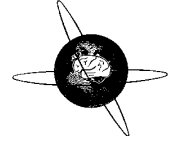


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Event-related desynchronization related to the anticipation of a stimulus providing knowledge of results

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Abstract

In the present paper, event-related desynchronization (ERD) in the alpha and beta frequency bands is quantified in order to investigate the processes related to the anticipation of a knowledge of results (KR) stimulus. In a time estimation task, 10 subjects were instructed to press a button 4 s after the presentation of an auditory stimulus. Two seconds after the response they received auditory or visual feedback on the timing of their response. Preceding the button press, a centrally maximal ERD is found. Preceding the visual KR stimulus, an ERD is present that has an occipital maximum. Contrary to expectation, preceding the auditory KR stimulus there are no signs of a modality-specific ERD. Results are related to a thalamo-cortical gating model which predicts a correspondence between negative slow potentials and ERD during motor preparation and stimulus anticipation. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Event-related desynchronization; Slow potentials; Stimulus anticipation; Motor preparation

1. Introduction

Anticipatory behavior serves the goal of a faster and/or more efficient information processing. It can occur both at the input and at the output stages of information processing (Gottsdanker, 1980). The processes involved can be referred to as anticipatory attention and motor preparation, respectively. Two EEG measures seem particularly adequate to study these anticipatory processes: negative slow potentials and event-related desynchronization (ERD). Negative slow potentials are interpreted to reflect a depolarization of cortical cells, indicating an increase in the readiness of cells to fire. ERD reflects the interruption of synchronized activity in functionally related groups of cortical neurons, which again can be seen as a correlate of increased cellular excitability (cf. Pfurtscheller, 1994).

Motor preparation has been extensively studied with slow potentials. It manifests itself as the readiness potential (RP, Kornhuber and Deecke, 1965), which can be recorded prior to simple self-paced movements (for reviews, see Brunia et al., 1986; McCallum, 1988). The RP starts as early as 1500–1000 ms before movement onset, as a bilaterally symmetric negativity that is largest over the pre- and postcentral scalp areas. At about 500 ms prior to movement onset RP amplitudes become larger contralateral to the movement side, at least with finger movements. This has been termed ‘the negative slope’ (Shibasaki et al., 1980). At about movement onset, the negativity reaches its peak amplitude over the contralateral scalp. This so-called motor potential is thought to be a reflection of the activation of the pyramidal tract (see Arezzo et al., 1977). The most prominent neural generators of the RP are situated in the primary motor cortex (e.g. Bötzel et al., 1993; Toro et al., 1993; Böcker et al., 1994a,b).

A number of studies have investigated patterns of event-related synchronization (ERS) and desynchronization (ERD) in the alpha and beta frequency bands in a voluntary movement paradigm (e.g. Pfurtscheller and Aranibar, 1977;

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Pfurtscheller and Berghold, 1989; Pfurtscheller, 1992; Derambure et al., 1993; Toro et al., 1994; Stancák and Pfurtscheller, 1995; Pfurtscheller et al., 1996; Defebvre et al., 1996). These studies show consistent results, that can be summarized as follows: the first sign of ERD can generally be found at around 1500 ms pre-movement, and is strictly localized to the contralateral pre- and postcentral scalp. At approximately 750–500 ms before movement onset desynchronization of a comparable magnitude can be measured over the ipsilateral scalp as well. Simultaneously, starting at about 1000 ms prior to the movement, an ERS can be measured over the occipital cortex. After movement onset, there is a slow recovery of the power both in the alpha and the beta frequency bands at pre- and postcentral leads, with the higher frequencies (20–30 Hz) recovering fastest. The higher frequencies eventually show an ERS at about 1000 ms post movement, that has not yet been reported for the lower frequencies (8–12 Hz). In conclusion, although the time courses and spatial distributions of the RP and the pre-movement ERD show a relatively good correspondence, there is an obvious difference in the lateralization of both measures: the RP starts symmetrically and becomes contralaterally dominant at about 500 ms pre-movement, whereas the pre-movement ERD starts contralaterally and becomes symmetric at about 500 ms pre-movement. Although both measures are interpreted as a reflection of preparatory processes related to movement execution, the underlying mechanisms are different. It is unclear at present what might cause these differences between slow potentials and ERD.

