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RESEARCH ARTICLE

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Conscious and preconscious adaptation to rhythmic auditory stimuli: a magnetoencephalographic study of human brain responses

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Abstract This study was triggered by the experimental evidence that subjects required to tap in synchrony with a heard rhythm spontaneously time their tapping to variations in rhythm frequency even when these variations are so small that they are not consciously detectable. We performed a series of magnetoencephalographic (MEG) measurements, aimed at investigating whether the response of the auditory cortex discriminates randomly administered series of brief tones differing from each other only by their interstimulus intervals (ISI). Moreover, by combining psychophysical measurements, conscious and preconscious adjustments of tapping to rhythm variations were compared with brain cortical responses. The ISIs were varied by 2% or 20% from a "central" value of 500 ms. Subjects always consciously detected the 20% ISI changes and easily adjusted their tapping accordingly, whereas they never consciously detected the 2% ISI changes, even though they always correctly adjusted their tapping to them. Analysis of the auditory evoked fields (AEFs) showed that the intensity of the M100 component decreased with decreasing ISI both for 20% and 2% variations in a statistically significant manner, despite the fact that the 2% variation was not consciously perceived. The M100 behavior indicated that connections between auditory and motor cortexes may exist that are able to use the information on rhythm variations in the stimuli even when these are not consciously identified by the subject. The ability of the auditory cortex to discriminate different time characteristics of the incoming rhythmic stimuli is discussed in this paper in relation to the theories regarding the physiology of time perception and discrimination.

Key words Rhythm perception · Auditory evoked fields · Auditory-motor synchronization · Human

Introduction

Good timing is always needed for the execution of skilled movements and many experiments have been devoted to studying the cerebral processes related to timekeeping: auditory pattern recognition (Fitzgibbons et al. 1974; Povel and Essen 1985; Ross and Houtsma 1994), rhythmic perception (Monahan and Hirsh 1990; Dawe et al. 1995), and time perception as connected to timing ability in sensorimotor synchronization tasks (Kagerer et al. 1990; Collyer et al. 1992; Franek et al. 1994; Vos et al. 1995; Thaut et al. 1998) are some of the more investigated issues. Nevertheless, all these studies have used behavioral responses as observable parameters characterizing the human ability to process and discriminate rhythmic patterns. Since results based exclusively on behavioral performances are often conflicting, due to the high variability of many psychophysical measurements, and do not discriminate between subcortical and cortical mechanisms, a direct analysis of functional brain activation related to auditory-motor synchronization with elevated time discrimination and high sensitivity to cortical activation is of major importance (Miller et al. 1994; Treisman et al. 1994; Rao et al. 1997; Mayville et al. 1999).

In the present study we used magnetoencephalography (MEG) to investigate the response of the human auditory cortex to incoming rhythmic stimuli. The study was triggered by previous experimental evidence demon-

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strating that subjects required to tap their fingers in synchrony with a rhythmic metronome sequence spontaneously adjust their tapping to perturbations of the rhythm frequency even when these perturbations are so small as to be undetectable consciously (Thaut et al. 1998).

MEG is a noninvasive technique capable of spatially localizing the firing of small cortical and subcortical neuronal areas both when this firing is spontaneous and when it is evoked by externally delivered stimuli. MEG has been used in the past largely to study the response of the auditory system to tone bursts (Hari et al. 1980, 1987) or to temporally modulated stimulation (Romani et 1982; Makela et al. 1987), and more recently its spatial identification of activation areas has been precisely related to anatomical structures through the use of MRI (Pantev et al. 1990; Papanicolau and Banmann 1990). Mismatch fields (MMF) have been detected following variant (Sams et al. 1991), omitted (Joutsiniemi and Hari 1989), or changing interstimulus interval (ISI) in auditory stimuli (Hari et al. 1989; Levanen et al. 1996), showing a link between the auditory system and time perception. In contrast, only a few studies have been devoted to brain processing of repetitive auditory stimuli characterized by rhythm variations. Lu et al. (1992a) have demonstrated that the M100 intensity changes as a function of ISI and that this dependence is exponential. Pantev et al. (1993) have investigated auditory fields evoked (AEFs) by brief tone pips at different stimulus rates (0.125–39 Hz). To our knowledge, the linkage, if any, between cortical auditory responsiveness as reflected by M100 intensity and conscious and preconscious perceptions of ISI changes has never been investigated.

