Different Effects of Voluntary and Involuntary Attention on EEG Activity in the Gamma Band.

Voluntary attention and Gamma

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Key Words: Faces, Attention, Cueing, Eeg [Electro-Encephalogram], Gamma, Visual Selectivity
Abstract

Recent studies in animals and humans have shown that EEG activity in the gamma range can be modulated by attention. In the present study we compared this activity for voluntary and involuntary spatial attention in a spatial-cueing paradigm with faces as targets. The stimuli and trial timing were kept constant across attention conditions with only the predictive value of the cue changing. Gamma-band response was linked to voluntary shifts of attention but not to the involuntary capture of attention. The presence of increased gamma responses for the voluntary allocation of attention, and its absence in cases of involuntary capture, suggests that the neural mechanisms governing these two types of attention are different. Moreover, these data allow a description of the temporal dynamics contributing to the dissociation between voluntary and involuntary attention. The scalp distribution of this correlate of voluntary attention is consistent with a top-down process involving primarily contralateral anterior and posterior regions.
Introduction:

Behavioral evidence suggests that spatial attention can be summoned in at least two ways. One way is goal directed and engages top down control mechanisms, while the other is automatic and independent of the task. The former is often referred to as endogenous or voluntary attention (Posner 1978) and the latter as exogenous or involuntary attention (Jonides 1981).

Ample evidence, using the spatial-cueing paradigm (Posner 1978), Figure 1a), indicates that for both voluntary and involuntary attention, targets are detected and discriminated faster at a validly-cued location compared to invalidly-cued locations (the “validity effect”). It is often assumed that both forms of attention enhance perceptual processing similarly and are controlled by the same neural mechanisms (Gazzaniga et al. 1998). However, behavioral evidence indicates that voluntary and involuntary attention might have different time courses and consequences (Müller and Rabbitt 1989; Berger et al. 2005).

In the present study a cueing task was combined with electrophysiological measures, to examine and compare voluntary and involuntary attention in identical stimulus conditions. Of particular relevance was the ability of EEG to distinguish neural activity elicited during different
stages of selective spatial attention (i.e. spatial cue processing vs. target processing).

Previous work coupling electrophysiology with cueing paradigms have typically focused on Event-Related Potentials (ERPs). These studies often focused on differences in ERPs to cued targets compared to uncued targets. The most consistent finding is an increase in early sensory potentials (P1 component) elicited by a cued target compared to an uncued target (Mangun and Hillyard 1991; Hopfinger and Ries 2005). Later components may also be modulated, but the results are less consistent. For example, while some authors reported greater N1 on valid trials (Luck et al. 1994) others found the reverse (greater N1 on invalid trials, (Hopfinger and Ries 2005). Hopfinger and West (2006) measured interactions between voluntary and involuntary attention with a paradigm manipulating the two types of attention concurrently. Their findings indicated that although mutually affecting each other, voluntary and involuntary attention act on different stages of processing. However, in the procedure used by Hopfinger and West the voluntary and involuntary cues were visually different, and were presented at different times in a given trial. Voluntary and involuntary attention effects have seldom been directly compared under equal stimulus conditions within the same ERP study. Studies that attempted this
comparison, revealed no marked differences in the amplitudes of either P1 or N1 (Doallo et al. 2005).

Recent work in both animals and humans examined the spectral content of the EEG signal (Gruber et al. 1999; Fries et al. 2001; Vidal et al. 2006; Fan et al. 2007) suggesting that activity in the gamma range (>20Hz, Tallon-Baudry, and Bertrand, 1999) is modulated by attention. We therefore focused on the gamma-band response as it relates to voluntary and involuntary attention. Whereas ERPs did not distinguish voluntary from involuntary attention, we report clear differences between these two attention systems in the gamma band.