Anticipatory attention for an upcoming stimulus has been studied in a series of experiments employing a time estimation 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; for reviews, see Brunia, 1988, 1993a, 1997; van Boxtel, 1994pp. 15–18). Its onset has been reported to be at least as early as 2000 ms pre-stimulus (Damen and Brunia, 1994; Böcker et al., 1994c). The SPN has a widespread scalp distribution, with a frontal plateau and a parietal ramp-like potential, usually with a right-hemisphere preponderance (Brunia and Damen, 1988). It has been recorded prior to auditory and visual stimuli. The SPN has been recorded in different experimental paradigms: preceding instruction stimuli (e.g. Rösler, 1991; van Boxtel and Brunia, 1994), probe stimuli (Chwilla and Brunia, 1991, 1992) and KR stimuli (Grünwald and Grünwald-Zuberbier, 1983; Damen and Brunia, 1985, 1987; Brunia and Damen, 1988), and preceding stimuli evoking emotional arousal (Simons et al., 1979; Klorman and Ryan, 1980; Rockstroh et al., 1989). However, the SPN has been recorded unequivocally in two experimental conditions only: prior to KR stimuli and prior to stimuli

evoking emotional arousal. Both situations have two things in common: there is no immediate relation to motor activity, and the stimuli have an affective-motivational valence. Thus, the anticipatory attention is confounded with the anticipation of an affective stimulus, but not with motor preparation. The scalp distribution of the SPN varies with the type of stimulus that is anticipated. Prior to KR stimuli, a right-hemispheric dominance is usually found. Instruction and probe stimuli, however, have a more direct relation to subsequent motor activity. This has consequences for hemisphere differences. Preceding instruction stimuli, the results are contradictory: sometimes a left- and sometimes a right-hemispheric dominance is found (e.g. Rösler, 1991; van Boxtel and Brunia, 1994). and sometimes no SPN is found at all (e.g. Damen and Brunia, 1994). Prior to probe stimuli, Chwilla and Brunia (1991, 1992) found an SPN with a left hemispheric preponderance.

So far, with the exception of one study (Lang et al., 1984), no evidence has been found for a contribution of modality-specific processes to the SPN, contrary to what would be expected if the SPN were to reflect anticipatory attention. Thus, anticipatory attention per se does not seem to be a sufficient condition for an SPN to develop (see Damen and Brunia, 1994). It has been suggested that the occurrence of an SPN depends on whether the anticipated stimulus has an affective-motivational value (Damen and Brunia, 1994). This interpretation is further supported by a spatiotemporal dipole modelling study (Böcker et al., 1994c), where a large part of the pre-KR SPN could be explained by a pair of dipoles which probably represents activity in the *Insulae Reili*, a bilateral cortical structure buried within the Sylvian fissure. This structure has connections which suggest that the insular cortex is involved in the processing of affective-motivational stimuli (Mesulam and Mufson, 1985). In conclusion, slow potential research has as yet not been very successful in identifying physiological correlates of anticipatory attention per se.

In the present study, it will be investigated whether ERD might constitute a better candidate for identifying physiological correlates of preparation for perception, since there is a remarkable lack of experimental data on this topic. To our knowledge, there are no studies that have explicitly investigated ERD phenomena during the anticipation of a stimulus. Two studies should be mentioned, however, which provide some indirect support for the hypothesis that there is an ERD component reflecting anticipatory attention. Pfurtscheller (1992 Fig. 3) discusses an experiment in which subjects had to perform a reading task. Starting from 1 s pre-stimulus, ERD was localized on occipital electrode positions, while at central locations an ERS was measured. In another experiment, Pfurtscheller and Klimesch (1991) asked subjects to perform a visual-verbal reading and classification task. Preceding the presentation of the visual stimuli that were to be classified, he found a widespread, long-lasting (± 1 s) ERD with a left-hemisphere dominance in the 8–10 Hz band. The author interpreted