Our study was aimed at characterizing the response of the auditory cortex to a randomly administered series of rhythmic auditory stimuli differing from each other by small variations in ISI, in order to investigate whether brain responses possibly involved in the sensory stimulus processing are specifically linked to conscious or preconscious motor synchronization to the dispatched rhythm.

Subjects and methods

The study was approved by the local ethics committee. Ten healthy volunteers (35–45 years old; seven men, three women, all right-handed) were enrolled after informed consent was obtained.

Stimuli

Stimuli consisted of sequences of acoustic bursts (30 ms long, 2000 Hz frequency, 2 rise-time cycles, intensity of 70 dB sound pressure level above subjective threshold) delivered in blocks, each characterized by a different ISI and a random duration between 15 and 25 s. They were produced by a computer-driven Grass tone control module and transduced into a nonmagnetic, echo-free plastic tube that terminated in the subject's left ear. In one set of measurements, the stimulus ISI varied from block to block by 2% of a "central" frequency, chosen to be 2 Hz in order to reproduce the stimulus frequency range used by Thaut et al. (1998) in their original study: in other words, successive blocks had ISIs of 500 ms, 510 ms, 500 ms, 490 ms, 500 ms, and 510 ms. In a separate set of measurements, this variation was increased to 20%; i.e., successive blocks had ISIs of 500 ms, 600 ms, 500 ms, 400 ms, 500 ms, and 600 ms (Fig. 1). In neither case were subjects to perform any movement during the stimulation, but, in order to maintain attention, they were asked to mentally count how many times the ISI changes occurred. Prior to the MEG recordings, within the same session, the subjects' ability to adjust their tapping to ISI variations was checked by recording the timing of the subject's motor responses by means of a piezoelectric device.

Recording procedure

The spatial distribution of the brain's magnetic field over the scalp was measured with a 28-channel system (Tecchio et al. 1997) featuring 16 first-order axial gradiometers (1.8 cm coil diameter and 8 cm baseline), nine magnetometers (pickup area 81 mm^2), and three balancing magnetometers for noise cancellation coupled to low-noise, d.c. SQUIDs, with an overall sensitivity of about 5–7 fT/Hz$^{0.5}$. The 25 active sensors were uniformly distributed (about 2.5 cm apart one from each other) over a spherical surface covering an area of about 180 cm^2. All measurements were performed inside a magnetically shielded room (Vacuumschmelze).

The array of sensors was positioned over the right midtemporal lobe, centered 1.5 cm above the T4 position of the 10-20 International EEG System, and recorded the AEFs contralateral to the stimulated ear. The right hemisphere was chosen according to the known prevalent brain laterality of this side of the brain in controlling tapping rhythmicity (Fries 1990) and in processing music in nonmusicians (Berman 1981). The exact position of the array with respect to the subject's head was determined by using five current-fed coils (Ernè et al. 1987) attached to anatomical landmarks of the head (nasion, the two preauricular points, vertex and inion), whose three-dimensional (3D) positions were digitized (Polhemus Isotrack) prior to the recording session. The entire recording procedure lasted about 90 min.

Data analysis

About 500 artifact-free trials were acquired to obtain each evoked response (1 kHz sampling frequency, 0.48–250 Hz bandwidth). Data recorded in each block of constant ISI were averaged and expressed relative to a baseline represented by the data mean during the time interval between two successive stimuli. Only 50% of the trials relative to the "central" ISI stimulations were se-

