Independent Effects of Attentional Gain Control and Competitive Interactions on Visual Stimulus Processing

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Attention filters behaviorally relevant stimuli from the constant stream of sensory information comprising our environment. Research into underlying neural mechanisms in humans suggests that visual attention biases mutual suppression between stimuli resulting from competition for limited processing resources. As a consequence, processing of an attended stimulus is facilitated. This account makes 2 assumptions: 1) An attended stimulus is released from mutual suppression with competing stimuli and 2) an attended stimulus experiences greater gain in the presence of competing stimuli than when it is presented alone. Here, we tested these assumptions by recording frequency-tagged potentials elicited in early visual cortex that index stimulus-specific processing. We contrasted the processing of a given stimulus when its location was attended or unattended and in the presence or the absence of a nearby competing stimulus. At variance with previous findings, competition similarly suppressed processing of attended and unattended stimuli. Moreover, the magnitude of attentional gain was comparable in the presence or the absence of competing stimuli. We conclude that visuospatial selective attention does not directly modulate mutual suppression between stimuli but instead acts as a signal gain, which biases processing toward attended stimuli independent of competition.

Keywords: biased competition, human visual cortex, sensory gain control, steady-state visual evoked potentials, visual attention

Introduction

Cluttered visual scenes pose a challenge to capacity-limited human perception (Neisser and Becklen 1975). Adaptive behavior in such environments requires attentional selection of currently relevant and suppression of irrelevant information, a process that is thought to be governed by a “biased competition” mechanism (Desimone and Duncan 1995; Desimone 1998; Kastner and Ungerleider 2001). Originally put forward by Moran and Desimone (1985), this idea accounts well for neuronal attention effects in single-cell studies. They found that placing 2 stimuli in a neuron’s receptive field (RF) that corresponds to a currently unattended location, the response (spike rate) is a weighted average of the responses to the singly presented stimuli. A stimulus that usually elicits a high response (“preferred” stimulus) and that usually elicits a weak response (“poor” stimulus) placed within the same RF gives an intermediate response. Allocating attention to one of the stimuli shifts the neuron’s response toward the response given when it is presented alone. These results led to the hypothesis that multiple simultaneously presented stimuli enter a competition; thereby suppressing each other’s neuronal processing. Attention is thought to bias competition by releasing a selected stimulus from mutual suppression. Numerous single-cell studies have supported this assumption (Luck et al. 1997; Reynolds et al. 1999; Reynolds and Chelazzi 2004). In a paradigm that used a design similar to human event-related potential (ERP) studies on attention, Luck et al. (1997) measured attention effects on neuronal spike rates in monkey visual cortex. Attended and unattended stimuli were either presented simultaneously (allowing for competition between stimuli) or sequentially (no competition) to the same RF. When 2 stimuli were presented simultaneously, attention effects were substantially larger. Collectively, these findings suggest that biased competition provides a conclusive model for effects of attention on neuronal processing.

Importantly, biased competition predicts that attention influences neuronal stimulus processing maximally, if not exclusively, in situations where 2 or more stimuli fall into the same RF. The dynamic range of the attentional bias is hence confined to the limits set by the responses to the individual stimuli. Moreover, competition in the absence of an attentional bias refers to the suppression of the characteristic response to an individual stimulus. Thus, when a “poor” stimulus is attended in the presence of a “preferred” stimulus, the attentional bias may also decrease the neuron’s net response (Reynolds and Chelazzi 2004).

Due to these supportive findings in single-cell research, the biased competition framework has since been adopted to account for large-scale neural effects of human visual attention (Desimone and Duncan 1995; Duncan et al. 1997; Desimone 1998). In a functional magnetic resonance imaging (fMRI) study, Kastner et al. (1998) presented a display of 4 colorful visual stimuli, either simultaneously or sequentially, similar to the single-cell study byLuck et al. (1997) (see above), and instructed participants to attend to one of the stimuli or to central fixation. In-line with biased competition, the 2 core findings were that 1) activity in color-sensitive visual cortical area V4 was suppressed in the simultaneous compared with the sequential presentation condition and 2) attention to 1 stimulus counteracted this suppression.