**Materials and Methods:**

*Task and Procedures* – Participants performed an easy face-discrimination task under conditions of voluntary and involuntary attention conditions. As shown in Figure 1a, one of two faces was presented immediately after a cue offset, either to the left or to the right of fixation, and the participants reported which face had been presented by pressing one of two keys as rapidly as possible. A peripheral cue preceded the target face in both voluntary and involuntary conditions. Voluntary attention was measured in the predictive-cue condition. In this condition the face appeared more often in the cued location (70% valid) than the uncued location.
Involuntary attention was measured in the nonpredictive-cue condition. In this condition the cue location was unrelated to target location. Both conditions included target-absent trials, which allowed evaluation of cue-related activity in isolation of a target face. A third key was used to report the absence of a target. The only difference between the attention conditions was the proportion of valid, invalid, and cue-only trials. This design enabled examination of the physiological time course of cue and target processing for voluntary and involuntary attention without confounding physical stimulus parameters. The predictive-cue-condition consisted of six 100-trial blocks separated by breaks. The nonpredictive-cue-condition consisted of five 112-trial blocks (see figure 1a). Each participant completed one cue-condition before starting the other cue-condition, and cue conditions were counterbalanced between subjects. Each cue condition began with a short practice block (20 trials).

Note that in the predictive cue-condition (voluntary) the participant was encouraged to utilize the cue when it appeared, and anticipate the probable location of the target. In the nonpredictive cue-condition (involuntary) participants were instructed to ignore the cues as they are independent of target location. Here, predictive and nonpredictive cue conditions were used as operational variables for voluntary and involuntary
attention. With a predictive cue voluntary attention would be allocated when
the cue appears. With a nonpredictive cue voluntary attention will not be
allocated until the target appears.

Insert figure 1 about here

Stimuli  - Stimuli were presented on a 20” monitor. Seen from 155
cm, the visual angle of each cueing square was 2.2°, and they were centered
2.7° from a 0.4° fixation cross. Faces appeared centered in one of the
squares and were 2.4° wide.

Participants - Sixteen UC-Berkeley undergraduates participated in the
experiment for class credit. All participants had normal or corrected-to-
normal visual acuity. All gave informed consent as approved by the UC-
Berkeley IRB before participation began.

EEG acquisition and post processing - EEG was recorded by a
Biosemi Active Two system at a sampling rate of 256 Hz from 64 electrode
sites of a modified 10-20 system montage. Horizontal electrooculographic
(EOG) signals were recorded at the left and right external canthi, and
vertical EOG signals were recorded below the right eye. Scalp electrodes, as
well as the EOG electrodes were referenced off line to the tip of the nose.
Preprocessing of the data was done in Brain Vision Analyzer. Trials with
eye movement or blinks were removed from the data using an amplitude
criterion of $\pm 150\mu V$ or lower. Ongoing EEG was segmented into epochs from 200 ms before cue onset to 1000 ms after cue onset of correctly performed trials. These data were then exported to EEGLAB (Matlab Toolbox; Delorme and Makeig 2004) for spectral analysis.

EEG spectral analysis - To measure the spectral power at each frequency band and time point, the data were processed using the “timef” function of EEGLAB (Delorme and Makeig 2004). For each experimental condition, approximately 60 randomly-selected EEG epochs were convolved with Gaussian-windowed sinusoidal wavelets of two-cycle duration (identical results were obtained using fixed moving window Fast Fourier Transform). At each frequency band, the mean spectral energy of the pre-stimulus baseline (from -200 to -50 ms, excluding the last 50ms of fixation in which fixation changed color) was subtracted from the pre- and post-stimulus time frequency energy. The absolute power measure was converted to decibels (dB; $10 \times \log (\mu V^2)$). Baseline levels in the two attention conditions were equivalent as revealed by a planned paired t-test $[t(15)=1.05, p=0.92]$. The resulting time-frequency maps were averaged across trials for each subject to form the event-related spectral perturbation (Makeig, 1993). The individual subject maps were averaged to create grand average ERSP maps (figure 2).
For statistical analysis an unbiased time by frequency range of maximal gamma-band response was selected from the averaged data for cue related responses and target-related responses separately (Yuval-Greenberg 2007). The average power within these regions for each condition was then used as the dependent variable in an ANOVA with repeated factors. Due to the wide scalp distribution the data were collapsed for analysis into three groups (anterior, central and posterior) in each hemisphere (Gruber et al. 1999; see Supplementary Material 1).