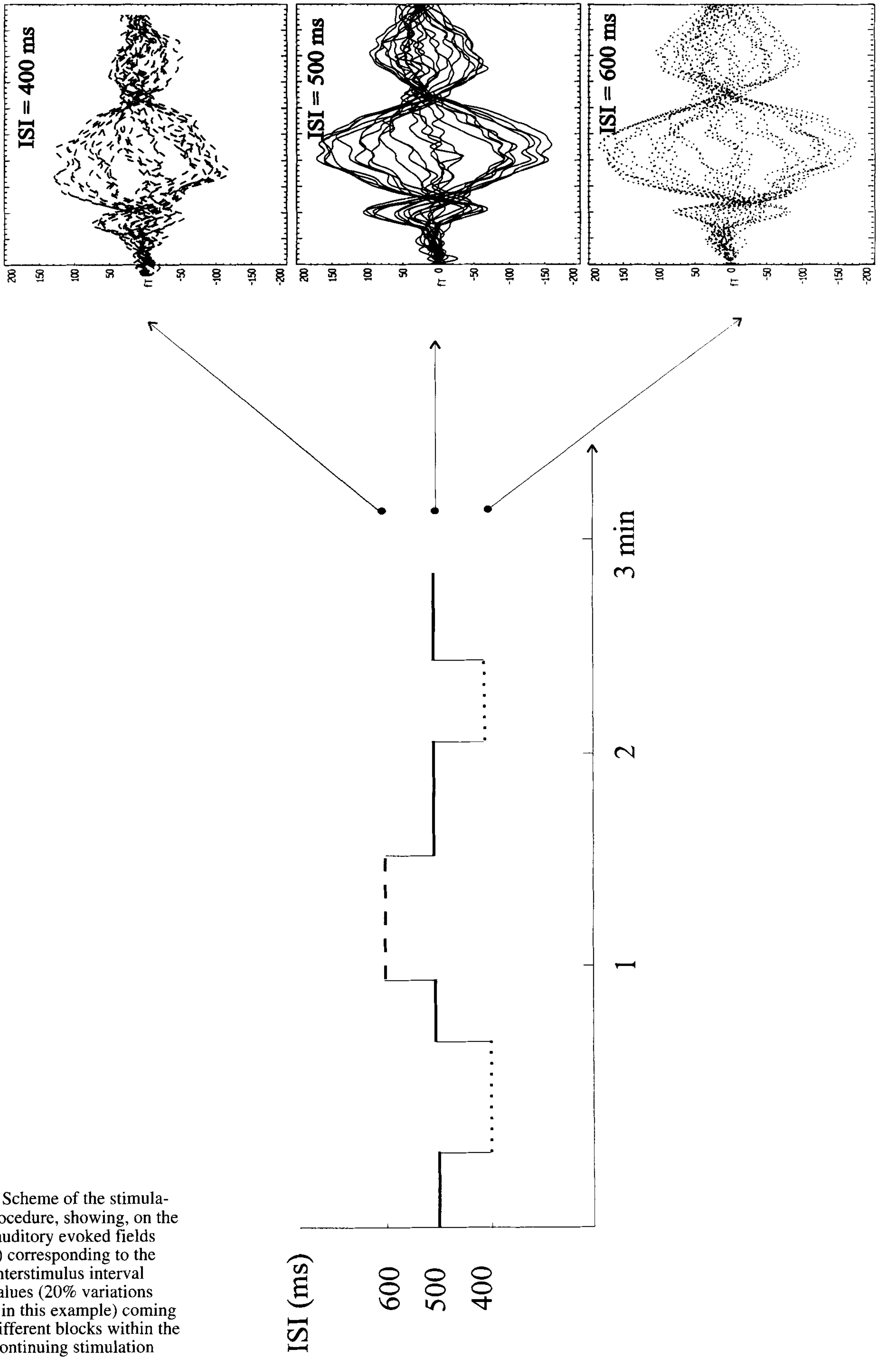


Fig. 1 Scheme of the stimulation procedure, showing, on the *right*, auditory evoked fields (AEFs) corresponding to the three interstimulus interval (*ISI*) values (20% variations shown in this example) coming from different blocks within the same continuing stimulation

lected in order to obtain means with the same number of traces for each ISI.

Two components of the AEFs were studied in particular: one elicited at about 40 ms after stimulus onset (middle-latency AEF, latency 10–50 ms; Pellizzone et al. 1987; M40), the second elicited at about 100 ms (slow AEF, latency 40–250; Reite et al. 1978; Hari et al. 1980; M100). The amplitudes of these components are known to be related to ISI changes: Hari and colleagues (Hari et al. 1982) showed that M100 intensity increases with increasing ISIs between 1 and 16 s. Pantev et al. (1993) showed that both M40 and M100 intensities decrease with decreasing ISIs when the latter are in the range 8–1 s and that the M100 even disappears when the ISI is as short as 0.1 s: at these ISI values a "steady state" is reached in which individual components are melted together and the brain shows a sinusoidal response, oscillating at the stimulating frequency. Lu et al. (1992a) have demonstrated that the M100 amplitude exponentially saturates with progressively longer ISI, giving an indication of the duration of time over which an event remains available for processing by the working memory; in particular they demonstrated that the lifetime of the neuronal activation trace in primary auditory cortex predicts the psychophysical duration of the memory of the loudness of a tone (Lu et al. 1992b).

