side of the Landolt square, whereas the gap was either at the top or at the bottom. Therefore, although both line ends will be perceptually pushed away from the focus of attention, the magnitude could vary because their distance from the focus of attention differs, potentially creating an effect on perceived gap size.

Receptive field shifts might provide the physiological basis of the observed change in perceived stimulus size. By now a number of reports on the attentional modulation of the appearance of various stimulus parameters have been published though, which are not likely linked to spatial distortions of visual processing. Of all stimulus features so far tested, color (hue) seems to be the only one that is not perceived differently when attended. Hue is different from the other tested stimulus features: Although parameters like size, contrast, saturation, or motion coherence are varied quantitatively (prothetic scale), the variation of hue results in qualitatively different perceptual experiences (metathetic scale; see Fuller & Carrasco, 2006; Stevens & Galanter, 1957). From a functional perspective, attentional modulation of quantitative features like contrast or saturation could be beneficial because increasing those features could enhance discrimination of secondary features (it is easier to see the orientation of a high contrast pattern than that of a low contrast pattern), but there is no reason to assume that the variation of a qualitative feature would increase signal strength in the same way (judging the orientation of a purple stimulus should not be easier than judging the orientation of a blue stimulus). Following this line of thought, attentional modulation of appearance might not only be a side product of other attentional effects but might itself be functional for enhanced processing. The modulation of the appearance of many different quantitative but not qualitative features suggests that attention acts on a general level: Instead of modulating the appearance of several specific stimulus features via different unrelated physiological mechanisms, attention might generally increase the saliency of an attended stimulus and this enhanced saliency might then manifest itself in several distinct perceptual illusions.

Conclusions

In summary, we show that transient spatial attention increases the apparent size of moving visual stimuli. The increase in perceived size varies inversely with stimulus size, which is consistent with receptive field shift data (Womelsdorf et al., 2006). In addition, attention biases subjects to select the attended stimulus for perceptual judgment, possibly by decreasing the difficulty of the second task.

Acknowledgments

We thank Dr. Tzvetomir Tzvetanov for help with data analysis, Ralf Brockhausen for technical assistance, and Sabine Stuber for administrative assistance.

This work was supported by the International Max Planck Research School for Neurosciences, Goettingen, and the German Ministry for Education and Science Grant BMBF 01GQ0433 to the Bernstein Center for Computational Neuroscience, Goettingen.

Commercial relationships: none.
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