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Selective visual attention ensures constancy of sensory representations: Testing the influence of perceptual load and spatial competition

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Abstract

We report findings from several variants of a psychophysical experiment using an acceleration detection task in which we tested predictions derived from recent neurophysiological data obtained from monkey area MT. The task was designed as a Posner paradigm and required subjects to detect the speed-up of a moving bar, cued with 75% validity. Displays varied according to number of simultaneously presented objects, spatial distance, and difficulty of the task. All data obtained under different levels of competition with multiple objects were compared to a corresponding condition, in which only a single moving bar was presented in the absence of any interfering distracter object. For attended objects, subjects did not show any difference in their ability to detect accelerations, regardless of the strength of inter-object competition or spatial distance. This finding was consistent in all of the experiments, and was even obtained when the acceleration was made hardly detectable. In contrast, increasing competitive interactions either by enhancing number of objects or spatial proximity resulted in strong reduction of performance for non-attended objects. The findings support current noise reduction models and suggest that attention adjusts neuronal processing to ensure a constant sensory representation of the attended object as if this object was the only one in the scene.

Keywords: Human; Psychophysics; Motion; Velocity; Noise reduction; Attentional load; Acceleration

1. Introduction

Several recent neurophysiological studies have shown that directing attention to a stimulus over the receptive field (RF) of a cortical visual neuron is usually accompanied by an attention-dependent increase of the firing rate. That is, the neuron fires more spikes in response to the attended object than to the non-attended object. Recently, it was shown that such firing rate increases can also be observed when comparing neuronal responses to an attended target with purely sensory responses to a neutral, i.e., behaviorally irrelevant stimulus (Treue & Martínez Trujillo, 1999), or when comparing baseline activity at the spatial position of an upcoming target with baseline activity at an uncued location (Luck, Chelazzi, Hillyard, & Desimone, 1997; Reynolds, Chelazzi, & Desimone, 1999). These firing rate modulations are thought to allow for a more efficient activation of post-synaptic targets and may reflect neuronal mechanisms enhancing perceptual discrimination of an attended object (e.g., Cameron, Tai, & Carrasco, 2002; Carrasco, Williams, & Yeshurun, 2002). Another possible prediction regarding the perceptual consequences may be derived if attention-dependent changes of neuronal stimulus selectivity are analyzed instead of absolute firing rate. A recent study on the influence of sustained attention on direction selectivity of neurons in macaque area MT (Wegener, Freiwald, & Kreiter, 2004) suggests that attention may adjust neuronal

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activity in order to ensure a constant, undisturbed sensory representation of the attended content, rather than enhancing its neuronal representation. In that study, monkeys were trained on a task requiring them to selectively attend a precued moving target in the presence of a motion distracter and to detect a slight acceleration of the target's velocity while always ignoring distracter accelerations. Analysis of the firing pattern prior to acceleration showed that neurons suffer from reduced direction selectivity when responding to the non-attended distracter, but keep high and constant selectivity when responding to an attended target. In particular, the results showed almost equal levels of direction selectivity when comparing a neutral fixation condition (with no attention paid to the stimulus) with two attended conditions employing different inter-stimulus competition, despite remarkable rate changes. Direction selectivity for non-attended stimuli, however, was progressively impaired with enhanced inter-stimulus competition. Well in line with recent psychophysical work (Baldassi & Burr, 2000; Dosher & Lu, 2000; Lu & Dosher, 2004; Shiu & Pashler, 1994, 1995), these data support the view that attention ensures the optimal sensory representation of the attended content by reducing noise from unattended channels.

Given the close relation between activity patterns in area MT and perceptual judgments (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Salzman, Britten, & Newsome, 1990) these findings suggest the following predictions for the detectability of slight velocity changes under different conditions of attention. First, if attention ensures a constant neuronal representation of the attended content, then detectability of the acceleration of an attended bar will not be influenced by increasing competitive interactions with other objects. Second, because increasing inter-stimulus competition results in stronger degradation of neuronal stimulus selectivity for non-attended objects, perceptual performance on non-attended objects will decrease likewise. Third, if attentional mechanisms serve to adjust a constant, optimal representation of the same target under different conditions of stimulus competition, perceptual performance should be independent of stimulus competition not only for well visible, but also for hardly perceivable accelerations. We tested these predictions in psychophysical experiments very similar to those used in our former neurophysiological study. The results show a remarkable correspondence between the influence of attention on neuronal stimulus selectivity and perceptual judgments, indicating that noise reduction is a key feature of selective attention allowing for a constant representation of the attended content.

2. Materials and methods

2.1. Subjects

Twelve subjects (all female, mean age 23.5, range 20–36 years) took part in the study. All participants had normal or corrected to normal vision as confirmed by means of the *Freiburg Visual Acuity and Contrast Test* (Bach, 1996). Each of the three experiments described below was conducted with five subjects. Thus, some participants took part in more than one experiment. All subjects volunteered for the study and gave their written informed consent. The study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki) and was approved by the local authorities.

2.2. Visual stimulation

Subjects sat 45 cm in front of a 22 in. monitor (NEC MultiSync FE2111SB, NEC Display Solutions, Munich, Germany) with the head stabilized by a head-chin rest (NovaVision AG, Magdeburg, Germany). Stimuli consisted of high-contrast, moving bars with a size of 1.9° by 0.4°, generated on a Pentium computer with a Nvidia Quadro NVS graphics card, and displayed on a dark background at 100 Hz refresh rate. Eye movements were measured using a custom-made remote videooculography system, based on a CCIR Monochrome Camera (DMK 83 Micro/C, The Imaging Source, Bremen, Germany) and self-written software.