In the present study, the amplitudes of the M40 and M100 components were evaluated as functions of all the ISIs used and compared with the subjects' ability to consciously discriminate rhythm changes. The signal amplitude was defined as the difference between maximum and minimum peaks in those channels that detected the strongest signal. Means of 15 ms around the maximum or minimum power values were taken into account.

A model based on a single equivalent current dipole (ECD) inside a homogeneously conducting sphere (Elberling et al. 1982; Gallen et al. 1992; Pantev et al. 1993) was used to localize the generator of the M100 component. The brain magnetic field distributions recorded within a 16-ms-wide time interval centered at the time that showed maximum total power was used for each component to calculate the ECD position and strength. Our model was chosen according to previous studies (Sams et al. 1993) showing that the magnetic response in the contralateral hemisphere could be accounted for by a single dipole when ISI is shorter than 1 s. Localization results were accepted only if their explained variance was above 90%. The ECD position was expressed in the individual Cartesian coordinate system, defined as follows: the x-axis passing through right and left preauricular points, outgoing rightward; the positive y-axis through the nasion; and the z-axis perpendicular to the point of bisection between the x- and y-axes.

Statistical analysis

In order to analyze all sources of variance, an initial two-way ANOVA for repeated measures with PROTOCOL (±20%, ±2%) and ISI (short, baseline, long) as "within-subjects" factors was performed. After assessing in this way the significance of both the main and the interaction effects, a separate ANOVA was run for each protocol. We described the ISI effects by "repeated contrasts" (i.e., baseline vs short, long vs baseline). No correction to α-inflation was applied, since comparisons were preplanned and only orthogonal contrasts were chosen. Before performing ANOVA, we applied a logarithmic transformation to the original data in order to achieve a better Gaussian fit and to limit heteroschedasticity. The significance threshold was set at 0.05. A Greenhouse-Geisser correction was applied to the degrees of freedom when appropriate.

Results

Subjective perception

All subjects counted the ISI changes correctly when their variation was 20% of the central frequency, whereas in no case were they able to identify the 2% ISI changes. Despite this, all subjects were able to adjust quickly (within 1–2 motor responses) to the new ISI, both of 20% and 2%, with an appropriate interresponse interval (IRI, Fig. 2). Our results therefore agree with previous studies suggesting conscious and preconscious tuning to rhythm changes in the above conditions (Thaut et al. 1998).

AEF morphology

In agreement with others, auditory cortical responses in our ten subjects showed a high intersubject variability, in both AEF morphology and M100 dependence on ISI. Figure 3a,b represents two subjects for whom the shape of morphological responses are very different (Lu et al. 1992b).

Table 1 Summary of statistical analysis for both original and log-transformed data

Protocol		fT		log(fT)		P-value
		Mean	SD	Mean	SD	
20%	ISI400	138.1	56.9	4.85	0.43	0.005
	ISI500	169.4	70.6	5.05	0.42	<0.001
	ISI600	211.7	76.1	5.29	0.37	
2%	ISI490	153.4	72.4	4.94	0.44	0.006
	ISI500	174.0	76.1	5.07	0.44	0.032
	ISI510	191.8	92.6	5.16	0.46	