this ERD as being related to the anticipation of the stimulus. These two instances of an occipitally localized ERD prior to visual stimuli suggest a modality specificity of ERD during anticipatory attention. In the present study, we will more explicitly investigate ERD related to anticipatory attention. More specifically, we will investigate the patterns of synchronization and desynchronization prior to the presentation of auditory and visual KR stimuli, paying specific attention to possible modality specific effects on ERD. The subjects performed a time estimation task, and received feedback about the timing of their response by means of an auditory or a visual KR stimulus. We expected five components to become manifest: (1) an ERD which is localized at the primary motor cortex prior to response execution; (2) a centrally maximal ERS following response execution; (3) an ERD which is localized at primary auditory cortex prior to auditory KR stimuli, reflecting a modality-specific anticipation of the auditory KR; (4) an ERD which is localized at the primary visual cortex prior to visual KR stimuli, reflecting a modality-specific anticipation of the visual KR; and (5) a frontotemporal ERD prior to KR stimuli in both modalities, reflecting anticipatory activity in the *Insulae Reili*, which is related to the affective-motivational value of the KR stimulus.

2. Methods

2.1. Subjects

Ten right-handed subjects (4 men and 6 women) aged 21–36 years (mean 24.7 years) participated in the experiment. They were volunteers, and received Dfl. 7.50/h for participating in the experiment.

2.2. Design and procedures

The experiment consisted of three conditions: voluntary movement, time estimation with auditory KR, and time estimation with visual KR. In the voluntary movement task, subjects were instructed to produce rapid self-paced flexions of index-finger and thumb at a slow pace (4–6 movements per minute, with a minimum inter-response interval of 6 s), with either the left or the right hand. A total of 100 trials were recorded for each hand.

The other two conditions consisted of a time estimation task, in which the subjects were instructed to produce a rapid unilateral flexion of index finger and thumb, starting at 4000 ms after the onset of an auditory warning stimulus (1000 Hz, 70 dB(A), 60 ms). Two seconds after the response they were informed about the correctness of the estimated time interval, by either an auditory or a visual KR stimulus. The auditory KR stimulus was a 500 Hz tone at 70 dB(A), the visual KR stimulus consisted of the illumination of two red LEDs mounted inside a box with a circular translucent front, placed about 1.5 m in front of the subject. In both

modalities, the information conveyed by the KR stimulus was encoded in its duration, which was either 50, 250 or 750 ms, corresponding to the estimation of an interval that was too short, correct or too long, respectively. The length of the time interval considered correct was individually adjusted during a training block, in order to obtain about 40% of correct trials. A total of 100 trials was recorded for each hand in each KR-modality. The voluntary movement condition always preceded both time estimation tasks, in order to prevent carry-over effects from the time estimation to the voluntary movement task.

2.3. Electrophysiological recordings

For the EEG-recordings, 23 non-polarizing Beckman 8 mm Ag-AgCl electrodes were affixed to the scalp, most of them placed according to the international 10–20 system. Standard positions were Fp1, Fp2, F7, F3, F4, F8, T3, Cz, T4, P3, Pz, P4, O1, and O2. Non-standard positions were C3' and C4', which are 1 cm anterior to C3 and C4, respectively; T5an, T5po, T6an and T6po, which are at one third and two third of the distances between T3 and O1 and between T4 and O2, 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. Electrode impedance was kept below 5 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 30 Hz (–42 dB/octave) lowpass filter. Epochs of 3000 ms pre-movement to 3500 ms post movement were AD-converted with a sampling frequency of 128 Hz.

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).

Next, an automatic artifact detection was performed, discarding trials containing spikes that exceeded 100 μ V and trials containing large drift. Two criteria were used to define drift: after applying a 2 Hz lowpass filter to the data (1) individual sample values in an epoch may not differ from each other by more than 80 μ V, and (2) the mean amplitude in 4 subsequently sampled intervals of equal length may not differ from the baseline by more than 35 μ V.

2.4. ERD computation

In order to obtain reference-free data and to remove ERD/ERS effects at the reference electrodes, the recorded potentials were transformed to scalp current density (SCD) fields by estimating a spherical spline function, which is the recommended procedure by Perrin et al. (1987, 1989); see Böcker et al., 1994c for the resulting SCD maps). This method has the advantage of yielding reliable estimates of the SCD at electrode positions that are at the border of the electrode montage, so it is preferable to computing a local average reference (Hjorth, 1975), as is mostly done in ERD computation (e.g. Pfurtscheller, 1991).

