

# Visual Grouping and the Focusing of Attention Induce Gamma-band Oscillations at Different Frequencies in Human Magnetoencephalogram Signals

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## Abstract

■ Neural oscillatory synchrony could implement grouping processes, act as an attentional filter, or foster the storage of information in short-term memory. Do these findings indicate that oscillatory synchrony is an unspecific epiphenomenon occurring in any demanding task, or that oscillatory synchrony is a fundamental mechanism involved whenever neural cooperation is requested? If the latter hypothesis is true, then oscillatory synchrony should be specific, with distinct visual processes eliciting different types of oscillations. We recorded magnetoencephalogram (MEG) signals while manipulating the grouping properties of a visual display on the one hand, and the focusing of attention to memorize part of this display on the other hand. Grouping-related gamma oscillations were present in all conditions but modulated by the grouping properties of

the stimulus (one or two groups) in the high gamma-band (70–120 Hz) at central occipital locations. Attention-related gamma oscillations appeared as an additional component whenever attentional focusing was requested in the low gamma-band (44–66 Hz) at parietal locations. Our results thus reveal the existence of a functional specialization in the gamma range, with grouping-related oscillations showing up at higher frequencies than attention-related oscillations. The pattern of oscillatory synchrony is thus specific of the visual process it is associated with. Our results further suggest that both grouping processes and focused attention rely on a common implementation process, namely, gamma-band oscillatory synchrony, a finding that could account for the fact that coherent percepts are more likely to catch attention than incoherent ones. ■

## INTRODUCTION

Oscillatory synchrony has been associated with a number of cognitive processes and, in particular, with visual grouping, attention, and memory (Herrmann, Munk, & Engel, 2004; Tallon-Baudry & Bertrand, 1999). How can the same neural mechanism be associated with processes as different as visual grouping, attention, and memory? This could indicate that oscillatory synchrony is a nonspecific phenomenon, accompanying any demanding task (Shadlen & Movshon, 1999; Usrey & Reid, 1999). On the other hand, it could indicate as well that oscillatory synchrony is a fundamental basic mechanism engaged whenever neural cooperativity is required (Tallon-Baudry & Bertrand, 1999; Singer & Gray, 1995). If oscillatory synchrony is indeed a specific mechanism, then two distinct visual processes should elicit two distinct types of oscillatory synchrony. We examined this possibility by testing whether the oscillatory synchrony involved in visual grouping and the one elicited by the focusing of attention were distinct.

Experimentally, oscillatory synchrony in the gamma range (30–120 Hz) increases in response to coherent stimuli requiring visual grouping in animals (Woelbern, Eckhorn, Fries, & Bauer, 2002; Castelo-Branco, Goebel, Neuenschwander, & Singer, 2000; Gail, Brinksmeier, & Eckhorn, 2000; Fries, Roelfsema, Engel, Konig, & Singer, 1997; Gray & Viana Di Prisco, 1997; Kreiter & Singer, 1996; Fries, Eckhorn, Bauer, Woelbern, & Kehr, 1994; Kreiter & Singer, 1992; Engel, Konig, Gray, & Singer, 1990; Gray, Konig, Engel, & Singer, 1989) and humans (Gruber & Muller, 2005; Goffaux, Mouraux, Desmet, & Rossion, 2004; Kaiser, Buhler, & Lutzenberger, 2004; Grice et al., 2001; Gruber, Keil, & Muller, 2001; Csibra, Davis, Spratling, & Johnson, 2000; Keil, Muller, Ray, Gruber, & Elbert, 1999; Rodriguez et al., 1999; Muller, Junghofer, Elbert, & Rochstroh, 1997; Revonsuo, Wilenius-Emet, Kuusela, & Lehto, 1997; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997; Muller et al., 1996; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). Oscillatory synchrony is also enhanced when focusing attention on a subset of the visual scene in monkeys (Bichot, Rossi, & Desimone, 2005; Fries, Reynolds, Rorie, & Desimone, 2001) and humans (Gruber, Muller, Keil, & Elbert, 1999), or when paying attention to the stimulus to

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memorize it (Tallon-Baudry, Bertrand, Henaff, Isnard, & Fischer, 2005; Shibata et al., 1999). Last, memory formation or maintenance is accompanied by gamma oscillatory synchrony (Gruber & Muller, 2005; Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002; Fell et al., 2001; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998), and the strength of this synchrony is modulated by memory load (Howard et al., 2003; De Pascalis & Ray, 1998).

However, in all these experiments, only one process was studied at a time—be it grouping, attentional selection, or memory encoding. Are the oscillations observed specific of the visual process studied or are they the same whenever a demanding visual task is proposed? To answer this question, we manipulated two visual processes independently (grouping and the focusing of attention) and analyzed the corresponding induced gamma oscillations.

Grouping may or may not depend on attention, depending on the type of grouping considered (Treisman, 1999; Moore & Egeth, 1997; Trick & Enns, 1997; Tsal, 1989). However, one type of grouping, namely, grouping by color similarity, is found to be a robust low-level phenomenon (Kimchi & Razpurker-Apfeld, 2004) that may even occur under conditions of inattention (Chang & Yeh, 2003). We therefore manipulated grouping by color similarity in our experiment (Figure 1), by showing the subject eight colored bars that were either all alike (*one-group* condition) or displays of eight bars that could be automatically split into two groups according to color similarity (*two-group* conditions, half of the bars are red and the other half green). Subjects had to memorize the display and, after a delay, indicate whether one of the bars of the test display changed in orientation.

The other process studied was the selective encoding of the display in short-term memory: Either subjects attended and memorized the whole display, or they at-

tended and memorized only half of it. The color of the central fixation cross indicated, at each trial, whether the subject should memorize the whole display (black or yellow cue, *distributed attention* conditions) or part of it: A red (respectively green) cross instructed the subject to attend and memorize only the red (respectively green) bars (*focused attention* conditions). To further distinguish between the neural correlates of grouping by color similarity and attentional focusing, the cue indicating the subject to focus his/her attention could be delivered at colored display onset or 600 msec later (*early* or *late focused attention* conditions). We thus varied both grouping by color similarity on the one hand, and the focusing of attention to memorize part of the scene on the other hand.