**ERP analysis:** Segmented data was averaged separately for each condition. Averaged waveforms were band pass filtered (0.8 Hz-17 Hz 24db/oct as in Zion-Golumbic and Bentin 2006) and baseline corrected from 100 ms pre-cue-onset. For each participant the P1 peak was determined as local maximum between 80-150 ms post target onset and the peak of the N170 face selective component (Bentin et al. 1996) was determined as local minimum between 130-220 ms. Amplitudes of these components at sites P8, PO8 and P10 over the right hemisphere and the homologue sites over the left were included in the analysis. ANOVA with repeated measures with factors cue-condition (predictive, nonpredictive), hemisphere (left, right), site (P7/8, PO7/8, P9/10), target-side (Left, Right) and Validity (Valid, Invalid) were
Results:

Performance:

Overall, discrimination of targets was faster for valid than invalid trials (Figure 1b). The validity effect was greater in the predictive than nonpredictive cue condition. These results were supported by a two-way ANOVA conducted for target-present trials. Overall, responses were slightly faster in the predictive than the nonpredictive cue condition. However this difference was not significant \([F(1,15)=3.32, \ p=0.09]\). The validity effect was significant \([F(1,15)=30.29, \ p<0.001]\), and interacted with cue condition \([F(1,15)=15.91, \ p<0.01]\). This interaction indicated that validity effects were larger in the predictive-cues-condition than in the nonpredictive-cue-condition. Planned paired comparisons indicated that in both cue conditions the validity effect was significant \([t(15)= 5.14, \ p<0.001]\) for predictive and \(t(15)= 3.4, \ p<0.01\) for nonpredictive]. For target absent trials, performance was identical for the two cue conditions (636 ms in both).

The percent correct for valid and invalid trials following predictive cues were 94.7% and 92.4% respectively. The corresponding accuracy rates following nonpredictive cues were 95.2% and 93%. ANOVA showed a
main effect of validity in error rates [difference=2.25%, F(1,15)=17.3, p<0.01] and no interaction with cue condition [F<1].

Spectral analysis:
Activity within the gamma range (30-70 Hz) was averaged for the temporal window from 150 to 225 ms post-cue-onset to measure cue-related activity and from 150 to 225 ms post-target-onset to measure target related-activity (figure 2, time frequency window selection process as described in the methods section).

Cue Related Activity -- Analysis of target-absent trials showed that gamma band power to cues was higher in the predictive than in the nonpredictive cue condition (Figure 2a). This observation was supported by an ANOVA with cue condition (predictive, nonpredictive), cue-side (left, right), hemisphere (left, right), and site (posterior, central, anterior). The main effect of cue condition was significant [F(1,15)=4.63, p<0.05] while the effects of all other factors were not (for the complete statistical analysis, see Supplementary Table 1).

Target Related Activity -- The gamma activity elicited in the predictive cue condition by invalid targets was higher than that elicited by valid targets. In the nonpredictive cue condition, to the gamma elicited by
both target types (valid and invalid) was similar (Figure 2b). An ANOVA with cue condition (predictive, nonpredictive), validity (valid, invalid), target-side (left, right), hemisphere (left, right), and site (posterior, central, anterior) as within subject factors showed a main effect of validity [F(1,15)=5.12, p<0.05], which interacted with cue condition [F(1,15)=4.7, p<0.05]. Paired planned comparisons showed that in the predictive cue condition gamma-band response was significantly greater on invalid then valid trials [F(1,15)=5.20, p<0.05]. In the nonpredictive-cue condition this was not the case [F(1,15)=3.51, p=0.08]. The trend in the non predictive case could be due to a number of factors. Importantly, the significant interaction reflects the reliable differences in gamma activity between valid and invalid conditions for predictive and nonpredictive conditions.

