

Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG/MEG study

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Abstract

Objectives: Our neurophysiological model of anticipatory behaviour (e.g. *Acta Psychol* 101 (1999) 213; Bastiaansen et al., 1999a) predicts an activation of (primary) sensory cortex during anticipatory attention for an upcoming stimulus. In this paper we attempt to demonstrate this by means of event-related desynchronization (ERD).

Methods: Five subjects performed a time estimation task, and were informed about the quality of their time estimation by either visual or auditory stimuli providing Knowledge of Results (KR). EEG and MEG were recorded in separate sessions, and ERD was computed in the 8–10 and 10–12 Hz frequency bands for both datasets.

Results: Both in the EEG and the MEG we found an occipitally maximal ERD preceding the visual KR for all subjects. Preceding the auditory KR, no ERD was present in the EEG, whereas in the MEG we found an ERD over the temporal cortex in two of the 5 subjects. These subjects were also found to have higher levels of absolute power over temporal recording sites in the MEG than the other subjects, which we consider to be an indication of the presence of a ‘tau’ rhythm (e.g. *Neurosci Lett* 222 (1997) 111).

Conclusions: It is concluded that the results are in line with the predictions of our neurophysiological model. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Event-related desynchronization; Anticipatory attention; Magnetoencephalography; Knowledge of results; Tau rhythm; Thalamo-cortical gating

1. Introduction

Most of the events that we experience everyday do not happen unexpectedly. This enables us to anticipate events that (probably) will happen in the near future. From a functional point of view, this anticipatory behaviour is aimed at a faster and better perception, and a faster and more accurate response than would have been possible under unwarned conditions. From a neurophysiological point of view, anticipatory attention is directed either at preparing the relevant brain structures to do in advance what can be done (e.g. Requin et al., 1991), or at reducing the threshold levels of the relevant brain structures (e.g. Birbaumer et al., 1990) in order to ensure a faster processing, given the available infor-

mation about the situation the subject is in. This should manifest itself as an anticipatory activation of the primary sensory cortex corresponding to the modality of the anticipated stimulus, which *precedes* the presentation of the stimulus. In other words, we think that the mechanism underlying anticipatory attention is independent of stimulus modality, although at the same time we expect topographic differences in cortical activation during the anticipation of stimuli in different modalities. Elsewhere, we have presented a neurophysiological model (Brunia, 1993; 1999; Bastiaansen et al., 1999a), in which we propose that anticipatory behaviour is based on a thalamo-cortical gating mechanism. This gating mechanism has previously been put forward by Skinner and Yingling to account for intermodal selective attention (Skinner and Yingling, 1977; Yingling and Skinner, 1977).

Anticipatory attention for an upcoming stimulus has been studied in a series of experiments employing a time estima-

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tion paradigm. In this paradigm subjects are instructed to press a button some seconds after a warning stimulus, and are subsequently confronted with a Knowledge of Results (KR) stimulus providing feedback about the accuracy of the estimated time interval. A negative slow potential can be recorded prior to the KR stimulus, which has been called the Stimulus-Preceding Negativity (SPN, Damen and Brunia, 1994; for reviews, see Brunia, 1993; 1999; Böcker and Van Boxtel, 1997). The SPN has been observed preceding auditory and visual KR stimuli. On the basis of our model for anticipatory behaviour we would in principle expect visual stimuli to be preceded by an occipitally maximal SPN, and auditory stimuli by a temporally maximal SPN; at the very least, we would expect the SPN to display differences in scalp distribution preceding stimuli of different modalities. However, this has not been found to be the case (Böcker et al., 1994), although results of a recent experiment in our laboratory suggests that there are tiny differences in SPN amplitude over the auditory and visual cortices preceding auditory and visual KR stimuli, which go in the expected direction. Furthermore, a spatiotemporal dipole analysis of the SPN prior to auditory and visual KR stimuli did not detect dipoles in the primary auditory or visual cortices (Böcker et al., 1994). In sum, the conclusion seems warranted that slow potential research has as yet not been very successful in identifying physiological correlates of anticipatory attention as described in the thalamo-cortical gating model.

Skinner and Yingling (1977) predicted that during selective attention for a specific sensory modality one should find a coincidence of negative slow potentials, enhanced evoked potential amplitudes and desynchronization of 10 Hz rhythmic activity over the corresponding sensory cortex. Support for the notion of desynchronization can be found in two comprehensive review papers by Steriade et al. (1990); Lopes da Silva (1991). These authors point out that under influence of the reticular nucleus, thalamic relay nuclei can operate in two modes. In burst mode the transmission of information from sensory afferents through the thalamus to the cortex is blocked. In the scalp-recorded EEG this is reflected in synchronized, rhythmic activity with a frequency of approximately 10 Hz above the corresponding cortical area. In the tonic mode afferent information is transmitted to the cortex. At the scalp this is reflected in a desynchronization of 10 Hz rhythmic activity. In terms of Skinner and Yingling, this would imply that synchronization of EEG activity over a sensory cortex indicates that the gate of the corresponding sensory modality to the cortex is closed, whereas desynchronization indicates an open gate.

These findings suggest that analyzing the spatiotemporal patterns of synchronization and desynchronization of the EEG might be another means of studying thalamo-cortical gating, that can be used in addition to slow potential analyses. An analysis method known as event-related desynchronization (ERD; Pfurtscheller and Aranibar, 1977) can be used to quantify such event-related changes

in rhythmic EEG activity. At a signal-analytic level, the major difference between slow potentials and ERD is that, due to the averaging procedure used in their computation, slow potentials only contain activity that is both time- and phase-locked to the occurrence of an event. For ERD it holds that the relevant phenomena need only be time-locked to the event, i.e. phase-locking is not required. Therefore ERD and ERP's may contain complementary information (see also Lopes da Silva, 1999; Pfurtscheller, 1999).

