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Research report

What is common to brain activity evoked by the perception of visual and auditory filled durations? A study with MEG and EEG co-recordings

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Abstract

EEG and MEG scalp data were simultaneously recorded while human participants were performing a duration discrimination task in visual and auditory modality, separately. Short durations were used ranging from 500 to 900 ms, among which participants had to discriminate a previously memorized 700-ms "standard" duration. Behavioral results show accurate but variable performance within and between participants with expected modality effects: the percentage of responses was greater and the mean response time was shorter for auditory than for visual signals. Sustained electric and magnetic activities were obtained correlatively to duration estimation, but with distinct spatiotemporal properties. Electric CNV-like potentials showed fronto-central negativity in both modalities, whereas magnetic sustained fields were distributed with respect to the modality of the interval to be timed. Time courses of these slow brain activities were found to be dependent on stimulus duration but not on its modality nor on the recording signal (EEG or MEG). Source reconstruction demonstrated that these sustained potentials/fields were generated by superimposed contributions from visual and auditory cortices (sustained sensory responses, SSR) and from prefrontal and parietal regions. By using these two complementary techniques, we thus demonstrated the involvement of frontal and parietal cerebral cortex in human timing.

Theme: Motor systems and sensorimotor integration: cortex
Topic: Neural basis of behavior: cognition

Keywords: MEG; EEG; Time perception; Auditory; Visual; Distributed source analysis

1. Introduction

Although numerous behavioral studies have explored functional properties of the human timing abilities, insights into the neural bases of them are still scarce. Despite the ubiquity of time, experimental psychology has come up to isolate one range of durations from this continuum: the so-called "short" or circa second durations, which span from some hundredths of a seconds to few seconds. The ability to handle temporal events in that range of durations is what Fraisse [20] named "time perception", as opposed to "time estimation" which concerns longer durations. The words "time perception" refers to the ability of human beings to apprehend such short intervals as unitary objects whether they are composed of either simple events (as a "beep" in a Morse code) or more complex sensory signals (as a piece of bird song). Yet, their subjective duration might differ according to many non-temporal factors among which, our own inner state or physical characteristics of the stimuli (such as sound intensity). Among them, the sensory modality involved in the timed interval has been widely demonstrated to play a major role in the perceived duration of any time interval as well as in the accuracy of this perception [26]. Contrasting with our unitary feeling of the passage of time, these discrepancies in the subjective timing of sensory events raise challenging questions: First, since any signal is primarily processed by the appropriate sensory channel, how much does sensory processing contribute to the perception of duration? And more fundamen-

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tally, to what extent can we isolate a supra-modal processing of duration—a hypothetical central single timing process, which might be involved independently of the sensory modality of the signal to be timed?

1.1. Behavioral aspects and EEG correlates of duration discrimination

To assess human performance in interval timing, many experimental procedures have been adapted from animal timing paradigms [1]. One of them is the ''temporal generalization'' first applied to human beings by Wearden [81]. This paradigm has proved to be highly sensitive to slight differences in behavioral results, such as those induced by modality effects [38,83]. Using temporal generalization, and other methods, psychophysical studies have quantitatively assessed the influence of modality on perceived duration. Auditory signals are thus judged longer than objectively equal visual ones [4,23,64,75,83], and with a greater accuracy and precision [25,27].

Functional investigations of the neural bases of time judgment may be traced back to the early 1960s. Although not dedicated to the study of human timing as such, a fixed-interval reaction time task provided the first insights into electrophysiological correlates of human temporal processing. In that task, participants had to respond as fast as possible to an ''imperative stimulus'' systematically preceded by a ''warning stimulus'' with a constant fore period. While recording scalp electroencephalography (EEG), Walter et al. [80] observed a widespread fronto-central negative potential developing during the interval separating the two stimuli, named ''contingent negative variation'' (CNV), which they associated with ''expectancy''. CNV has been extensively studied within a timing framework and various relationships between its properties and temporal judgment have since been established [15,53,58,73].

Amplitude and time course of the CNV are correlated to behavioral performance in the following way: CNV amplitude [53,66] and resolution (indexed by the zero crossing of the slow wave) [52,69,73] both correlate with subjective duration, and participants showing rapid CNV resolutions also manifest temporal accuracy [42]. Two recent studies by Pfeuty et al. [66] and Macar and Vidal [51] have also demonstrated that the peak of the CNV was dependent on the encoded duration in a duration discrimination protocol.

1.2. Addressing the role of modality in human timing with electromagnetic recordings

Contrasting with behavioral investigations, functional studies have hardly ever focused on modality effects in timing (but see Refs. [6,21]): On the ground of the behavioral results, two alternative explanations have been proposed to account for the fact that auditory signals are judged longer. First, the auditory clock might run faster than the visual clock. Second, auditory signals would be more readily processed. Consequently in both cases, the accumulated value for the same physical duration will be higher when signals are auditory. Following what has been said of CNV properties and time judgment, one could investigate sensory modality effects using the CNV as a window on physiological processes: Assuming that auditory signals lead to longer subjective duration, tone-elicited CNV amplitude would be larger and would resolve later in time than light-elicited CNV.

However, two possible confounds might impede such straightforward comparisons. Firstly, scalp EEG records electric potential due largely to whole brain activity with only remote contributions of the actual active regions, depending on their locations, orientation and on electrical diffusion across the tissues. As auditory and visual cortices are located in different regions of the brain, their contributions to the scalp EEG differ. Plain comparisons of scalp-recorded signal in visual and auditory conditions might thus be ill-grounded. Secondly, the time-course of sensory evoked responses also depends on the modality. Roughly speaking, auditory EEG responses are earlier than visual ones. Whether sensory components might contribute to the CNV has thus to be answered before anything is inferred from the CNV time-course. Each of the issues raised here will be discussed separately.

1.3. In search of the CNV generators

EEG responses to visual and auditory stimuli originate from different regions of the brain, mainly due to the occipital and temporal location of the visual and auditory cortices. This needs caution when scalp distributions and amplitudes of light- versus tone-evoked responses are to be compared. To circumvent this difficulty, one may attempt to isolate sources of the CNV from sensory processing activity, whose generators are located within the sensory cortices. In recent years, various attempts to identify the neural generators of CNV activity have been undertaken. Initially, based on the analysis of scalp topography, these studies inferred from the fronto-central distribution of CNV that it mainly originated from frontal regions [12,49]. These results were confirmed by epidural [80] and subdural recordings [29,37,43], the latter also showing implications of supplementary motor area and dorsolateral prefrontal cortex.

The study by Pouthas et al. [69] contrasted a duration discrimination task based on temporal generalization with an intensity discrimination task. Timing visual signals evoked a CNV whereas discriminating other aspects of the same stimulus did not. Using the results of a preceding positron emission tomography study, these authors could constrain positions of the dipoles within the regions showing increased regional cerebral blood flow. This dipole analysis demonstrated that even if the same regions were engaged in both tasks, time course of their activity differed.

In particular, right prefrontal dipole exhibited a CNV-like activity, reproducing the timing of its resolution as well, while left prefrontal source showed sustained activity whatever the task. These results are in line with those obtained by Pfeuty et al. [66] on a similar but auditory duration discrimination task, as well as with those by Monfort et al. [60] showing an enhanced negativity over right frontal areas when encoding and comparing duration information.

Magnetoencephalography (MEG) can be of precious help in analyzing neural bases of timing behavior owing to its high spatial resolution. Using dipolar or distributed source analyses, a few studies have tried to probe the "contingent magnetic variation" (CMV), the magnetic counterpart of the CNV [3,13,16,35]. Multiple generators located in frontal, premotor, sensory and associative areas form a complex picture, which may be partly due to the diversity of the tasks used (filled/empty intervals, auditory/visual modalities) and to a "considerable intersubject variability" [16] observed by all authors.

Furthermore, magnetic correlates of duration discrimination in the circa-second range have never been addressed directly. To our knowledge, only two studies have previously used MEG to deal with duration discrimination in the circa-second range. In the first study, by Hari et al. [31], duration discrimination of tones was used as a case of selective listening. They reported enhanced sustained activity correlative to attention to duration over temporal sensors were the auditory sustained response was recorded from. Sieroka et al. [76] have used an auditory oddball paradigm where longer targets had to be detected among 1-s tones. Augmented activity for the auditory sustained response was explained with a dipolar modeling by an additional parietal source whose moment's amplitude was correlated with duration discrimination performance by subjects.

1.4. Time-course of brain activity in duration estimation

The key feature of MEG-EEG is thus the millisecond resolution which allows one to follow the evolution of brain activity from the stimulus onset to the evaluation of its duration by the human observer leading ultimately to a motor response. Within the framework of time perception, this is of much value since timing the duration of any particular event is essentially a dynamic process. As mentioned above, a growing number of studies have focused on the waveform of event-related potentials/fields in a timing context. It has been demonstrated that timing performance was tightly related to the resolution of slow waves (e.g. the CNV), whose generators might comprise a distributed network of cortical regions. Much information can be gained from studying the time course of these particular slow potentials in relation to the anatomy of their generators.