2.3. Tasks

The tasks were designed to be as close as possible to the behavioral paradigm used in the corresponding neurophysiological study (Wegener et al., 2004) to allow for optimal comparability of results. We carried out three experiments to test the influence of attention on velocity perception under different levels of attentional load. The first experiment was conducted under circumstances of low spatial competition with one distracter only. In Experiment 2, we increased competitive interactions by decreasing the distance between the objects, and in Experiment 3 by adding two additional distracters to the display. In Experiments 1 and 3, objects were presented at 10.5° eccentricity. In Experiment 2, the second object was separated from the first by 6.5° with the center of its trajectory at 11.2°. Prior to all experiments, participants were familiarized with the task within up to 100 trials. The experimental design is illustrated in Fig. 1. The subject's task was to report an increase in velocity in any of the bars simultaneously present. The number of bars was either two or four. Which of the bars present on the display would undergo the acceleration was indicated by a spatial cue that appeared at the subsequent target's position in the beginning of a trial. The cue had a validity of 75%. Each trial started with the appearance of a fixation spot at the center of the screen (T_{sf}). Subjects started fixation and pressed a button to initiate the following stimulus sequence. The sequence started with the appearance of the cue shown for 500 ms (T_c), followed by a delay of 500 ms (T_d) and the subsequent appearance of the first bar. The second bar in Experiments 1 and 2 appeared with an onset asynchrony of 200 ms (T_{amo}). In Experiment 3 the three other bars appeared one after the other, each bar delayed by 100 ms relative to the former one. Following onset, bars moved back and forth along a trajectory of 3.8° length and with constant velocity of 2.5°/s. During the whole stimulation period subjects had to keep fixation within a $2° \times 2°$ fixation window. After a random time interval of 100–2700 ms (T_{acc}) length one of the bars underwent acceleration. Subjects were instructed to signal perception of this speed-up by releasing the button as fast as possible, and to minimize errors for correctly cued objects. With the latter instruction, we aimed to ensure that subjects preferentially attended the cued location instead of shifting attention between all possible locations. For all experiments, we tested seven different values of acceleration, each in a separate session. In the most salient condition the bar increased velocity by 85%, and in the most difficult condition by 25%. We started with the easiest condition and then increased difficulty by reducing acceleration strength by 10% each session. In case that performance reached very low levels already in the 35% speed-up session, we abstained from requiring subjects to participate in the 25% speed-up session. To allow for comparison of the behavioral data with a distracter-free condition we additionally estimated performance in a 1-bar condition. Here, target position of the forthcoming trial was cued prior to bar onset with 100% validity. Targets were placed at all possible target locations of the corresponding attention conditions. Thus, each session consisted of

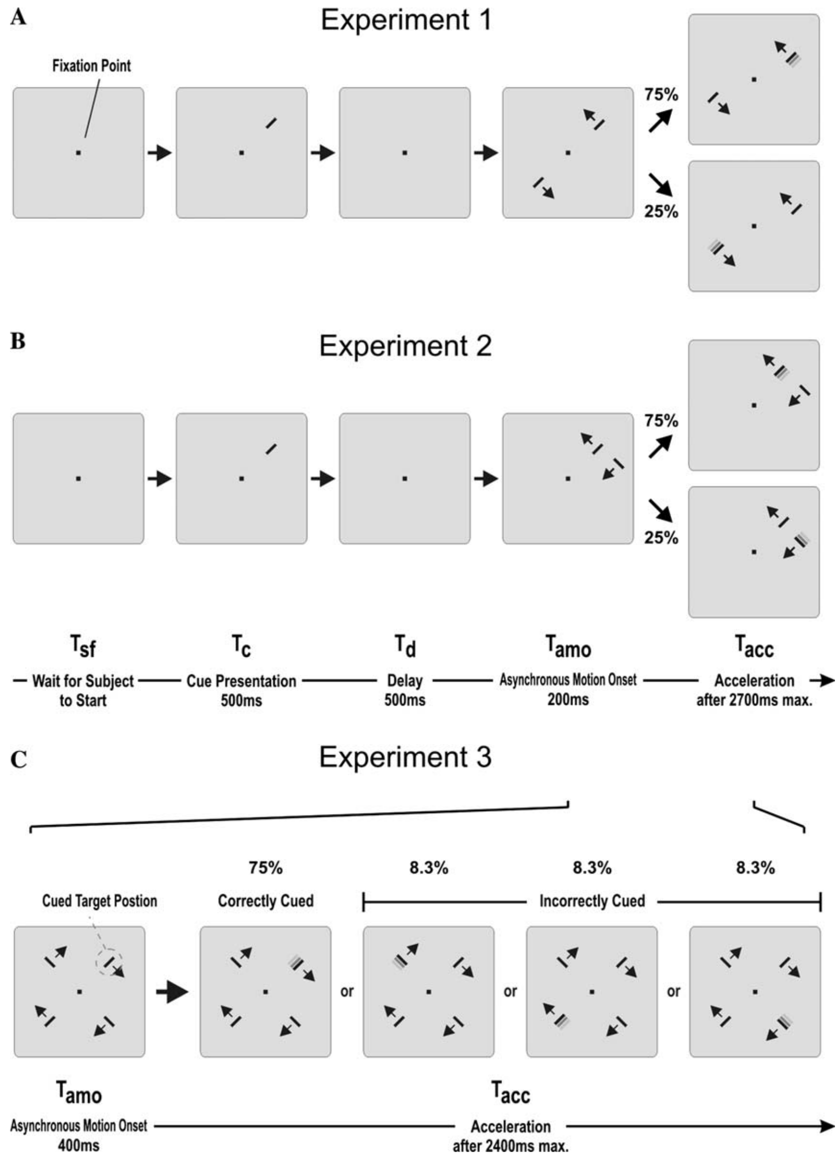

Fig. 1. Stimulus sequence and spatial arrangement of experiments. All experiments followed the same principal temporal pattern, but differed in terms of spatial separation, relative motion directions and number of objects. Each trial started with the appearance of a fixation point (T_{sf}) at the center of the screen. If subjects started fixation and pressed a button, the trial continued with a 500ms presentation of a spatial cue (T_c). The cue indicated the position of the upcoming target with a validity of 75%. Targets could appear in each of the four quadrants and on both motion trajectories of Experiment 2. After a delay of 500 ms (T_d), depending on the experiment, two or four bars appeared asynchronously (T_{amo}) and started to move immediately. The task of the subjects was to indicate a small acceleration of one of the bars occurring at a random point in time during the subsequent period (T_{acc}) by releasing the button. Responses had to occur within a response window specified for each subject prior to the experiments in a separate 1-bar condition. (A) Spatial arrangement of the bars in Experiment 1. Two bars were presented in opposite hemifields. The bars were mirrored across the fixation point and moved in counterphase. (B) In Experiment 2, the position of the first bar was identical to Experiment 1, but the second bar was placed in the same quadrant near the first one, and moved in orthogonal direction. (C) In Experiment 3, the display consisted of four bars, each in one of the quadrants. Positions of the bars were identical to the possible positions within Experiment 1.

two measurements: a 1-bar condition, in which targets were tested for one particular acceleration value, and the corresponding multiple-bar conditions that were tested in a separate block following directly afterwards. We never carried out more than one session the day.