In a previous study, we studied the spatiotemporal patterns of ERD based on EEG data of 10 subjects, during the anticipation of auditory and visual KR stimuli in a time estimation task (Bastiaansen et al., 1999b). On the basis of the thalamo-cortical gating model we expected an occipital ERD preceding the visual KR, and an ERD over the left and right temporal cortices preceding the auditory KR. Preceding visual KR stimuli we indeed found an ERD with an occipital maximum; however, preceding auditory KR stimuli no appreciable ERD was present. In summary, although we clearly found a topographic dissociation between the two modalities, we did not find evidence for anticipatory attention in the auditory modality.

Niedermeyer (1990, 1991) (see also Niedermeyer, 1997 for a review) reported the existence of rhythmic activity originating in the temporal lobe. This 10 Hz rhythm could be measured by means of epidural and intracortical EEG recordings, but could not be picked up by simultaneously recorded scalp EEG. This indicates that normal, scalp-recorded EEG is blind to this kind of rhythmic activity. Niedermeyer termed it the 'third rhythm', and showed that it could be functionally differentiated from alpha and mu activity on the basis of the observation that it did neither display any reactivity to opening or closing of the eyes, nor to activity of the somato-motor system. On the other hand, Tiihonen et al. (1991); Lehtelä et al. (1997) reported the existence of a magnetoencephalographic (MEG) rhythm originating from the temporal lobe, which was termed the tau rhythm (Hari, 1993; see also Hari et al., 1997 for a review). They demonstrated that the tau rhythm was, in most of the subjects, clearly attenuated following auditory stimulation. The suppression of the tau rhythm was found to be much stronger over the right than over the left temporal cortex. This, together with the fact that source analyses demonstrated that the sources of the tau rhythm were located very close to the sources of the auditory evoked responses, namely in the supratemporal plane, suggests strongly that the tau rhythm is an intrinsic rhythm of the auditory cortex.

Together, these studies demonstrate that the auditory cortex generates a 10 Hz rhythm that can be measured with MEG, but not with scalp-recorded EEG. This might be explained by the fact that MEG is particularly sensitive to sources that are oriented tangentially with respect to the cortical surface, which is mostly the case for cell columns in the supratemporal plane. The fact that EEG is blind for rhythmic activity from the auditory cortex might explain

why we did not find an ERD over the temporal cortex preceding auditory KR stimuli in our previous EEG study (Bastiaansen et al., 1999b): if we cannot pick up rhythmic activity from the auditory cortex with scalp EEG, then we surely cannot demonstrate a desynchronization of this rhythmic activity. The experiment described in the present paper is aimed at testing this possibility. Five subjects performed a time estimation task, and the ERD preceding the presentation of the – auditory or visual – KR stimulus was computed on both EEG and MEG. With the EEG data we expect to replicate the results of our previous study (Bastiaansen et al., 1999b), that is, an occipital ERD preceding visual KR stimuli and no ERD preceding auditory KR stimuli. With MEG we expect to find similar results preceding the visual KR, but we expect to find an additional ERD bilaterally over the temporal cortex preceding auditory KR stimuli.

2. Methods

2.1. Subjects

Five normal, healthy subjects (4 men, one woman, age range 25–35) participated in the experiment. They received Dfl.10,- (approximately 5 USD) per hour plus travel expenses for their participation. Informed consent was obtained from all subjects prior to their participation in the study.

2.2. Design and procedure

Our recording devices did not allow for simultaneous recording of EEG and MEG. Therefore each subject performed the experiment twice, first for the EEG recordings and then for the MEG recordings. The experimental conditions were highly similar for the two recording sessions, although there were small, and for the present purposes irrelevant, differences in the presentation of the KR stimuli (see later in this section).

Subjects were seated in a dimly illuminated, sound-attenuating chamber. The experiment consisted of two conditions: time estimation followed by auditory KR and time estimation followed by visual KR. For the time estimation task, subjects were instructed to shortly press a button (either with their left or their right hand, depending upon the experimental condition) 4000 ms after the onset of an auditory warning stimulus (WS; 1000 Hz, 70 dB(A), 100 ms). Two seconds after response onset they were informed about the correctness of the estimated time interval by either an auditory or a visual KR stimulus. The auditory KR stimulus could be a 2000, 1000 or a 500 Hz tone (80 dB(A), 200 ms), corresponding to the estimation of an interval that was too short, correct or too long, respectively. For the EEG recordings the stimuli were presented through a loudspeaker situated 1.5 m in front of the subject, for the MEG recordings the stimuli were presented binaurally through earphones.

The visual KR stimulus was presented on a computer screen (a VGA monitor for the EEG recordings, and an LCD screen for the MEG recordings) placed about 1.5 m in front of the subject, and could be a minus sign (for a premature response), a vertical bar (for a correctly timed response) or a plus sign (for a response that was too late). A response between 3700 and 4300 ms after WS onset was considered correct. Trials on which the estimated interval was shorter than 3500 ms were discarded from further analysis. The time-out was set at 4750 ms after WS onset (this led to an average of 1.04% timeouts), and was followed by a KR corresponding to a response too late; these trials were discarded from further analysis.

Subjects received a 20 min training on the task prior to data collection. Subsequently, both for the EEG and the MEG recordings a total of 180 trials was recorded for each condition, divided in two experimental blocks of 90 trials. The order of the resulting 8 experimental blocks (two response sides \times two KR modalities \times two blocks per condition) within each recording session was randomized over subjects.

2.3. Data recording

2.3.1. Behavioural data

Reaction times were measured from WS onset to response onset for each trial, and were stored for off-line analysis.