In addition, the analysis revealed evidence for laterality in the gamma-band response in the predictive cue condition. Both the hemisphere by target side interaction and the hemisphere by target side by site interaction were significant [F(1,15)=6.20, p<0.05 and F(2,30)=7.04, p<0.01, respectively]. Gamma power was higher over the hemisphere contralateral to the target location than over the ipsilateral hemisphere. The difference between the

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1 It is possible that this trend reflects an indirect influence of involuntary capture on the distribution of attention. While nonpredictive cues do not elicit gamma band activity (fig 2a cue only nonpredictive trials), the RTs suggest that they indeed affect the locus of visual attention in space (fig 1b significant validity effect in the nonpredictive cue-condition). Hence, attentional capture, while having different temporal dynamics and seemingly different neural signatures, might determine the starting point from which a voluntary attentional shift is initiated upon target display. This account is post hoc and would require further experimental investigation.
contralateral and ipsilateral response was significant for posterior and anterior sites \[F(1,15)=7.16 \ p<0.05 \text{ and } F(1,15)=0.33, \ p<0.01 \text{ respectively}\]. Figure 3 presents scalp distributions of the gamma-band response at three time points after target onset (Figure 3a-c) demonstrating the differences in the propagation of gamma over different scalp sites (also see supplementary materials 2). For the central sites the statistical test did not reveal significant laterality effects (no target-side by hemisphere effect \[F(1,15)=2.086, \ p=0.169, \ ns\]).

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Insert figure 3 about here

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**ERPs:**

P1 and N170 components did not differ between predictive and nonpredictive cue-conditions \(F<1\) for all relevant comparisons for both P1 and N170 components). Both components showed maximal response for sites located contralateral to the target side (hemisphere x target side significant interaction: \(F(1,15)=8.16, \ P<0.05\) for P1 and \(F(1,15)=8.67, \ p<0.05\) for N170). Consistent with previous reports in the literature (Mangun and Hillyard 1991; Hopfinger and Ries 2005), for both attention conditions the P1 component was larger for valid conditions compared to invalid conditions when the target was presented in the contralateral visual field (supplementary material). This effect was supported by a significant
hemisphere by target side by validity interaction \( F(1,15)=17.142, p<0.01 \).
For the N170 no such validity effect was found (hemisphere by target side by validity: \( F(1,15)=1.23, \text{ ns } p=0.28, \text{ ns} \)).

**Discussion:**

The present findings demonstrate that voluntary and involuntary attention have different effects on gamma-band response whereas both affect RT similarly. These effects were manifested in two stages. The first was in response to the cue: only voluntary attention induced gamma band increases to the cue alone (predictive-cue condition). The second was in response to targets: gamma band increased whenever a voluntary shift of attention was required to a target. These patterns of gamma response and the way they relate to voluntary and involuntary attention are detailed in the following paragraphs.

Replicating many past studies, valid targets were detected faster than invalid targets regardless of the cue’s predictive value. This is evidence that abrupt onsets of peripheral stimuli captured the observer’s attention reflexively. When the cue was predictive, however, participants also oriented voluntarily to the cued location, which lead to enhanced validity effects. Since the addition of voluntary attention was the only difference between the two conditions, the higher the gamma power elicited by the
predictive relative to nonpredictive cues reflects EEG activity associated with voluntary attention\(^2\).

Responses to the targets differed depending on whether the cue was predictive or nonpredictive. In the nonpredictive condition, when the target appears, a voluntary attention shift to the target is required to carry out the discrimination task (for both valid and invalid trials). EEG response in those trials reveals that after a target appears in the nonpredictive condition, there is an increase in the gamma-band response (Figure 2b). Hence for the nonpredictive cue condition, response to the targets is supporting the correspondence between gamma-band response and voluntary shifts of attention.

In the predictive cue condition, on valid trials, the cue summoned voluntary attention and there is no additional shift required to the target. In these trials, there was less gamma-band response because participants had already shifted their attention to the cued location. In contrast, in invalid trials, while a shift of attention has occurred to the predictive cue, attention has shifted to the wrong location and an additional shift of attention is required when the target appears. Examining the EEG response in these trials reveals a marked increase in gamma-band response on invalid trials.

\(^2\) The time course of the voluntary attention EEG modulation found here is consistent with previous work measuring SSVEPs in response to an attentional cue in a sustained attention paradigm (Müller et al, 1998).
Once again, EEG response in the gamma band seems to mirror the voluntary shift of spatial attention.

Previous investigations in the spectral domain of the EEG signals have suggested diverse roles for gamma activity which include perception, higher cognitive functions such as memory and object representation (Herrmann et al. 2004; Zion-Golumbic and Bentin 2006). Tallon-Baudry et al. (Tallon-Baudry and Bertrand 1999) have extensively examined the role of gamma band activity in perceptual binding. In initial studies gamma activity was measured to stimuli requiring perceptual integration to form a visible object. However, since the object requiring binding was also the object of attention, it was unclear whether the factor eliciting the increases in induced gamma in these studies was perceptual binding, attentional selection or some combination of the two (Tallon-Baudry et al. 2005).