## METHODS

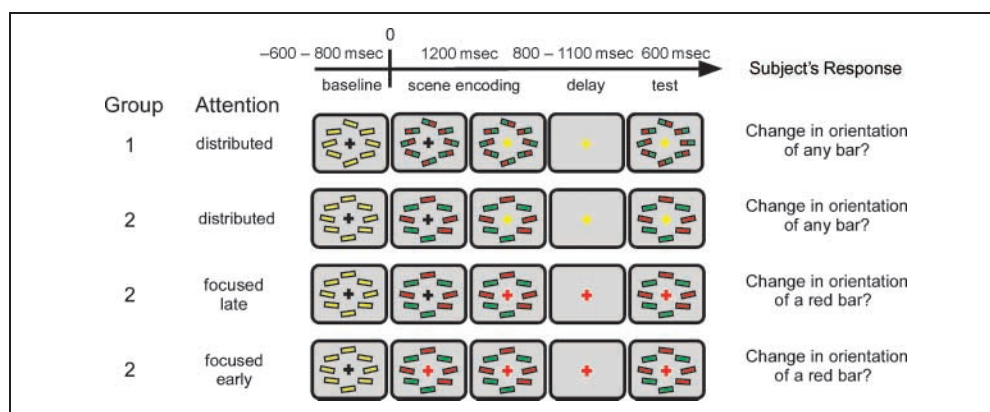
### Subjects

Twelve right-handed subjects (6 women, mean age: 23 years, range: 22 to 26 years) gave their informed and written consent and were paid to participate in the study. All subjects had normal vision. The study was approved by the local Ethical Committee on Human Research (CCPPRB no. 02033).

### Task

The experiment consisted in a delayed matching-to-sample task: Subjects were presented displays of eight oriented bars, and had to store in visual short-term memory the orientation of either half the display (four bars) or the whole display (eight bars) during the delay (blank screen). When the test stimulus appeared, subjects had to detect whether the orientation of one of

**Figure 1.** Subjects performed a delayed matching-to-sample task: They had to memorize the orientation of the bars in the display and after a delay decide whether or not one of the bars had changed in orientation. In the encoding phase, the display presented was either homogeneous (top row, all elements alike) or could be split in two groups according to color similarity (all other conditions). This resulted in two different grouping conditions, one



giving rise to the perception of a homogeneous group of eight items, the other in the perception of two groups of four items, one red and the other green. In addition, the color of the central fixation cross indicated the subject to focus his/her attention to either a subset of the display (a red cue indicates to pay attention and memorize the four red bars only) or to the whole display (a black or yellow cue indicates to pay attention and memorize the eight bars). Attention could thus either be focused on a subset of bars, or distributed on the whole display. In addition, to better disentangle the grouping by color similarity process from attentional focusing, the attentional cue (color of the fixation cross) could be delivered at scene onset or 600 msec after it (early focused attention or late focused attention conditions).

the previously memorized bars had changed. All four conditions have the basic structure of the above described delayed matching-to-sample task, that is, stimuli have to be encoded, stored, and retrieved from short-term memory. The visual processes of interest during scene encoding (color grouping and attentional focusing) were manipulated in four different experimental conditions. During encoding, each condition involves one type of grouping process (*one group* or *two groups*) and one type of attention (*distributed* or *focused*). This is summarized in the name of each condition, the first part referring to the grouping factor and the second part to the attentional state. In the one-group condition (top row), all bars were alike, half-red and half-green, whereas in all other conditions (*two-group* conditions), each bar was either red or green and the display could be segmented in two groups by color similarity. Attention could be either distributed across the entire display, or focused on one color group: If the central fixation cross turned yellow, the whole display had to be memorized (*distributed attention* conditions), if it turned red or green (*focused attention* conditions), only the four bars of that color had to be memorized. The color cue could be delivered at scene onset (*early focused attention* condition) or 600 msec after the beginning of scene encoding (*late focused attention* condition). The four conditions were randomly interleaved.

In the *two-groups, late focused attention* condition, each trial began with a display of eight yellow tilted bars (Figure 1, third row). The bars then changed color (but not orientation), becoming either red or green, forming spatially two color groups. After 600 msec, the black central fixations cross changed color: If it became red (respectively green), it indicated the subject to attend red bars (respectively green). After a delay of about 1 sec, the whole scene reappeared: Subjects had to detect a change in orientation of a bar of the selected group (red or green).

To control for the existence of an effective selective attention, we used the response behavior at test display (Figure 1). The yellow fixation cross indicated the subject to memorize the whole display (eight bars) in two conditions (*one-group, distributed attention* and *two-group, distributed attention* conditions). In the other two conditions (*early and late focused attention*), the subject memorized only four bars. The lower memory load in these two conditions should lead to better performances.

## Procedure

The experiment was divided in six recording blocks consisting of 80 trials each (20 trials per condition in randomized order). Subjects answered by pressing a button with one hand to signal a change, with the other hand to signal an absence of change. Response-to-hand

mapping was switched in the middle of the experiment and the whole sequence was balanced across participants. Subjects were asked to fixate the central cross during the whole trial. They were told to blink only when answering, or shortly after.

## Stimuli

Eight bars ( $0.55^\circ \times 0.14^\circ$ ) were displayed at  $0.8^\circ$  around a central fixation cross on a gray background (Figure 1). A new image was generated at each trial. The angle between each bar and the horizontal was randomly chosen between  $2^\circ$  and  $20^\circ$ . A change in orientation at test consisted in a rotation of the bar by  $-24^\circ$ . Stimuli were displayed by a video projector (refreshing rate 60 Hz) and back projected through a translucent screen at a viewing distance of 1.05 m. The video projector induced an additional delay of 25 msec to project the complete image on the screen as measured with a photodiode. The latencies reported in this article are not corrected for this delay.

## Recordings

Recordings were made with a CTF/VSM OMEGA 151 channels third-order gradiometers, high-end whole-head system magnetoencephalogram (MEG) system at the MEG-EEG Center, Pitié-Salpêtrière. Trials were recorded at a sampling rate of 1250 Hz (bandwidth 0–200 Hz) during epochs of 5.9 sec, beginning 0.8 sec prior to scene onset. Horizontal and vertical eye movements, as well as the electrocardiogram, were recorded. Raw signals were visually inspected, and trials containing muscle artifacts were manually rejected, as well as trials containing saccades larger than  $1^\circ$ . After artifact rejection, an average of 100 trials per subject was included in each condition. Cardiac artifacts picked up in the MEG signal were corrected by a correlation method (Gratton, Coles, & Donchin, 1983).

## Data Analysis

Behavioral data (performance and response times) were analyzed using an analysis of variance (ANOVA) with memory load as one factor. Response times were analyzed excluding outliers ( $<200$  msec and  $>2$  sec) and then excluding those reaction times outside two standard deviations from the mean.

Induced oscillatory activity, evoked oscillatory activity, and evoked field potentials were analyzed. Oscillatory activity was analyzed using a time–frequency (TF) representation on the basis of a Morlet wavelet transform of the signals. The wavelet family that was used was defined with the ratio  $f_0/\sigma_f = 7$  with  $f_0$  ranging from 8 to 120 Hz in 2 Hz steps (Tallon-Baudry & Bertrand,

1999; Tallon-Baudry, Bertrand, Delpuech, et al., 1997; Tallon-Baudry et al., 1996). This analysis was applied to single trials (induced and evoked oscillatory activity) and evoked fields. To isolate evoked components, we computed in addition the phase-locking factor (Tallon-Baudry et al., 1996) that varies between 0 (*purely non-phase-locked activity*) to 1 (*strictly phase-locked activity*).