2.3.2. Physiological data

The EEG was measured from 27 non-polarizing Beckman 8 mm Ag–AgCl electrodes, most of which were placed according to the international 10–20 system. Standard positions were Fp1, Fp2, F7, F3, Fz, F4, F8, T3, Cz, T4, P3, Pz and P4. Non-standard positions were C3p and C4p, which are 1 cm anterior to C3 and C4, respectively; TC3 and TC4, which are located at one third of the distance between T3 and C3, and between T4 and C4, respectively; TP3 and TP4, which are in the centre of T3, P3, T5 and C3 and in that of T4, P4, T6 and C4, respectively; O1p, Ozp and O2p, which are located 2 cm anterior to O1, Oz and O2, respectively; O1d, Ozd and O2d, which are located 1 cm posterior to O1, Oz and O2, respectively. Electrode impedance was kept below 3 k Ω . Software-linked mastoids served as a reference. The EEG was amplified by home-made amplifiers, with a 30 s time constant, and a 70 Hz (–42 dB/octave) lowpass filter. Epochs of 3000 ms pre-movement to 3000 ms post-movement were digitized with a sampling frequency of 256 Hz, and stored for off-line analysis. The horizontal EOG from the outer canthi, and the vertical EOGs of both eyes were recorded, and an off-line EOG correction was performed (van den Berg-Lenssen et al., 1989).

For the MEG recordings, we used a 64-channel whole-cortex MEG system (CTF Systems Inc., Vancouver, Canada). The 64 axial gradiometers are uniformly distributed on the helmet surface with mean spacing of 4.5 cm. Fig.

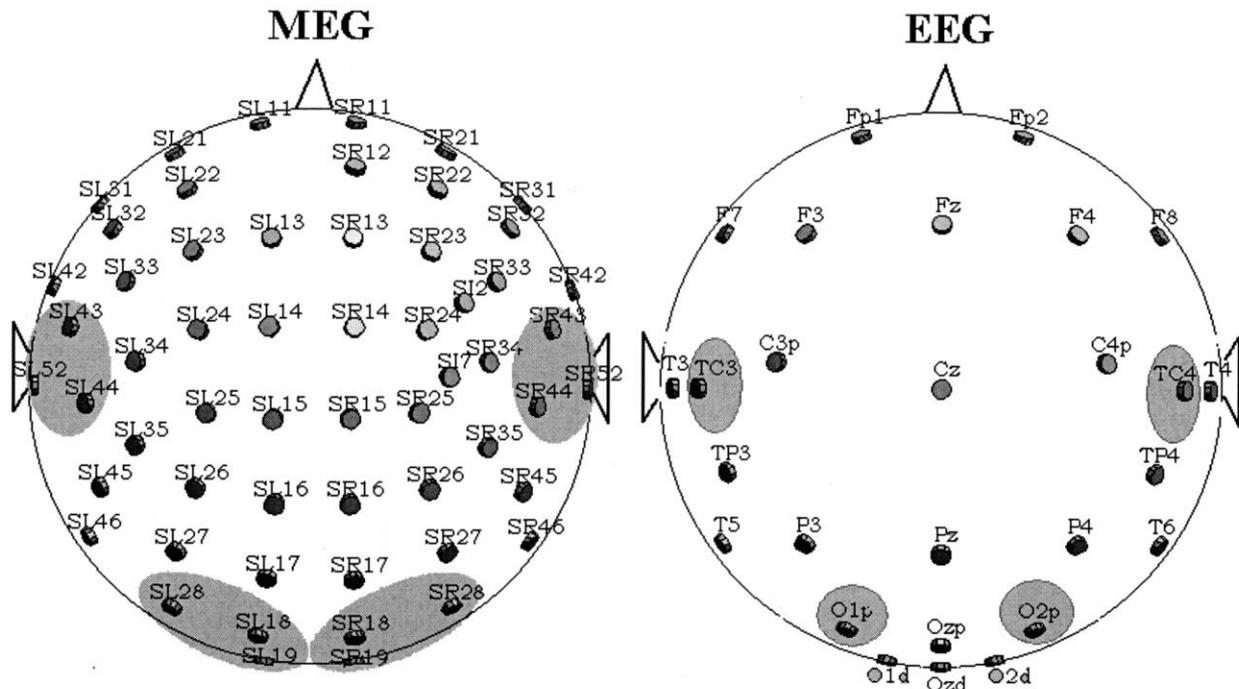


Fig. 1. Orthogonal projection of the electrode and gradiometer positions used for the EEG and MEG measurements. Shaded areas indicate regions of interest (ROIs) used for the statistical analyses.

1 presents the sensor configurations for the EEG and MEG measurements. MEG epochs from 3000 ms pre-movement to 3000 ms post-movement were digitized at 250 Hz, and stored for off-line analysis. Filter settings were from DC to 45 Hz, with additional notch filters at 50 and 60 Hz. The MEG data were later resampled to 256 Hz for practical purposes. Preceding and following each experimental block the position of the sensors relative to the subject's head was determined on the basis of 3 head localization coils attached to the nasion and both pre-auricular points, and the average of the pre- and post-run was used as the sensor position for that particular block. Subsequently, in order to allow for a comparison between experimental conditions and subjects, we extrapolated the data on a grid of averaged sensor positions using the algorithm developed by Hämäläinen and Ilmoniemi (1994).

2.4. Data reduction and statistical analyses

2.4.1. Behavioural data

Two behavioural measures were derived from the reaction time (RT) data. First, the quality of time estimation was monitored by computing the percentages of too fast, correctly timed or too slow responses. These data were analyzed by an ANOVA with Response category (too early, correct, too late), KR Modality (auditory, visual), Response side (left, right) and Recording Session (EEG, MEG) as repeated measures. Second, the effectiveness of the KR stimulus was assessed as follows: for trials with too early or too late responses, we computed the percentage of

subsequent trials for which the RT changed in the desired direction (that is, an RT decrease following a trial with a too late response, and an RT increase following a trial with a too early response). These data were analyzed by an ANOVA with KR Modality (auditory, visual), Response side (left, right) and Recording Session (EEG, MEG) as repeated measures. Where necessary, degrees of freedom were corrected using the Greenhouse–Geisser Epsilon (GGE, Vasey and Thayer, 1987).

2.4.2. Physiological data

On the EEG data, after the EOG correction a semi-automatic artefact detection was performed, discarding trials containing spikes that exceeded 100 μV and trials containing large drift. Two criteria were used to define drift: after applying a 2 Hz lowpass filter to the data (for artefact detection only), (1) individual sample values in an epoch may not differ from each other by more than 80 μV , and (2) the mean amplitude in 4 subsequently sampled intervals of equal length may not differ from baseline by more than 35 μV . The MEG data were visually inspected, and trials that contained eye-movement or other artefacts were discarded from further analysis.