Notably, this adoption of biased competition required a translation of the single-cell competition idea as described above. In the case of macroscopic brain responses, populations of neurons with a variety of possible preferences contribute to the measured activity. Here, competition in the absence of an attentional bias refers to the mutual suppression of the pooled responses to individual stimuli. An attentional bias will therefore always increase the pooled response (Kastner and Ungerleider 2001), thereby acting as a signal gain. In contrast to the single-cell situation, the neural response to an unattended singly presented stimulus (upper bound) and the suppressed response to the same unattended stimulus in the presence of...
neighboring competing stimuli (lower bound) confine the dynamic range of the attentional bias.

Nevertheless, a long tradition of human ERP research (for a review, see Hillyard and Anllo-Vento 1998), including steady-state visual evoked potential (SSVEP) studies (Morgan et al. 1996; Müller et al. 1998; Kim et al. 2007), has consistently demonstrated attention effects on the processing of individual stimuli that were presented in the absence of neighboring competing stimuli. Thus, in parallel to the development of biased competition, attention has also been conceptualized as a “sensory gain control,” which increases neuronal/cortical responses to stimuli at attended locations (Hillyard et al. 1998). The 2 positions are not mutually exclusive. With regard to the ERP studies, it may well be the case that attentional gain of a stimulus in the presence of a neighboring competing stimulus is larger compared to a presentation of the same stimulus in the absence of competing stimuli. However, in contrast to biased competition, sensory gain control does not explicitly predict such an interaction.

Here, we aimed to test for an interaction of 2 mechanisms of attention—gain and competition—as it is proposed in biased competition accounts of human visual attention (Desimone and Duncan 1995; Kastner and Ungerleider 2001; Beck and Kastner 2009). We probed how the presence or the absence of a competing stimulus (“competitor”) influenced the processing of a spatially attended or unattended stimulus. To this end, we recorded the electroencephalogram (EEG) while human subjects covertly attended to a stimulus in the left or right visual hemifield of a display and ignored a simultaneously presented stimulus in the opposite hemifield (see Fig. 1A). Both stimuli flickered at different frequencies, thereby eliciting separable SSVEPs. SSVEPs are continuous oscillatory brain responses to flickering stimuli, which have the same temporal frequency as the driving stimulus (Regan 1989). SSVEP amplitudes have been shown to index both attentional allocation (Morgan et al. 1996; Müller et al. 1998, 2003; Toffanin et al. 2009; Quigley et al. 2010) and mutual suppression by competition in a multistimulus display (Fuchs et al. 2008; Busse et al. 2009; Andersen and Müller 2010; Keitel et al. 2010). Thus, in the present context, they may quantify 1) how the neural response to a particular stimulus varies when it is presented alone versus when it is accompanied by a competitor and 2) whether response modulations in (1) change with attentional allocation to that stimulus. Importantly, our methodological approach allows a direct test of the effects of biased competition on the processing of individual stimuli in a multielement display for the first time. In contrast, previous fMRI studies that investigated biased competition based their conclusions on cortical responses to entire stimulus displays (Kastner et al. 1998; Bles et al. 2006; McMains and Kastner 2011).

A comparison of SSVEP amplitudes when participants attend or do not attend to a given stimulus under conditions when a competitor is present versus absent allows for the assessment of the influence of attentional gain and competition on the ongoing processing of simultaneously presented stimuli. If attention, in fact, resolves competition and releases a stimulus from mutual suppression, we expect spatially directed visual attention and the presence/absence of a competitor to interactively modulate stimulus processing (see Fig. 1B). Specifically, the SSVEP amplitude of an unattended stimulus should be substantially reduced in the presence of a competitor, which, in turn, should have only little influence on the amplitude of an attended stimulus. Moreover, in the absence of a competitor, attention should have only minor, if any, effects on SSVEP amplitude as there is no competition to be resolved.

