

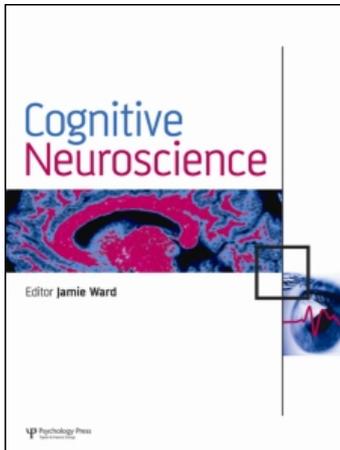
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Time is more than a sensory feature: Attending to duration triggers specific anticipatory activity

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Time is more than a sensory feature: Attending to duration triggers specific anticipatory activity

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Time processing requires the estimation of events' duration *per se*, but also seems to trigger attentional and memory processes. To isolate attentional processes, we investigated neural correlates of anticipatory attention when estimating stimulus duration. Magneto-encephalographic (MEG) activity was recorded in fourteen healthy right-handed volunteers, who were cued to attend to either the duration or the intensity of a visual stimulus. We report an increase of gamma-band oscillations over right fronto-central and parietal regions when subjects are prompted to attend to duration, which is not present when subjects are cued to attend to intensity. Cue-related alpha power decreases over occipito-parietal regions were similar in the two conditions. Our results support the hypothesis that the right fronto-parietal network observed repeatedly in time estimation imaging studies is indeed involved in attentional control rather than stimulus processing. Moreover, they underline the supramodal property of time dimension that goes beyond purely perceptual features.

Keywords: Time; MEG; Oscillations; Anticipatory Processes; Specific mechanisms.

INTRODUCTION

Perceiving accurately the duration of events and actions is crucial to many aspects of human performance. Time perception has some unusual characteristics. First, duration is not a typical sensory feature like contrast or color in the visual domain. Time is more abstract and needs some form of representation to be actively maintained during temporal processing. Second, time processing requires attentional resources. Indeed, estimation of stimulus duration varies depending on the degree of attention allocated to the time feature (Brown, 1997). In line with this idea, neuroimaging studies have provided substantial evidence suggesting the involvement of a right fronto-parietal network in time perception. Although still controversial, it is usually held that this network could be related to the attentional and memory processes

associated with duration estimation while the coding of duration *per se* would rely on the striatum, cerebellum, and supplementary motor area (SMA) (Coull, Nazarian, & Vidal, 2008; Harrington et al., 2004; Rao, Mayer, & Harrington, 2001).

Our objective was twofold. First, we wanted to characterize the anticipatory attention to duration. We therefore sought to determine what happens when preparing to attend to duration and not during duration processing *per se*. Based on the work done on visuo-spatial attention, we reasoned that the more a network is involved in attentional control, the more it should be active during anticipatory phases. Previous studies suggest that attentional modulations in sensory areas are preceded by the activation of fronto-parietal areas. This network is thought to be involved in the control of spatial attention, rather than in stimulus processing, because it is activated before stimulus

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onset (Capotosto, Babiloni, Romani, & Corbetta, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). If the fronto-parietal network activated in time perception tasks is involved in attentional control, it should therefore be active before stimulus onset. Our second objective was to test whether the attentional preparation for duration was of similar nature to that for another stimulus feature (luminance) and whether it relies on the same brain regions: Since duration is not a typical sensory feature, a question often raised in time studies is the specificity of the network involved in duration perception (Coull, Vidal, Nazarian, & Macar, 2004; Ferrandez et al., 2003; Pouthas, Garnero, Ferrandez, & Renault, 2000).

In practice, we tested whether preparatory baseline shifts in brain activity would differ depending on the stimulus feature participants anticipated to process. We recorded magneto-encephalographic (MEG) activity while subjects discriminated either duration or intensity of a visual stimulus. A cue about the relevant sensory feature was given at the beginning of each trial (Figure 1). The main aim of the present work being to study preparatory processes, we analyzed brain activity between the presentation of the cue and the appearance of the first stimulus. We focused particularly on the alpha and gamma frequency ranges. Typically, attentional cues suppress alpha-band oscillations (Thut et al., 2006; Wyart & Tallon-Baudry, 2008) and can increase gamma-band oscillations (Fries, Reynolds, Rorie, & Desimone, 2001; Wyart & Tallon-Baudry, 2009). If preparing to attend to time engages specific anticipatory processes,

then a dedicated functional network should be activated. Conversely, if attention to time engages similar processes to attention to intensity, then the two networks should closely match.