Behavioral data were obtained by estimating the number of correct responses to the velocity change of the moving bar. Responses had to be given within a predefined response window (RW). This approach was chosen to urge subjects to detect an increase in bar velocity rather than a difference in the absolute speed of multiple objects simultaneously present. The length of RW was estimated for each subject separately because inter-individual reaction times (RT) are known to show substantial variations in such kind of tasks (Brebner, 1980; Welford, 1977, 1980). To calculate RW, a 1-bar condition with an acceleration value of 55% and a fixed response window of 550 ms length had been conducted prior to the three main experiments. Subjects had to perform this experiment with at least 75% performance; otherwise they first received another training session. For each subject, the maximally allowed response time for all subsequent experiments was then calculated as mean RT plus one standard deviation. The minimally required response time was set to 100 ms in order to exclude responses that are too fast to be caused by the acceleration (Fig. 2). The chance level for a correct response was calculated as the probability that a response at a random point in time falls into RW. For this, we took the sum of the maximal stimulation length T_{acc}, the minimally required response time, and the length of RW and divided by RW. Due

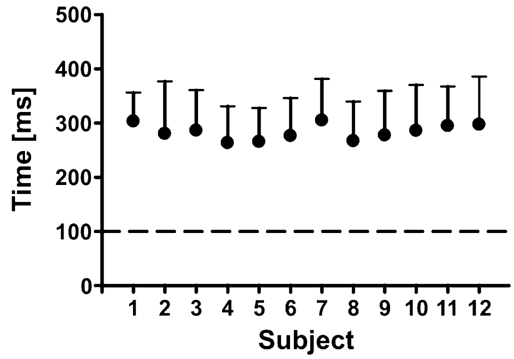

Fig. 2. Response window (RW). Mean RT for a 55% acceleration of a single moving bar were estimated for each subject prior to the experiments. The length of RW for all subsequent experiments was then calculated as the sum of the average RT and one standard deviation. The first 100 ms of the resulting interval were blocked due to an assumed minimal processing time for recognizing the speed-up and preparing and executing the motor response (dashed line).

to its dependency from RW, chance level slightly differed between subjects. In the following text and within figures, for any particular experimental condition we only refer to the chance level with the highest value obtained within the corresponding experimental condition.

2.4. Data analysis

To allow for comparison of performance on correctly and incorrectly cued targets across experiments and acceleration values we normalized data with a 1-bar condition. In this condition each target's position was cued with 100% validity, whereas for all conditions where two or four bars were presented the cue's validity was only 75%. This reduction of validity is accompanied by an increase in the subject's uncertainty about the occurrence of a velocity change. According to Signal Detection Theory (Green & Swets, 1966), increased uncertainty causes an increase in the probability of false alarms (FA). To avoid an influence of validity-dependent uncertainty on comparisons of performance we expressed subject's performance as the ratio between correct responses (CR) and the sum of CR and misses (MISS) disregarding FAs:

$$\text{Performance} = \text{CR}/[\text{CR} + \text{MISS}].$$

To ensure that the sum of CRs and MISSes used for the performance calculation was the same for each subject and acceleration value we collected a predefined number of such trials (n_{Tr}) in any experimental session. For each subject in Experiments 1 and 3, n_{Tr} was set to 80, and in Experiment 2 to 96. In the corresponding 1-bar measurement, n_{Tr} was 20 for each subject in Experiments 1 and 3, and 40 in Experiment 2. Furthermore, since false alarms increase the probability that CRs occur by accident we defined the following rule to discard datasets affected by an unusually large number of FAs. We calculated the number of FAs expected when a blind observer (BO)[1] knowing only the maximum length of the trial would try to produce the demanded number of trials. This number is obtained by multiplying the product of the probability of getting a false alarm (p_{FA}) and the reciprocal probability of getting either a correct response or a MISS (p_{CRMISS}) with the demanded number of trials (n_{Tr}):

$$n_{\text{FABO}} = p_{\text{FA}}(1/p_{\text{CRMISS}}) * n_{\text{Tr}}.$$

For each subject (SUB), this number was compared with the total amount of FAs in the 1-bar condition and the accompanying multiple-bar conditions, separately for each acceleration value. We defined the ratio between these FA-groups as the Uncertainty Index (UCI):

$$\text{UCI} = \text{FA}_{\text{SUB}}/\text{FA}_{\text{BO}}.$$

The UCI is 0 when a subject produces no FA, and 1 when the subject performs on chance level. If for one of the conditions a subject's UCI reached a value greater than the mean UCI of all subjects for that condition plus two standard deviations (SD), the subject's full dataset for that particular acceleration value was excluded from further analysis. In addition, we excluded a measurement if a subject reported being unaware of the acceleration and having produced responses essentially by guessing.

For each acceleration level in Experiments 1–3 we computed the index ΔPI to quantify performance (*P*) difference between correctly cued targets (cct) and incorrectly cued targets (ict):

$$\Delta\text{PI} = (P_{\text{cct}} - P_{\text{ict}})/(P_{\text{cct}}).$$

The index varies between 1, if a subject only detected the speed-up of correctly cued targets, and 0, if performance is the same for correctly and incorrectly cued targets.

Statistical significance of the results was tested in two ways. First, to compare performance between the 1-bar condition and the corresponding attention conditions of Experiments 1–3 for each acceleration value separately, we applied the non-parametrical Kolmogorov–Smirnov test. Second, for further analysis, performance data from the 2- and 4-bar conditions of Experiments 1–3, respectively, were normalized with the corresponding 1-bar condition. These normalized values were then subjected to further statistical procedures (*t*-test, Wilcoxon rank sum test, Mann–Whitney *U* test, ANOVA). Unless otherwise stated, all statistical tests were performed on a 95% significance level.

3. Results

In the present study, we performed three acceleration detection experiments with different levels of spatial and inter-object competition, each testing seven different speed-up values from five subjects. For all experiments, we also sampled data for a competition-free reference condition, presenting only a single bar. In five of 15 cases, subjects were not tested for the weakest acceleration value, due to poor performance already in the 35% condition (see Section 2). Thus, we obtained data from 200 measurements. The number of FAs was low for strong accelerations (6.19% of all trials, averaged over all conditions for a speed-up of 85%) but increased for weaker accelerations (reaching 20.25% for a speed-up of 25%, averaged over all conditions). The mean uncertainty index (UCI) in the 1-bar condition was 0.188 ± 0.156 (range 0.000–0.757, $n = 100$) and $0.202 \pm 0.0.159$ (range 0.000–0.893, $n = 100$) in the multiple-bar conditions. In a total of eight sessions, we estimated an UCI exceeding the mean by more than 2SD for at least one of the two measurements, or had a report of a subject to have had responded by guessing. Since these data did not meet the behavioral criteria we excluded them from further analysis. The resulting database included data from 184 measurements (58 from Experiment 1, 62 from Experiment 2 and 64 from Experiment 3). In this dataset, the UCI of all measurements in the 1-bar condition ranged from 0.000 to 0.444 with a mean of 0.163 ± 0.128. Within the multiple-bar conditions, the mean UCI was 0.171 ± 0.113 (range 0.000–0.574). The number of eye

[1] *Abbreviations used:* BO, blind observer; CR, correct response; FA, false alarm; P, performance; RF, receptive field; RT, reaction time; RW, response window; SD, standard deviation; SUB, subject; UCI, uncertainty index; ΔPI, performance difference index.