Materials and Methods

Participants

Nineteen participants took part in the experiment after giving informed written consent. Five participants were excluded from further data analysis because they showed systematic eye movements. The remaining participants (mean age = 24.6 years, 7 females) had normal or corrected-to-normal vision and no history of neurological disease or injury. The experiment was conducted in accordance with the declaration of Helsinki.

Stimuli

Visual stimuli were shown on a 19 inch cathode ray tube screen (refresh rate = 85 Hz) against a gray background (35.8 cd/m²) at
Procedure and Task
Participants were seated comfortably in an acoustically dampened and electromagnetically shielded chamber. For each of the 4 experimental conditions—attend left, competitor off; attend left, competitor on; attend right, competitor off; attend right, competitor on—150 trials were presented in 10 consecutive blocks. Participants started individual blocks by pressing a designated response button. The side to be attended was randomized on a trial-by-trial basis and indicated by presentation of a cue for 800 ms prior to stimulus onset (see Fig. 1A). Cue offset was followed immediately by the onset of the 2 textured brackets. Flicker stimulation lasted 367 ms followed by an intertrial interval of 800 ms during which participants were allowed to blink. Participants were instructed to report occasional brief local luminance increments on the cued textured bracket ("targets," duration = 282 ms, maximum luminance = 99.2 cd/m², 40.4% Michelson contrast) by pressing the response button while ignoring luminance decrements on the same side ("distractors," minimum luminance = 36.1 cd/m², 50% Michelson contrast, see Fig. 1A). Changes were centered at corresponding luminance maxima and minima on the textured outer brackets and spanned one half-cycle of the luminance modulation, which corresponded to 10% of the bracket's arc. Detection responses made between 300 and 1000 ms after target onset were considered hits. Similar responses after distractor onset were considered false alarms. Prior to the experiment, participants were trained in the task for at least 2 blocks. They received feedback regarding average hit rate and reaction time after each training and experimental block.

Behavioral Data Analysis
Accuracy was calculated as the total number of hits and correct rejections divided by the total number of target and distractor events. Behavioral data did not differ between attended sides. Thus, we averaged across left and right sides and tested accuracy and median reaction times for competitor present versus absent by means of paired t-tests.

SSVEP Recordings and Analysis
EEG was recorded from 64 Ag/AgCl scalp electrodes mounted in an elastic cap and amplified by an ActiveTwo amplifier (BioSemi, Amsterdam, Netherlands). Eye movements and blinks were monitored with 2 bipolar montages, one positioned above and below the right eye (vertical electrooculogram) and another at the outer canthii (horizontal electrooculogram, HEOG). In order to quantity stimulus processing with any possible influences of target and distractor processing, all trials containing such events were excluded leaving 75 trials per condition for SSVEP analysis. Individual trials were rejected automatically when contaminated with blinks or eye movements. Two criteria determined rejection due to eye movements: 1) HEOG amplitude exceeded a threshold corresponding to a horizontal gaze shift of 1.5° and 2) After (1) had been applied, a conservative leave-one-out iterative procedure was performed for "attend left" and "attend right" conditions separately. Trials were rejected, one per iteration, until the statistical threshold, namely no significant deviation of the HEOG from zero, was reached. An extended version of the "statistical control of artifacts in dense array EEG/MEG studies" procedure (Junghöfer et al. 2000) was used to identify and to correct further artifacts by channel interpolation where applicable. Total average rejection rate was 28% of trials. Subsequently, data were referenced to average reference and averaged for each participant and experimental condition separately. SSVEP amplitudes of both stimulation frequencies were quantified by a Fourier transform of the time interval 500–3500 ms after display onset. SSVEP amplitudes were divided by the mean amplitude across conditions to yield normalized amplitudes which allowed us to average across both stimulation frequencies. Averaged normalized amplitudes were compared by a 2-way repeated measures analysis of variance (ANOVA) with factors of attention (attended = A+ vs. unattended = A-) and competition (competitor present = C+ vs. absent = C−). Basic data-processing steps such as extraction of epochs from the continuous recordings, re-referencing and plotting scalp isocountour voltage maps made use of EEGLAB (Delorme and Makeig 2004) in combination with custom routines written in MATLAB (The Mathworks, Natick, MA).