METHODS

Subjects

Fourteen healthy right-handed volunteers (six females, mean age 24.78 ± 3.4), with normal or corrected to normal vision took part in the MEG experiment after signing an informed consent. The study was approved by the Ethical Committee on Human Research (CCP-PRB, Hôpital de la Pitié-Salpêtrière).

Apparatus and stimuli

The apparatus consisted of a black panel located in front of the subject, on which a translucent screen (16 cm wide \times 10 cm high) and a light emitting diode were mounted. All instructions were projected on the screen by a video-projector placed outside the MEG room by a system of mirrors. The distance between the LED that served also as fixation point and the position of the warning stimulus or attentional cue was 1 cm. The cue was either a “D” or an “I” for the Duration and Intensity condition respectively. The stimulus had durations of 150 or 300 ms and intensities of 0.04 or 0.06 cd/m^2 . These values were crossed

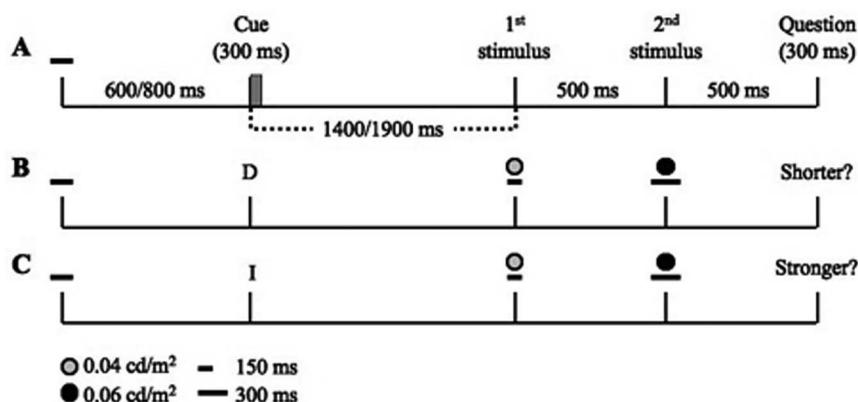


Figure 1. (A) Timeline of a trial. (B) Example of an “attend duration” trial. The subject was cued to attend the upcoming stimuli duration by the letter “D”. After the two stimuli were displayed, the subject was prompted to decide which stimulus (first or second one), was the shorter one. Here, the correct response would be “1st stimulus”. The question (“shorter?” or “longer?”) was randomly chosen on each “attend duration” trial, and the position of the shorter stimulus (1st or 2nd) randomly varied between trials. (C) Example of an “attend intensity” trial. The subject was cued to attend the upcoming stimuli intensity or visual brightness by the letter “I”. After the two stimuli were displayed, the subject was prompted to decide which stimulus (first or second one), was the stronger one. The question (“stronger?” or “weaker?”) and the position (1st or 2nd) of the stronger stimulus were randomly varied from trial to trial.

to form four different combinations of stimuli: short/weak (150 ms/0.04 cd/m²), short/strong (150 ms/0.06 cd/m²), long/weak (300 ms/0.04 cd/m²) and long/strong (300 ms/0.06 cd/m²). The question could be for the duration condition “court?” (short) or “long?” (long) and for the intensity condition “faible?” (weak) or “fort?” (strong).

Paradigm

Stimuli presentation was computer-controlled by in-house software (Stimulat). Trial proceeded in the following order: warning stimulus (600 or 800 ms), cue (300 ms, D or I), random interval after cue onset (1.400/1.900 ms), first stimulus (one of the four stimuli described above), fixed interstimulus interval (ISI) (500 ms), comparison stimulus (note that if the first stimulus was, for example, short/strong the comparison one had to be long/weak), fixed ISI (500 ms), question (300 ms, depending on the condition) and a random intertrial interval (2.200/3.200 ms) (Figure 1).

The attentional cue signaled to the subject which stimulus feature to pay attention to. Subjects had to indicate which stimulus corresponded to the question using a two button-device pressing with the right index finger on the left button or the right medium finger on the right button to indicate the first or the second stimulus respectively. Subjects were asked to fixate the LED during all the experiment and to answer as fast as possible. Before MEG recording subjects were familiarized with the task. The MEG session consisted of 256 trials divided into four blocks. In each block the two conditions as well as the different questions were presented in equal number in a randomized order.