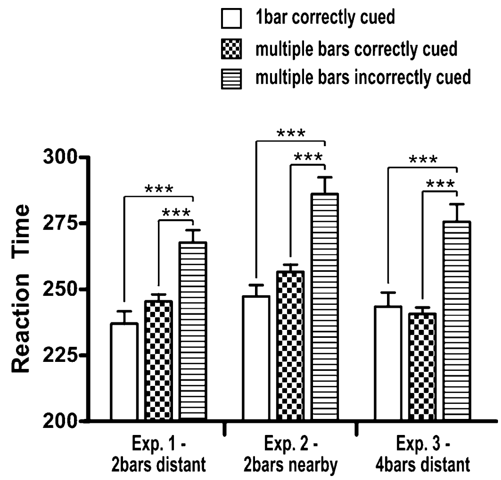

Fig. 3. Reaction times. For the easiest acceleration conditions in the three experiments, a speed-up of 85%, we compared mean RT in order to test whether subjects used the cue to direct their attention. As expected for selective attention, RTs for incorrectly cued trials were significantly longer than for correctly cued trials in both, the 1-bar condition and the multiple-bar conditions.

errors was very low in all experiments (1.42% all trials in 1-bar measurements, 1.76% in multiple-bar measurements).

In order to control whether subjects used the cue to direct their attention instead of dividing attention between multiple objects, we compared RT for correct responses for the easiest conditions, i.e., for speed-ups of 85% (Fig. 3). In all of these measurements, the reduction of RT for correctly cued trials in both the 1-bar condition and the multiple-bar conditions as compared to incorrectly cued trials was highly significant (Kruskal–Wallis test, $p < 0.001$). Interestingly, in none of the experiments did we find a significant difference in RT for correctly cued trials between 1-bar and multiple-bar conditions (Kruskal–Wallis test, $p > 0.05$).

3.1. Effect of selective attention on acceleration detection for different speed-up values with and without a distracter

Experiment 1 was conducted to test differences in the ability of subjects to report the acceleration of a moving bar when this bar was the only object on the screen versus a situation in which two bars were displayed at distant positions. In the 2-bar conditions, the spatial position of the target bar was cued with 75% validity, whereas in the 1-bar condition the cue's validity was 100%. Subjects were required to report any acceleration, but to minimize errors at the cued location. We tested seven different values of acceleration, each in a separate block of trials. Fig. 4 summarizes the results of this experiment. Fig. 4A shows the performance of each subject individually in the 1-bar condition. In blocks with the strongest target acceleration, subjects easily reported a speed-up of the moving bar showing correct responses in 80–100% of the trials. For slightly weaker accelerations, performance was still very good, and only for accelerations of 45% and less correct responses clearly decreased. However, even for the slightest speed-up of 25% subjects still performed well above the 9% chance level. Fig. 4B and C give the corresponding data from the 2-bar condition. In Fig. 4B, responses to correctly cued targets are shown. The overall pattern of the graphs is similar to those from the 1-bar condition. For accelerations between 85% and 55% subjects performed on a high level reaching 85–97% correct responses. Target accelerations of 45% and below were more difficult to detect and thus led to more misses, but again even for the weakest speed-up of 25% performance was far above chance and reached ratios similar to those in the 1-bar condition. In contrast, for incorrectly cued targets performance was much worse. It fell down towards levels below 25% for the lowest acceleration values (Fig. 4C). This difference in performance is reflected by a median ΔPI of 0.28 ($n = 30$; mean = 0.33).

Fig. 4D and E show averaged results for the three conditions. To control whether performance changed between the distracter-free 1-bar condition and the perceptually more demanding 2-bar condition, we normalized the results separately for each subject and acceleration value. Normalization was achieved by dividing performance data for correctly cued and incorrectly cued trials obtained from the 2-bar conditions with the corresponding data from the 1-bar condition. Normalized data were then fitted with a straight line. Fig. 4F shows the results along with the 95% confidence bands. For correctly cued targets, the fitted line has an intercept of 0.995 and a slope of −0.0003, indicating that performance in the 2-bar condition almost perfectly mirrored performance in the 1-bar condition. To verify these results statistically, we applied two tests. As a first test we used the non-parametrical Kolmogorov–Smirnov test to compute the probability that for a given acceleration value data from the 2-bar conditions derived from a different distribution than those obtained in the 1-bar condition. For rejection of the null hypothesis, indicating equal distributions of data obtained from the 1-bar and the 2-bar conditions, we allowed a 10%-error probability. The results are shown in Fig. 4F. For correctly cued targets, there was a clear correspondence between the distribution of data from the 2-bar condition and the corresponding 1-bar condition for all acceleration values. Thus, even for the slightest, and hence most difficult to detect, speed-up of a bar performance did not differ significantly between the two conditions, even with the high error allowed by the statistical test. In contrast, for incorrectly cued targets, data for all acceleration values were likely to be drawn from a different distribution than the corresponding 1-bar data with the only exception of the most salient speed-up of 85%. The second test was performed in order to control whether the overall performance for correctly cued targets in the 2-bar condition matches that of the 1-bar condition. If so, the mean of the whole set of normalized data is expected to equal 1.0. The actual mean of the data is 1.013 ± 0.0087 SD ($n = 29$). We used the D'Agostino and Pearson omnibus KS to verify Gaussian distribution, and