Source Localization
Cortical regions generating SSVEPs were localized by subjecting the complex Fourier coefficients at each stimulation frequency to variable-resolution electromagnetic tomography (VARETA, Bosch-Bayard et al. 2001). Similar to the normalization procedure on SSVEP amplitudes in sensor space (see above), prior to localization, complex Fourier coefficients were divided by the mean across conditions for each individual participant and frequency. Cortical currents giving rise to SSVEP modulation by attention and competition were revealed by comparing the source localizations between attended versus unattended and competitor-absent versus competitor-present conditions by means of Hotelling's T²-statistic.

Results
Behavioral Data
The presence of the behaviorally irrelevant competitor led to a small but consistent decrease in performance (accuracy: 82.3 ± 1.4% competitor present and 86.0 ± 1.3% competitor absent, mean ± standard error of the mean, t133 = −3.10, P < 0.001) but did not affect reaction times (579.5 ± 15.9 ms competitor present and 574.0 ± 12.0 ms competitor absent, t133 = 0.74, P = 0.47).

Electrophysiological Data
The topographical distribution of SSVEP amplitudes averaged across all experimental conditions was maximal at occipital electrode sites for both stimulation frequencies (Fig. 2A). Notably, lateralized flicker stimulation is likely to drive tangentially projecting dipoles due to the retinotopic organization of early visual cortex. This results in a "smearing" across hemispheres and limits the identification of focused amplitude maxima that are contralateral to the driving stimulus (see, e.g., Andersen et al. 2011). For further analyses, we thus averaged SSVEP amplitudes across a unified cluster of 13 occipital and parietal electrodes as indicated in Figure 2A. As in previous studies (Müller et al. 2003; Andersen et al. 2008, 2011), the higher flicker rate elicited an SSVEP of smaller absolute amplitude at the fundamental frequency of the signal (Fig. 2B). For both frequencies, SSVEP amplitudes were greatest for attended brackets with competitor absent (A+C−) and smallest for unattended brackets in the presence of a competitor (A−C+). Attended brackets with competitor present (A+C+) reached. An extended version of the "statistical control of artifacts in dense array EEG/MEG studies" procedure (Junghöfer et al. 2000) was used to identify and to correct further artifacts by channel interpolation where applicable. Total average rejection rate was 28% of trials. Subsequently, data were referenced to average reference and averaged for each participant and experimental condition separately. SSVEP amplitudes of both stimulation frequencies were quantified by a Fourier transform of the time interval 500–3500 ms after display onset. SSVEP amplitudes were divided by the mean amplitude across conditions to yield normalized amplitudes which allowed us to average across both stimulation frequencies. Averaged normalized amplitudes were compared by a 2-way repeated measures analysis of variance (ANOVA) with factors of attention (attended = A+ vs. unattended = A−) and competition (competitor present = C+ vs. absent = C−). Basic data-processing steps such as extraction of epochs from the continuous recordings, re-referencing and plotting scalp isocountour voltage maps made use of EEGLAB (Delorme and Makeig 2004) in combination with custom routines written in MATLAB (The Mathworks, Natick, MA). A general alpha criterion of P < 0.05 was used for all statistical comparisons performed.
elicited intermediate SSVEP amplitudes that were somewhat larger than those elicited by unattended brackets with competitor absent (A–C–) (Figs. 2B and 3A).