To test for the existence of an induced response, the non-baseline-corrected data were compared with the mean power in the baseline (from -400 to -50 msec, before colored scene onset) using the nonparametrical Wilcoxon test for matched pairs.

Comparisons between conditions were performed on TF energy values that were baseline-corrected (division by the mean power in the baseline -400 to -50 msec) and log-transformed. The result has no unit. Positive (or negative) values thus indicate an increase (or decrease) in power with respect to baseline. This correction was performed independently for each frequency band. Data analysis was based on a segmentation in regions of interest defined in space (groups of sensors, time, and frequency). The definition of each region of interest is described in the Results section and illustrated in the corresponding figures. The mean power in these regions of interest was computed in each condition, and differences between conditions were analyzed using a nonparametrical Friedman test followed by Conover post hoc procedures for pairwise comparisons (Conover, 1980).

As a first approach, both correct and error trials were included in the analysis. This procedure has the advantage of balancing the number of trials analyzed in each condition. To check whether any of the significant results could be due to a difference between correct and incorrect trials, we systematically compared the mean power averaged across sensors of interest, in the corresponding TF windows, for correct and incorrect trials (Wilcoxon test for matched pairs).

## RESULTS

### Behavioral Results

Performance was higher in the two conditions with a low memory load compared with the two conditions

with a high memory load [Table 1, one-factor ANOVA  $F(2,10) = 70.5, p < .0001$ ]. There was no significant effect on reaction times [ $F(2,10) = 1.7, p = .2$ ]. Performance was thus better in the two conditions in which the subject was prompted to attend and memorize only part of the display (*focused attention* conditions), indicating that subjects effectively focused their attention on one color when instructed to.

### Grouping-related Activities

A high-frequency gamma response was present in all experimental conditions, in the 70–120 Hz band at central occipital sensors (Figure 2A–C). To test for the existence of a gamma response, we compared the mean (not baseline-corrected) TF activity in the 70–120 Hz band to baseline level (-400 to -50 msec). All conditions showed a high-gamma activity induced by the colored scene at central occipital sensors significantly larger than baseline (mean 180–430 msec, 70–120 Hz, averaged across MLO11, MRO11, MZPO2 and MRP31, nonparametrical Wilcoxon test, all conditions larger than baseline,  $p < .01$ ). This 70–120 Hz response was further modulated by the grouping properties of the stimulus (Figure 2B and C): It was larger in the one-group condition than in all other two-group conditions (Friedman test:  $F = 9, p < .001$ ; post hoc Conover procedures: one-group condition larger than all other conditions,  $p < .01$ ). The grouping-related 70–120 Hz response did not differ between correct and incorrect trials (Wilcoxon test for matched pairs, one-group condition,  $p = .87$ ).

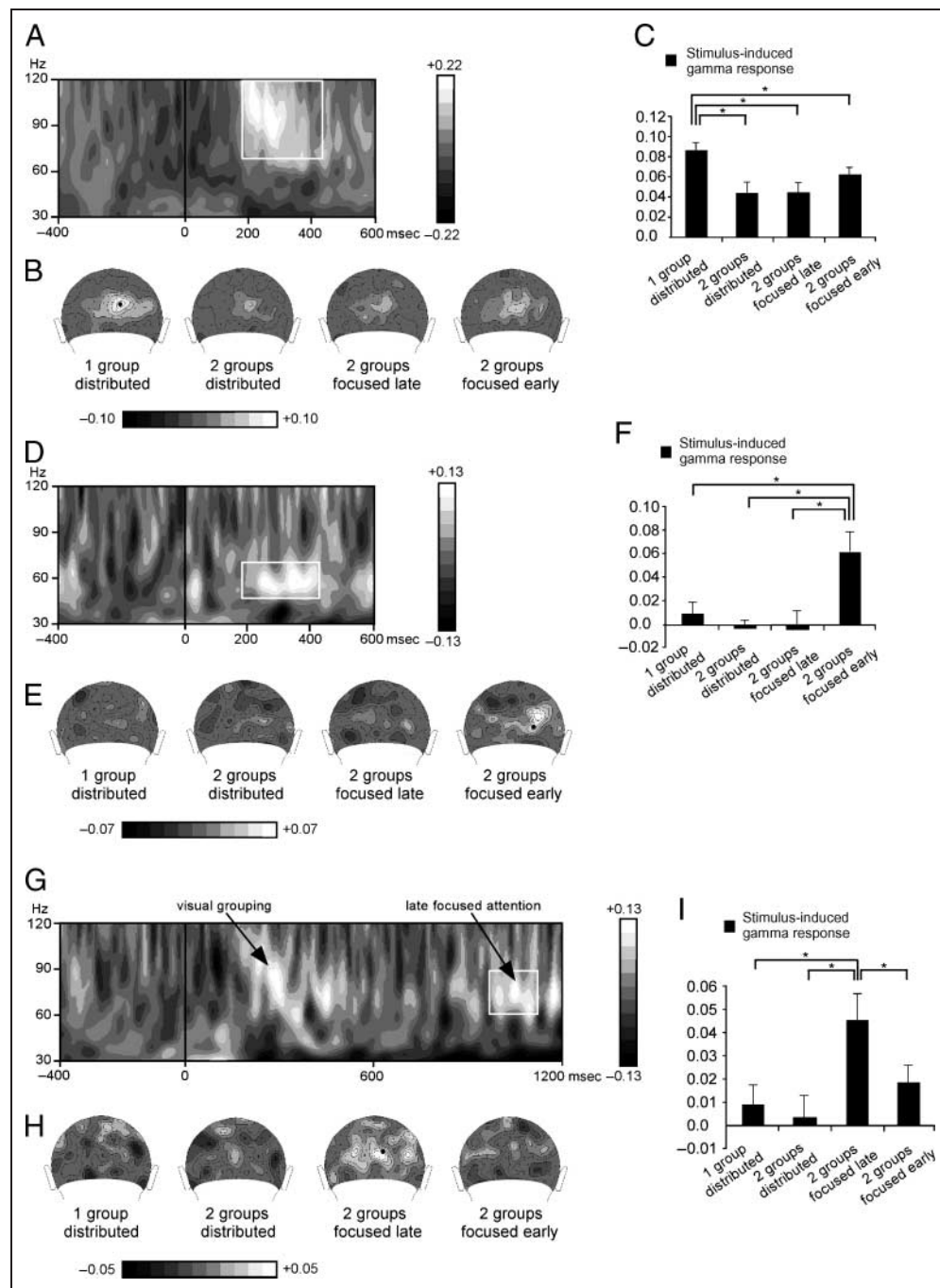
These results thus indicate that all stimuli elicited a high-frequency (70–120 Hz) induced gamma response at midline occipital sensors. This response was modulated by the grouping properties of the stimulus, being larger when all items were alike than when they could be split into two subsets according to their color. It should be noted that the 70–120 Hz gamma response was unaffected by the type of attention paid to the stimulus, being similar between the two-group, focused attention and two-group, distributed attention conditions (Figure 2B and C).