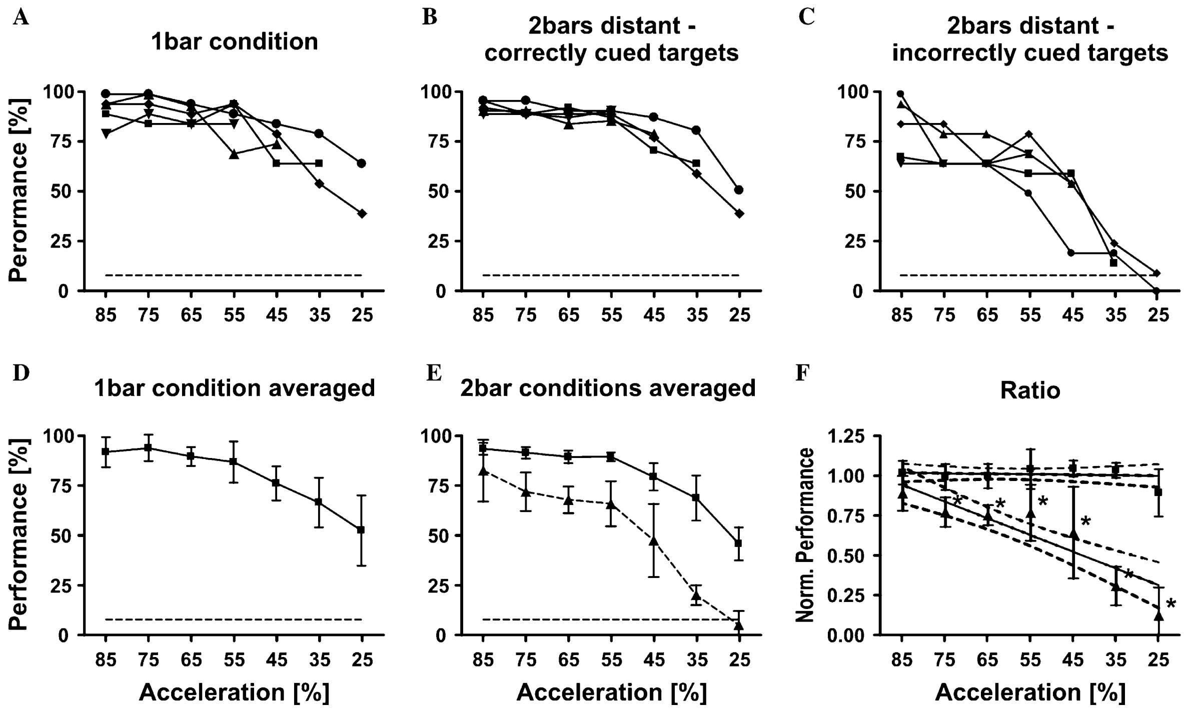

Fig. 4. Results of Experiment 1. (A) Individual performance of subjects for seven acceleration values for a validly cued single bar. The dashed horizontal line indicates the maximal chance level. (B) Performance of the same subjects in the 2-bar condition for correctly cued targets, and (C) incorrectly cued targets. (D and E) Averaged performance for correctly cued (■) and incorrectly cued (▲) targets, respectively. Error bars indicate standard deviation throughout the figure. For correctly cued targets, the difference in SD between the 1-bar condition and the 2-bar condition disappears when equal amounts of trials are computed. (F) Normalized performance, obtained by dividing performance data from the two conditions of the 2-bar condition with corresponding data from the 1-bar condition. The straight line shows the result of a first-order polynomial fit, dashed lines show the confidence bands. Asterisks indicate the results of a Kolmogorov–Smirnov test calculating the probability that the distribution of data from the two 2-bar conditions derived from a different distribution than those from the 1-bar condition. Analysis shows no such trend for data obtained from trials with correctly cued targets, but for incorrectly cued trials this trend was observed for all accelerations with the exception of the most salient value of 85%. The results of the experiment show that adding a second, potentially relevant bar to the display did not change the performance level compared to the 1-bar condition, regardless of the difficulty of the task. A hypothetical increase of attentional effects was observed only within the results obtained with non-attended objects for which relative performance decreased the more difficult the required perceptual judgement was made.

then applied a *t*-test to test the actual mean against the hypothetical mean of 1. We found no significant difference. Further, we used the non-parametrical Wilcoxon signed rank test to test the actual data against a hypothetical median of 1. Again, we found no significant difference. In summary, for correctly cued targets in Experiment 1, performance of subjects in the 2-bar condition equaled that of the same subjects in the corresponding 1-bar condition, although in the 2-bar condition uncertainty caused by the limited validity of the cue as well as perceptual load were increased.

3.2. Effects of increasing inter-stimulus proximity

In Experiment 2, we tested whether increasing spatial proximity of the two bars would decrease behavioral performance of subjects for correctly cued targets. In our corresponding neurophysiological experiment (Wegener et al., 2004), we not only increased proximity but also changed the second bar's orientation by 90° in order to minimize modulatory effects from the surround of the receptive field. For reasons of comparability, we adopted this stimulation for the current study. Consequently, targets could appear at two orthogonal trajectories in each quadrant (cf. Fig. 1B). In order to test whether subjects performed differently depending on the trajectory of the target we compared behavioral results from the two trajectories. Averaged over all acceleration values, the mean performance was 72.6% (SD = 15.7%) on the first trajectory and 74.4% (SD = 16.2%) on the second. Applying a *t*-test to the data revealed no significant difference.

Fig. 5 shows the results of Experiment 2. As in Experiment 1, subjects detected accelerations of correctly cued targets in similar ratios in the 1-bar and 2-bar conditions. In contrast, incorrectly cued targets were often missed and an appreciable decrease in performance was visible already for the highest acceleration value. To test for constancy of performance, we again normalized data from the 2-bar conditions separately with the 1-bar condition and fitted a straight line to the data points. For correctly cued targets, the line has an intercept of 1.065 and a slope of 0.0007, again showing strong correspondence of performance. For each of the tested acceleration values, the Kolmogorov–Smirnov test revealed no hint that data from correctly cued targets of the 2-bar condition derived from a different distribution than those from the 1-bar condition,