In order to obtain reference-free data, the EEG data were transformed to scalp current density (SCD) fields by estimating a spherical spline function (Perrin et al., 1987; 1989). This step was omitted for the MEG data, since MEG data are inherently of a reference-free nature. Thus, the ERD was computed on reference-free data both in the case of EEG and of MEG. It should be noted here that as a

result of computing the ERD on the SCD (which acts as a spatial high-pass filter) rather than on the raw EEG data, activity originating from superficial sources is enhanced at the expense of activity originating from deeper sources, since the latter produce potentials with low spatial frequencies. This is not the case for the ERD on the MEG data. The general implication of such an approach is that one should be careful in interpreting effects that appear in the ERD on MEG data as widespread phenomena but are absent from the ERD on EEG data: in this case it might be expected that widespread effects have been filtered out of the EEG. As will be seen in the results section however, such effects do not appear in the present data.

The ERD was subsequently computed as follows. The (EEG and MEG) data were bandpass filtered using an FFT filter. Two different frequency bands were thus obtained: 8–10 and 10–12 Hz. These frequency bands were chosen because it has previously been suggested that ERD in the upper and lower alpha bands reflect different cognitive processes (Pfurtscheller and Klimesch, 1990). These authors proposed that ERD in the lower alpha band reflects attention and expectancy, whereas ERD in the upper alpha band reflects task-specific cortical activation. The data then were transformed into power values by squaring the amplitudes. Intervals of 64 consecutive samples were averaged, giving rise to 24 time intervals of 250 ms each. Since the data were recorded on a trial-by-trial basis, the first and the last 250 ms intervals of the 6000 ms sampling epoch were invalid because of an inherent discontinuity in the data. For each subject data were averaged over trials, and ERD was computed as the percentage power increase (or event-related synchronization, ERS) or decrease (or event-related desynchronization, ERD) for a particular time interval in a particular frequency band, relative to the reference interval from 2500 to 2000 ms pre-movement (It might be suggested that the auditory warning stimulus (WS) presented at the beginning of each trial induced a suppression of the tau rhythm, and that therefore the baseline power was calculated when the tau rhythm was suppressed. This is however highly unlikely for the following reason. The shortest estimated time interval for a trial to be accepted at the behavioural level was 3500 ms. The baseline was defined from 2500 to 2000 ms pre-movement. Thus, even in the small percentage of trials in which the estimated interval was not more than 3500 ms, there is still a 1500 ms delay between the WS and the baseline interval, while in most of the trials this delay was longer. Lehtelä et al. (1997) have demonstrated that the suppression of the tau rhythm induced by auditory stimulation lasts maximally 1500 ms (this was actually the longest suppression they found, in only one subject, while in the other subjects the suppression was more transient; in their study the suppression typically reached its maximum between 300 and 500 ms after stimulus onset). Therefore, in the present design we can be sure that the tau rhythm was already recovered at the moment the baseline power was computed.). The end of this reference

interval corresponds to the point in time when movement-related ERD starts (e.g. Pfurtscheller and Berghold, 1989).

For the statistical analyses we restricted ourselves to the ERD in the last 250 ms interval immediately preceding the presentation of the KR stimulus, which is the primary interest of the study. The pre-movement ERD will be presented only at a descriptive level. Since there was a large inter-individual variability in the pre-stimulus ERD (see Section 3), and because of the small sample size, we decided to perform the statistical analyses at the level of individual subjects.

In order to obtain reliable spatial estimates of the event-related power changes, for each subject sensors overlying the auditory and visual cortices were pooled into 4 topographic regions of interest (ROIs): left temporal (LT), which included electrode TC3 for the EEG, and gradiometers SL43, SL44 and SL52 for the MEG; right temporal (RT), which included the same sensors at homologous positions over the right hemisphere; left occipital (LO), which included electrode O1p for the EEG, and gradiometers SL18, SL19 and SL28 for the MEG, and right occipital (RO), which included electrode O2p for the EEG, and gradiometers SR18, SR19 and SR28 for the MEG. See Fig. 1 for the resulting ROIs. The distinction between left and right hemisphere was made for two reasons. First, we want to be able to compare our results to those of Lehtelä et al. (1997), who found a clear right-hemisphere dominance in the reactivity of the tau rhythm to auditory stimuli. Second, we want to relate the pre-stimulus ERD to the results that have previously been obtained with slow potential studies, and the latter have consistently demonstrated a right-hemisphere preponderance of the SPN, at least in the time estimation paradigm that is used in the present study (Damen and Brunia, 1994).

For each ROI, the power in the 750 ms baseline interval and the power in the 250 ms pre-KR interval were averaged over sensors (gradiometers) for each single trial. Then, for each subject and each condition, non-parametric sign tests were used to assess the significance of the power decrease (ERD) or increase (ERS) in the pre-KR interval relative to the baseline interval, for all 4 ROIs separately, using single trials as observations. This was done for both frequency bands (8–10 and 10–12 Hz) separately.

3. Results

3.1. Behavioural data

With respect to the quality of the time estimation, the ANOVA on the percentages too early, correct and too late responses reveals only one significant effect: subjects produced more correct responses (64%) than too early or too late responses (16 and 20%, respectively; main effect of Response Category: $F_{2,8} = 29.29$, $P = 0.0016$, $GGE = 0.689$). There were no statistically significant differ-