Given this identical pattern, we pooled amplitudes across frequencies, that is, left and right stimuli, for statistical analysis. In order to avoid biasing the results toward the stimulus that evokes a greater SSVEP amplitude, we normalized amplitudes prior to averaging (see Materials and Methods). Pooled normalized amplitudes were subjected to a repeated measures ANOVA with the 2 factors of attention (attended vs. unattended) and competition (competitor present vs. absent). Amplitudes were significantly greater when the corresponding bracket was attended compared with when it was unattended (main effect attention, $F_{1,13} = 47.37, P < 10^{-7}, \eta^2 = 0.60$) and significantly reduced when competitors were present compared with when they were absent (main effect competition, $F_{1,13} = 18.25, P < 0.001, \eta^2 = 0.11$). Contrary to the prediction of biased competition accounts of human visual attention, we found no indication that attentional gain depends on the presence or the absence of a competitor (interaction attention × competition, $F_{1,13} = 0.02, P = 0.89, \eta^2 < 10^{-3}$). Thus, attentional gain and competition modulated SSVEP amplitude in an independent additive fashion (Fig. 3B).

Further contrasts (two-tailed paired $t$-tests) were calculated to confirm specific effects of attention and competition. They revealed that attention increased SSVEP amplitude significantly in both the absence ($t_{13} = 6.63, P < 0.001$) and the presence ($t_{13} = 5.40, P < 0.001$) of the competitor. Vice versa, the presence of a competitor suppressed SSVEP amplitude significantly both when the stimulus was attended ($t_{13} = 3.00, P < 0.05$) and when it was unattended ($t_{13} = 3.55, P < 0.01$). A comparison of the magnitudes of the attentional gain (attended minus unattended) and the suppression by competition (competitor absent minus present) on stimulus processing showed that gain influenced SSVEP amplitude more strongly ($t_{13} = 2.85, P < 0.05$).

Although our experiment was not designed to investigate temporal characteristics of neural attentional gain and competition mechanisms, an exploratory analysis of SSVEP amplitude time courses suggested that the effects were consistent across entire trials (see Supplementary Data and Fig. S1a).

**Source Localization**

As depicted in Figure 2C, effects of attentional gain and competition on SSVEPs were generally localized to occitoparietal areas contralateral to the driving bracket. The Montreal Neurological Institute (MNI) coordinates (Evans et al. 1993) of the maximum attentional modulation were 28, −92, and −10 (x; y; and z) for the SSVEP driven by the left bracket and −15, −99, and −2 for the SSVEP driven by the right bracket. Maximum modulation by competition was localized to MNI coordinates 21, −92, and −10 (left bracket) and −27, −92, and −10 (right bracket). Loci of maximum modulation by attentional gain and competition showed large congruencies for both stimulation frequencies. Occipital regions centered on respective lingual gyri included early visual areas V1, V2, and

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**Figure 2.** SSVEP topographies, grand average spectra, and cortical sources. (A) Spline-interpolated voltage maps of SSVEP amplitudes for both stimulation frequencies (i.e., response to each stimulus) averaged over all experimental conditions. Dashed black lines show the cluster of 13 occipital and parietal electrodes surrounding electrode Oz used in further analyses. (B) Grand-average power spectrum obtained by a Fourier transform of SSVEP waveforms for each condition averaged across the occipital electrode cluster described in A. Peaks correspond to the respective stimulation frequencies. (C) Statistical parametric maps of the cortical current density distributions giving rise to the SSVEP amplitude increases for attended versus unattended (A+ vs. A−, upper panel) and presented alone versus presented with competitor (C− vs. C+, lower panel) for left (left panel) and right brackets (right panel), respectively. Color scale represents $T^2$ values above the $P < 0.001$ threshold (corrected for multiple comparisons).
We recorded frequency-tagged visual-evoked responses to assess the influences of 2 mechanisms of attention—gain and competition—on the processing of individual simultaneously presented stimuli. Our results corroborate earlier findings that attending to a flickering stimulus increases its corresponding SSVEP amplitude (Müller et al. 2003; Quigley et al. 2010; Andersen et al. 2011) even when it is presented in the absence of a nearby competitor (Morgan et al. 1996; Müller et al. 1998; Kim et al. 2007). Also in accordance with recent studies the presence of nearby competitors suppressed SSVEP amplitudes (Fuchs et al. 2008; Busse et al. 2009; Keitel et al. 2010). The corresponding diminished processing of task-relevant stimuli was further reflected in decreased performance in the behavioral task. Processing of attended and unattended stimuli was equally suppressed by the presence of a competitor in close spatial proximity. Moreover, attentional gain influenced SSVEP amplitude more strongly than competition. Cortical sources of attentional gain and competition effects largely overlapped suggesting common neural generators.