Next, data were bandpass filtered in the frequency domain according to the following procedure. First, an FFT was performed on the entire sampling epoch, after which the data were smoothed twice using a moving Hamming window with a 3-sample length. Next, the weights for frequencies outside the desired band were set to zero, and finally the data were transformed back to the time domain. Five different frequency bands were thus obtained: 8–10 Hz, 10–12 Hz, 12–16 Hz, 16–20 Hz, and 20–25 Hz.

The data were then transformed into power values by squaring the amplitudes. Intervals of 32 consecutive samples were averaged, giving rise to 26 time intervals of 250 ms each (since the lowest frequency band considered was 8–10 Hz, this 250 ms interval still covers two periods of the slowest frequency component in this band). Since the data were recorded on a trial-by-trial basis, the first and the last 250 ms intervals of the 6500 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 (ERS) or decrease (ERD) for a particular time interval in a particular frequency band, relative to the reference interval from 2750 to 2000 ms pre-movement. The end of this reference interval corresponds to the point in time when movement-related ERD starts (Pfurtscheller and Berghold, 1989). Finally, percentages ERD were averaged over all subjects for display purposes.

2.5. Statistical analyses

2.5.1. *t* Tests

In order to assess whether the power during the performance of the task differs significantly from the power in the reference interval, i.e. whether ERD or ERS is significant, we performed single-sample *t* tests. These tests are essential since differences in ERD or ERS between conditions, which are assessed by an ANOVA for repeated measures (see below), can only validly be tested if there is a significant ERD or ERS.

In order to limit the number of *t* tests, tests were performed only on a selection of time intervals and channels: an early pre-movement interval (from 1000–750 ms pre-response), which is probably dominated by a contralateral ERD at central (C3' and C4') channels; a late pre-movement interval (250–0 ms pre-response), where we expect a bilaterally symmetric ERD at central (C3' and C4') channels, and a pre-KR interval (250–0 ms pre-KR), which is the main interest of this study: here we do not only expect post-movement ERS at central (C3' and C4') channels, but also ERD related to the anticipation of the KR stimulus at occipital (O1, O2), temporal (T3, T4) and frontotemporal (F7, F8) channels. These tests were performed in all 5 frequency bands for all 3 conditions.

We subtracted the grand averages of the ERD percentage in the voluntary movement condition from the ERD percentage in both time estimation conditions. On these subtracted

data, similar *t* tests were performed as on the non-subtracted data. The *t* tests concerning the movement-related ERD after subtraction can be used to assess if the subtraction effectively eliminated the movement-related ERD. If this is the case, the power changes related to the anticipation of the KR stimulus can be assessed without running the risk of confounding pre-KR activity with post-movement activity. A 5% significance level was adopted for the *t* tests. However, since using a large number of *t* tests could result in an overall increase of type I errors, only those results that show a consistent pattern of significances will be considered relevant? (for example, movement-related effects should be consistent over conditions, while pre-KR effects should be consistent over response sides).

2.5.2. ANOVAs

Next, differences in power changes between conditions were tested by an ANOVA for repeated measures. Similar time intervals and electrode positions were selected to those of the *t* tests. Factors were task condition (voluntary movement, auditory KR, visual KR), response side (left, right), frequency band (8–10, 10–12, 12–16, 16–20 and 20–25 Hz), time interval (early pre-movement: late pre-movement, pre-KR), electrode position (F, C, T, O) and hemisphere (left, right).

The subtracted data were subjected to a second ANOVA, which now included only two task conditions (auditory and visual KR).

Where necessary, Greenhouse-Geisser corrected degrees of freedom were used (Vasey and Thayer, 1987). A 5% significance level was adopted for the ANOVAs. Significant interactions were clarified, either by breaking them down into simple effects or by computing post-hoc contrasts.

A statistical analysis of the behavioral data and the potential data, as well as a spatiotemporal dipole model of the potential data have been presented elsewhere (Böcker et al., 1994c).