The evoked fields in the one-group condition differed from those in the two-group conditions around 90 msec

**Table 1.** Effect of Memory Load on Behavioral Data

Conditions	Memory Load	% Correct Responses $\pm$ SE	Reaction Times (msec) $\pm$ SE
One group distributed	8	64.66 $\pm$ 1.94	656.01 $\pm$ 33.76
Two groups distributed	8	65.22 $\pm$ 1.52	684.82 $\pm$ 37.56
Two groups focused late	4	83.82 $\pm$ 1.61	635.98 $\pm$ 34.72
Two groups focused early	4	75.37 $\pm$ 2.17	627.56 $\pm$ 30.62

**Figure 2.** Visual grouping and focused attention induced gamma responses (grand averaged across 12 subjects). Time–frequency (TF) power was normalized by prestimulus values, and the log-transformed resulting value has no unit. Error bars indicate the standard error of the mean. (A–C) Grouping-related gamma oscillations, 180–430 msec and 70–120 Hz. (A) The TF representation of power in the one-group, distributed attention condition at a central parietal sensor (MRP31) shows an increase in power in the 180–430 msec and 70–120 Hz interval (white rectangle). (B) Topographical map, back view, of the mean power in this interval. The black dot indicates the MRP31 sensor. (C) The mean 180–430 msec and 70–120 Hz power averaged across central occipito-parietal sensors is significantly larger in the one-group condition than in all other conditions (Friedman test:  $p < .001$ ). (D–F) Early focused attention-related gamma oscillations, 180–430 msec and 44–66 Hz. (D) TF power in the two-group, early focused attention condition at a right occipital sensor (MRO22). (E) Topographical maps, back view. The black dot indicates the MRO22 sensor. (F) Mean power averaged across a right parietal group of sensors is significantly larger in the two-group, early focused attention condition than in all other conditions (Friedman test,  $p < .01$ ). (G–I) Late focused attention-related oscillations, 850–1100 msec and 60–90 Hz. (G) TF power in the two-group, late focused attention condition at a central right occipito-parietal sensor (MZP02). (H) Topographical maps, back view. The black dot indicates the MZP02 sensor. (I) The mean power averaged across the central occipito-parietal group of sensors is significantly larger in the two-group, late focused attention condition than in all other conditions (central sensor group, Friedman test,  $p < .05$ ).



at left central sensors and around 170 msec at bilateral temporal sensors (Figure 5A–D), with larger field amplitudes in the one-group condition than in all other two-group condition (mean 85–95 msec amplitude averaged across sensors MLC23, MLC24, MLC31, MLC32, MLC33, MLC42, and MLP13:  $F = 4.97$ ,  $p < .01$ ; post hoc Conover procedures: one-group condition larger than all other conditions,  $p < .01$ ; mean 170–180 msec averaged

across left sensors MLT15, MLT16, MLT25, MLT26, MLP32, MLP33:  $F = 6.92$ ; post hoc Conover procedures: one-group condition larger than all other conditions,  $p < .01$ ; mean 170–180 msec averaged across right sensors MRO22, MRO33, MRT15, MRT25, MRT26, MRT35:  $F = 3.45$ ,  $p < .05$ ; post hoc Conover procedures: one-group condition larger than all other conditions,  $p < .05$ ).

### Early Focused Attention-related Activities

We observed activities related to the early focusing of attention on one color in the two-group, early focused attention condition, the only condition in which attentional focusing took place within the first 600 msec. A gamma activity, occurring in a lower-frequency range than the grouping-related gamma oscillations, was significantly larger in the early focused attention than in all other conditions (Figure 2D–F) at right parietal sensors (mean 44–66 Hz, 180–430 msec TF energy averaged across sensors MRO22, MRT16, MRP32, MRP33, and MRP34; Friedman test:  $F = 5.2$ ,  $p < .01$ ; post hoc Conover procedures: two-group, early focused attention condition larger than all other conditions,  $p < .01$ ). The attention-related 44–66 Hz response did not differ between correct and incorrect trials (Wilcoxon test for matched pairs, early focused attention condition,  $p = .48$ ).

To test for the existence of a gamma response, we compared the mean (not baseline-corrected) TF activity to the baseline level in all conditions. Only the early focused attention condition showed a significant 44–66 Hz, 180–430 msec response larger than baseline (nonparametrical Wilcoxon test, two-group, early focused attention larger than baseline,  $p < .005$ ; all other conditions,  $p > 0.2$ ). This 44–66 Hz response thus appears as an additional activity related to the focusing of attention, absent from all other conditions.

In the evoked fields, a peak was observed at occipito-parietal sensors (Figure 5E and F) at  $\sim 200$  msec after scene onset. The mean field amplitude averaged on left occipito-parietal sensors between 210 and 220 msec was significantly larger in the early focused attention condition compared with all other conditions (mean across MLO11, MLO12, and MLP31,  $F = 4.53$ ,  $p < .01$ ; post hoc

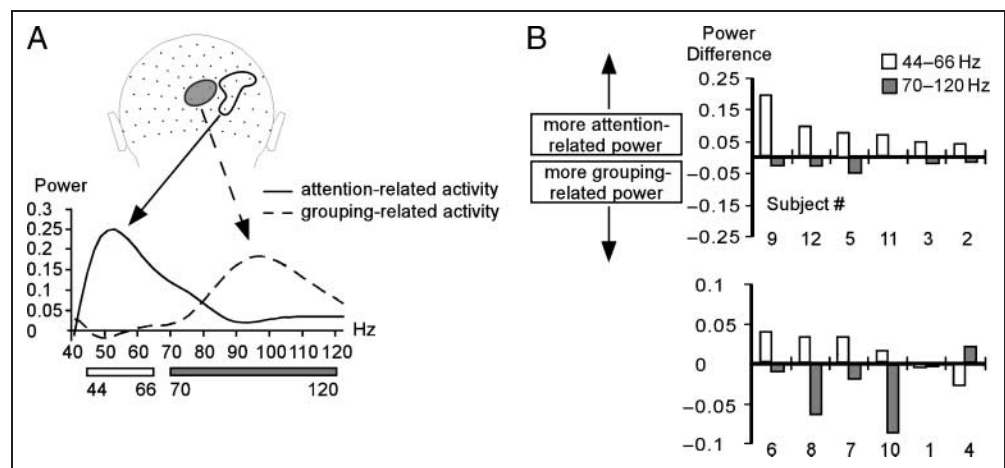
Conover procedures: two-group, early focused attention larger than all other conditions,  $p < .05$ ).