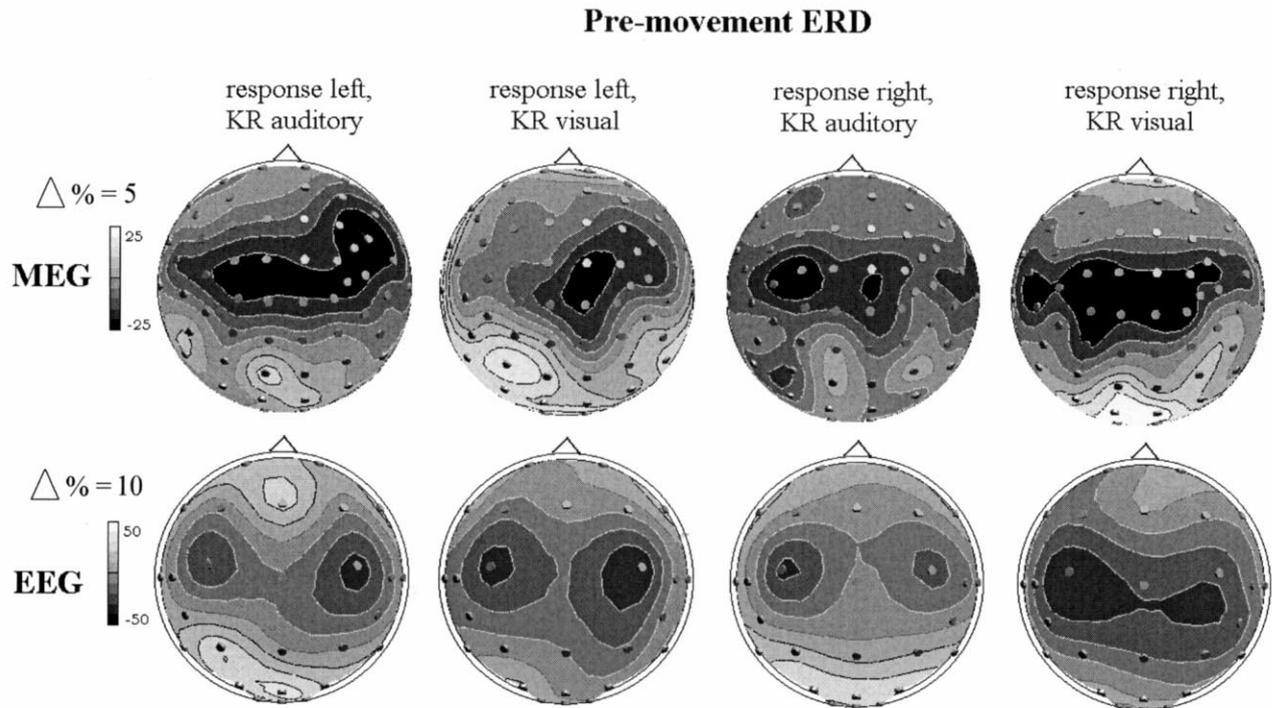


Fig. 2. Grand average ($n = 5$) pre-movement ERD maps in the 8–12 Hz frequency band, for all 4 conditions. The top row presents the ERD on MEG data, the bottom row the ERD on EEG data. ERD, or power decrease, is depicted in dark grey surrounded by white contour lines, while ERS, or power increase, is depicted in light grey, surrounded by black contour lines. The grey contour lines correspond to zero power change. Spacing of contour lines is 5% power change for the MEG, and 10% power change for the EEG. Scaling as indicated in the figure. Note the contralateral dominance of the pre-movement ERD, both in the EEG and MEG data.

ences in these figures between recording session, response side and KR modality.

KR stimuli indicating that a response was too early or too late resulted, on the subsequent trial, in an average of 79% of the cases in an adjustment of the RT in the desired direction. The ANOVA on these figures revealed no statistically significant differences in the percentage correctly adjusted RT's between recording session, response side or KR modality. In sum, the lack of effects of Recording Session in the behavioural data indicates that subjects performed equally well on the task during the EEG and the MEG measurements and suggests that the experimental conditions were indeed very similar over recording sessions.

3.2. Physiological data

A first point of concern was whether pooling the ERD on the MEG data into ROIs, which gives more reliable spatial estimates of the prestimulus ERD, could result in a loss of relevant information at the level of the individual gradiometers. We therefore visually compared, for each subject, the ERD traces at the individual MEG gradiometers that were included in the ROIs, to the timecourse of the ERD trace of the ROI itself. The global finding of this visual inspection was that all the individual gradiometers showed timecourses that were comparable in shape to the timecourses of the pooled data, although there was obviously

some variation in ERD magnitude between individual sensors. Therefore the ROIs could be used as a reliable spatial estimate of the prestimulus ERD over the temporal and occipital cortices.

3.2.1. Pre-movement ERD

Visual inspection of the grand average pre-movement ERD on EEG and MEG data in the 8–12 Hz frequency band (see Fig. 2) reveals the usual pattern of an ERD with a central maximum and a contralateral preponderance, both in the EEG and in the MEG. Fig. 2 also suggests that the pre-movement ERD is of a larger magnitude in the EEG than in the MEG.

3.2.2. Pre-stimulus ERD

In Fig. 3 subject averages of the ERD in the 8–10 Hz band are presented, for the conditions in which a right-hand response was required. A quick view on Fig. 3 reveals that for the MEG there is a considerable amount of individual variation in the pre-stimulus ERD, while for the EEG the effects are much more consistent over subjects. Initial analyses showed that the results of the statistical analyses were highly comparable for both response sides; therefore it was decided to average the ERD results over response sides in order to limit the number of sign tests. Table 1 summarizes the results of the statistical analyses of the pre-stimulus ERD, for both frequency bands. A general