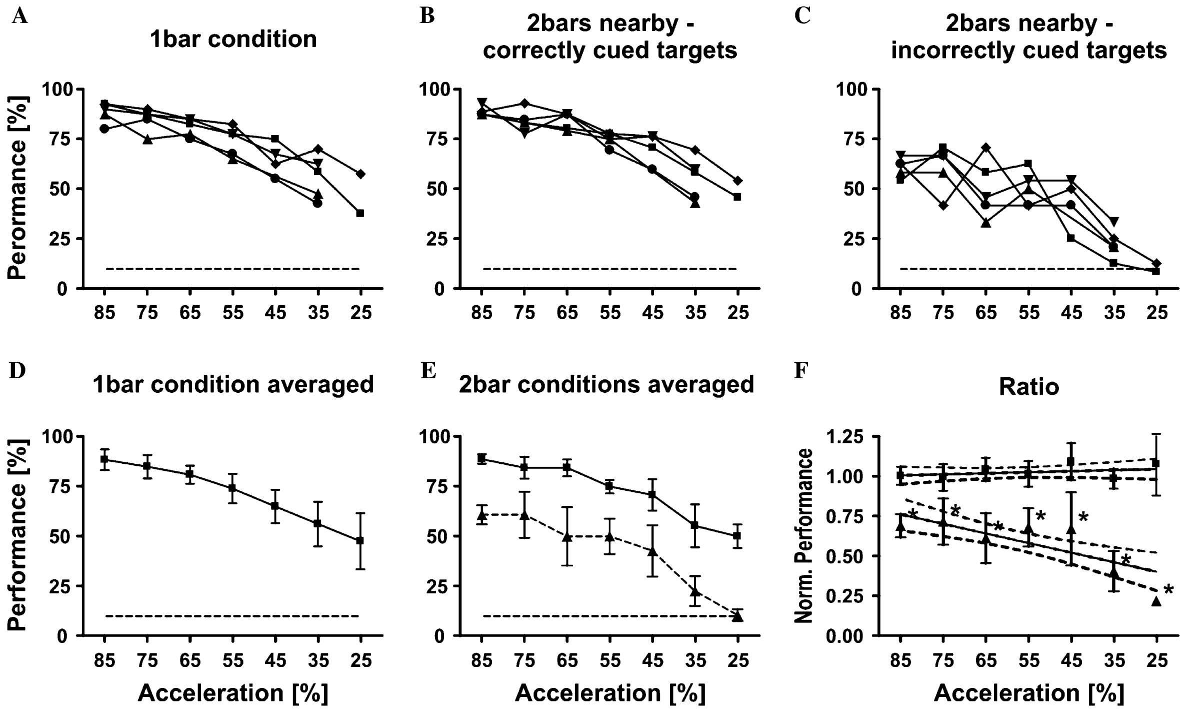

Fig. 5. Results of Experiment 2. Conventions as in Fig. 4. Within Experiment 2 spatial competition was enhanced by decreasing inter-stimulus distance. No effect of enhanced competitive interactions was observed for correctly cued targets of the 2-bar condition when compared to the 1-bar condition, demonstrating again constant performance at all levels of task difficulty. In contrast, performance for incorrectly cued targets further decreased when compared to Experiment 1.

even when accepting an error up to 10% within this statistical test. This indicates that both datasets were indeed drawn from the same distribution. In contrast, for none of the accelerations we found such a correspondence between incorrectly cued targets and the 1-bar condition. For the entirety of correctly cued targets averaged over all acceleration values, we additionally performed a *t*-test and a Wilcoxon signed rank test to control the actual mean (1.026 ± 0.0864) and median (1.000) of the normalized data for any deviation from the hypothetical value of 1. The tests did not reveal significant differences. In summary, as in Experiment 1, for correctly cued trials the performance in the 2-bar condition equaled that of the 1-bar condition, although spatial inter-stimulus competition was markedly increased. The higher attentional effort necessary to correctly detect the speed-up of the target bar is reflected only in the performance for incorrectly cued targets, for which in comparison to Experiment 1 the acceleration is more often missed. Over all accelerations, this is expressed by the median ΔPI of 0.35 ($n = 31$, mean = 0.42), which is significantly higher as compared to the ΔPI of 0.28 in Experiment 1 (Mann–Whitney *U* test, $p < 0.05$), indicating a further decrease of performance on incorrectly cued targets in Experiment 2 as compared to Experiment 1.

3.3. Effects of increasing set size

In Experiment 3, we tested the effect of increasing perceptual load by enhancing the number of distracters. The results are illustrated in Fig. 6. The 1-bar condition of this experiment equaled that of Experiment 1. For correctly cued targets, subjects showed similar performances as compared to the former experiments. For incorrectly cued targets, mean performance did not exceed 50% even for the strongest acceleration, and dropped down to values around 10% for the weakest speed-up. Performance differences between correctly and incorrectly cued trials reached a median ΔPI of 0.57 (mean = 0.56, $n = 32$), indicating significantly weaker performance for incorrectly cued targets as compared to Experiment 1 (Mann–Whitney *U* test, $p < 0.001$) and 2 (Mann–Whitney *U* test, $p < 0.01$).

Within Experiment 3, running the Kolmogorov–Smirnov test again found no differences for the distribution of data obtained with correctly cued targets, while for incorrectly cued targets there was a clear trend that all data derived from a different distribution than those from the corresponding 1-bar condition. Fitting normalized data from correctly cued trials with a straight line revealed an intercept of 1.015 and a slope of 0.0002, again indicating strong correspondence for performance on correctly cued targets in the 1-bar and 4-bar conditions. Testing mean (1.002) and median (1.010) values against the hypothetical value of 1 did not reveal significant deviation (*t*-test, Wilcoxon signed rank test). In summary, increasing perceptual load of the task did not influence the performance on correctly cued trials, but was accompanied by a further decrease of performance to incorrectly cued trials.

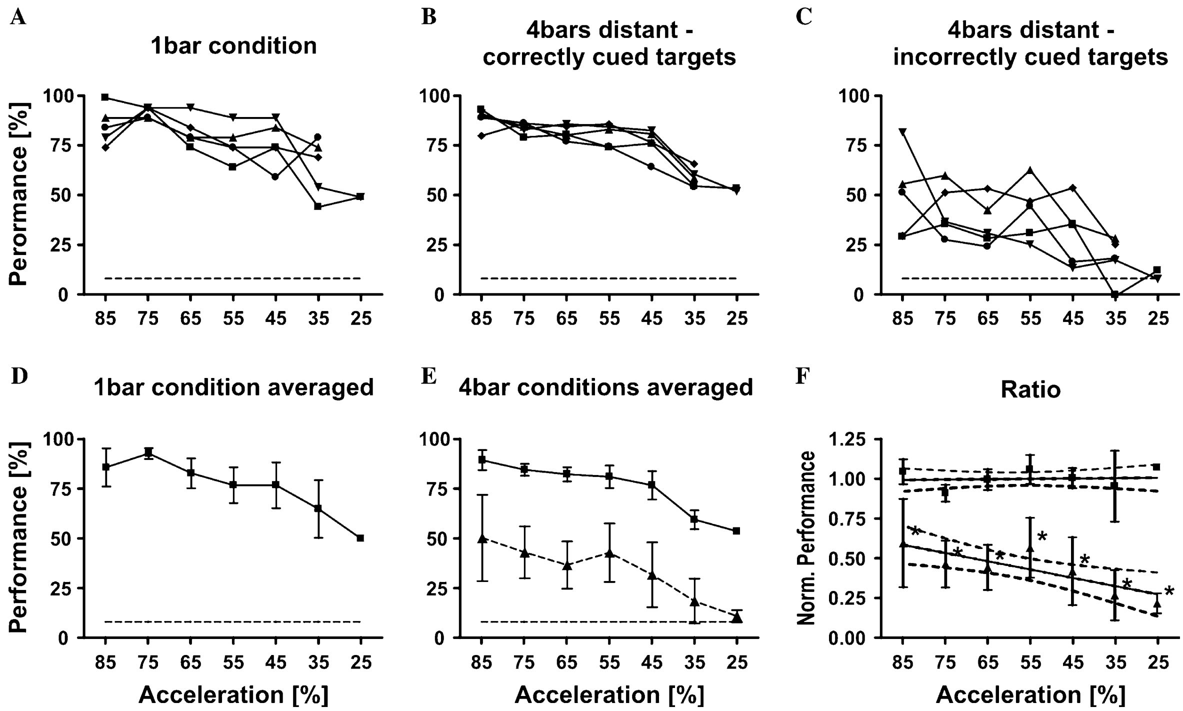

Fig. 6. Results of Experiment 3. Conventions as in Fig. 4. Within Experiment 3 inter-stimulus competition was enhanced by increasing the number of distracters. As in Experiment 2, for correctly cued targets no effect of increasing competition was observed as expressed by the offset and slope of the upper straight line in (F). However, for incorrectly cued targets performance in Experiment 3 was further reduced as compared to the other experiments showing weak performance already for salient acceleration values.