Recording, data processing and analysis

Continuous data were collected at the MEG Centre, Hôpital Pitié-Salpêtrière (Paris, France) using a CTF/VSM OMEGA 151-channels third-order gradiometer, whole head system (CTF System, Vancouver, Canada) at a sampling rate of 1250 Hz, together with electrocardiogram, as well as vertical and horizontal electrooculograms (EOGs). Subjects' head position was monitored and no deviation larger than 0.5 cm was allowed. Signal was cut in epochs of 6 s around the first stimulus trigger. In order to enhance the signal to noise ratio we restricted the discarding procedure of artifacted trials to the window of interest that is the period between the warning stimulus and the appearance

of the first stimulus. All trials containing blinks, saccades that exceeded 50 μ V or muscle artifacts were discarded from the analysis. Only trials in which subjects answered correctly were used for further analysis. A wavelet transform was applied to each trial (–800 to 1700 ms around the attentional cue, 200 ms blackman window) at each sensor, using complex Morlet wavelets characterized by the ratio $f_0/\sigma_f = 10$, resulting in an estimate of power at each sample in time at each frequency (1 Hz step) between 8 and 90 Hz. The resulting time–frequency data were then averaged across trials separately for each condition. For statistical comparison time–frequency data were then divided by the corresponding baseline (–500 to –100 ms before the cue) and log transformed to approach a normal distribution (Kiebel, Tallon-Baudry, & Friston, 2005). Data preprocessing and wavelet analysis were performed using in-house software.

Sources of power modulation registered at scalp level were tentatively reconstructed using a beamformer technique (Dynamical Imaging of Coherent Sources) described by Gross et al. (2001). The alpha power modulation was easily localized at occipitoparietal areas in both conditions. By contrast, no reliable sources could be obtained for the γ -band modulation. This difficulty was probably due to a weak signal/noise ratio. Indeed, in accordance with the literature, our results show that alpha band activity has a size effect several times greater than higher frequencies. Results of these analyses are not described below.

RESULTS

Behavioral results

Performance in the two attentional conditions was similar. Statistical analysis did not show any significant difference either for the percentage of correct answers (duration: mean = 80.5 ± 12.4 ; intensity: mean = 78.9 ± 11.12 ; $t(13) = 0.82$, $p > .4$) or for reaction times (duration: mean = 1026.72 ± 188.11 ms; Intensity: mean = 1009.74 ± 162.59 ms; $t(13) = 0.72$, $p > .4$).

Induced power modulation

We were particularly interested in alpha and gamma band power modulation. For the alpha-band we found decreased activity in the upper alpha range (11–13 Hz) over posterior regions, as expected from the literature.