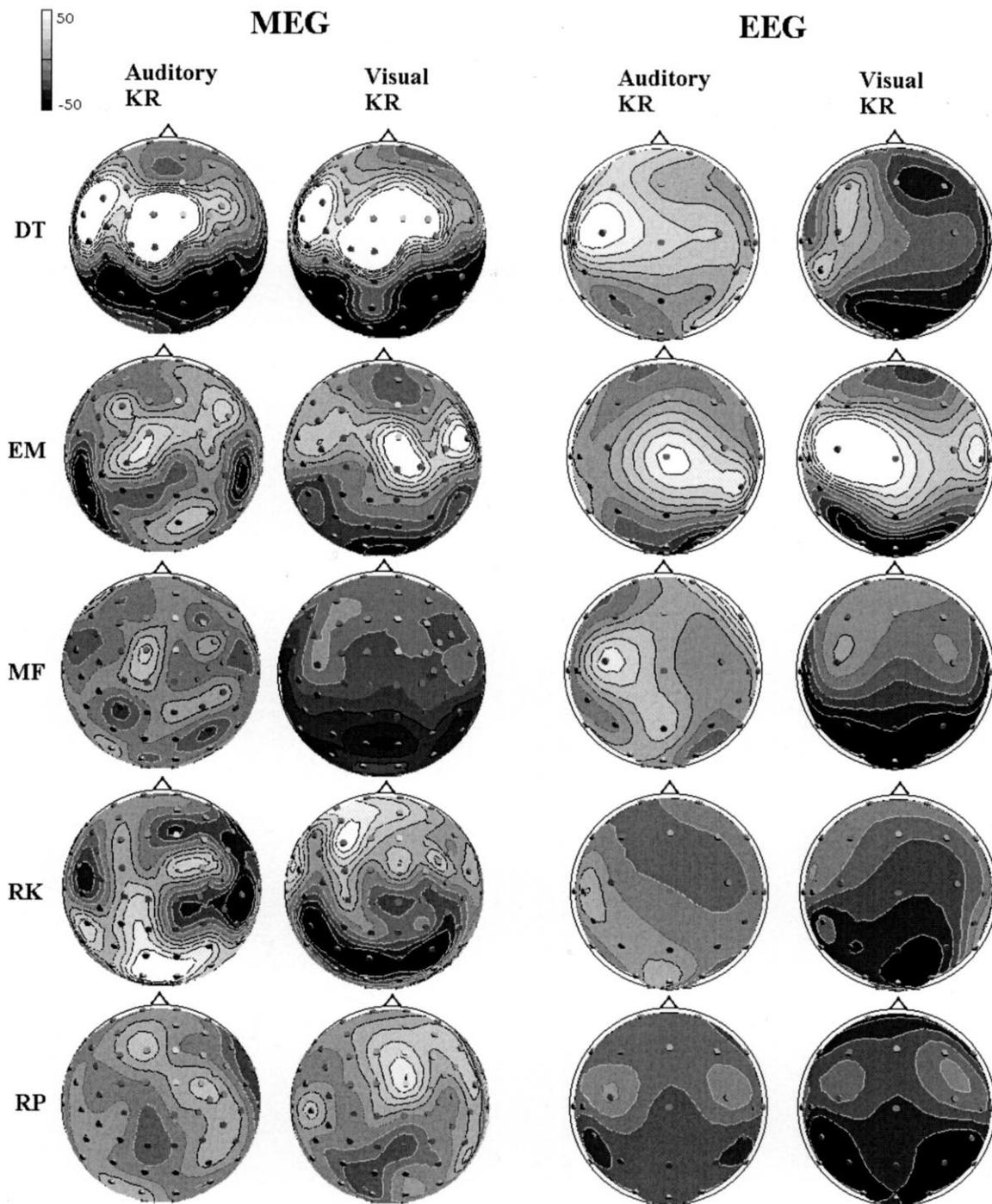


Fig. 3. Subject averages of the ERD in the 8–10 Hz frequency band, in the last 250 ms interval preceding the presentation of the KR stimulus. Left-hand panel: ERD on MEG data. Right-hand panel: ERD on EEG data. ERD, or power decrease, is depicted in dark grey surrounded by white contour lines, while ERS, or power increase, is depicted in light grey, surrounded by black contour lines. The grey contour lines correspond to zero power change. Scaling as indicated in the figure. Spacing of contour lines is 5% power change. Data are from right-hand responses.

inspection of Table 1 indicates that, although similar for the two frequency bands, the effects shown in Fig. 3 are more pronounced in the 8–10 than in the 10–12 Hz frequency band.

The ERD computed on EEG data (see Fig. 3, right-hand panel) reveals that all the subjects studied display an ERD

with an occipital maximum preceding the visual KR stimulus. For all subjects, this effect is significant at both left and right occipital ROIs, irrespective of response side and frequency band (see Table 1). It should be noted that for subjects MF and RP the ERD preceding the visual KR stimulus is rather widespread, and is occasionally significant at left

Table 1
Significance levels of the sign tests on the change in power from baseline interval to pre-KR interval^a

		ERD 8–10 Hz							
		MEG				EEG			
Subject	ROI → KR ↓	Left Temp	Right Temp	Left Occ	Right Occ	Left Temp	Right Temp	Left Occ	Right Occ
DT	Aud	+		---	---				
	Vis	+		---	--		-	-	--
EM	Aud	---	--						-
	Vis			---	---		+	--	--
MF	Aud								
	Vis			--	-	--	--	---	---
RK	Aud	--	---	++	++				
	Vis			--	---			--	--
RP	Aud		-						-
	Vis				--	-	-	---	---
		ERD 10–12 Hz							
DT	Aud			-	--				
	Vis			-	---		++	---	---
EM	Aud	-	--	+					
	Vis			---	---			-	--
MF	Aud				+				
	Vis			-	--		-	---	---
RK	Aud	--	--		+				
	Vis			---	--			-	-
RP	Aud				++			-	
	Vis			-	-	-		--	---

^a For each subject, results are presented separately for the 8–10 and 10–12 Hz bands. Data are pooled over left- and right-hand responses. Power decrease (ERD): - = $P < 0.05$; -- = $P < 0.01$; --- = $P < 0.001$. Power increase (ERS): + = $P < 0.05$; ++ = $P < 0.01$; +++ = $P < 0.001$.

and right temporal ROIs as well. There are no clear differences in ERD between left- and right occipital ROIs. Preceding auditory KR stimuli, none of the subjects display an appreciable ERD, irrespective of response side and frequency band (see Fig. 3 and Table 1). In essence the ERD results on the present EEG data are a confirmation of the results of our previous study (Bastiaansen et al., 1999b).