However when the participants have to time a visual or an auditory signal, one shall also be concerned with the concurrent cortical activity which is elicited within sensory cortices, as both kinds of signals evoke transient and sustained responses. In EEG, transient activity is described as a succession of positive–negative potentials labeled after their electrical sign and their latency [22,63]: the main visually evoked potentials recorded from the occipital or parieto-occipital sites are the P1 (positive, 80–130 ms after stimulus onset), the N1 (negative, 130–200 ms) and the P2 (positive, 200–300 ms). The main auditory electric components are recorded from fronto-central sites (because of the dispersion of the electric field by the head tissues); they consist of a small positive component, the P50 (50–60 ms), followed by a larger negative shift, the N1 (100–120 ms) and then a positive deflexion, i.e. the P2 (150–200 ms). The magnetic counterparts of these electric potentials are labeled likewise: P50m, N1m and P2m.

The functional significance of these early components is still a matter of debate as it is now acknowledged that each of them might be divided into multiple overlapping subcomponents differentially affected by behavioral context or stimulus properties [55,61]. However, the main sources of the transient responses are mainly located within the corresponding sensory cortices (supratemporal cortex for auditory signals and inferior occipital cortex but also in dorsal occipital and medial occipito-parietal cortices for visual stimuli [14]).

Besides these transient responses, continuous sensory stimulation (i.e. signals longer than few tens of milliseconds) additionally evoke sustained responses whose distributions are very similar to those of the primary sensory responses (as their cortical generators largely overlap [28,63]) and which persist until stimulus offset. On scalp recordings, these sustained responses may overlap with other slow waves, such as those elicited by cognitive processes. However, contrary to task-related components, these sustained responses ordinarily show a plateau-shaped waveform, i.e. constant amplitude throughout the duration of the stimulation [67,76].

Since timing procedures commonly use visual or auditory stimuli to define the interval to be timed, valid inferences on electrophysiological correlates of human timing thus require to distinguish between sensory evoked potentials/fields (especially sustained ones) and timing-related activity. Two lines of evidence can be drawn upon: (1) as stated above, the main correlate of human timing is the CNV which develops in relation to the interval to be timed. Its time course allows one to distinguish it from the sustained potentials that it could be mistaken for: whereas the CNV peaks at a point in time corresponding to the target-duration (or its subjective representation), the sustained response shows a steady plateau waveform with constant amplitude. (2) According to the location of the generators of the sustained sensory responses (SSR), their electric and magnetic signatures might differ from scalp recordings of the CNV, whose generators lie in distinct (although unclear) cortical regions. Source reconstruction is here of great profit as it enables to identify distinct subsets of generators for these two types of evoked responses that might otherwise appear very similar providing their electric/magnetic scalp distributions.

1.5. Objectives of the present study

The present experiment was thus aimed at investigating the neural bases of timing in a duration discrimination task. Besides fMRI, which has been extensively used with timing tasks (see reviews by Lewis and Miall [48] and Macar et al. [54]) but lacks temporal accuracy, MEG supplies information on the anatomy of the cortical substrates involved in a particular cognitive task, while at the same time providing the same high temporal accuracy as EEG. Whereas most BOLD-based studies provide little information on the evolution of brain activity (event-related fMRI allows promising insights on that question [70]), we looked at the precise time course of the electrophysiological correlates of the processes involved in timing duration whilst source analyses were conducted to identify their anatomical substrates.

To extend the results of previous EEG studies carried out in our laboratory [66,69], EEG recordings were simultaneously acquired throughout the experiment. Direct comparison of EEG and MEG signals is not straightforward since MEG—contrary to EEG—is known to be "blind" to radially oriented or deep cerebral currents [32]. As a consequence, some electric components may not show an obvious magnetic counterpart in the simultaneously acquired MEG data. Hence, measuring MEG and EEG simultaneously provides a full picture of brain activity (for comparison of auditory MEG and EEG responses, see Ref. [36]).

Works by Pouthas and her coworkers [66,69] have used, respectively, visual and auditory signals, but none have used both modalities with the same participants. Because of the questions raised concerning the role of modality in timing, we were interested in having the same participants perform identical task in visual and auditory modalities, in order to compare auditory and visual blocks within the same study. We assumed that common mechanisms to visual and auditory timing should therefore be activated in both conditions, while modality specific processes should differ in-between. According to the results of the work cited above, we hypothesized that sensory processing-related and timing-related activities might display distinct time-courses. The former (being stimulus-driven) would be reflected by early and middle latency transient components followed by plateau-like sustained potentials/fields over the scalp surface. On the contrary, time course of components related to the timing task should reflect temporal processing of events with little or no dependency on the stimulus actually presented. From what is known about electrophysiological correlates of time perception, we expected to observe fronto-central activity whose resolution should occur at the end of the target duration used in our task. However, analyses solely based on electromagnetic scalp signals may be impeded by the diffusion of electric potentials due to head tissue and also by the concurrent activation of a scattered set of cortical generators. We used distributed source reconstruction in order to separate those contributions on the basis of their neuroanatomical locations. In sum, the spatiotemporal analysis of electromagnetic correlates of timing processes should provide helpful insights on their functional properties in comparison to those of stimulus driven activities.

2. Materials and methods

2.1. Participants

Thirteen right-handed healthy young male volunteers (ranging in age from 21 to 29 years, mean 24.6) participated in the study. All had normal hearing and vision. It was controlled that participants were not under medication and did not suffer from any central nervous system abnormality or injury. Informed consent was obtained from each participant. Participants were paid for their participation. The study was approved by the French Ethical Committee on Human Research (CCPPRB, Hôpital Pitié-Salpêtrière).

2.2. Design and procedure

Our study used a temporal generalization task. The session was divided in two parts: one in the visual modality, the other in the auditory modality. Order of presentation was counter-balanced across participants. Each part was composed of three blocks. Each block started with six successive presentations of the 700-ms "standard stimulus". Participants had to memorize its duration in order to compare it to each of the following "test stimuli" which could be: 490, 595, 700, 805 or 910 ms, designated as "short", "intermediate short", "standard", "intermediate long" and "long". Every block was thus made of 6 standard presentations and 100 test stimuli randomly presented. Participants had to respond by pressing a button for each test stimulus, with the right thumb if its duration was identical to that of the standard or with the left thumb if it was different. Since there were 20 presentations of the 5 test-durations in every block, participants should have pressed the left button in 80% of trials, and the right button for the 20% remaining. Inter-trial interval was random between 1500 and 2300 ms (mean: 1900 ms).

2.3. Stimuli

Auditory stimuli were 500 Hz pure tones, 490, 595, 700, 805 or 910 ms long, including a 3-ms rise/fall time. Sounds were produced by piezoelectric transducers and conducted through plastic tubing and molded earplugs to both ears of the participant. Intensity was initially set around 70 dB, adjusted according to the comfort of each participant, and then kept constant during the whole session. Visual stimuli were produced by a green light emitting diode (LED) placed outside the shielded room to prevent magnetic artifacts. The beam light was guided through an optical fiber to a translucent aperture in the middle of a black panel placed 65 cm from the participant's face. The light was piloted by a computer with a millisecond precision. Light duration was identical to tone duration, i.e. 490, 595, 700, 805 or 910 ms. Sixty trials by participant were recorded for each duration, in each modality.

2.4. Simultaneous EEG and MEG

In a dimly lit electromagnetically shielded room, each participant was seated in a chair with eyes open gazing at a white circle in the middle of the black panel holding the optical fiber used for visual stimulation.

Magnetic fields were measured with a 151-DC-SQUID whole-head type MEG system (Omega 151, CTF Systems, Port Coquitlam, B.C., Canada [79]). Three small coils were attached to reference landmarks on the participant: at the left and right pre-auricular points and at the nasion. At the beginning of each block, the head position relative to the coordinate system of the MEG helmet was calculated from the position of those coils in order to register possible head movements during the experimental session.

Electrical activity was recorded simultaneously with a 64 Ag/AgCl unipolar electrode cap and processed by the MEG system. Electrode placement followed the Extended International 10–20 system and position of each electrode in the participant's coordinate system was digitized with a Polhemus Fast Track system (Polhemus, Colchester, VT, USA). EEG signal was referenced on-line against the linked earlobe potential.

All operations were controlled by a computer (PC) with < 1 ms precision running in MS-DOS mode. This PC also recorded participant's responses and triggered MEG/EEG acquisition on every trial. Electromagnetic activity was recorded with a digitization sampling-rate of 625 Hz after passing through a DC to 100 Hz on-line filter.

Each trial was 2 s long including 100 ms pre-trigger and 1900 ms post-trigger periods. The 100-ms pre-stimulus epoch served as a baseline for MEG or EEG amplitude.

Participants were instructed to maintain their gaze fixed on the optic fiber at the center of the panel and to avoid blinking in the interval from stimulus onset to their response. Eye-blinks or movements and cardiac artifacts were monitored for later off-line correction with three pairs of disposable electrodes placed laterally on the temples, at the outer canthus of each side for horizontal electrooculogram (EOG), above and below the right eye for vertical EOG, and on the shoulder and stomach for the electrocardiogram (ECG). One extra-channel served as a control track, recording the signal derivated from the stimulation system.