### Activity in Two Distinct Gamma Frequency Bands

We thus observed the existence of two distinct oscillatory activities, related to two distinct visual processes, occurring in two different frequency bands, and peaking at distinct sensors. The grouping-related oscillations occurred between 70 and 120 Hz and peaked at midline occipital locations, whereas the attentional focusing-related oscillations showed up between 44 and 66 Hz at right occipito-parietal locations.

This balance between two anatomical regions and two frequency bands is illustrated in Figure 3A for one subject: power between 44 and 66 Hz was large at right occipito-parietal sensors in the two-group, early focused attention condition, power between 70 and 120 Hz was large at central locations in the one-group, distributed attention condition. To investigate the existence of a functional specialization within the gamma band on a subject-by-subject basis, we measured the difference between grouping-related power and focused attention-related power in the two frequency bands of interest, 44–66 Hz and 70–120 Hz (Figure 3B). A positive difference in the 44–66 Hz range indicates the predominance of attention-related oscillations in the low gamma range, whereas a negative difference in the 70–120 Hz range indicates a predominance of grouping-related oscillations in the high gamma range. As can be seen from Figure 3B, 10 subjects out of 12 followed this pattern. The presence of a functional specialization in the gamma range, with grouping-related oscillations showing up at higher frequencies than

**Figure 3.** Activity in two distinct gamma frequency bands. (A) Power spectrum in the 180–430 msec interval in Subject 9, over central occipito-parietal sensors in the one-group, distributed attention condition (dashed line, grouping-related activity), and over right occipito-parietal sensors in the two-group, early focused attention condition (solid line, attention-related activity). The grouping-related activity peaks at 96 Hz, the attention-related activity at 54 Hz. (B) Difference between the grouping- and attention-related gamma powers in two frequency bands, 44–66 Hz (white) and 70–120 Hz (gray), for each subject. Positive values indicate more attention-related power and negative values more grouping-related power. Ten subjects out of 12 display the same functional specialization in frequency, with more attention-related power in the 44–66 Hz band and more grouping-related power in the 70–120 Hz band.



focused attention-related oscillations, is thus a robust phenomenon that can be observed on a subject-by-subject basis.

### Late Focused Attention-related Activities

An induced gamma activity in the 60–90 Hz range was observed in the two-group, late focused attention condition only, at about 850 msec after the onset of the visual scene, that is, ~250 msec after the onset of the attentional cue (Figure 2G). This power increase occurred at three locations: central, left, and right occipitoparietal sensors (Figure 2H).

Induced gamma activity was averaged between 60 and 90 Hz and between 850 and 1100 msec after scene onset. At all three locations, gamma power was significantly larger in the late focused attention condition than in all other conditions [left group (MLP32 and MLT16):  $F = 6.68$ ,  $p < .005$ ; central group (MRP31, MLO11, MRO11, MRO12, and MZPO2):  $F = 3.45$ ,  $p < .05$ ; right group (MRT14, MRT15, MRP34, and MRC24):  $F = 6.6$ ,  $p < .005$ ; post hoc Conover procedures: for all three locations, two-group, late focused attention condition larger than all other conditions,  $p < .05$ ]. The 60–90 Hz response did not differ between correct and incorrect trials in any condition (Wilcoxon test for matched pairs,  $p > .13$ ). The two conditions requiring attentional selection (early and late focused attention conditions) thus both present gamma oscillations, about 250 msec after the onset of the attentional cue, in partially overlapping frequency bands and topographies.

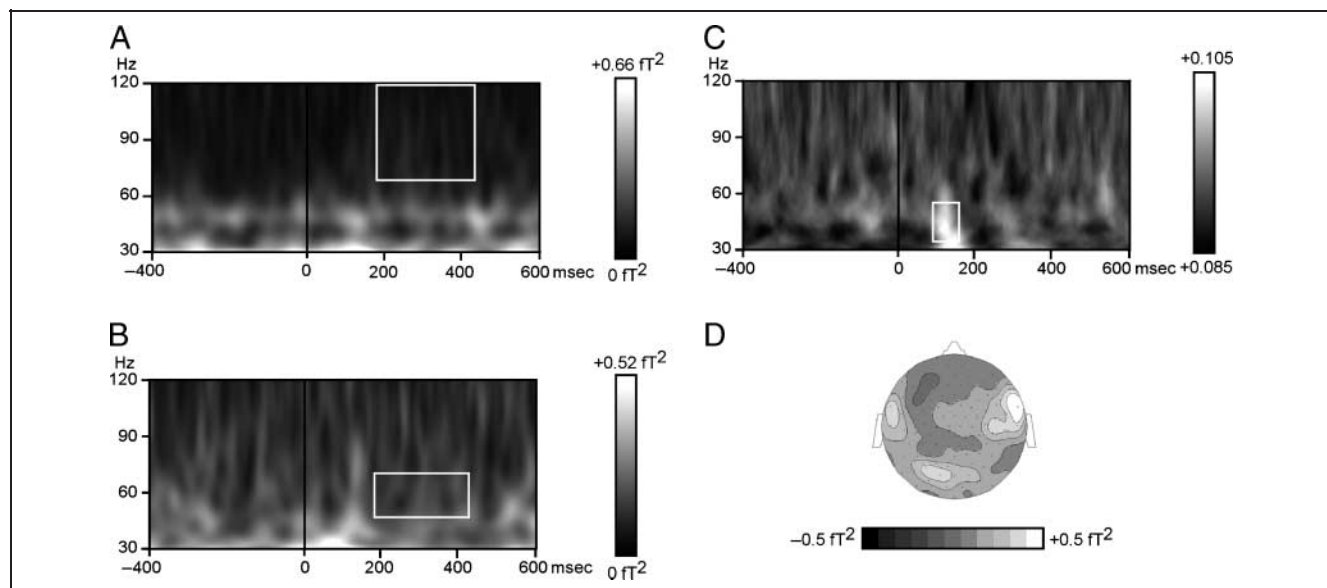
A significant difference was found in the averaged evoked fields between 850 and 950 msec (Figure 5G and H) in a group of right fronto-temporal group of sensors between the late focused attention condition and all other conditions (mean amplitude between 850 and 950 msec averaged across sensors MRT11, MRT12, MRT21, MRT22, MRT23, MRT31, MRT32, MRT42, and MRF34,  $F = 4.71$ ,  $p < .01$ ; post hoc Conover procedures: two-group, late focused attention condition larger than other conditions,  $p < .05$ ).