3. Results

Fig. 1 shows the time courses of the movement-related ERD at central electrode positions. At the early pre-movement time interval, a centrally maximal contralateral ERD is present in all three task conditions, as indicated both by the *t* tests¹ and the ANOVA (see Table 1; T * R * H and E * T * R * H; simple effect of response side * hemisphere in the early pre-response interval at central positions: $F_{1,9} = 5.68$; $P = 0.0410$). Note that although the ANOVA indicates no differences between frequency bands, the *t* tests show that the contralateral ERD is consistently significant in the 8–10 and 10–12 Hz bands only.

¹ For the sake of brevity, the *t* test results will be presented only if their interpretation could be considered equivocal. Full significance tables can be obtained from the corresponding author.

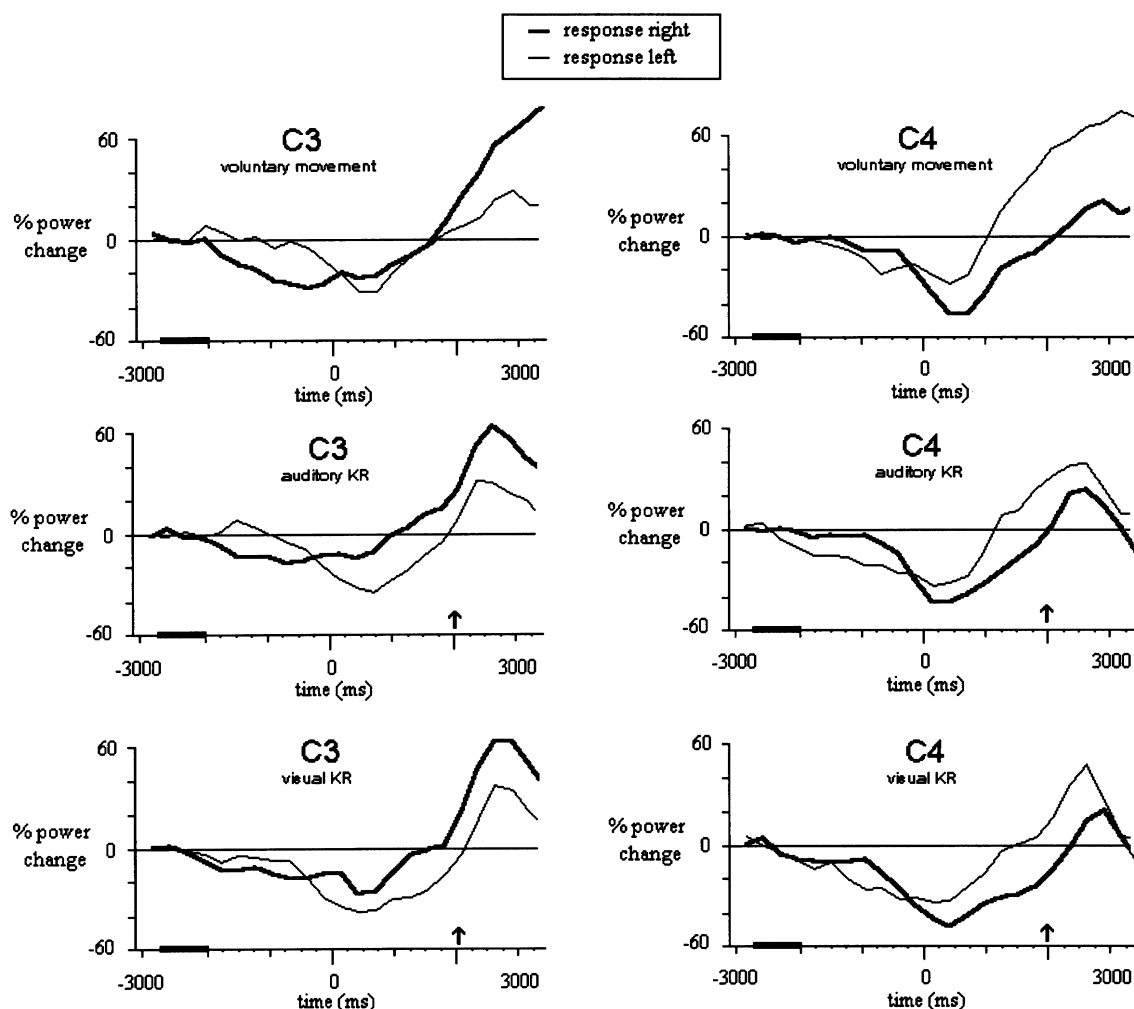


Fig. 1. ERD/ERS time courses on non-subtracted data, for left- and right-hand responses at central channels in the 10–12 Hz frequency band. The Y-axis indicates magnitude of power change. Marked area on the x-axis indicates reference interval. Arrows indicate presentation of KR stimulus. The initially contralateral pre-movement ERD gradually develops into a post-movement ERS in all 3 conditions. Note the similarity of movement-related ERD in the 3 conditions.

At the late pre-movement interval, *t* tests indicate that in all three task conditions, the contralateral ERD has shifted to a bilateral ERD that is consistently present in the 8–10, 10–12 and 20–25 Hz bands. This is further supported by the ANOVA, which shows simple effects of response side * hemisphere in this time interval.