2.5. Data analysis

Three behavioral indexes were computed from responses. Generalization gradient was computed as the rate of "Yes, it is the Standard" responses (%Yes) according to the duration of the stimulus actually presented. Percentage of correct responses (%Correct) was the mean of the rate of true positive, i.e. "Standard" responses to standard durations (S) and the rates of true negative, i.e. "Not the standard" responses to the longer or shorter than standard durations (C, IC, IL and L). Response time (RT) was computed from stimulus's offset. Analyses of variance (ANOVA) were carried out using a two within-subject factors: modality (visual/auditory) and duration (five levels: C, IC, S, IL, L) corrected for multiple comparisons. *T*-tests comparing conditions were corrected with the Bonferroni method.

Two participants were discarded from the following analysis because of a large amount of movement and blinking artifacts. Trials during which responses occurred less than 125 ms after the offset of any stimulus were also rejected. Trials showing deflections of EOG were corrected using an automatic off-line method [24]. Likewise, cardiac artifacts were removed from the signal by subtracting the average activity time-locked to the QRS complex. Trials with EEG changes exceeding 50 μV or MEG changes exceeding 0.5 pT were discarded. For further analysis, data were then low-pass filtered under 20 Hz.

To even out differences in head position across participants, co-registration was applied on inter-individual MEG data: MEG signal was first modeled in a high-dimension space (151 virtual dipoles) and then re-projected on a single array of sensors, which was the same for all participants. This allowed a more precise inter-individual averaging of scalp MEG data.

Event-related potentials (ERP) and event-related fields (ERF) were obtained by computing separate averages of the data for each stimulus duration, from each modality independently of the subject's response (i.e. whether it was correct or not). To increase signal to noise ratio, all durations were pooled together to investigate early components, that is before 490 ms. Indeed, until that point, all stimuli were physically identical.

To analyze transient components, data were filtered with a 20-Hz low-pass zero-phase digital filter. Electric N1 latency was measured as the latency of the maximum negative deflexion in EEG trace occurring around 180 ms at parieto-occipital sites (PO7 and PO8) in the visual condition, and around 100 ms at fronto-central sites (FC5 and FC6) in the auditory condition. Its magnetic counterpart (N1m) was measured on temporo-parieto-occipital sensors (MLT26 and MRT26) in the visual condition and on temporal sensors (MLT22 and MRT22) in the auditory condition at the first maximum deviation after stimulus onset.

Slow potentials were analyzed from 8-Hz low-pass filtered data. Maximum amplitude and latency of this maximum was collected from the same EEG and MEG sites as those used for the transient responses. Slow wave resolution was defined as the latency of the half-height amplitude between the maximum and the peak following stimulus offset. Finally, the latency of this latter peak was recorded as an index of the transient off response.

These data were statistically analyzed with an analysis of variance (ANOVA) separately for EEG and MEG signals using the following within-subject factors: modality (visual/auditory) × duration (5 levels) × side (left/right) × position (fronto-temporal/parieto-occipital) corrected for multiple comparisons: The Huynh-Feldt correction (ε_{HF}) was applied on EEG/MEG measurements instead of the Greenhouse–Geisser (ε_{GG}), provided that ε was above 0.75 (and degrees of freedom larger than 1).

All statistics were calculated using Statistica software [77].

2.6. Source analysis

Distributed source analyses used The BrainStorm Toolbox [2] to perform a minimum-norm analysis. For this purpose, anatomical magnetic resonance images (MRI) were obtained for each participant on a separate session with a 1.5-T Sigma MRI scanner (General Electrics, Milwaukee, WI) at the *Service de Neuroradiologie de l'Hôpital de la Pitié-Salpêtrière* (Paris, France). Sequence used a high resolution volume inversion-recuperation fast spoiled gradient recalled echo structural imaging (IR-FSPGR) along an axial scan plane, time of repetition = 14.3 ms, time of echo = 6.3 ms, time of inversion = 400 ms, field of view = 24 × 24 cm, matrix = 256 × 192, number of excitations = 1, number of slices = 124, contiguous 1.3 mm thick. Scan time was 9′ 43″. Grey matter and grey matter/white matter interface segmentations were performed using Anatomist software [56]. The scalp data used for source reconstruction was an average of co-registered individual datasets: trials of 700, 805 and 910 ms duration were pooled together to increase signal to noise ratio. On these grand-mean datasets, distributed source analyses were performed using a template brain segmentation co-registered with the template sensor array (a similar source reconstruction using grand-mean data has been used by Hopf et al. [34]). Because 700, 805 and 910 ms stimuli were physically indiscernible up to 700 ms (the shortest of the three durations), distribution of sources was computed from this average until 700 ms.

3. Results

3.1. Behavioral data

3.1.1. Generalization gradient

Average behavioral results show that the maximum rate of "standard" responses was obtained for the standard (700 ms) duration (68% in the visual condition and 68.8% in the auditory condition) in comparison to other longer or shorter stimuli, leading to the classical centered gradient shape (Fig. 1).

3.1.2. Percentage of correct responses

Behavioral performance was assessed by computing the rate of correct responses (true positive plus true negative). Participants performed with 63.2% of correct responses in visual blocks and 70.2% in auditory blocks. A two within-subject factor ANOVA was conducted using modality and duration as independent variables: 2 modalities × 5 durations, corrected for multiple comparisons. The effect of modality on correct responses was significant ($F = 14.1$, $p < 0.01$) indicating that stimuli were better recognized in the auditory modality than in the visual modality. The effect of duration was also significant ($F = 6.1$, $p < 0.05$, $\varepsilon_{GG} = 0.46$). There was no interaction between modality and duration ($F = 1.4$, $p = 0.27$, $\varepsilon_{GG} = 0.47$). Interestingly, post-hoc comparisons revealed that the percentage of correct responses was significantly higher for the extreme (490 and 910 ms) durations than for the intermediate short duration (595 ms), and also for the long duration (910 ms) than for the intermediate long (805 ms) duration ($p < 0.05$ in every case). There were no differences for any other comparison. This shows that the intermediate durations (595 and 805 ms) tend to be more easily confounded with the standard than the extreme durations (490 and 910 ms).

3.1.3. Response times

Response times, computed from signal offset, varied monotonically with stimulus durations: the longer the dura-

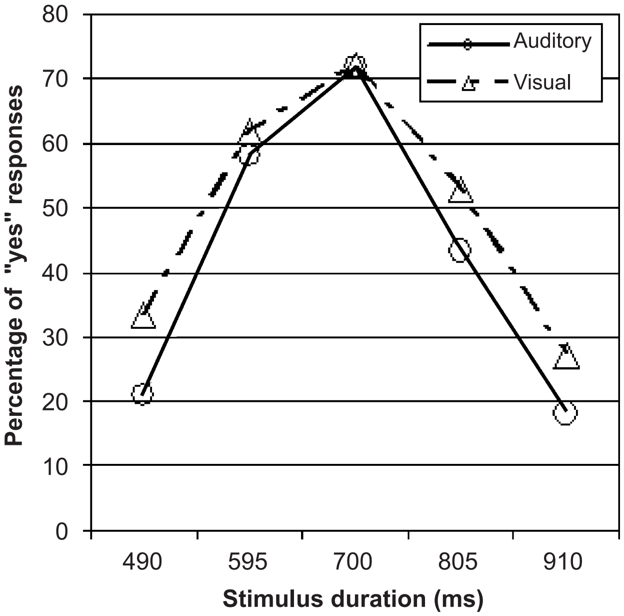

Fig. 1. Generalization gradient in both modalities. Percentage of "equal to standard" responses (ordinate) according to stimulus duration.

tion, the shorter the response time (548.5 ms for "long" vs. 748.5 ms for "short" stimuli). Auditory signals were answered earlier than visual signals (667.6 and 723.0 ms, respectively) (Fig. 2). These observations were assessed by statistical analyses: significant effects of duration ($F = 30.8$, $p < 0.01$, $\varepsilon_{GG} = 0.48$) and modality ($F = 8.0$, $p < 0.05$) on response times were obtained. Interaction between these two factors did not lead to any significant effect ($F = 1.7$, $p = 0.21$, $\varepsilon_{GG} = 0.39$). Post-hoc comparisons showed significant differences between the response times to the shortest durations (either 490-, 595- or 700-ms stimuli) and the responses times to the longest ones (805- or 910-ms durations) ($p < 0.05$ in every pair wise comparison). Participants were faster at identifying the longest durations.

3.2. EEG and MEG data in the visual condition

EEG recordings were made up of a transient response followed by a sustained response. Firstly, three-component early and middle latency responses occurred with a positive–negative–positive sign over occipital regions (Figs. 3, top, and 5). These transient responses were then followed by a sustained potential showing occipital positivity and fronto-central negativity. MEG recordings showed a transient middle latency response maximal over temporo-parietal sensors followed by a sustained activity over the same regions (Figs. 3, bottom, and 5).