Our findings obtained with the given stimulation cannot easily be reconciled with the idea of attention resolving competition by releasing an attended stimulus from mutual suppression as put forward in biased competition accounts of human visual attention (Desimone and Duncan 1995; Duncan et al. 1997; Kastner and Ungerleider 2001). They are better captured by a combination of assumptions from biased competition and sensory gain control. Specifically, rather than modulating suppressive interactions per se, here, the attentional bias acts to enhance stimulus processing at attended locations. An attended stimulus is thus never released from mutual suppression but processing is still biased toward it. The present data support this notion as we found that 1) stimulus processing was subject to attentional gain even if no nearby (<1°) competitor was present. 2) The gain effect was greater than the competition effect and thus exceeded the limit that could be explained by a release from mutual suppression. This is well in-line with other recent studies indicating that attentional gain and competition could indeed influence stimulus processing independently (Scalf and Beck 2009; Scalf et al. 2011) and on different time scales (Andersen and Müller 2010). Recent computational models also acknowledge an attentional bias that extends beyond the modulation of mutual suppression by implementing an independent attentional gain factor (Womelsdorf et al. 2008; Boynton 2009; Reynolds and Heeger 2009). We simulated data based on our experimental stimulation with the Normalization Model of Attention (Reynolds and Heeger 2009; Herrmann et al. 2010) and found them to closely resemble the experimental results (see Supplementary Data and Fig. S2). In fact, an early computational model of biased competition derived from single-cell results might already be compatible with our data (Reynolds et al. 1999). Interestingly, this model also preserves the inhibitory influence of a competitor on the attended stimulus when presented to the same RF. Complementing this result, another body of single-cell research demonstrated that attention may well modulate processing of single stimuli in an RF (Spitzer et al. 1988; Connor et al. 1997; Treue and Martínez Trujillo 1999; Ghose and Maunsell 2008).

Previous fMRI research has provided strong support for biased competition as an account of human visual attention without the need to assume additional sensory gain control (Kastner et al. 1998; Bles et al. 2006; Beck and Kastner 2009). In particular, a very recent study by McMains and Kastner (2011) provides compelling evidence for attentional gain interacting with competition in human visual cortex (areas V1-V4). However, these studies measured cortical responses to an entire multistimulus display that was presented only transiently (usually 250 ms). To our knowledge, the present study was the first to vary spatial attention and local competition while allowing a measurement of stimulus-specific processing. In
contrast to the above-mentioned studies, this enabled a direct comparison of individual stimulus processing between conditions "attended, competitor absent" and "attended, competitor present." Additionally, the present experimental paradigm featured a more naturalistic presentation that took several seconds. Effects of endogenously cued attention have been shown to take a substantial amount of time to build up (Müller et al. 1998; Andersen and Müller 2010; Buffalo et al. 2010; Bouvier and Engel 2011). In particular, suppressive effects on unattended stimuli only peak around 800 ms after cue (Andersen and Müller 2010). Hence, it is possible that previous fMRI studies sampled a highly dynamic process before it reached asymptote.