At the pre-KR interval, a centrally maximal, contralaterally dominant ERS is present in all three task conditions, including the voluntary movement condition. The *t* tests show that this effect is present in all frequency bands, but that in the 20–25 Hz band the ERS is also present over the ipsilateral hemisphere. The contralateral ERS is supported by the ANOVA (simple effect of response side * hemisphere in the pre-KR time interval at central channels: $F_{1,9} = 10.21$; $P = 0.0109$), but again the ANOVA does not indicate differences between frequency bands.

Together, the pre-movement ERD and the pre-KR ERS produce a cluster of interactions in the ANOVA on the non-subtracted data (Table 1; $T * R * H$; $E * R * H$; $T * E *$

$R * H$). Over frequency bands, however, the magnitude of the pre-KR ERS is such that in addition to the above-mentioned interactions it produces both the main effect of time interval (over electrode positions, response side and hemisphere an ERS is present at the pre-KR interval) and the interaction $T * E$ (this effect is strongest at central electrode positions). Note that since the pre-KR ERS is also present in

Table 1

Significant ($P < 0.05$) effects of the ANOVA on non-subtracted data

Effect	<i>F</i>	d.f.	<i>P</i>	ϵ
Time interval	6.41	2, 18	0.0139	0.80
B * E	2.82	12, 108	0.0334	0.37
T * E	12.20	6, 54	0.0038	0.20
T * R * H	12.08	2, 18	0.0050	0.56
E * R * H	6.64	3, 27	0.0066	0.68
E * T * R * H	7.99	6, 54	0.0110	0.22

B, frequency band; E, electrode position; T, time interval; R, response side; H, hemisphere; ϵ , Greenhouse-Geisser epsilon.