3.2.1. Visual early and middle latency responses

Visual stimulation led to a typical pattern of P1, N1, P2 components recorded on left (PO7) and right (PO8) parieto-occipital electrodes, respectively 123, 192 and 230 ms after light onset. (Fig. 3, second row) At fronto-central sites, a large positive deflection, peaking 200 ms after light onset, was recorded (Fig. 3, first row). Magnetic counterparts of the N1 and the P2 components, namely N1m and P2m, peaking respectively 160 and 210 ms after stimulus onset, were recorded with maxima on left (MLT26) and right (MRT26) temporo-parieto-occipital sensors (Fig. 3, third row). ANOVA analyses show no effect of stimulus duration on N1 and N1m latencies or amplitudes ($F < 1$, $p > 0.5$ for all main effects).

3.2.2. EEG visual sustained response

After those early and middle latency components, a negative fronto-central slow potential developed. This slow wave can be labeled as a CNV firstly described by Walter et al. [80] and observed in a similar condition to ours (e.g. Pouthas et al. [69]). Its location was distinct from that of the transient sensory response, being maximal on the fronto-central electrodes (Fig. 5). This broad slow component was also prominent at lateral fronto-central sites (FC5 and FC6) as shown on Fig. 3 (first row). The mean latency of the maximum was 655 ms (S.D. = 118 ms). No significant effect of duration was obtained ($F = 2.5$, $p = 0.11$, $\varepsilon_{GG} = 0.60$). CNV resolution showed a slow decrease in amplitude from the maximum followed by a steeper slope. This deflexion marked the end of the sustained potential following LED extinction. Two separate components seemed thus to occur concurrently at the resolution of the CNV: first, a slow resolution of the negativity starting around 650–700 ms independently of the duration of the stimulation (except

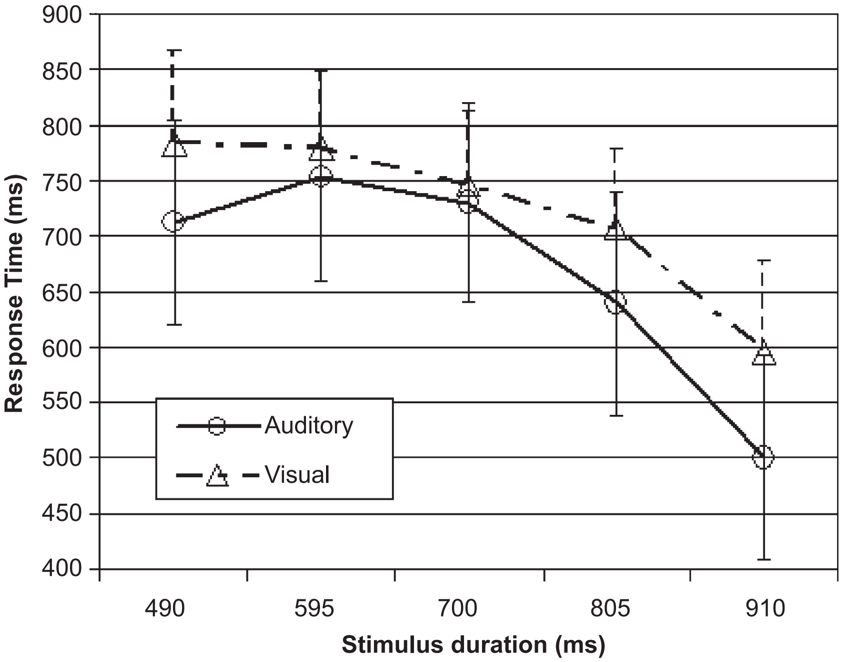

Fig. 2. Mean response times for each stimulus duration in the visual and auditory modality.

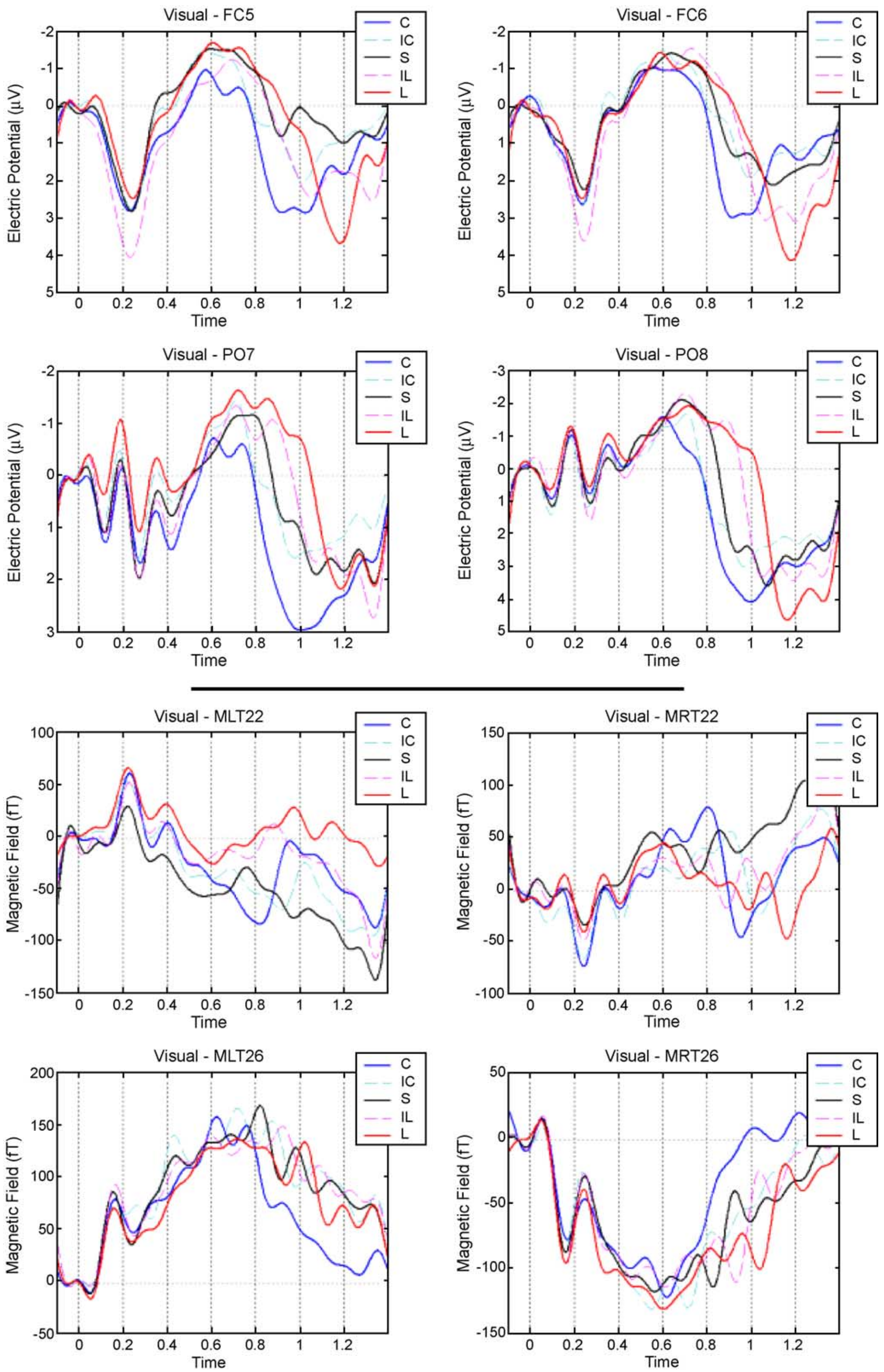

Fig. 3. Time-course of EEG-MEG activity in the visual condition. The two upper rows display the time-course of the electrical scalp potential in the visual condition recorded from left and right fronto-central sites (FC5 and FC6, respectively) and from left and right parieto-occipital sites (PO7 and PO8, respectively). The two bottom rows display the time-course of the magnetic field recorded from left and right anterior temporal sensors (MLT22 and MRT22, respectively) and from temporo-parieto-occipital sensors (MLT26 and MRT26). Colors mark the different conditions as indicated in the legend. The C-condition corresponds to the presentation of a short stimulus (490 ms), IC is for intermediate-short (595 ms), S is for standard (700 ms), IL is for intermediate-long (805 ms) and L is for long stimulus (910 ms).

the shortest one, 490 ms), then a fast positivity time-locked to the light offset. Sustained activity was also present on parieto-occipital and occipital electrodes, i.e. on the putative projection area of visual cortex, but with smaller amplitude. However, contrary to what has been described concerning fronto-central regions, the sustained negativity resolution was modified by the actual duration. On these posterior sites, resolution occurred in time with the offset of the stimulation, which contrasts from what was observed on fronto-central sites. On Fig. 3, one can see a clear separation of the waveforms according to stimulus duration on posterior sites (second row) but not on frontal sites (first row).