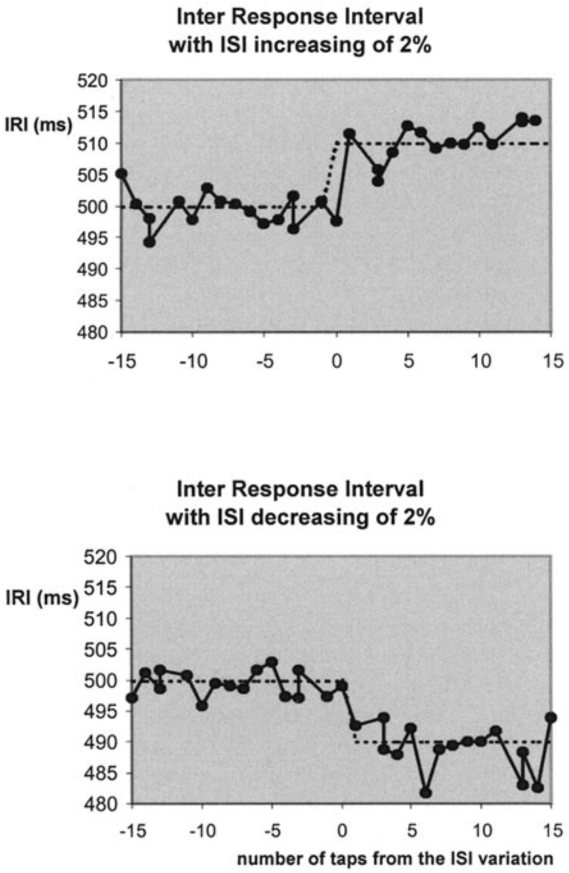


Fig. 2 Intermotor response intervals (*IRI*) related to changes toward larger (i.e., from 490 to 500 ms and from 500 to 510) or briefer ISI (i.e., from 510 to 500 ms and from 500 to 490). Fifteen taps before and 15 after the change are shown. The values are the means of around 50 ISI variations, grand-averaged across two subjects. Notice that within 1–2 taps following the ISI variation, the interval between two motor responses is adjusted to the new ISI

M100 component

M100 wave amplitude significantly increased with increasing ISI duration. This was present for both 20% and 2% variation, despite that the former was always correctly identified, whereas the latter was never detected (Fig. 4).

Statistical analysis

Table 1 summarizes the results of our analysis, showing the means and standard deviations of both the original and the log-transformed measures. The initial two-way ANOVA indicated no difference between the two protocols as main effect (F=0.8, df=1,9; P=0.782), but a strongly significant effect of the ISI variations (F=72.3, df=2,18; P<0.001). Since also the interaction term (Protocol × ISI) was statistically significant (F=5.3, df=2,18; P=0.015), the ISI effect was not homogeneous across the two protocols. Focusing on the 20% protocol, the significance of ANOVA (F=41.7, df=2,18; P<0.001) stems from the differences both between 500 ms and 400 ms (P=0.005) and between 600 ms and 500 ms (P<0.001). Also in the 2% protocol, ANOVA was significant (F=14.6, df=2,1; P<0.001), owing to the significant increments of AEF amplitudes both between 490 ms and 500 ms (P=0.006) and between 500 ms and 510 ms (P=0.032). Therefore, a similar pattern in the two protocols was identified, and the significance of the interaction term could be attributed to the fact that the line was steeper when 20% ISI modulation was applied. In other words, a clear dependence of M100 amplitude on minimal ISI variations (2%) was also verified, although to a significantly lesser extent.

Localization of the sources of the M100 component showed an explained variance greater than 90% in 43 out of 60 trials. In such cases it showed a complete stability of the M100 source position (Fig. 5) and latency with changing ISIs. In all these cases, the source strength showed the regular decrease in relation to the ISI decrease, explaining the M100 intensity variation.