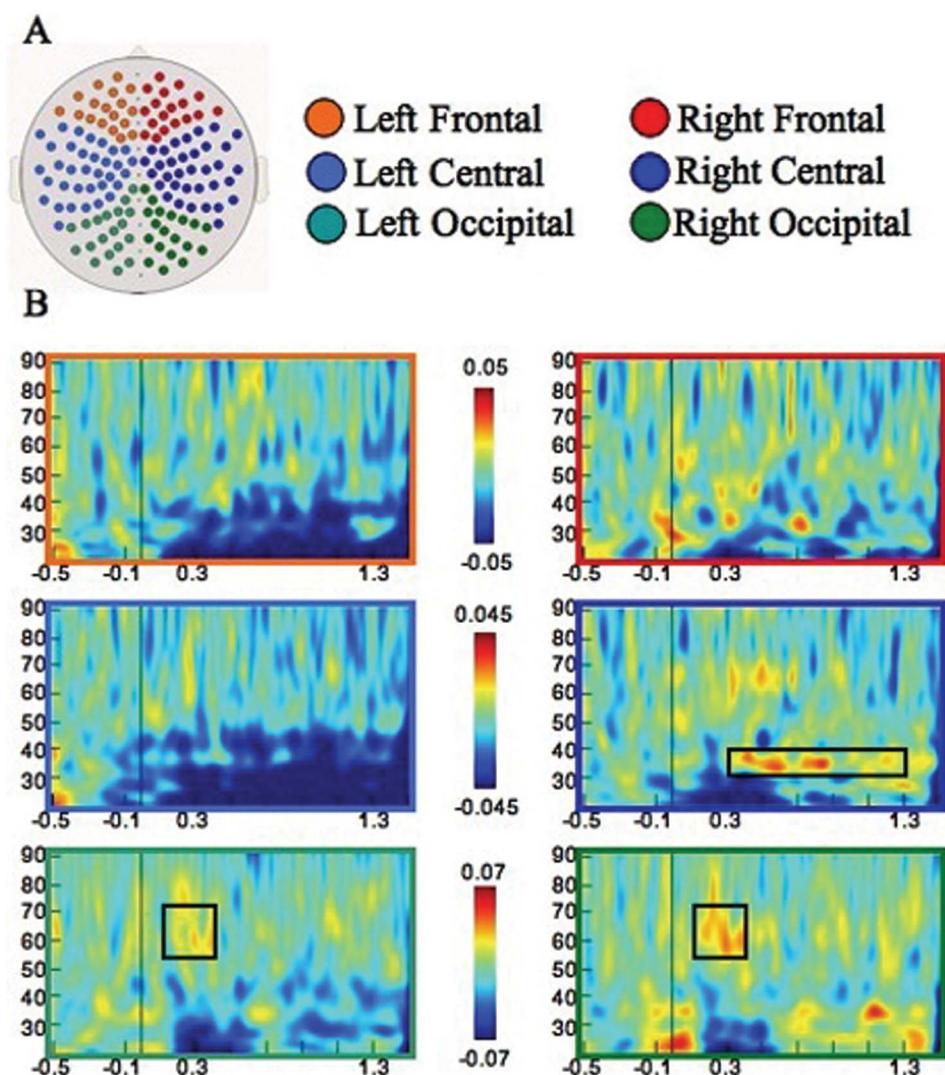


Figure 2. (A) A priori subdivision of the scalp sensors in six regions of interest: left frontal, right frontal, left central, right central, left occipital and right occipital. (B) Time-frequency charts for each region of interest obtained by averaging the mean time-frequency data for the two conditions (Duration and Intensity) across all sensors in each region. These time-frequency charts revealed the existence of response to the cue in the high gamma range over visual regions, followed by a sustained activity in the lower gamma band range over the right central region of interest. Subsequent analysis is focused on this 34–38 Hz sustained activity occurring while subjects prepared to attend the stimulus.

However, since narrow-band gamma-band modulations can be observed across a wide frequency range, from 20 to 90 Hz, we could not use a priori frequency settings. To determine whether power increases could be observed within the gamma range we computed the mean time-frequency data across the two conditions and then we averaged that mean across sensors in six a priori defined regions of interest (Figure 2A). These time-frequency charts revealed a sustained power increase in a narrow frequency range (34–38 Hz) over the right central region (Figure 2B). This frequency band was therefore considered for further analysis.

In the alpha range power in the most reactive band (11–13 Hz) was averaged between 300 and 1300 ms after cue onset over sensors of interest (Figure 3A). Alpha-band desynchronization occurred in both conditions (comparison with baseline, duration: $t(13) = -2.43$, $p < .04$; intensity: $t(13) = -2.17$, $p < .05$), but did not differ between conditions, $t(13) = -0.28$, $p > .7$) (Figure 3B).

The picture that emerged in the gamma range was more complex. The attentional cue elicited a right power increase in the attend duration condition as well as a left frontal power suppression common to the two conditions (Figure 4A and 4B). To test for

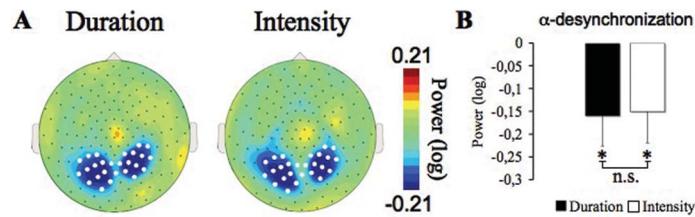


Figure 3. Induced alpha-band modulation. (A) Power's scalp distribution averaged between 11 and 13 Hz in the time window of interest (300–1300 ms after cue onset). White dots represent sensors included in the analysis. (B) Statistical comparison between each condition and the baseline and between the two conditions. Error bars indicate SEM, * $p < .05$, *ns*.