3.2.3. MEG visual sustained response

Magnetic data also showed a sustained response over temporo-parietal and parieto-occipital sensors (Fig. 5, top right). This field was maximal on left (MLT26) and right (MRT26) temporo-parietal sensors and its waveform displayed a CNV-like pattern with a steep increase after the P2m component of the transient response, followed by a plateau with constant amplitude around 120 fT (Fig. 3, fourth row). Resolution of this sustained field was time-locked to stimulus offset. However, a decrease in this field could be observed for the longest duration, where an analogue of the slow positive electric component described above started at 700 ms, and then was over-ridden by a N1m–P2m complex corresponding to the offset response. The same pattern was observed over both hemispheres. On the temporo-parietal recording sites, where maximal field was recorded, the latency of the maximal amplitude was not significantly dependent on stimulus duration ($F=2.6$, $p=0.098$, $\varepsilon_{GG}=0.54$) nor was its amplitude ($F=1.22$, $p>0.1$).

3.2.4. EEG and MEG scalp distributions

Topography of the electric signal due to early sensory activity was mainly posterior with negativity peaking on parietal and occipital sensors. On the contrary, the sustained potential was a negative fronto-central slow wave paired with a centro-parietal positivity. The magnetic signal showed a very different pattern: there was a great similarity in the distributions of the evoked fields due to the early response and the distributions of the fields due to the sustained activity. At both latencies, peak activity was bilaterally localized on temporo-parieto-occipital sensors reflecting posterior activity.

3.3. EEG and MEG data in the auditory condition

EEG recordings showed negative transient responses followed by a sustained negativity, centered on fronto-central electrodes. MEG recordings also showed a transient response, which was maximal over fronto-temporal and temporo-parietal sensors and followed by a sustained activity over the same regions (Fig. 4).

3.3.1. Transient EEG and MEG responses

105 ms after auditory stimuli onset, a transient N1 component peaked on fronto-central electrodes (left, FC5, and right, FC6, Fig. 4, first row). The corresponding magnetic response (N1m) peaked 108 ms after tone onset bilaterally on temporal sensors, namely MLT22 and MRT22, respectively, left and right sensors (Fig. 4, fourth row). The corresponding outgoing/ingoing counterpart of the evoked magnetic field was located on temporo-parieto-occipital sensors (MLT26 and MRT26, Fig. 4, fourth row). ANOVA analyses show no effect of stimulus duration on N1 and N1m latencies or amplitudes ($F<1$, $p>0.1$).

3.3.2. EEG auditory sustained response

After the early sensory response, a slow negative potential developed over the frontal region, with its maximum centered on fronto-central electrodes. This slow negative potential peaked around 570 ms (S.D. = 152 ms) and then decreased slowly until the end of the auditory stimulation (Fig. 4, first row). We found a significant effect of stimulus duration on the latency of the peak ($F=12.1$, $p<0.01$, $\varepsilon_{GG}=0.60$), but not on its amplitude ($F=0.13$, $p>0.1$). This slow wave was much larger over anterior electrodes than over posterior ones ($F=53.7$, $p<0.01$, $\varepsilon_{GG}=0.63$) revealing the fronto-central focus of this slow potential.

Following Pfeuty et al. [66], who used a similar methodology, we interpreted that sustained negative activity as a CNV. While this slow wave was maximal around 570 ms, a slow positive shift arose from that point in time leading to a decrease in the amplitude of the CNV, up to the occurrence of the P2 offset-sensory response which finally inverted the polarity of the slow wave, peaking 200 ms after sound's offset (Fig. 4, first raw).

3.3.3. MEG auditory sustained response

The simultaneous magnetic field showed a similar sustained activity, but distributed over temporal regions reflecting bilateral activity (Fig. 4, bottom part). Its amplitude was about 250 fT and was not affected by duration ($F=0.37$, $p>0.1$). Time course of this sustained field was somewhat different from that of the fronto-central negativity observed in EEG within the same modality. Whereas the auditory CNV peaked around 570 ms, this sustained field showed different pattern according to electrode position (on an anterior/posterior axis): whereas anterior frontal sensors showed a peaked slow wave, posterior sensors displayed a steady-state component from 500 ms until the end of the to-be-judged duration. Later on, the end of the stimulation triggered an offset response.

3.3.4. Scalp distribution

The transient auditory response and the late sustained potential both display a maximum negativity on fronto-central regions (Fig. 5, bottom left). A similar observation can be drawn from the MEG data, as the distribution of

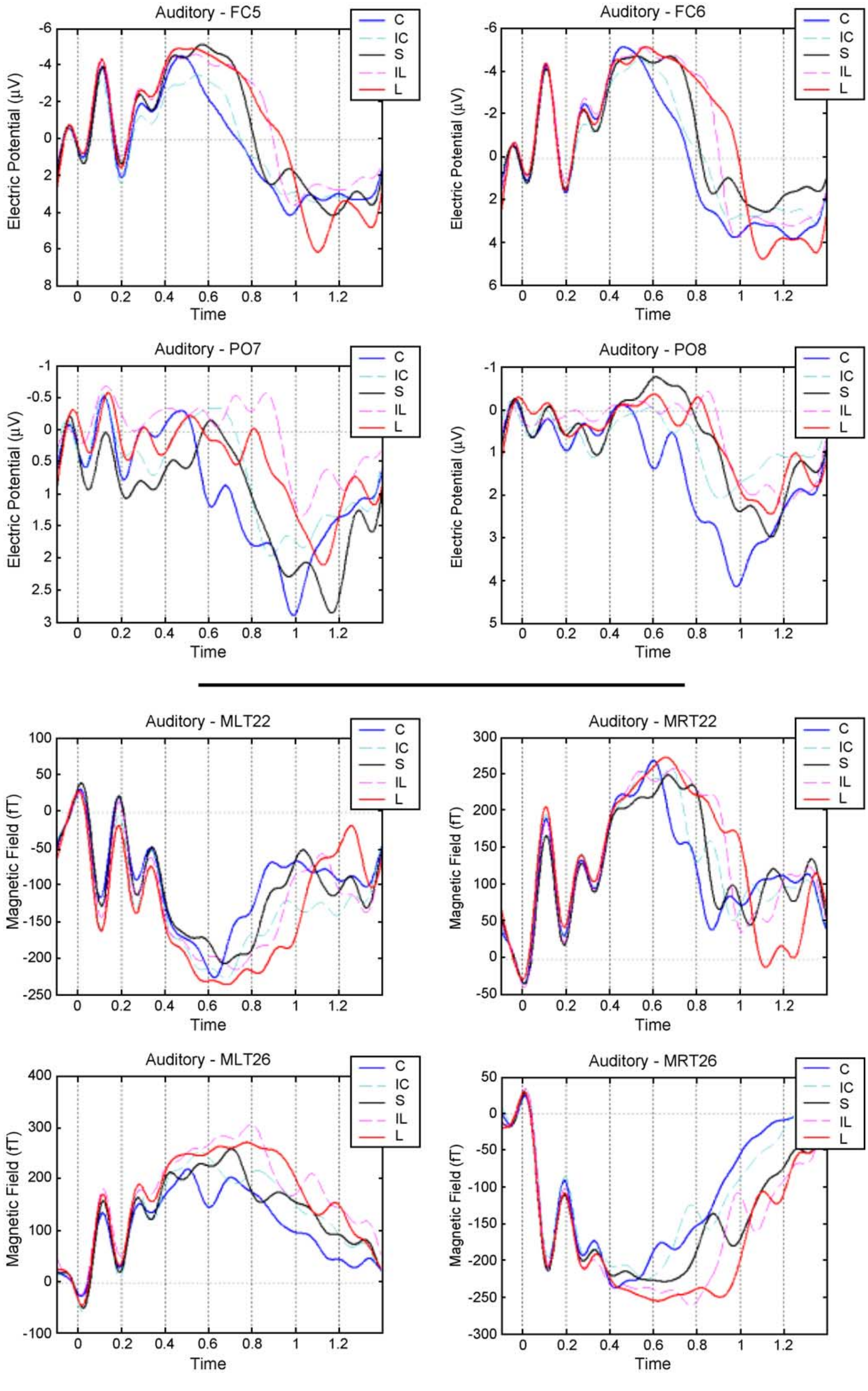

Fig. 4. Time-course of EEG-MEG activity in the auditory condition. The two upper rows display the time-course of the electric scalp potential in the auditory condition recorded from fronto-central sites (FC5 and FC6, respectively, left and right) and from parieto-occipital sites (PO7 and PO8, respectively, left and right). The two bottom rows display the time-course of the magnetic field recorded from left and right anterior temporal sensors (MLT22 and MRT22, respectively) and from temporo-parieto-occipital sensors (MLT26 and MRT26). Colors mark the different conditions as indicated in the legend. The C-condition corresponds to the presentation of a short stimulus (490 ms), IC is for intermediate-short (595 ms), S is for standard (700 ms), IL is for intermediate-long (805 ms) and L is for long stimulus (910 ms).