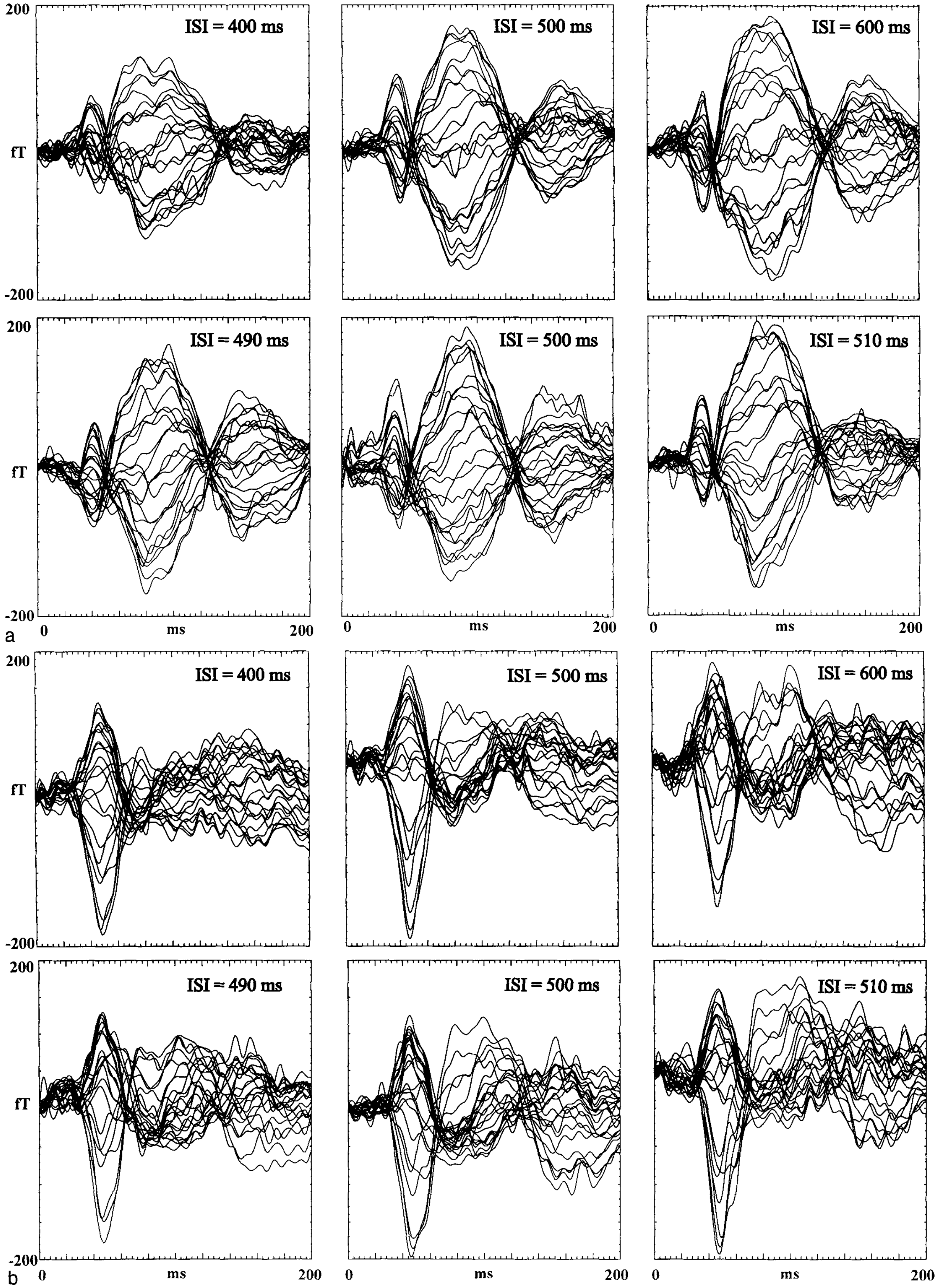
M40 component

The M40 amplitude did not show any regular relationship with the ISI, either for 20% ISI variations or for the 2% ones.

Discussion

The present work reveals for the first time that the amplitude of a specific component (M100) of the brain magnetic field evoked by rhythmic auditory stimuli increases when the time interval between stimuli gets longer regardless of whether the subject is consciously identifying rhythmic changes or not. In fact, this effect is observable even when a 500-ms ISI is varied by a percentage as small as 2%, at a level where the subject is still able to adapt and rapidly synchronize the motor output, but at a preconscious level. The dependence of the M100 intensity on the ISI, known to be exponential over the scale of seconds (Lu et al. 1992a), is represented by a straight line in the brief tested interval (400–600 ms total). Previous studies never addressed the issue of the M100 intensity-ISI relationship in a time frame as brief as the one close to the threshold between conscious and preconscious perception. The present findings suggest that rhythm discrimination is at least in part taking place at the auditory cortical level and that the auditory cortex may contribute directly to synchronize the motor output, in particular via common thalamic projections shared