### Induced versus Evoked Responses

Evoked gamma activity in TF windows corresponding respectively to the induced oscillatory activity related to visual grouping (70–120 Hz, 180–430 msec), early focused attention (44–66 Hz, 180–430 msec), and late focused attention (60–90 Hz, 850–1100 msec) was not significant between conditions (for all,  $p > .15$ ). The gamma oscillations described above, related to grouping and attentional selection, are thus induced.

### Evoked Gamma Response

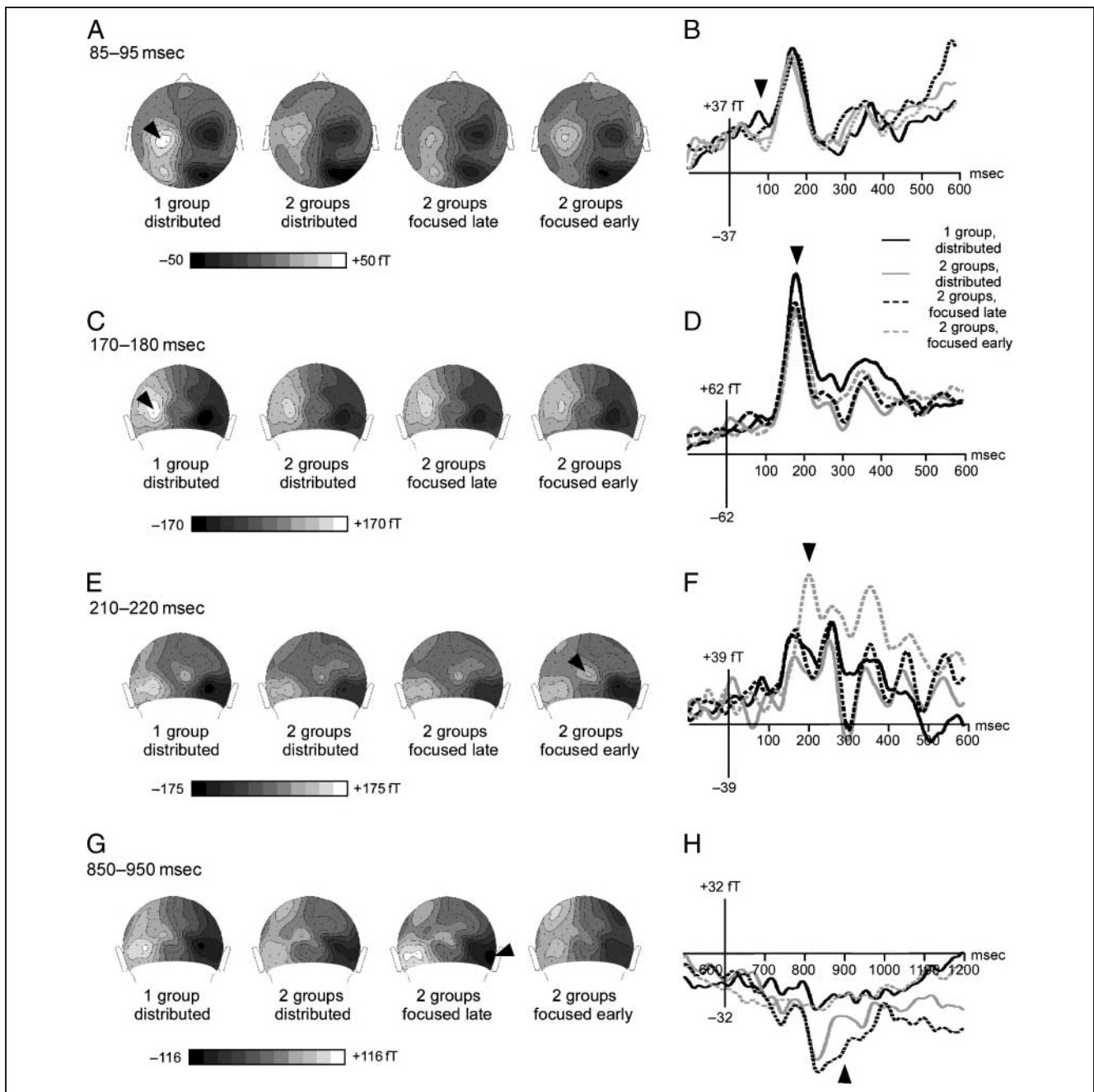
The phase-locking factor averaged across all subjects and sensors revealed an increase around 120 msec and 40 Hz (Figure 4C). The mean evoked power in the interval of 34–54 Hz and 90–160 msec revealed three regions of interest: one central occipital and



**Figure 4.** Evoked gamma responses. (A, B) Time–frequency (TF) representations of evoked fields at the sensors displaying the maximal induced gamma power, related to grouping (MRP31, A) and attentional focusing (MRO22, B). No evoked activity can be observed, neither in the high nor low gamma band (white rectangles). (C) Phase-locking factor in the one-group, distributed attention condition, grand-averaged across subjects and sensors. An increase is observed in the 90–160 msec and 34–54 Hz interval (white rectangle). (D) Topographical map (top view) of the evoked gamma response (mean power in the 90–160 msec and 34–54 Hz interval).

two fronto-temporal bilaterally (Figure 4D; left fronto-temporal: MLC15, MLF45, MLT12, MLT13, and MLT14; right fronto-temporal: MRC15, MRF34, MRF45, MRT12, and MRT13; central occipital: MLO11, MLO12, MLP31,

MLP32, MRO11, MRP31, MZO01, and MZP02). The mean evoked power averaged across each group of sensors revealed no significant difference between conditions (for all,  $p > .28$ ).



**Figure 5.** Evoked fields, grand-averaged across subjects. (A) 85–95 msec, topographical maps (top view). A group of left central sensors presents a larger peak in the one-group, distributed attention condition (arrow). (B) Evoked fields averaged over the left central occipito-parietal group sensors. An early positive peak can be observed in the one-group, distributed attention condition (arrow). (C) 170–180 msec, topographical maps (back view). Left occipito-temporal sensors show a large positive peak in the one-group, distributed attention condition (arrow). (D) Evoked fields averaged over the left occipito-temporal group of sensors. The M170 peak is largest in the one-group, distributed attention condition (arrow). (E) 210–220 msec, topographical maps (back view). A group of central sensors presents a larger peak in the two-group, early focused attention condition than in all other conditions (arrow). (F) Evoked fields averaged over the central occipito-parietal group sensors. An early peak can be observed in the two-group, early focused attention condition (arrow). (G) 850–950 msec, topographical maps (back view). A group of right fronto-temporal sensors presents a larger sustained activity in the two-group, late focused attention condition (arrow). (H) Evoked fields averaged over the right fronto-temporal group of sensors. A sustained negative field, larger in the two-group, late focused attention condition can be observed (arrow).