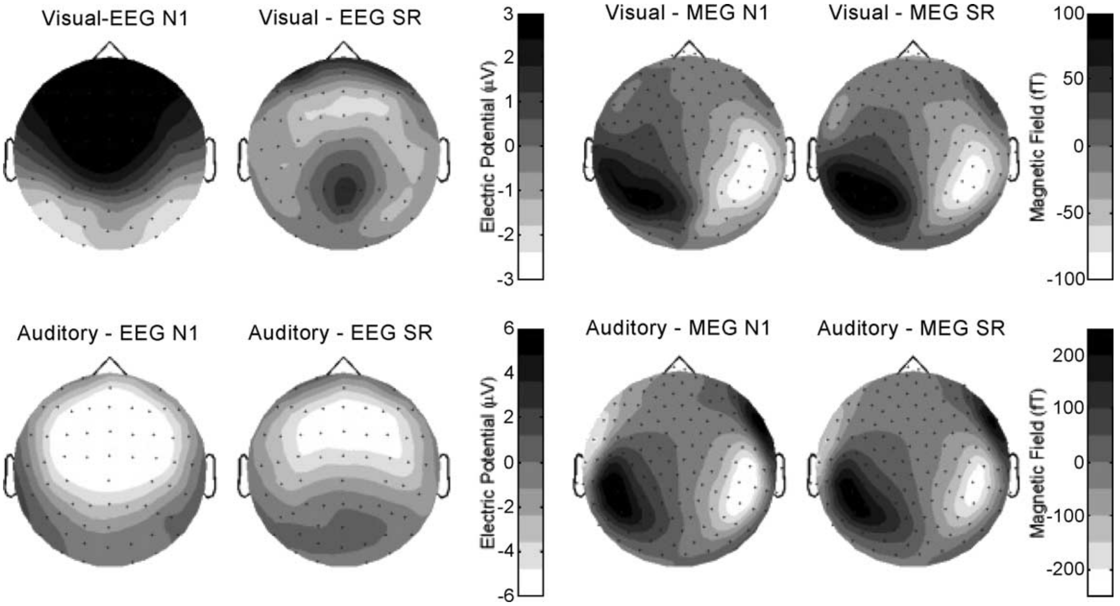

Fig. 5. Scalp distribution of EEG and MEG signals in the visual and auditory condition during transient and sustained responses. Maps show scalp distribution of electric (left part of the figure) and magnetic (right part) signals at two different latencies in each experimental condition: visual (top row) and auditory (bottom row). Two different latencies are displayed: the transient (N1/N1m) response and the sustained response (right). Sustained activity is computed as the average of signal over a window from 500 to 700 ms after stimulus onset in 700, 805 and 910 ms conditions.

early magnetic response and late sustained fields superimpose (Fig. 5, bottom right).

3.4. Comparison between auditory and visual conditions

A striking difference between visual and auditory conditions lays in the scalp distribution of sustained activity. A significant interaction was observed between the factors modality and antero-posterior position ($F = 7.5$, $p < 0.01$, $\varepsilon_{GG} = 0.62$) as a posterior sustained negativity developed in the visual but not in the auditory condition. When considering fronto-central electrodes only, CNV amplitude for auditory stimuli was significantly larger than that for visual stimuli (6 vs. 2 μV; $F = 9.8$, $p < 0.005$, $\varepsilon_{GG} = 0.65$).

Regarding CNV time-course, the effect of modality did not reach significance, possibly because CNV peaks in the visual condition were more variable. CNV resolution showed a distinct time-course between anterior and posterior electrodes in the visual condition: whereas posterior slow wave resolved in time with stimulus duration, fronto-central CNV resolution was less dependent on stimulus duration. From MEG data, an analogous topographical distinction is unobvious as visually evoked magnetic signal is mainly temporo-parietal (Fig. 5, top right). In the auditory condition, a similar distinction could be made as posterior MEG sensors showed a steady-state response profile, whereas anterior sensors showed a inverted U-shape slow wave (Fig. 4, bottom part). In the auditory condition, little difference was observed between scalp magnetic distribution of the transient and sustained responses (Fig. 5, bottom right). In this condition, contrary to what was the case in the visual one, scalp distribution of transient and sustained electrical responses are both fronto-central (Fig. 5, bottom left), which did not allow us to separate stimulus driven from less time-locked activity.

3.5. Distributed sources analysis

To assess the possible concurrent activation of distinct generators in each condition, we performed a distributed source analysis on the mean signal over a 200-ms window around the latency of the peak amplitude of the sustained response, i.e. between 500 and 700 ms, using only the three longest durations (700, 805 and 910 ms). This reconstruction was compared to the sources obtained for the corresponding transient sensory response.

3.5.1. Visual condition

Transient N1 sources where located mainly in both dorsal part of the occipital cortex (precuneus and cuneus) and ventral part of the occipito-temporal junction, bilaterally (Fig. 6, top left). Sources reconstructed from the magnetic signal were located in the same regions showing more acute distribution on medial dorsal parieto-occipital cortex (Fig. 6, mid-top left). Visual sustained activity, as recorded by EEG, was modeled by a segregated pattern of activation including the medial parieto-occipital cortex and bilateral prefrontal cortices. Weaker activation was also reported from superior temporal gyrus (Fig. 6, top right). The same analysis performed on MEG data resulted in activation foci partially overlapping the EEG results: The medial parieto-occipital cortex showed transient and sustained activity, but in contrast with EEG, no frontal nor prefrontal activity was

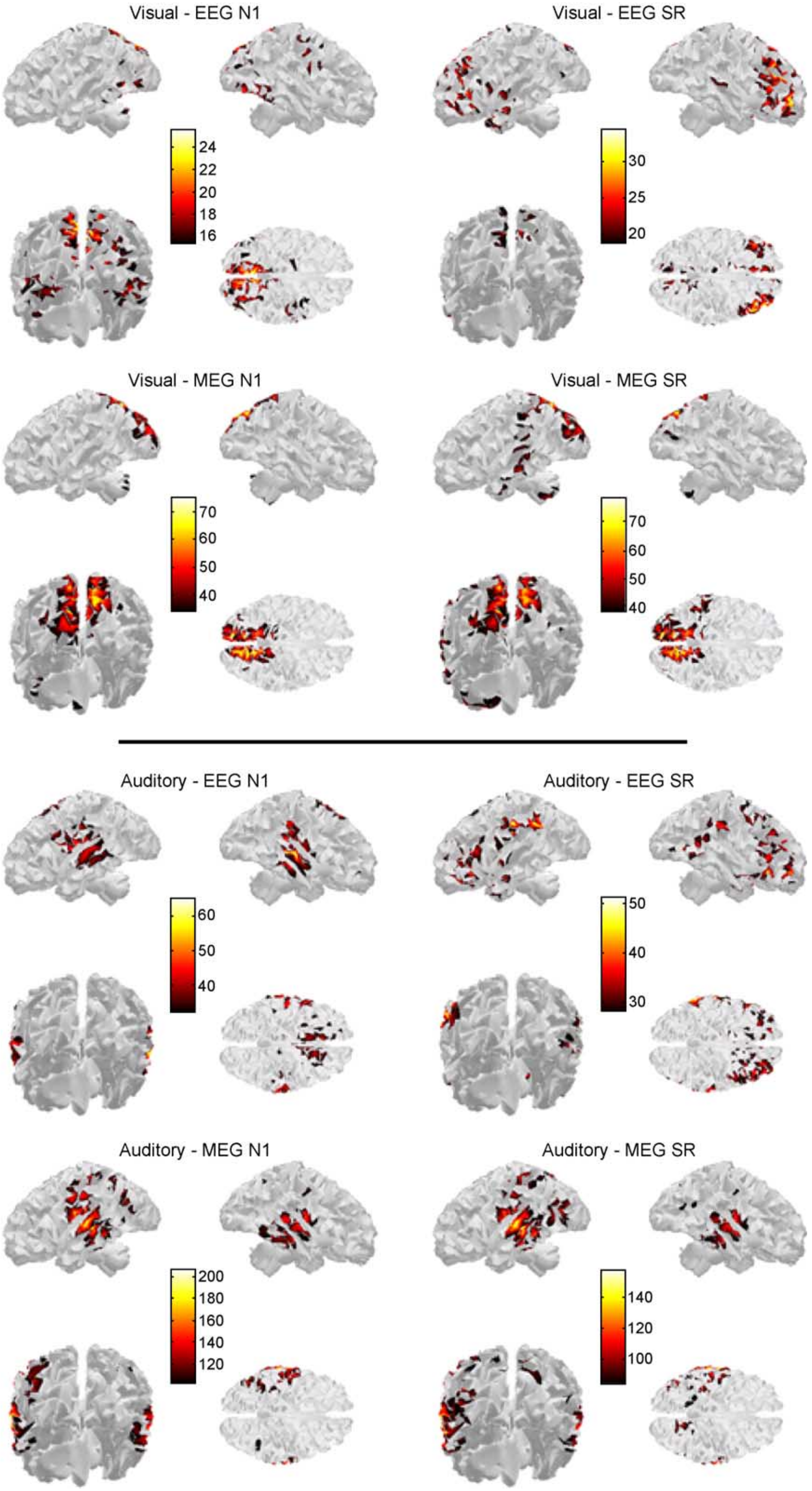

Fig. 6. Distributed source reconstructions. Source reconstructions are shown on the template brain which has been used for the distributed source estimate from the grand average data in eight experimental conditions. Visual vs. auditory × EEG vs. MEG × transient (N1) vs. sustained (SSR) responses. For each experimental condition, four views of the cortex are displayed, from left to right, top to bottom: left hemisphere view, right hemisphere view, backwards view and top view. Source reconstructions of electric (top row) and magnetic (bottom row) slow waves in visual (left column) and auditory (right column) conditions were computed on the mean signal between 500 and 700 ms from 700, 805 and 910 ms conditions. Color scale has been adjusted in each condition to provide optimal viewing.

obtained. Simultaneous activity was also reported in temporal regions on the banks of the superior temporal and middle temporal sulci but also within superior parietal lobe. (Fig. 6, mid-top right).