Our exploratory analyses suggest time-invariant influences of attentional gain and competition on visual stimulus processing (see Supplementary Data and Fig. S1a). Future frequency-tagging studies may employ paradigms including baseline periods to investigate time courses of stimulus processing more closely (see, e.g., Müller et al. 1998; Andersen and Müller 2010).

Regarding suppressive effects on SSVEP amplitude by competition, it is noteworthy that Kastner et al. (2001), using colored stimuli, demonstrated greater mutual suppression with increased RF sizes of cortical neurons. They found only minimal suppression for stimuli with a spatial separation of 1° of visual angle in primary visual cortex (V1) and maximal suppression in area V4. However, we localized cortical currents giving rise to suppressive effects on SSVEPs to V1–V3 with minor contributions from midtemporal motion sensitive area (MT/V5). The fact that we find robust effects of competition between achromatic stimuli might be due to 2 reasons. First, the textured outer brackets and competitors have a spatial separation of 0.62° of visual angle and thus are closer in space as compared with Kastner et al. (2001). The smaller distance corresponds well to the typical RF sizes of <1° in V1 (Dumoulin and Wandell 2008) and might have caused greater mutual suppression between stimuli. Second, our source analysis revealed suppressive effects on SSVEPs in cortical areas beyond V1. Neurons in these areas (V2 and V3) have RF sizes >1° (Kastner et al. 2001; Dumoulin and Wandell 2008) and therefore also contribute to the overall competition effect.

One might argue that our competitor-absent conditions should not be considered pure no-competition conditions as there is always 1 stimulus presented to each visual hemifield (see Fig. 1a). Therefore, conditions with competitors present versus absent might rather represent cases of more versus less competition when taking into account a possible competition between hemifields. Such an interhemifield competition might lead to an underestimation of competitive effects within the unattended hemisphere. Ultimately, our finding that attentional gain has a stronger influence on stimulus processing than competition might be partially explained by this underestimation. However, Schwartz et al. (2005) have demonstrated that interhemifield competition affects stimulus processing earliest in inferioparietal cortex but has no effect on retinotopically organized areas of occipital visual cortex during sustained stimulus presentation (20 s). Moreover, minimal stimulus separation between hemifields was above 5° of visual angle, a distance that has previously been shown to be sufficient to abolish suppressive effects on SSVEP amplitude even within hemifields (Fuchs et al. 2008). Another line of research suggests that processing concurrent stimulation in different visual hemifields might draw on largely independent resources (Alvarez and Cavanagh 2005; Delvenne et al. 2011; Delvenne and Holt 2012). As a consequence, 2 stimuli, each presented to one hemifield, would not have to compete for one common resource. Taken together, the above findings render interhemifield competition unlikely to affect the present results.

In conclusion, we here put a long-standing conceptualization of human visual attention to a new test. Based on findings that biased competition, a concept derived from single-cell studies, may well account for large-scale neural effects of attention, we expected spatially selective attention to release a stimulus from mutual suppression with a simultaneously presented competitor. Moreover, singly presented stimuli should have experienced smaller attentional gain as compared with when a nearby competitor was present. A macroscopic measure of human brain response allowed us to investigate these questions at the level of individual stimulus processing in multistimulus displays. Our findings challenge previous adoptions of biased competition as accounts of human visual attention. An attended stimulus was not released from mutual suppression in early human visual cortex. Instead, attention acted as a sensory gain control, equally modulating the processing of stimuli either presented alone or in the presence of a competitor. In-line with recent computational models of attention (Womelsdorf et al. 2008; Boynton 2009; Reynolds and Heeger 2009; see Supplementary Data), this critical finding argues for a conceptualization of human visual attention that is not only defined in the context of mutually suppressive stimulus interactions. It supports an extension of the bias in "biased competition" to an independent gain control mechanism to account for a more comprehensive range of attentional effects on conscious perception.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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Notes

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