3.4. Cross-comparison of experiments

If performance for correctly cued targets stays constant, we expect equal values not only within but also across experiments. We therefore divided the mean normalized response for a given acceleration value in Experiment 1 by the corresponding value from Experiment 2. This was repeated for all acceleration values across these two experiments as well as for the corresponding comparison between Experiments 1 and 3 and between Experiments 2 and 3, respectively. If performance to correctly cued targets is constant across all three experiments then the mean value of the division described above should be near to 1, regardless of which experiments are compared. Fig. 7 shows the results. For the comparison of Experiment 1 with Experiment 2, we obtained a mean of 0.99 ± 0.0909 (median = 0.980), and for the comparison with Experiment 3 the mean was 1.011 ± 0.0958 (median = 1.000). Comparison of Experiment 2 with Experiment 3 resulted in a mean of 1.023 ± 0.0496 (median = 1.030). We found no significant differences between these values using the non-parametric Friedman test, nor did we find any significant deviation from a theoretical median of 1 (Wilcoxon signed rank test).

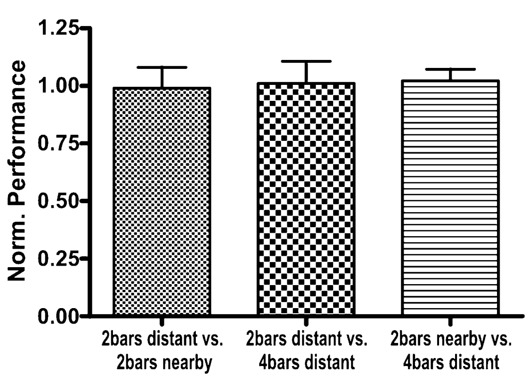

Fig. 7. Cross-comparison of behavioral performance on correctly cued targets between the three experiments. For each acceleration value, relative performance level was calculated by dividing normalized results from one experiment with corresponding data of the other experiment. Bars show the mean ratio across all acceleration values for every combination of experiments. Error bars indicate standard deviation. The results of the analysis show that the relative performance on correctly cued trials was almost identical in all of the experiments, despite substantial differences regarding the strength of spatial and perceptual competition.

4. Discussion

The aim of the present study was to examine how attention influences detectability of small increments in the velocity of a moving object, depending on inter-stimulus competition and difficulty of the task. Using the classical Posner paradigm (Posner, 1980), we carried out three experiments with different attentional load (Lavie, 1995) and for each of the experiments tested seven different values of acceleration ranging from salient to weak. The results show that for correctly cued targets performance was similar in all tested conditions. We did not find any effect of adding one or three distracters to the display, or changing spatial distance between the objects. In each experimental condition, subjects performed as well as in the 1-bar condition where there was no competition for motion processing resources. This holds true not only for salient accelerations but also for very weak speed-ups that were much harder to detect. In contrast, performance on incorrectly cued targets was significantly reduced already in the weakest load condition, and decreased further with increased inter-stimulus competition.

4.1. Methodological considerations

The results were obtained by estimation of behavioral performance defined as the ratio between correct responses and missed responses within a given RW. For each subject, the RW was calculated individually, based on the subject's mean RT for detection of the median acceleration in validly cued 1-bar trials. This approach was used because we wanted subjects to detect changes of the velocity rather than absolute differences in velocity between the bars. This requires tracking of the moving object and a fast response as soon as a speed-up occurs. Such a purely acceleration-based performance cannot be estimated within a classical reaction time experiment because a subject who failed to detect the speed-up may recognize an absolute difference in velocity between simultaneously presented objects somewhat later. Thus, subjects may use different perceptual strategies in order to produce the required response, making unambiguous interpretation of the data difficult. Therefore, we limited the response time and urged subjects to respond as quickly as possible. A failure to respond within RW can therefore be attributed to either a prolongation of RT, or a complete failure to detect the speed-up of the bar. Both causes are well-known consequences for non-attended objects (cf. Pashler, 1998; van der Heijden, 1992). Furthermore, for every experiment we instructed subjects to detect as much acceleration events as possible but to minimize errors at the cued location. By this, we aimed to prevent subjects from using a divided attention strategy, which would not allow comparing data from the multiple-bar conditions with the 1-bar condition, since attention in the latter condition is always directed to the same object. We tested the direction of attention by a RT-comparison for salient accelerations, for which sufficient performance was obtained in all behavioral conditions. For a divided attention strategy, equal reaction times independent of the cue's validity are expected, whereas for selective attention RT is expected to be shorter for correctly cued trials. The results indicated that subjects indeed used the cue to direct their attention, since for each subject RTs were faster for correctly cued targets than for incorrectly cued ones.

4.2. Comparison with neurophysiological results

The behavioral results of the present study are in good correspondence with recent neurophysiological findings suggesting that in the presence of distracters attention serves to keep sensory representations constant (Wegener et al., 2004). In that study, direction selectivity of single neurons in area MT was first measured under competition-free circumstances in a fixation task. When these data were compared with the results from two attention experiments, it was found that in the presence of distracters attention modulates neuronal responses as to ensure the same direction selectivity as measured before in the competition-free condition. In contrast, direction selectivity in response to the non-attended distracter bar was significantly reduced, and the reduction even increased when spatial competition was enhanced. The psychophysical data described here suggest corresponding attentional effects on the behavioral level. In each of the three experiments, our results indicate that attending the cued bar results in equal levels of performance, regardless of whether the bar was shown in the presence or absence of distracters. Neither enhancing inter-stimulus proximity nor increasing the number of objects induced a performance decrease for the attended object, indicating that the strength of competition did not influence the performance level for the attended object. All modulations occurring with increased competition only occurred for non-attended objects. Thus, our data point towards a noise reduction mechanism (Baldassi & Burr, 2000; Dosher & Lu, 2000; Lu & Dosher, 2004; Shiu & Pashler, 1994, 1995) that goes along with a stronger suppression of non-attended content with increasing competitive interactions between target and distracter objects. The behavioral results thereby exactly confirm the corresponding predictions drawn from attention-dependent modulation of stimulus selectivity in monkey area MT.