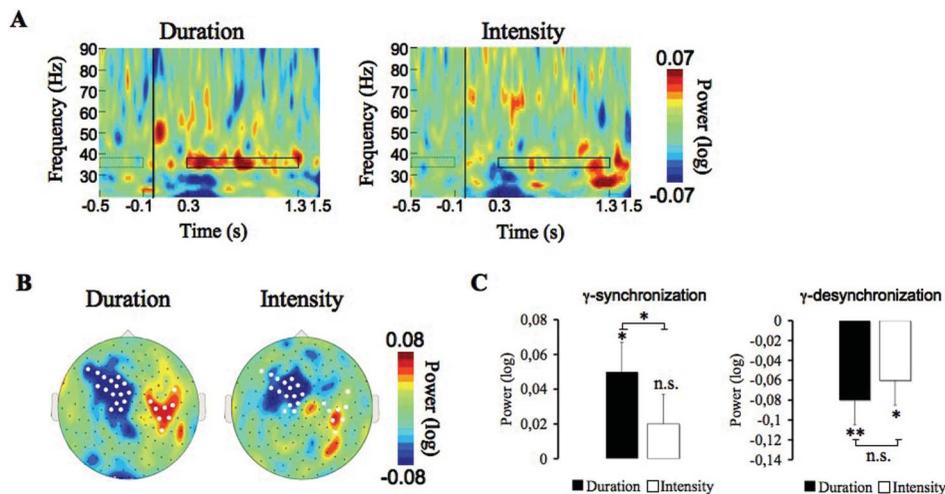


Figure 4. Induced gamma-band modulation. (A) Time–frequency charts, for duration and intensity conditions, obtained by averaging across sensors of interest. The black vertical bar indicates cue onset (time 0), the dotted rectangle indicates the baseline and the black rectangle the window of interest. (B) Power's scalp distribution averaged between 34 and 38 Hz in the time window of interest (300–1300 ms after cue onset). White dots represent sensors included in the analysis. (C) Statistical comparison between each condition and the baseline and between the two conditions for gamma-band synchronization in the right hemisphere and gamma-band desynchronization in the left hemisphere to the left and right respectively. Error bars indicate SEM, ** $p < .01$, * $p < .05$, *ns*.

statistical differences we averaged power between 300 and 1300 ms and 34 and 38 Hz over sensors of interest (Figure 4B) and we entered these values in a 2×2 ANOVA with hemisphere (right, left) and condition (duration, intensity) as factors. We found a significant effect of hemisphere, $F(1, 13) = 28.35$; $p < .001$, and a significant interaction between the factors hemisphere and condition, $F(1, 13) = 9.38$; $p < .01$, but no main effect of condition, $F(1, 13) = 0.19$; $p > .6$.

Further testing revealed that gamma-band increase was specific to the attend duration condition (attend duration vs. baseline, $t(13) = 2.81$, $p < .02$; attend intensity vs. baseline, $t(13) = 0.93$, $p > .3$; attend duration vs. attend intensity, $t(13) = 2.19$, $p < .05$) and that gamma-band desynchronization was similar in the two conditions (attend duration vs. baseline, $t(13) = -3.11$, $p < .01$; attend intensity vs. baseline,

$t(13) = -2.38$, $p < .04$; attend duration vs. attend intensity, $t(13) = -0.84$, $p > .4$) (Figure 4B and 4C).

DISCUSSION

The present study aimed at investigating the neural correlates of anticipatory attention to process time and to determine whether these correlates were specific to time processing. To address the issue of specificity, the choice of the control task is crucial. The first requirement is that the timing task and the control task use the same stimuli (Coull et al., 2004; Livesey, Wall, & Smith, 2007), which was the case in the present study. Moreover, the two tasks should require the same cognitive demands apart from timing (Coull et al., 2004; Lewis & Miall, 2003; Rao et al., 2001). Equivalent levels of performance were obtained,

suggesting that task difficulty and attentional load were correctly balanced between conditions. Thus, such factors cannot be considered as confounds for the interpretation of our results. The most important finding was that significant gamma synchronization occurred over right fronto-central and parietal regions only when subjects prepared to attend to duration. This specific oscillatory activity was associated with alpha desynchronization over parieto-occipital areas and gamma desynchronization over left fronto-central areas which were conversely observed in both conditions. No specific oscillatory activity was found in the attend intensity condition. Alpha desynchronization, observed in both attentional conditions, is usually associated with increasing demands in attentional resources (Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Thut et al., 2006; Wyart & Tallon-Baudry, 2008), alertness and task load in general (Klimesh, Doppelmayr, Russegger, Pachinger & Schwaiger, 1998; Müller, Lutzenberger, Preissl, Pulvermüller & Birbaumer, 2003). This alpha desynchronization is typically observed in parieto-occipital areas, occipito-parietal sulcus and areas around the calcarine sulcus (Gómez, Marco-Pallarés & Grau, 2006; Siegel et al., 2008). Although the role of alpha oscillations might be more complex than previously thought (Palva & Palva, 2007), our data fit well with the generally accepted idea that alpha desynchronization reflects inhibition suppression that could in turn facilitate sensory processing. Large-scale synchronization in the alpha range implies that neurons with very different selective properties are coupled. This in turn prevents the emergence of sharply tuned stimulus-selective responses (Jokisch & Jensen, 2007). Preparing to perform a task would suppress this unselective correlation between sensory neurons (Cohen & Maunsell, 2009), resulting in a strong suppression of alpha-band oscillations before stimulus onset. The important point here is that alpha desynchronization was similar in both conditions. This finding suggests that the level of attentional and intentional preparation was indeed similar and engaged the same neural mechanisms.