Fig. 3 a AEFs of subject S1 corresponding to the five different, ▶ constant ISI values. The AEFs related to the ISI of 500 ms is shown twice, coming from the stimulation with 2% and 20% ISI variations. The AEF morphology shows the prevalence of the M100 component, usually common for ISI longer than 1 s. **b** The same for subject S2. The M40 is much larger than the M100


200
fT
-200
ISI = 400 ms
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ISI = 500 ms
ISI = 510 ms
a
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ms
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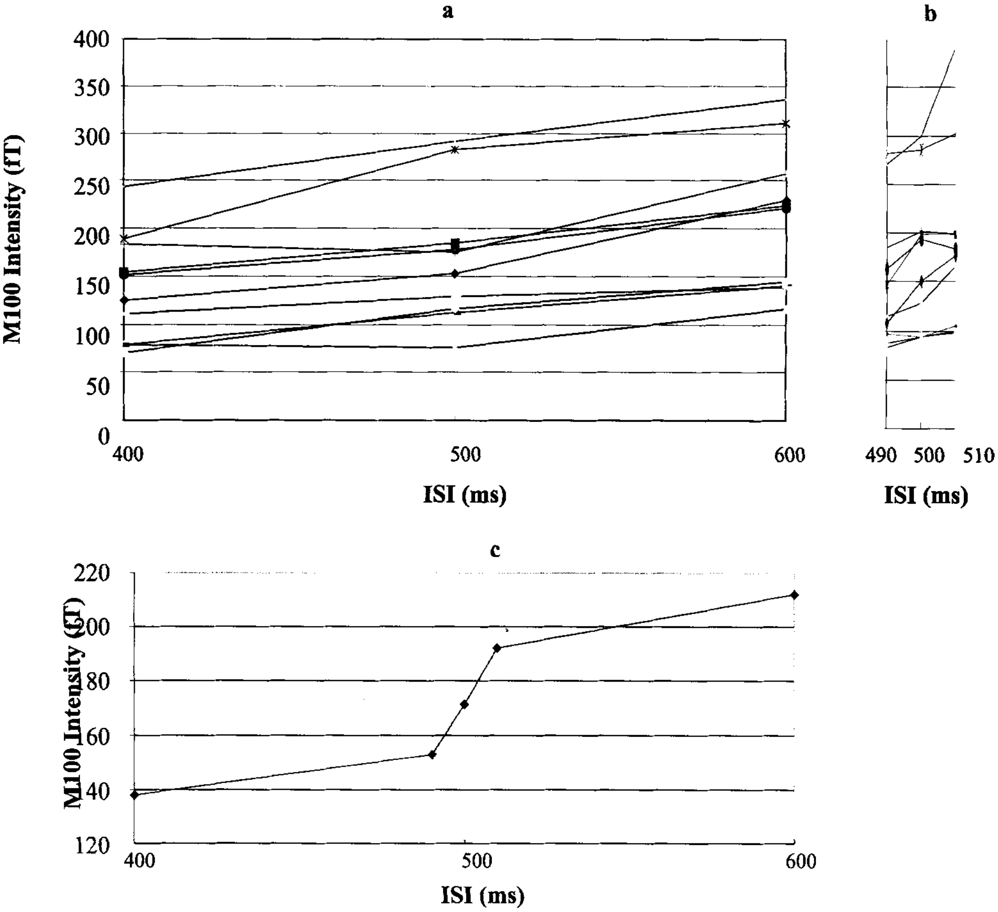

Fig. 4 **a** M100 intensities of all subjects for the 20% ISI variation. **b** The same for 2% ISI variation. **c** The means across all subjects