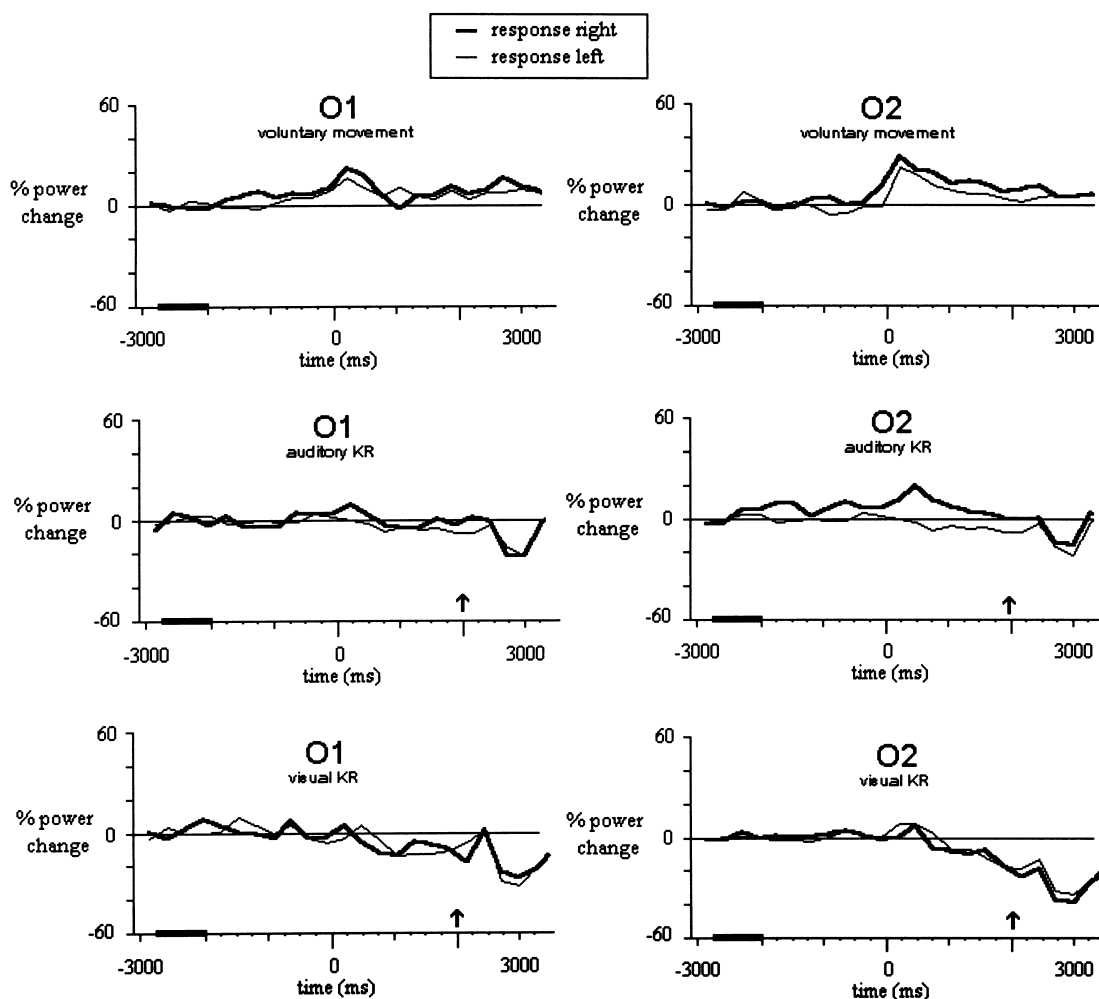


Fig. 2. ERD/ERS time courses on non-subtracted data, for left- and right-hand responses, at occipital channels. The 12–16 Hz frequency band is displayed because in this band the *t* tests indicate a significant ERD (see Table 2). Legends as indicated in Fig. 1. Note the relatively large ERD preceding visual KR stimuli only.

the voluntary movement conditions, it should be attributed to post-movement processes rather than to the anticipation of the KR stimulus. The initially contralateral pre-movement ERD and the post-movement ERS are displayed in Fig. 1.

Over time intervals, the power changes at central elec-

trode positions are different in the different frequency bands: the alpha bands (8–10 Hz and 10–12 Hz) are dominated by ERD, while the higher frequency bands are dominated by ERS (Table 1; B * E: contrast of alpha vs. beta at central channels: $F_{1,9} = 6.76$; $P = 0.0287$).

Fig. 2 shows the ERD time courses in the 12–16 Hz

Table 2

Significance levels of *t* tests on pre-KR ERD (250–0 ms pre-KR) at occipital electrode positions before ($^+P < 0.05$; $^{++}P < 0.01$) and after ($*P < 0.05$; $^{**}P < 0.01$) subtraction of RP conditions from KR conditions. S indicates significant ERS. In the 10–12 Hz band a significant ERD appears as a result of the subtraction indicating that movement-related ERD was masking this effect before subtraction. In the 12–16 Hz bands the ERD is consistently significant before as well as after subtraction

	Auditory KR				Visual KR			
	Response left		Response right		Response left		Response right	
	O1	O2	O1	O2	O1	O2	O1	O2
8–10 Hz					*			
10–12 Hz						*	*	*
12–16 Hz					+*	+*	+**	+**
16–20 Hz				S+			+	
20–25 Hz	S+	S++				*		

frequency band at occipital electrode positions. Preceding visual KR stimuli, there is an ERD that is not present preceding auditory KR or following the voluntary movement. Although the ANOVA revealed no condition effects, the *t* tests indicate that the above-mentioned effect is significant (see Table 2): irrespective of response side a significant ERD is consistently present preceding visual KR stimuli, not preceding auditory KR. Because these effects are never present in the voluntary movement condition, they can truly be attributed to the presentation of the visual KR stimulus.