3.5.2. Auditory condition

Three active regions were observed during the auditory N1 potential: Both left and right temporal cortices (especially superior and middle temporal gyrus) and medial fronto-central regions (Fig. 6, mid-bottom left). Auditory CNV was modeled by strongly active sources stemming from bilateral inferior parietal lobe and a widespread activation over bilateral prefrontal cortices (Fig. 6, mid-bottom right). MEG data in the auditory condition resulted in a very different distribution pattern of activity: Whereas bilateral temporal cortex was also intensely active during both transient and sustained response, no prefrontal activity was generated. However, distributed activity was observed within superior parietal regions (especially left ones) and at temporo-occipital junction (posterior inferior temporal gyrus and inferior occipital gyrus) (Fig. 6, bottom).

4. Discussion

4.1. Behavioral data

As reported in previous studies, proficient temporal generalization performance was characterized by a central tendency to respond positively (i.e. "identical to the standard" by a right button-press) to the test duration corresponding to the initially-presented "standard". Better discrimination was achieved for extreme short (490 ms) or long (910 ms) durations in comparison to the intermediate (595 or 805 ms) even if some participants showed variable performance (which is often observed when no feed-back is given, see Ref. [82]). Concerning modality influence, auditory signals are generally reported as being perceived longer and with a greater accuracy [27,64,83]. Here, a significant effect of modality was observed on duration discrimination in line with those previous studies since auditory stimuli led to better discrimination than visual ones.

In addition to discrimination performance, response times (RT) show here two remarkable features:

(1) The longer the test-duration, the faster the response. One possible interpretation of this result might be that participants made their decision while the test duration was elapsing and, as soon as the timed duration exceeded the memorized standard, they could categorize the on-going signal as a non-standard duration, since they were in a two-alternative choice procedure. As noticed by Leon and Shadlen [45], the conditional probability of categorizing a signal according to its duration is a monotonic function of time. Although this hypothesis may explain behavioral results for a short/long categorization, it fails within the context of generalization were uncertainty would be a bimodal function of time for a perfect observer. Instead of this bimodal pattern, RT in our study were monotonically decreasing with the duration to be timed. In a different timing task, Lacouture et al. [41] also noticed a decrease in RTs with the duration to be timed, independently of the bow-effect, which describes shorter RTs when discrimination is easier. A possible explanation of this could be that the shorter-than-standard and the longer-than-standard stimuli are differently processed. Categorizations of the longest (805 and 910 ms) durations would occur as soon as standard duration has elapsed. On the contrary, this categorization could not happen earlier than the standard duration and would even require a constant time to be performed.

(2) Auditory stimuli are more rapidly discriminated than visual stimuli. The 60-ms difference between auditory and visual RT is in accordance with results showing better performances in auditory than visual timing task and similar modality effects on RT are reported in other timing tasks by Ford and Hillyard [19] and Rousseau and Rousseau [72]. This can be interpreted as a better efficiency of the auditory channel to process time, but alternative hypotheses such as speed differences in sensory processing cannot be discarded (see Ref. [25]).

4.2. Electromagnetic data

This present study was aimed at comparing cortical activity simultaneously monitored with MEG and EEG within a single group of participants while they were performing the same timing task in both modalities. Fronto-central sustained event-related potentials (CNV) occurred in both auditory and visual modalities while participants were performing a duration discrimination task. Time-course of this slow EEG potential was shown to be dependent on the duration to be timed, while its topography was shown to be modality independent. However, classifying the duration-dependent sustained magnetic activity as a magnetic equivalent of the electric CNV (a CMV) is uncertain because the magnetic fields topography did not reproduce the frontal distribution of the CNV. On the contrary, its distribution was similar to that of modality specific early sensory responses. The EEG–MEG recordings showed that during duration perception of filled intervals timing-dependent activity and sustained sensory response (SSR) occurred concurrently. However, separating these slow waves was uneasy especially in the auditory modality.

These results were supported by modeling the distributed sources of the sustained electric and magnetic responses in each modality. Beside sensory cortices, prefrontal cortices in EEG and temporo-parietal or parietal cortices in MEG showed activity as the stimulus duration was being judged.

4.2.1. EEG data in the visual condition

In line with previous studies, whilst participants were performing duration discrimination of visual signals, we observed a fronto-central CNV that peaked on fronto-central sites. The latency of this maximum was around 600 ms after stimulus onset. As sensory activity within the visual cortex projects onto the parieto-occipital regions of the scalp, SSR and CNV were easily distinguishable. Moreover, CNV time-course differed from that of the SSR. Whereas sustained negativity at parietal or parieto-occipital electrodes showed a steady-state profile, which resolved after light offset, fronto-central negativity peaked around 650 ms for all but the shortest stimulus, and then resolved independently of the duration to be judged (see the superimposed traces on Fig. 3 for 595, 700, 805 and 910 ms conditions). The marked differences in the time course of activity between fronto-central and parietal/parieto-occipital regions indicate that these two slow waves are due to concurrently active but distinct generators. From this condition, we can conclude that timing visual filled intervals leads to a sustained activity within the corresponding sensory regions and to a simultaneous fronto-central scalp negativity which cannot be accounted for by the sensory processing of the visual stimulation to be timed. It should be noted at that point that although the actual duration of the stimulation to be timed does not seem critical for the peak latency of the CNV negative deflexion, it determines the latency of the positive shift which marks the end of the CNV resolution. The CNV seems thus here to be composed of two different components: a slow negative wave peaking at 655 ms and a fast resolution crossing baseline towards a positive peak. These two components are differentially modulated by the duration discrimination task: the slow negative wave might reflect a true timing process (as its peak latency does not correlate with the duration of the on-going stimulation but is rather modulated by the encoded "standard" duration); the fast positive resolution, on the contrary, is dependent on the real stimulus duration and it may thus reflect the processing of the stimulus offset.

4.2.2. EEG data in the auditory condition

By recording electric scalp activity while participants were performing duration discrimination of continuous tones, we observed a fronto-central negativity whose time course was duration dependent. Contrary to what could be inferred from EEG data in the visual condition, possible superimposition of timing-dependent activity and sensory sustained activity cannot be readily assessed from scalp distributions. It has indeed been repeatedly shown [30,67,68] that, outside any explicit timing context, long-lasting tones also generate a fronto-central negative potential, the auditory sustained potential (ASP), the resolution of which being time-locked to the offset of the sound. Nonetheless, attention to time has also been reported to modulate ASP: In a thorough study of ASPs, Picton et al. [67] demonstrated that enhanced ASPs were recorded when participants were requested to detect durations deviants among continuous tones (but not when they were attending frequency deviants). The temporal component of the task seemed critical for this effect and these authors concluded on the possible superimposed contributions of frontal and temporal generators to the ASP. Our data suggest that such a sustained sensory activity would be superimposed on task specific cortical slow components. Whereas ASP show a steady-state profile, the present slow potentials peaked at a specific point in time independent of the duration to be timed. Afterwards, the fronto-central negativity amplitude decreased (compare our Fig. 5 with Fig. 1 from Picton et al. [67]). The present results therefore support the concurrent activity of generators whose electric signature lies on frontal regions of the scalp during the timing of auditory filled intervals.

4.2.3. MEG data in both conditions

The most striking observation concerning MEG data in the present experiment is the similarity between the distribution of this slow potential and the transient sensory response (N1m). Moreover, time course of the sustained potential followed the duration of the sound to be timed: the shorter the duration, the earlier the resolution of the sustained field. The present slow cortical field might thus reflect the contribution of a common set of generators responsible for both the N1m and a sustained sensory response. As a result, no magnetic counterpart of the CNV could be identified from the scalp data at late (>300 ms) latencies.

Generators of the sustained responses have been reported to lie in the same cortical regions of those of the transient sensory responses. This hypothesis is supported, at least in the auditory modality, by many studies that showed that auditory sustained fields (ASF) could be repeatedly recorded with MEG. Source modeling of these ASF demonstrated that their generators were also located in the auditory supratemporal cortex, which is the reason why they are so easily detectable with MEG [28,30,36,63,76]. However, in keeping with observations made on their electric counterpart (ASP), Hari et al. [31] also reported enhancement of ASF with selective listening, in particular while participants performed a duration discrimination task while the N1m, which shares anatomically common generators with the ASF, was not modulated by selective attention to duration. However, in the present task, there was no control condition to compare our timing condition with.