Recent work has shown that gamma-band response can be related to selective attention. Gruber et al. (Gruber et al. 1999) have reported increases in gamma band activity at parieto-occipital sites contralateral to attended movement, and recently Vidal et al. (Vidal et al. 2006) have dissociated between the response to visual grouping and focused attention. In this study however participants were requested to selectively attend to a subset of the stimuli in a display for later report of the items orientation, a task involving a
memory component in addition to the selective attention components. Fan et al. (Fan et al. 2007) have recently reported increases in gamma-band response to a peripheral predictive cue, as we found here. The authors term this effect a spatial-orienting effect. However in their study it is unclear whether these increases are due to the peripheral sensory stimulation, the exogenous capture of attention by the peripheral cue or the voluntary deployment of attention to the cued location (cues were 100% predictive).

Our data rule out a sensory interpretation for these findings and suggest that increases in gamma-band response are related to voluntary rather than involuntary deployment of attention. Because mechanisms of selection and perceptual organization are thought to be highly interactive, perceptual binding and attention are difficult to tease apart. In the present study we circumvented this problem by observing the effects of voluntary and involuntary attention on gamma band activity in the absence of sensory differences between these two attention conditions. It might be the case that the neural mechanisms that support voluntary shifts of attention are also involved in perceptual binding (Treisman and Gelade 1980), however these questions await further investigation.

In contrast to gamma, ERPs did not discriminate between voluntary and involuntary attention. Similar to previous studies (Mangun and Hillyard
1991; Schuller and Rossion 2001; Hopfinger and Ries 2005) we found evidence for early sensory processing for validly cued compared to invalidly cued locations (as indicated by a larger P1 component on valid trials). However, this difference was largely unaffected by cue predictability (Doallo et al. 2005). This dissociation between higher frequency responses in the gamma band range and the low frequency responses in ERPs suggest that high- and low-frequency EEG activity reflect different neural mechanisms.

Our findings in the gamma-band response relate to previous findings from single unit recordings. In monkey V4, gamma activity correlates with attentional selection (Fries et al. 2001). Recordings in this study were limited to the extra-striate regions. Our data are complementary to the animal work, as they reveal contralateral responses to predictive cues and attended targets that initially appear in anterior regions and then propagate to posterior regions (figure 3 and supplementary movie). Such contralateral fronto-parietal distribution is consistent with evidence from both fMRI studies in humans and investigations in animals showing the relevance of cortical regions such as the frontal eye fields (FEF) in selective voluntary attention (Corbetta 1998; Buschman and Miller 2007).
Other frequency bands may also show interesting modulations with attention. EEG Activity in the alpha-band has been shown to be modulated by sustained voluntary attention (Worden et al. 2000, Thut et al. 2006). However, these modulations typically take 400ms to develop after the onset of a spatial cue. It is possible that alpha-band and gamma-band-responses are linked, and future studies could address this issue using longer cue target intervals than those used here. The present study was designed to allow a direct comparison between voluntary and involuntary attention requiring relatively short cue to target intervals.

The differences in neural response between voluntary and involuntary attention conditions fit well with the hypothesis that they involve different mechanisms and suggest how these two types of attention may affect performance and perceptual processing. Previous support for this hypothesis can be found in both behavioral and imaging work. RT studies showed that involuntary attention effects dissipate rapidly and reverse at long cue-target SOAs while the effects of voluntary attention on performance are sustained (Berger et al. 2005). Prinzmetal et al. (2005) suggest that there are several cases where voluntary attention affects accuracy while involuntary attention does not within identical stimulus conditions. fMRI studies also report differences between voluntary and involuntary attention, mostly in dorsal
regions (Mayer et al. 2004; Kincade et al. 2005). A recent study by Esterman and colleagues (Esterman et al. under review) demonstrated that BOLD response to faces in the fusiform face area (FFA; Kanwisher et al. 1997) increased when a target face was presented at a cued location compared to an uncued location, but only if the cues were predictive of target location. The current EEG study provides insight to the temporal dynamics of voluntary and involuntary attention and reveals that gamma-band response reflects voluntary shifts of attention.
References


Esterman, M., W. Prinzmetal, et al. (under review). "Voluntary and Involuntary Attention Effect Face Discrimination Differently."