For the MEG data the picture is more complex. Therefore we will discuss the results separately for each subject (see Table 1 and Fig. 3, left-hand panel). Two of the 5 subjects (subjects EM and RK) show a clear modality-dependent ERD scalp distribution in the MEG. Preceding auditory KR stimuli these subjects display a clear, focal ERD over the left and right temporal ROIs, that is highly significant for both response sides in the 8–10 Hz frequency band, and to a lesser extent in the 10–12 Hz frequency band. At the same time an ERS is present over both occipital ROIs that reaches significance only for subject RK. It should be noted that these effects are not present in the ERD computed on the EEG data for these two subjects. Preceding visual KR stimuli, subjects EM and RK display an ERD over both occipital ROIs, while no ERD is present over temporal sites. One subject (subject DT) shows an occipitally maximal ERD, irrespective of KR modality, response side and frequency band. Finally, subjects MF and RP show a signif-

icant ERD preceding the visual KR stimulus (although for subject RP this effect only borders on significance in the 8–10 Hz frequency band). Preceding the auditory KR stimulus subjects RP and MF do not show any ERD. For none of the subjects there are clear differences in pre-stimulus ERD between left and right hemispheres.

In order to investigate the possibility that individual differences in the ERD over the left and right temporal ROIs preceding auditory KR stimuli were caused by between-subject differences in the level of power during baseline intervals, we computed for each frequency band the absolute power (averaged over trials, conditions and response sides, and over left and right ROIs) during all the baseline intervals, for each subject separately. Means and 95% confidence intervals ($M \pm 2$ SD) are depicted in Fig. 4, and clearly indicate that the two subjects that display a temporal ERD preceding auditory KR stimuli (subjects E.M. and R.K.) have significantly higher levels of absolute baseline power than the subjects in which this effect is not present.

4. Discussion

We investigated the event-related power changes (ERD and ERS) related to the anticipatory attention for an upcom-

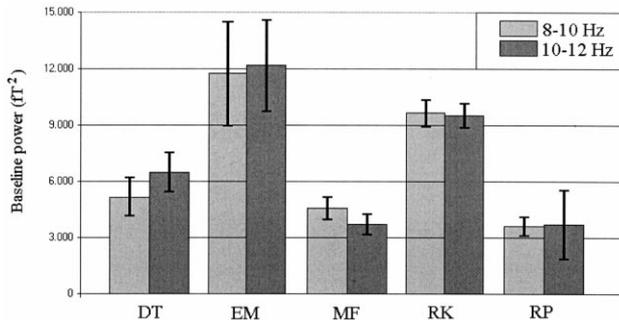


Fig. 4. Means and 95% confidence intervals (mean \pm 2 times the standard deviation) of absolute power of the MEG averaged over both temporal ROI's during the baseline interval, for the 8–10 and 10–12 Hz frequency bands separately. For each subject, means and confidence intervals are computed over conditions, response sides, and averaged over left and right temporal ROIs. Note that the baseline power for subjects E.M. and R.K. is significantly larger than for the other subjects.

ing stimulus in the EEG and MEG of 5 subjects, using a paradigm in which the subjects were instructed to perform a time estimation task, and were informed about the quality of their time estimation by either an auditory or a visual KR stimulus.

The results of the ERD computed on the EEG data are a confirmation of the results from our previous study (Bastiaansen et al., 1999b). For all 5 subjects we investigated, an ERD with an occipital maximum was present preceding the visual KR stimuli, whereas preceding the auditory KR stimuli no ERD was found at all. It should be noted however, that in the present study the occipital ERD was strongest in the 8–10 Hz frequency band, whereas in the earlier study we found the strongest effects in the 10–12 Hz and even in the 12–16 Hz frequency bands. These differences between studies in maximally reactive frequencies may well be accounted for by the fact that we did not select frequency bands based on individual alpha peak frequencies, as is sometimes done in ERD research (e.g. Klimesch et al., 1997). Klimesch (1996, 1997) points out that individual alpha peak frequency is negatively correlated with age, and that even within a group of subjects of the same age an inter-individual difference in alpha peak of 2 Hz is quite common. We admit that our results might have been more consistent with respect to the maximally reactive frequency band, but this does not compromise our finding that anticipating a visual stimulus is consistently reflected by a desynchronization of rhythmical EEG activity with a frequency of *approximately* 10 Hz over the occipital cortex, as we hypothesized on the basis of our thalamo-cortical gating model.

For the MEG, we found an occipital ERD preceding visual stimuli in all of the subjects studied. There was however a large inter-individual variability in the ERD preceding auditory stimuli: we found a clear ERD over temporal recording sites during anticipatory attention for an auditory stimulus only in two out of the 5 subjects. Thus, these two subjects displayed the differences between

EEG and MEG we expected on the basis of previous research (Niedermeyer, 1990; 1991; Tiihonen et al., 1991; Lehtelä et al., 1997; see Niedermeyer, 1997; Hari et al., 1997 for reviews). In addition, we found significantly higher levels of absolute power in the MEG over temporal recording sites for these two subjects than for the other 3 subjects. Of the other 3 subjects, two displayed no ERD preceding auditory stimuli, while the third displayed an occipitally maximal ERD preceding auditory stimuli.