The unexpected gamma-band decrease over left fronto-central sensors was also common to both attentional conditions. With a few notable exceptions (Hirata et al., 2004; Lachaux et al., 2008; Pulvermüller et al., 1996), gamma-band desynchronization has rarely been reported in the literature. Interestingly, all the studies listed above used written words or letters: it therefore seems likely that the observed left fronto-central gamma-band desynchronization was related to the translation of the cue letter (D or I) into the corresponding word (Duration or Intensity).

The only activity specific to the attend duration condition was a gamma power increase over right fronto-central and parietal areas. This effect was restricted to quite a narrow frequency band. There is growing evidence that distinct cognitive functions elicit oscillations at different frequencies within the gamma range (Chaumon, Schwartz, & Tallon-Baudry, 2009; Vidal, Chaumon, O'Regan, & Tallon-Baudry, 2006). However, there is no simple one-to-one relationship between a frequency range and a cognitive function (Tallon-Baudry, 2009): for instance, depending on the experimental paradigm, neural correlates of attention can be found in the high or low gamma-range (Vidal et al., 2006). The increase in gamma-band power was observed only when subjects prepared to process duration, suggesting that such activity played a specific role in the anticipatory attention to duration. Gamma-band oscillations before stimulus onset have already been reported in the literature (see, e.g., Wyart & Tallon-Baudry, 2009). Here, they would reflect a task-specific preactivation of areas involved in time estimation. Indeed, many studies have proposed that right frontal and parietal areas are key structures for time processing (Lewis & Miall, 2006; Pouthas et al., 2000; Rao et al., 2001). Gamma activity increase might be due to the synchronization of neurons coding the duration feature of the visual stimulus, as has been shown for other stimulus features (see, e.g., Müller & Keil, 2004). However, right frontal and parietal areas are usually considered to control the attentional and memory processes involved in time perception, time estimation *per se* being a role attributed to the striatum (in connection with the SMA) (Pouthas et al., 2005; Rao et al., 2001) or the cerebellum (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). Attending to duration triggers oscillatory activity in associative regions also involved in cognitive control (Cho, Konecky, & Carter, 2006). This is in line with Lewis and Miall (2006), who stated that the "cognitive time measurement" depends on prefrontal and parietal regions independently of the temporal range to be processed. By contrast, the specific oscillatory activity we found in associative regions could appear at odds with intrinsic models. These models have postulated that the representation of very short time intervals could be ubiquitous, arising from the intrinsic dynamics of nondedicated neural mechanisms, particularly through the amount of activation of sensory processes (Buonomano, 2000; Ivry & Schlerf, 2008). This led us to think that, whatever the temporal range, duration is not equivalent to a simple stimulus feature and encompasses supramodal properties. This is consistent with a MEG-electroencephalography (EEG) study (N'Diaye, Ragot, Garnero, & Pouthas,

2004) and a recent functional magnetic resonance imaging (fMRI) study (Shih, Kuo, Yeh, Tzeng, & Hsieh, 2009) that used duration discrimination tasks in visual and auditory modalities. Authors reported modality-dependent activity within the associated sensory areas as well as modality-independent activations. In the MEG study the modality-independent activity was located within prefrontal and parietal cortices; in the fMRI study common activation across modalities were found in dorsolateral prefrontal cortex (DLPFC), SMA, and basal ganglia.

To conclude, directing attention in a top-down manner to process the duration of a visual stimulus recruits gamma-band oscillations in a right fronto-parietal network. Based on results by N'Diaye et al. (2004) we propose that this activity could reflect supramodal processing of duration, complementary to sensory features processing. The functional role of this activity would be to support the supramodal properties of a time dimension that goes beyond purely perceptive features.

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