4.3. Relation to load theory of attention

The behavioral data of the current study and the neuronal data from the former MT-study both indicate that non-attended objects suffer from a reduced representation when inter-object competition between target and distracters is enhanced. Under highly competitive circumstances neurons in area MT show strongly reduced direction selectivity (Wegener et al., 2004), and for the same condition a strong decrease in behavioral performance on non-attended objects is found. This part of our results would be compatible with an early selection account stating that non-attended information is not processed because of capacity limits (Broadbent, 1954, 1958; but see Navon, 1989 and Lavie & Tsal, 1994 for discussion). However, since the extent to which non-attended objects are processed depends on spatial distance and number of objects the data suggest that the processing of unselected information is determined by the strength of competitive interactions. Thus, our data strongly support Lavie's recent load theory of attention (Lavie, 1995, 2005) stating that "...processing load in a relevant task determines the extent to which irrelevant distracters are processed" (Rees, Frith, & Lavie, 1997, p. 1616). In other words, distracter processing depends on the extent to which processing of the relevant information utilizes the system's processing capacity.

4.4. Strength of competitive interactions

In line with earlier psychophysical work (Bahcall & Kowler, 1999; Cutzu & Tsotsos, 2003; Eriksen & Spencer, 1969; Mounts, 2000) our data show that both increasing number of objects as well as decreasing inter-object distance goes along with a decrease in performance for non-attended objects, which is likely to reflect stronger competitive interactions. This is in good correspondence with (a) recent electrophysiological studies from both ventral and dorsal stream areas suggesting that competition for processing resources increases with decreasing spatial separation among objects (Luck et al., 1997; Moran & Desimone, 1985; Treue & Maunsell, 1996), probably involving a local network of reciprocal inhibitory connections (Chelazzi, 1995); and (b) neuroimaging data that show increasing suppressive effects in areas V1, V2, V4 and TEO (Kastner, DeWeerd, Desimone, & Ungerleider, 1998) when the number of objects simultaneously present in the display is enhanced. However, also in the latter case the magnitude of effects decreased with increasing distance among objects (Kastner et al., 2001), supporting the view that competition for processing resources takes place most strongly at the level of receptive fields (e.g., DeWeerd, Peralta, Desimone, & Ungerleider, 1999; Reynolds et al., 1999). Therefore, with respect to our findings it might be surprising that performance for non-attended objects was more impaired in Experiment 3 where we used four bars with relative large inter-object distance than in Experiment 2 with two nearby objects. A similar finding was reported by Eriksen and Rohrbaugh (1970) who described an increase in attention effects when using a distributed multiple-item display in comparison to a spatially more narrow display with fewer items. Are these findings in disagreement with the notion that within visual areas competition among resources is inversely related to the degree of spatial separation among objects? We do not think that this is necessarily the case. First, the poor performance for non-attended bars in Experiment 3 may reflect competitive effects at later processing stages, e.g., in parietal cortex, where receptive fields are larger. In this case, processing of stimuli at earlier stages with smaller receptive fields, e.g., area MT, may be largely unaffected. Corresponding results have been obtained in the ventral visual stream (e.g., Moran & Desimone, 1985). Second, stronger impairment of performance for incorrectly cued targets in Experiment 3 might also be caused by statistical reasons. Here, incorrectly cued accelerations may occur at one out of three locations (instead of only one), resulting in increased uncertainty and reduced performance (cf. also Eriksen & Spencer, 1969).

4.5. Comparison to psychophysical results

The results presented here support current hypotheses stating that a main effect of attention is noise reduction (e.g., Baldassi & Burr, 2000; Dosher & Lu, 2000; Lu & Dosher, 2004), although they do not exclude the possibility of additional signal enhancement (Bashinski & Bacharach, 1980; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Yeshurun & Carrasco, 1999). According to the latter, it would have been necessary to test performance on attended targets against performance on neutral stimuli, which is difficult within the behavioral paradigm used in the present study. However, the independence of performance on the strength of competitive interactions found in the present study indicates that a major neuronal mechanism allowing for the constant representation of the attended object is the exclusion of external noise by diminishing the impact of non-attended stimuli. This is well in line with several psychophysical studies employing static objects. First, data from cueing studies with supra-threshold stimuli show that in the absence of competing objects spatial cueing has, if any, only little influence on the detectability of target stimuli when compared to neutral stimuli (Nakayama & Mackeben, 1989; Posner, 1980; Prinzmetal, Presti, & Posner, 1986; Shiu & Pashler, 1994, 1995), indicating that attentional mechanisms do not necessarily enhance performance. Second, from several studies using recognition tasks it is known, that non-target stimuli can quite successfully be ignored, and that the number of these stimuli has little effect on target identification (cf. Bundesen, 1990; Duncan, 1980). The extent to which non-selected objects may be processed strongly depends on inter-stimulus interferences (e.g., Kahnemann & Chajczyk, 1983), and under highly competitive circumstances, e.g., having a large number of distracters, evidence for unselective processing of distracter objects virtually disappears (Yantis & Johnston, 1990). Third, several recent studies demonstrated that enhancing complexity of a stimulus display is not necessarily accompanied by changes in the performance for the attended stimulus. For example, Palmer (1994) required subjects to judge the relative orientation between pairs of small, black-and-white squares. Subjects showed similar performance in blocks where only a subset of a larger display was cued compared to blocks where only this subset was present, suggesting that subjects successfully excluded irrelevant objects but kept target representation constant. Caputo and Guerra (1998) required subjects to perform a line discrimination task and concluded from their results that if knowledge is given about the relevant target features, irrespective of the presence of a distracter, attention "[...] places discriminability at the level attainable if no object other than the target was present on the image".

5. Conclusions

The results of Caputo and Guerra (1998) and others (e.g., Baldassi & Burr, 2000; Dosher & Lu, 2000; Lu & Dosher, 2004) as well as the results of the present study strongly support the view that under conditions of high perceptual load (Lavie, 1995) successful allocation of attention is inextricably associated with the reduction of external noise. Recent research on attention deficits suggests that the inability to ignore distracting information might be a major cause in several forms of attention-deficit-hyperactivity-disorder (Tsal, Shalev, & Mevorach, 2005) as well as in milder forms of attention difficulties (Shalev & Tsal, 2003). The consistence between the behavioral results in the current study and the predictions drawn from the MT data suggests that this inability might be caused already in early sensory processing. Future research has to clarify in more detail by which neuronal mechanisms noise reduction can be accounted for. Aside from firing rate modulations, neurophysiological data from a single cell study in monkeys performing the same paradigm (Wegener & Kreiter, 2004) showed attention-dependent frequency differences in oscillatory activity patterns when responding to a target or distracter stimulus, indicating that the temporal structure of neural activity is one possible candidate mechanism underlying the attentional gating process.

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