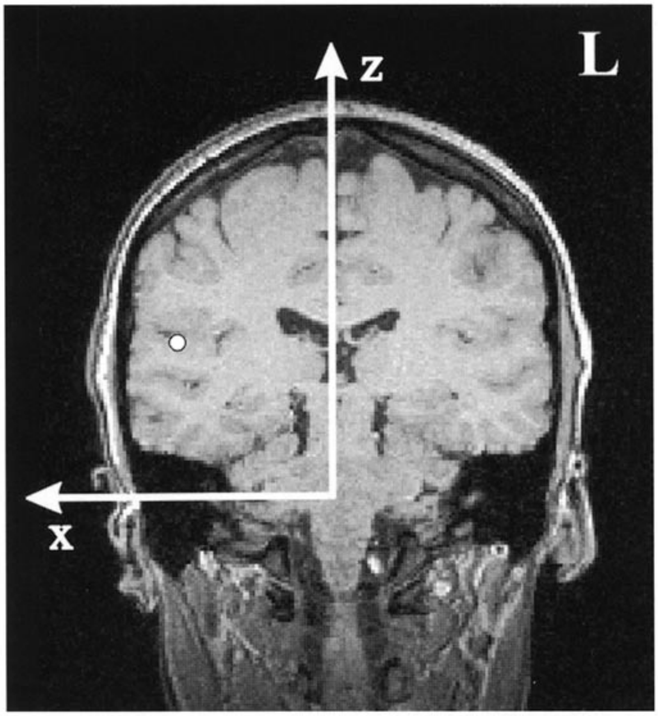

Fig. 5 Localization of the M100 generator in one sample subject, showing the source in the supratemporal Heschl's gyrus (primary auditory cortex)

with supplementary motor area, as observed in musicians tapping different rhythms (Lang et al. 1990).

Moreover, it is suggested that the local sensory memory, which retains processed information about an auditory sequence for about 10 s (Cowan 1984; Lu et al. 1992a; Sams et al. 1993), is characterized by a sensitivity of at least 2% in the 2 Hz rhythmicity. In particular, the M100 behavior is due to the increase in strength of a cortical generator stable in position and latency, indicating that what is changing in the cerebral response is the number of activated neurons within a neural pool fixed in position. It is worth noticing that a link between the M100 intensity and stimulus temporal characteristics was also found by Imada et al. (1997), by demonstrating the dependence of this component on the pause duration immediately preceding the stimulus arrival. It is natural to believe that the subcortical relays preceding the primary auditory cortex may not only contribute to generate the pattern of activity found at cortical levels, but also trigger those neuronal loops necessary for the motor performance. Indirect support for this hypothesis comes from Rossignol and Melvill Jones (1976), who demonstrated the increased excitability of motoneuronal pools at the spinal level induced by an auditory burst.

The ability of the auditory cortex to process the temporal characteristics of incoming stimuli seems to support the idea that separate neural networks are intrinsically able to process temporal information. This would support one of the two main hypotheses about the physiology of time perception and discrimination. In particular, some researchers believe that the neuronal pathway that connects the ear to the auditory cortex (cochlear nucleus, superior olive nucleus, inferior colliculus, and thalamic medial geniculate nucleus) is a neuronal network intrinsically able to process temporal characteristics of auditory input (Buonomano and Merzenich 1995; Buonomano et al. 1997; Buonomano 2000). Others claim that such a network needs instead the interaction with the basal ganglia, which function as an "internal clock," working on the time scale of milliseconds in a way similar to the circadian timing system, which works on the scale of hours or days (Meck and Church 1987; Ivry and Keele 1989; Wearden and Penton-Voak 1995; Rao et al. 1997; West et al. 1997; Woodward et al. 1998).

The increase in the mean M100 amplitude versus the ISI increase was nonlinear: this effect could indicate some particular role of the 2-Hz rhythm in human perception. While studying the increase in motoneuronal pool excitability induced by auditory stimuli, Rossignol and Melvill Jones (1976) found that facilitation lasted about 460 ms, indicating that audiospinal potentiation is enabled at a rate of about 2 Hz. This frequency has been indicated also as preferred hopping frequency (Melvill Jones and Watt 1971). On the other hand every hypothesis on the role of the 2-Hz frequency could be understood only by measuring the M100 intensity at different ISIs by using nonhomogeneous (large and small) variations to check for nonlinearities as a way to detect context-dependent variations.

We found no regular variation of the M40 component. In fact, no systematic behavior of its intensity with ISI changes was detected in our data, although this could be simply due to unfavorable directions of the dipolar sources located in some regions of the temporal lobe, possibly including contributions from subcortical areas (Woods et al. 1987; Kraus et al. 1988).

In conclusion, it is clearly shown that the auditory cortex discriminates rhythmic variations of incoming stimuli, even when the subject does not identify them consciously, and new light is cast on brain mechanisms underlying rhythmic perception.

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