The main question is then, why did we find evidence for anticipatory attention for the auditory stimuli only in two out of 5 subjects? A possible explanation may be that the spatial sampling used in the MEG was insufficient to detect localized changes in power in the temporal region. However, visual inspection of Fig. 3 suggests that the prestimulus ERD in the subjects that do display the temporal ERD preceding auditory KR stimuli spreads over a number of gradiometers. Therefore we consider it unlikely that the relatively poor spatial sampling is the reason why only two out of 5 subjects display the expected ERD prior to auditory stimuli in the MEG. For a more plausible answer to this question we have to take into consideration that in these two subjects we found a larger level of absolute power over the temporal cortex. An explanation then might be that only these two subjects had a well-developed tau rhythm, or that only in these two subjects the generators of the tau rhythm were oriented in such a way (namely tangentially to the cortical surface) that their activity could be measured with the MEG sensors. The relative absence of a tau rhythm in the other 3 subjects might then explain the lack of desynchronization in these subjects over the temporal cortex preceding auditory KR stimuli. Such an explanation finds support in the results of Lehtelä et al. (1997), where (the reactivity of) the tau rhythm could not be demonstrated for all subjects, although the ratio of 8 out of 9 was much higher in the latter study. A tentative explanation for the higher ratio of tau-responsive subjects in the latter study as compared to the present study may be the following: Lehtelä et al. (1997) (p. 113) note that 'the observed remarkable interindividual variance in the abundance of temporal-lobe rhythms may be in part due to differences in vigilance', with more prominent tau rhythm being recorded in drowsy than in alert subjects. This is in agreement with results reported by Lu et al. (1992). In the experiment of Lehtelä et al. (1997), subjects had no task but to listen to auditory stimuli. In contrast, in the present experiment subjects performed a time estimation task, and made active use of the KR stimuli, as indicated by the behavioural data. Therefore a tentative, and somewhat speculative, explanation of the lower ratio of tau-responsive subjects in the present study as compared to the study by Lehtelä et al. (1997) may be that subjects were more drowsy in the latter study, which led to prominent, recordable tau rhythm in more of the subjects studied.

An important difference between the results of the present study and those of Lehtelä et al. (1997) is that we did not

find evidence for a right-hemisphere dominance in the reactivity of the tau rhythm. It is unclear at present what might have caused this difference. In any case the data provide supportive evidence for the existence of a 'tau' rhythm that is suppressed when the auditory cortex engages in active processing (cf. Tiihonen et al., 1991; Hari, 1993; 1997; Lehtelä et al., 1997) or, as in the present study, in anticipatory attention. The results are also in line with the idea that scalp-recorded EEG is not suited to measure rhythmic activity originating from the temporal cortex, as has been demonstrated by Niedermeyer (1990, 1991).

It is interesting to note that both in the EEG and in the MEG, the central and occipital cortices display antagonistic patterns of ERD/ERS: preceding movement execution there is ERD at central electrodes together with ERS at occipital electrodes, while preceding visual KR stimuli the opposite pattern is found. In addition, the two subjects that display ERD at temporal sensors preceding auditory KR stimuli in the MEG show an ERS over occipital recording sites at the same time, while preceding visual KR stimuli these subjects display an occipital ERD (but no ERS at temporal sensors however). These results support the idea that cortical areas not involved in the execution of the task display ERS while involved areas display ERD (see e.g. Pfurtscheller, 1992). The data also partly support the notion of 'focal ERD/surround ERS' that has been proposed by Suffczynski et al. (1999) on the basis of neuronal network simulations.

For our present purpose the most important conclusion is that the data support the notion that anticipatory attention in the auditory modality can be detected by studying the patterns of synchronization and desynchronization of 10 Hz rhythmical activity of the MEG, at least in some subjects. Anticipatory attention in the visual modality on the other hand can be demonstrated both with EEG and with MEG-based ERD/ERS. The combined results of this and the previous study are for a large part in accordance with the predictions of the neurophysiological model of anticipatory attention that we have described elsewhere (e.g. Brunia, 1999; Bastiaansen et al., 1999a).

The results obtained with the ERD/ERS technique are in contrast with the results that are usually obtained with slow potential studies (e.g. Damen and Brunia, 1994; cf. Böcker and Van Boxtel, 1997 for a review). These studies have demonstrated that although anticipatory attention for auditory and visual stimuli is accompanied by a negative slow potential, which has been termed Stimulus-Preceding Negativity (SPN; Damen and Brunia, 1987), the SPN neither shows any differences in scalp topography preceding stimuli of different modalities, nor maximal amplitudes over the sensory cortex corresponding to the modality of the anticipated stimulus (Böcker et al., 1994). Although preliminary results of a recent experiment performed in our laboratory suggest that there may be small but significant differences in SPN scalp topography preceding stimuli of different modalities that go in the expected direction, the global pattern of results suggests that the SPN, in contrast to the prestimulus

ERD reported in the present paper, does not primarily reflect anticipatory attention for upcoming stimuli in a certain modality, but rather the presetting of (supramodal) cortical areas necessary for the execution of the task at hand (cf. Bastiaansen et al., submitted, for a detailed discussion).

In order to establish a firmer experimental basis for our neurophysiological model for anticipatory behaviour, a number of issues have yet to be clarified. First, just as differences in movement parameters have been shown to influence reactivity of EEG and MEG (e.g. Salmelin et al., 1995; Pfurtscheller et al., 1998), it has to be established whether differences in stimulus parameters will have an effect on the pre-stimulus ERD. For example, we would expect that pre-stimulus ERD is larger preceding degraded stimuli than preceding normal stimuli, because degraded stimuli are more difficult to perceive and thus will require more anticipation. This would be convincing evidence for the notion that the pre-stimulus ERD we have reported here truly reflects anticipatory attention. Furthermore, demonstrating anticipatory attention in the somatosensory modality would be the obvious complement to the experiments we carried out up until now, that addressed only the auditory and visual modalities. The spatial proximity of the motor and somatosensory cortices have made it difficult in the past to separate post-movement activity from pre-stimulus activity in this modality in our time estimation paradigm, especially with slow potential research. Results of recent experiments comparing 10 and 20 Hz rhythms generated in the motor and somatosensory cortices suggest that there may be a qualitative difference between these two frequency components (e.g. Salmelin and Hari, 1994; Salmelin et al., 1995). With the frequency-based functional segregation of motor and somatosensory rhythms proposed by these authors, it may now be possible to study anticipatory attention to somatosensory stimuli without running the risk of confounding post-movement processes with pre-stimulus processes in the time estimation paradigm employed in the present study.

Finally, it should be assessed whether the ERD effects obtained in the time estimation paradigm, in which only KR stimuli are used, can be replicated when different types of stimuli are used to induce anticipatory attention. If the interpretation of the present ERD effects in terms of (the perceptual process of) anticipatory attention is correct, then we would expect to obtain similar results with other types of stimuli. Such evidence would provide a strong case for interpreting the presently found prestimulus ERD as truly reflecting anticipatory attention for an upcoming stimulus.

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