Figure Captions:

**Figure 1:** a) trial structure: After 1s of fixation (fixation changed color for the last 50ms pre-cue onset) a cue (one rectangle changed to red, denoted by the dotted rectangle) was displayed for 250 ms, followed by one of two face targets displayed for 300 ms or a blank screen. Below the illustration are the probabilities (and trial numbers) of each trial-type (valid, invalid, cue-only) in the different cue conditions (predictive and nonpredictive). Participants indicated by a key press which face appeared or whether no face appeared. 
b) Reaction time performance. In addition to the simple effects there was a significant validity effect and a significant interaction between validity and cue condition.

**Figure 2:** Time (x-axis)/frequency (y-axis) plots for nonpredictive (left column) and predictive (right column) conditions. (a) Data from cue only trials. Cue onsets at zero -- marked by an arrow. (b) Data from target present trials (valid in the first row, invalid in the second row). Target onsets at zero -- marked by an arrow. Dark rectangles mark the time/frequency window used in the statistical analysis.

**Figure 3:** The scalp distributions of gamma band activity at different time points on invalid trials in the predictive cue condition. (a-c) Scalp distributions at latencies 141ms, 198ms and 236ms respectively. Frequencies 30-70 Hz were collapsed, and scales changed in order to emphasize differences in activity between different sites at a given time point. A dynamic representation of this activity is shown in supplementary material 2.
Supplementary Material

**Figure S1:** A schematic of the sites grouped for the spectral analysis statistics. Anterior, central and posterior groups outlined in dashed, gray and black lines respectively.

**Movie S2:** A dynamic demonstration of the distribution and the propagation of gamma band activity across the different scalp sites. Invalid trials with targets on the left side of the screen from the predictive block were used. Gamma activity was averaged for the range of 30-70 Hz. Activity to target is depicted from 100 ms following target onset to 300 ms following target onset.

**Figure S3:** ERP waveforms to voluntary and involuntary cue conditions (a and b respectively) at contralateral-to-target channels (P7/8, PO7/8, P9/10 collapsed over side). Cue only trials were subtracted from target present trials and wave forms were baseline corrected from 100 ms pre target onset to produce this figure.
a) trial structure: After 1s of fixation (fixation changed color for the last 50ms pre-cue onset) a cue (one rectangle changed to red, denoted by the dotted rectangle) was displayed for 250 ms, followed by one of two face targets displayed for 300 ms or a blank screen. Below the illustration are the probabilities (and trial numbers) of each trial-type (valid, invalid, cue-only) in the different cue conditions (predictive and nonpredictive). Participants indicated by a key press which face appeared or whether no face appeared.

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<th>Non Predictive</th>
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b) Reaction time performance. In addition to the simple effects there was a significant validity effect and a significant interaction between validity and cue condition.
Time (x-axis)/frequency (y-axis) plots for nonpredictive (left column) and predictive (right column) conditions. (a) Data from cue only trials. Cue onsets at zero -- marked by an arrow. (b) Data from target present trials (valid in the first row, invalid in the second row). Target onsets at zero -- marked by an arrow. Dark rectangles mark the time/frequency window used in the statistical analysis.
The scalp distributions of gamma band activity at different time points on invalid trials in the predictive cue condition. (a-c) Scalp distributions at latencies 141ms, 198ms and 236ms respectively. Frequencies 30-70 Hz were collapsed, and scales changed in order to emphasize differences in activity between different sites at a given time point. A dynamic representation of this activity is shown in supplementary material 2.
Figure S1
ERP waveforms to voluntary and involuntary cue conditions (a and b respectively) at contralateral-to-target channels (P7/8, PO7/8, P9/10 collapsed over side). Cue only trials were subtracted from target present trials and wave forms were baseline corrected from 100 ms pre target onset to produce this figure.
Supplementary Table 1: Complete statistical analysis of the gamma band response

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