## Alpha and Beta Band Activities during Visual Grouping and Attention Focusing

Oscillatory activity in the 8–12 Hz (alpha) band and the 15–20 Hz (beta) band decreased below baseline level at scene onset in all conditions. In the 8–12 Hz band, this decrease is pronounced in the 350–600 msec interval, at occipito-parietal sensors (MZP01, MZP02, MRP21, MRP31, MRP32, MRT16, and MRO12). In the 15–20 Hz band, this decrease occurs later, in the 500–600 msec interval at occipito-parietal sensors (MLP21, MRP21, MRP31, MRP31, and MZP02). In both frequency bands, the suppression was large in the two-group, early focused attention condition (alpha:  $F = 15.76$ ,  $p < .0001$ ; post hoc Conover procedures: two-group, early focused attention larger than all other conditions,  $p < .05$ ; beta:  $F = 14.55$ ,  $p < .0001$ ; post hoc Conover procedures: two-group, early focused attention larger than all other conditions,  $p < .05$ ), intermediate in the two-group, late focused attention and two-group, distributed attention conditions, and weak in the one-group, distributed attention condition (alpha:  $F = 15.76$ ,  $p < .0001$ ; post hoc Conover procedures: all other conditions larger than the one-group, distributed attention condition,  $p < .05$ ; beta:  $F = 14.55$ ,  $p > .0001$ ; post hoc Conover procedures: all other conditions larger than the one-group, distributed attention condition,  $p < .05$ ).

The suppression observed in both the alpha and beta range during the first 600 msec of scene encoding thus follows the probability that attention focusing may occur. Both the suppression and this probability are maximal in the two-group, early focused attention condition (the cue is already present), intermediate in the two-group, distributed attention and two-group, late focused attention conditions (before 600 msec, 50% of chances that attentional focusing will be requested in these two conditions), and minimal in the one-group, distributed attention condition (subjects know that attention will remain distributed in this condition). The suppression in the alpha and beta bands at the beginning of scene encoding is unlikely to reflect directly the focusing process itself because it appears in the two-group, late focused attention condition and the two-group, distributed attention condition, in which there is no focusing until 600 msec.

## DISCUSSION

This experiment was designed to test whether distinct visual processes elicit different types of gamma-band activity. Two distinct induced gamma-band activities were observed, one modulated by the visual grouping properties of the stimulus, the other induced by the focusing of attention on one color. The grouping-related and attention-related activities occurred at different frequencies (70–120 Hz vs. 44–66 Hz) and appeared at different locations (central occipito-parietal vs. right

parietal). This difference in topography and frequency band, depending on the process involved, could be reliably identified in 10 subjects out of 12. It thus seems that gamma oscillations can participate in both visual grouping and focused attention, but that the corresponding neuronal assemblies recruit different areas at different frequencies depending on the process required. This is the first evidence of a functional specialization within the gamma-frequency range, with visual grouping and focused attention processes showing up at different frequencies.

## Evoked and Induced Gamma Oscillations in MEG Recordings

Evoked gamma oscillations have been described earlier in MEG recordings (Herrmann & Mecklinger, 2000; Tallon-Baudry, Bertrand, Wienbruch, Ross, & Pantev, 1997), and the latency and frequency observed here are in keeping with previous literature. However, in our data, these early evoked oscillations did not differ between conditions, although both stimulus features (Bodis-Wollner, Davis, Tzelepi, & Bezerianos, 2001; Tzelepi, Bezerianos, & Bodis-Wollner, 2000) and task difficulty (Senkowski & Herrmann, 2002; Herrmann & Mecklinger, 2001) have been shown to influence the early evoked gamma response. However, the modulation of the visual features and task difficulty used here is not very pronounced and may not have been sufficient to generate large differences in evoked gamma power.

Despite few notable exceptions (Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006; Hall et al., 2005; Adjamian et al., 2004; Kaiser et al., 2004), stimulus-induced gamma oscillatory activity has seldom been described in MEG recordings. Grouping-related induced gamma oscillations elicited by visual stimuli typically appear in scalp electroencephalogram (EEG) recordings between 250 and 350 msec, between 30 and 50 Hz (Muller & Keil, 2004; Grice et al., 2001; Csibra et al., 2000; Gruber et al., 1999; Keil et al., 1999; Tallon-Baudry & Bertrand, 1999; Revonsuo et al., 1997). In the present study, magnetically recorded gamma oscillations begin earlier, last longer, and show up at much higher frequencies than their scalp EEG counterparts, as already noted in the auditory modality (Kaiser, Hertrich, Ackermann, Mathiak, & Lutzenberger, 2005). This discrepancy in frequency range and time course between scalp EEG and MEG may account for previous failures in detecting induced gamma oscillations in MEG data (Tallon-Baudry, Bertrand, Wienbruch, et al., 1997).

The difference between scalp EEG and MEG data may be due to the different spatial resolution of the two techniques. Indeed, intracranial recordings that are, by definition, close to the neural sources of oscillatory synchrony reveal visually induced oscillations similar to those observed here with MEG, in the high gamma

range and with a sustained time course in humans (Lachaux et al., 2005; Tanji, Suzuki, Delorme, Shamoto, & Nakasato, 2005) and animals (Siegel & Konig, 2003; Rols, Tallon-Baudry, Girard, Bertrand, & Bullier, 2001). This local, within-area oscillatory synchrony could be directly picked-up by MEG due to its high spatial resolution, while a compound signal, mixing oscillations at different frequencies from different areas, would reach scalp EEG electrodes.

### Grouping-related Activities

An induced gamma oscillatory response could be observed in all conditions, in the high gamma range (70–120 Hz) at midline occipital sensors. This activity was modulated by image grouping properties, being larger in the one-group condition than in the two-group conditions. Our results thus add further support to the idea that visual grouping is accompanied by gamma oscillations in the human EEG (Gruber & Muller, 2005; Goffaux et al., 2004; Grice et al., 2001; Gruber et al., 2001; Csibra et al., 2000; Keil et al., 1999; Rodriguez et al., 1999; Muller et al., 1996, 1997; Revonsuo et al., 1997; Tallon-Baudry, Bertrand, Delpuech, et al., 1997; Tallon-Baudry et al., 1996) and MEG (Kaiser et al., 2004). In addition, our results are consistent with those of Muller's group showing that the perception of one object elicits larger gamma oscillations than the perception of two objects (Muller et al., 1996, 1997). Indeed, if two assemblies, coding for two different objects, are superimposed within the same area, the resulting compound signal is likely to be attenuated compared to the signal of one assembly only.

The one-group and two-group conditions differed along another dimension, namely, spatial frequency. Gamma oscillations have been shown to increase with spatial frequency in humans (Adjamian et al., 2004). In our experiment, spatial frequency is multiplied by two in the one-group condition. According to Adjamian, this would lead to a 25% increase of the gamma power, while we observed a 100% increase. Although spatial frequency differences may contribute to our results, the effects described by Adjamian et al. do not seem sufficient to account for the increase in gamma oscillations in the one-group condition compared to the two-group conditions.