4.2.4. Sustained response generators

To separate activity stemming from sensory regions from signal due to other sources, we performed a minimum-norm constrained distributed source imaging. As a result, we were able to reconstruct the main generators that contributed to the slow potentials/fields within each condition (auditory and visual) as recorded either by EEG or MEG. Interestingly, EEG data not only showed weak activations of sensory cortices but also strongly activated bilateral parietal and prefrontal regions. Frontal activations reported for each of the two conditions (visual or auditory) largely overlapped. Surprisingly MEG data also led to much greater activation foci within respective visual occipital or auditory supratemporal cortices, while no frontal generators were observed. However, extended temporo-parieto-occipital and parietal regions showed sustained activity while participants were timing the intervals in both modalities.

As clearly seen from scalp data, EEG and MEG signals showed undoubtedly different aspects of the brain activity. Source analyses confirmed this view since different subsets of sources were reconstructed from each recorded signal. An explanation for the absence of a magnetic counterpart to the fronto-central electric slow wave can be given by the physical characteristics of the MEG signal: While electric potentials are produced by both radial and tangential sources (with respect to the surface of the scalp), magnetic signal reflects only the contributions of the latter. As a consequence, tangential sources (like those in the calcharine sulcus) might generate a stronger magnetic than electric response, which would therefore hide contributions from other sources, especially if they are radially oriented as it may be the case on frontal gyri [11,71].

Moreover, as EEG captures signal from deeper generators than MEG, these sources might be reflected in widespread distribution on the cortical surface. Apparent frontal activity in the present data might thus be explained by activation from deep neural structures. One candidate for this may be the basal ganglia whose contribution in interval timing [59] but also at shorter duration ranges [17,70] has been widely documented.

Auditory and visual EEG data also showed medial activations. Contribution from the supplementary motor area (SMA) is possible since other timing studies have demonstrated the involvement of this area in temporal tasks [17,50]. Activity from this structure has appeared to be difficult to record with MEG possibly because of its anatomical configuration: bilateral activity on the medial wall of both hemispheres would result in two opposite dipoles facing each other, whose activity might partially cancel out, producing a very small magnetic field on the scalp surface [44].

4.2.5. Comparisons between visual and auditory conditions

Using filled intervals in both conditions, we observed sustained activity on the scalp projection areas of sensory cortices with both recording techniques. One could thus question the specificity of the slow cortical responses as regards timing processes. To our knowledge, only one MEG study [16] has used filled (auditory) interval to investigate CMV. Like us, the authors were unable to clearly separate CMV from sustained auditory activity, although some arguments allowed them not to confound them: intersubject variance was greater for the CMV, and single dipoles failed to explain this sustained activity. On balance, it is worth noticing that Dammers and Ioannides [13], even when using empty intervals, found consistent CMV generators within auditory and sensorimotor cortices. CNV-dedicated studies generally use empty intervals, but filled intervals have also been used [66,69,73] and authors rarely comment on the possible superimposition of sensory sustained activity over other ERP. However, some arguments strengthen our conclusion drawn from our analyses of EEG and MEG scalp recordings. On the one hand, even if concurrent sustained activity in sensory regions was recorded, it may not be crucial to duration discrimination itself as demonstrated by its time course. On the other hand, common cortical networks were shown to be active during the timing task, independently of the modality. We can therefore conclude that these particular networks were specifically engaged by the timing task and provide substrate for cognitive processes such as time perception.

Firstly, timing of visual and auditory signals evoked strong sustained activity in respective visual and auditory sensory regions. These activities may correspond to an enhancement of sensory processing (as signal offset detection is crucial to the task) rather than time processing per se. Indeed, preservation of auditory duration discrimination has been evidenced with patients suffering from bilateral auditory cortex lesions [78]. However, the involvement of sensory regions in duration processing can not be totally excluded, especially regarding auditory regions where increased metabolic activity has been shown to occur when participants were timing duration of short (~ 300 ms) auditory signals [5]. In the present experiment, possible rehearsal of the memorized signal may have been used as a strategy by the participants to perform the task in the visual condition as well, since superior temporal regions were also active while participants were timing visual signals.

Moreover, temporal information provided by the waveform of the EEG recordings, especially in the visual condition, showed distinct time courses between the fronto-central negativity and the electric negative potential recorded on parietal and occipital sites. These latter sites correspond to the projecting areas of the visual cortex which the visual sustained potential is generated from. The time course of the fronto-central negativity can thus not be fully attributed to the sustained activity reflecting visual processing. Even if no strict correlation could be established between electrophysiological activity and behavioral performance, CNV amplitude (measured at fronto-central sites, in both conditions, increased continuously until the standard duration had elapsed, after what it started to decrease. These results are in line with those of Pfeuty et al. [66] showing positive correlation between this CNV activity and the memorized standard duration. Fronto-central slow cortical responses recorded in timing tasks using filled intervals thus reflect contribution of sustained responses from sensory regions but also from additional sources specifically involved in duration discrimination.

Finally, the similar scalp distribution of these task-specific fronto-central responses to visual and auditory durations (though less ample in the visual modality) and the common networks activated independently of the sensory modality involved strengthen the conclusion that the slow fronto-central negative component which develops in both conditions, may reflect supra-modal timing processes.

4.3. Synthesis

The critical observations we made in the present study were (1) that slow electric potentials or magnetic fields were simultaneously recorded by EEG and MEG when participants were performing duration discrimination of filled visual or auditory intervals; (2) that sustained modality-dependent activity occurred within the associated sensory areas; (3) that from the scalp-recorded slow potentials/fields, one could partially isolate modality independent activations within prefrontal and temporo-parieto-occipital or parietal cortices, differently recorded by EEG or MEG. Contributions of these generators superimpose to produce the scalp distributions of these slow cortical potentials/fields.

From our source reconstruction, common cortical networks located in bilateral prefrontal cortex might be the generators of this modality-independent frontal activity. Prefrontal cortex has been repeatedly reported to play a major role in interval timing [9,17,33,47,57,62,69,70]. But its role in working memory [46] has also been assessed for long. The temporal generalization task is heavily demanding on working memory, since the standard has to be memorized for the whole block, which generally led the participants to update it according to the durations they were presented. Furthermore, decisional processes might also involve the prefrontal cortex [39]: the critical point in time from which the visual and auditory CNV started to resolve nearly corresponds to the standard duration. One can therefore hypothesize that the outcome of memorized vs. stimulus duration comparison is processed in line and the decision is made from then on.

According to distributed source reconstructions, generators of these modality-independent activities may be modeled as widespread parietal and temporo-parietal activations. These results are in line with those recently obtained by Sieroka et al. [76] in an auditory duration discrimination task. Sustained magnetic components were indeed explained by the joint contribution of bilateral dipoles located within supratemporal cortices and an additional parietal dipole. Interestingly, they report large inter-individual variability in the locations obtained for this dipole.

Possibly as part of a fronto-parietal network, the parietal lobe has been reported to be involved in human timing [8,54,57,69,70,74] and a recent study using intra-cortical recordings confirmed these results at the neuron level in rhesus monkeys [45]. Midline precuneus/cuneus regions were active in a temporal order task reported by Cabeza et al. [7]. This region is known to be anatomically connected to the dorsal frontal cortex [65] and was shown to be activated during auditory [84] or visual [18] imagery task. Possible processing of the duration to be timed might thus be reflected in this parietal activation, but other concurrent cognitive processes could also be the cause of it. Whether parietal activity is linked to attentional, memory, response preparation or specifically temporal processes cannot be discussed under the sole light of the present data.

Sensory activations may reflect processing of the stimulation but their role in timing is harder to assess. Although auditory cortex has been repeatedly proven able to detect temporal deviance, its integration windows within which it can perform temporal processing, seems limited to 200 ms [10] or slightly longer [40]. Moreover, left temporal cortex was active during the visual condition. It is possible that this focus corresponds to auditory imagery process. Post-test interview revealed that most subjects used this strategy to perform the visual task. fMRI studies also reported temporal activation in visual duration discrimination tasks [17,47]. These sources were either superimposed (or at least very close to) the most active sources in the auditory condition. This is coherent with Zatorre et al. [85] suggesting that auditory imagery share common neural bases with actual auditory perception.

5. Conclusion

Taken together, these results suggest that timing-dependent cortical activity might be reflected in an electric negative sustained CNV-like potential on fronto-central regions of the scalp present in both modalities. This CNV was concurrently observed with sustained activity from sensory regions evoked by the on-going stimulation. Simultaneous sustained evoked related magnetic fields showed markedly different distributions with regard to the modality of the signal to be timed. Complementary electric and magnetic images of sustainedly active brain regions proved to require the simultaneous use of EEG and MEG recordings to be fully captured: As opposed to EEG data, MEG recordings seemed to be more sensitive to the sources from sensory regions since the distribution of the sustained activity was very similar to that of the primary sensory response in the corresponding modality. Source reconstruction demonstrated that these sustained potentials/fields were generated by superimposed contributions from visual and auditory cortices and from prefrontal and parietal regions. These results suggest the involvement of both sensory and supra-modal associative regions in the duration discrimination of filled time intervals.

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