### Focused Attention-related Activities

An induced gamma band appeared at parietal locations about 200 msec after the delivery of the attentional color cue indicating the subject to focus his/her attention on a set of colored bars. A neutral color cue (yellow cue in the two-group, distributed attention condition) activity did not elicit such oscillatory activity. These results thus confirm the idea that selective attention processes are related to the oscillatory synchronization of underlying neuronal assemblies as shown in previous studies in

humans (Muller & Keil, 2004; Gruber et al., 1999) and monkeys (Bichot et al., 2005; Fries et al., 2001).

Gamma oscillations in the *early focused attention* and *late focused attention* conditions have different but partially overlapping frequency bands and topographies. These differences may be related to the fact that they occurred respectively simultaneously or after visual grouping. When the focusing of attention is concomitant with the grouping process that occurs in the high gamma range, attention-related oscillations occupy the low gamma range (44–66 Hz). When focused attention is requested after grouping process completion (late focused attention condition), it occupies an intermediate frequency range (60–90 Hz).

The frequency of selective attention-related gamma activity thus seems to depend on whether it is concomitant with a grouping process or not. However, the opposite is not true: the frequency of grouping-related gamma activity is not affected by the presence or absence of a simultaneous attentional focusing. This adds further support to the idea that grouping by color similarity can be independent of the attentional state of the subject (Kimchi & Razpurker-Apfeld, 2004; Marcus & Van Essen, 2002).

Because our task is distinct from both classical visual search tasks and short-term memory tasks, the attentional focusing process involved is only loosely defined. Indeed, attentional focusing resulted in the selection and memorization of four bars only. The memory load in the two focused attention conditions was thus lower than in the two distributed attention conditions. Task difficulty was also reduced in the two focused attention conditions, as shown by the better subjects' performance in these conditions. However, a decreased memory load or task difficulty should lead to reduced gamma oscillations (Howard et al., 2003; Posada, Hugues, Franck, Vianin, & Kilner, 2003; Senkowski & Herrmann, 2002), whereas we observed an increase. It thus seems more likely that the additional gamma oscillations observed are due to the focusing of attention rather than to a decreased memory load or overall task difficulty. Moreover, attention-related gamma oscillations show up at parietal locations, a region associated with attentional processes rather than with memory encoding.

However, it is clear that subjects focused their attention to be able to memorize the relevant part of the visual display: As often (Naghavi & Nyberg, 2005; Lebedev, Messinger, Kralik, & Wise, 2004; Pashler, 1998; Desimone, 1996), attention and memory are strongly coupled in this task. In any case, the most relevant point is that these oscillations were distinct both in topography and in frequency from those related to the grouping process.

### Gamma-band Functional Specialization

We observed a functional segregation between frequency bands: visual grouping occurs in the 70–120 Hz range

and the focusing of attention in the 44–66 Hz range. We show here that two distinct gamma-frequency bands can correlate functionally with distinct visual processes and that they can be identified on a subject-by-subject basis. This functional specialization probably reflects a neural strategy to separate two oscillation-based processes operating simultaneously. Altogether, these results suggest that oscillatory synchrony is selective for a given visual process, and thus, is unlikely to reflect a mere epiphenomenon.

The functional significance of different frequency ranges has been a matter of discussion in the recent years, although experimental data remains scarce (but see Kayser & Konig, 2004; Siegel & Konig, 2003; Bernasconi, von Stein, Chiang, & Konig, 2000). It has been suggested that the different frequency bands reflect the different spatial scales of neuronal interactions: Low frequencies would reflect long-range interactions, whereas local interactions would rely on high frequencies (Engel, Fries, & Singer, 2001; von Stein, Chiang, & Konig, 2000). An alternative proposal is that oscillatory activity in low (theta, alpha, beta) frequency bands would reflect top-down processing and that oscillations in high (gamma) frequency bands would reflect stimulus-dependent bottom-up processing (von Stein et al., 2000). In our experiment, the highest frequency range was devoted to automatic color grouping processes, which are likely to be mainly bottom-up. Attentional focusing, involving more top-down processing, occurred in the lower gamma range. Our data could thus fit with the idea that bottom-up processes show up at higher frequencies than top-down processes. However, the fact that in our experiment attention-related oscillations appear at different frequencies depending on whether they are concomitant with the grouping process suggests that the number of simultaneous active processes has a strong influence on the frequency range occupied by attentional processes.

## Conclusion

Our data show that both visual grouping and attentional focusing elicit induced gamma oscillations, although at different locations and in distinct frequency bands. Gamma activity induced by automatic similarity grouping was always present, but it was modulated by the number of perceptual groups formed (one or two). It showed up in the high gamma range (70–120 Hz). Selective attention-related activity appeared as an extra component in conditions requiring selection. Its frequency varied between 44–66 Hz (*early focused attention*) and 60–90 Hz (*late focused attention*). Our results thus strongly suggest that functional specialization occur within the gamma band, different processes being assigned to different frequency ranges.

This study adds to the view that oscillatory assemblies can implement a variety of neuronal operations associated with different perceptive and cognitive processes

such as grouping, attention, and memory (Tallon-Baudry & Bertrand, 1999). It might seem counterintuitive to suggest that the same mechanism underlies distinct cognitive processes. On the other hand, it may be economical to use the same organizational mechanism for distinct operations that all require interactions between large neuronal populations. When a coherent visual object is presented to the visual system, oscillatory synchrony between distributed neurons would signal relatedness between various bits of information (Singer & Gray, 1995). Some of these synchronized neurons project on a common downstream target. This target thus receives synchronized waves of synaptic potentials that lead to a strong dendritic summation, efficient in driving the target cell. The signal from synchronized neurons is thus more likely to be amplified at the next processing stage than the signal from unsynchronized ones, a mechanism that could be the neural basis of an attentional filter (Fries et al., 2001; Niebur & Koch, 1994). In addition, if the target neuron that receives synchronized inputs emits action potentials, those synapses that are active are likely to be reinforced by spike-time-dependent plasticity (Dan & Poo, 2004). Synchronized input and output spikes could hence foster the formation of new memories in distributed cell assemblies (Gruber & Muller, 2005; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004; Tallon-Baudry et al., 2001). Common implementation rules for perception, attention, and memory could thus account for the strong interdependency between these three fundamental processes: coherent percepts are more likely to catch attention, and attended stimuli are more likely to be memorized.

## Acknowledgments

This work was supported by grants from the French Ministry of Research (ACI Neurosciences Intégratives et Computationnelles, ACI Nouvelles Interfaces des Mathématiques). We thank Antoine Ducorps and Denis Schwartz for their help during data acquisition and Dr. Pascale Pradat-Diehl for her assistance throughout the experiment.

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