At temporal electrode positions, the *t* tests indicate a significant ERD preceding both auditory and visual KR stimuli following left-hand movements only (see Table 3). Fig. 3 shows that the ERD at temporal electrode positions is small and rather inconsistent. Moreover, Fig. 3 shows that it is also present in the voluntary movement condition, although in the latter condition it is not significant according to the *t* tests.

After subtraction of the voluntary movement condition from the KR conditions, the *t* tests reveal that both the pre-movement ERD and the post-movement ERS are almost entirely eliminated. This is supported by the ANOVA on the subtracted data, where the only movement-related effect is an intricate condition * response side * frequency band * electrode position * hemisphere interaction ($F_{12, 108} = 2.56$; $P = 0.0368$; $\epsilon = 0.44$). This interaction is considered to be uninterpretable, since none of the possible simple effects reach significance. Because this interaction includes the factors response side and hemisphere, its significance is probably caused by some small and inconsistent residual movement-related ERD.

With respect to the pre-KR ERD, the results are more clear-cut than before the subtraction. At occipital channels, a consistent ERD is found preceding a visual KR both in the 10–12 and the 12–16 Hz bands, while no ERD is present preceding auditory KR stimuli (see Table 2). At temporal electrode positions however, the *t* tests reveal no consistent ERD (see Table 3). This difference between KR modalities is supported by the ANOVA, which indicates that the ERD is larger prior to visual than prior to auditory KR stimuli (condition * time interval interaction: $F_{2, 18} = 8.63$; $P = 0.0074$; $\epsilon = 0.70$; simple effect of condition at the pre-KR

interval: $F_{1, 9} = 6.31$, $P = 0.0332$; see Fig. 4). It should be noted that the factor ‘electrode position’ is not included in this interaction, although the *t* tests clearly indicate that the ERD is significant at occipital channels only. The difference in ERD between KR conditions, as well as the posterior maximum of the ERD preceding a visual KR is illustrated in Fig. 4.

Finally it should be noted that at electrode positions F7 and F8 no consistent ERD or ERS was found, neither before nor after subtraction.

4. Discussion

We investigated the event-related power changes (ERD and ERS) in the EEG related to the anticipation of a stimulus, using a paradigm in which subjects were instructed to perform a time estimation task, and were informed about the quality of their time estimation by a KR stimulus. These event-related power changes are characterized by three components: (1) an initially contralateral, centrally maximal ERD preceding the response; (2) a contralaterally dominant, centrally maximal ERS following the response; and (3) an ERD with a posterior maximum preceding the visual KR stimulus.

The statistical analyses indicated that there were no differences, neither in time course nor in spatial distribution, between the three conditions in the pre-movement central ERD and the post-movement central ERS. The pattern of effects replicates the findings usually described in the literature (e.g. Pfurtscheller and Berghold, 1989), which formed the basis for hypotheses (1) and (2) formulated in the introduction.

The absence of statistically significant differences in movement-related ERD/ERS between conditions justifies the subtraction of the voluntary movement condition from the KR conditions: since the movement-related ERD/ERS pattern was similar in all three conditions, the subtraction effectively eliminated the movement-related effects from the KR conditions. This is indicated by the *t* tests, which show only a sporadic significant result after subtraction, and by the fact that the ANOVA on the subtracted data shows

Table 3

Significance levels of *t* tests on pre-KR ERD (250–0 ms pre-KR) at temporal electrode positions before ($^+P < 0.05$; $^{++}P < 0.01$) and after ($*P < 0.05$; $^{**}P < 0.01$) subtraction of RP conditions from KR conditions. Note that the inconsistent effects before subtraction become even more inconsistent as a result of the subtraction

	Auditory KR				Visual KR			
	Response left		Response right		Response left		Response right	
	T3	T4	T3	T4	T3	T4	T3	T4
8–10 Hz	++**	*			+	+		
10–12 Hz	+					+		
12–16 Hz					++*			
16–20 Hz								
20–25 Hz	S++		S+					

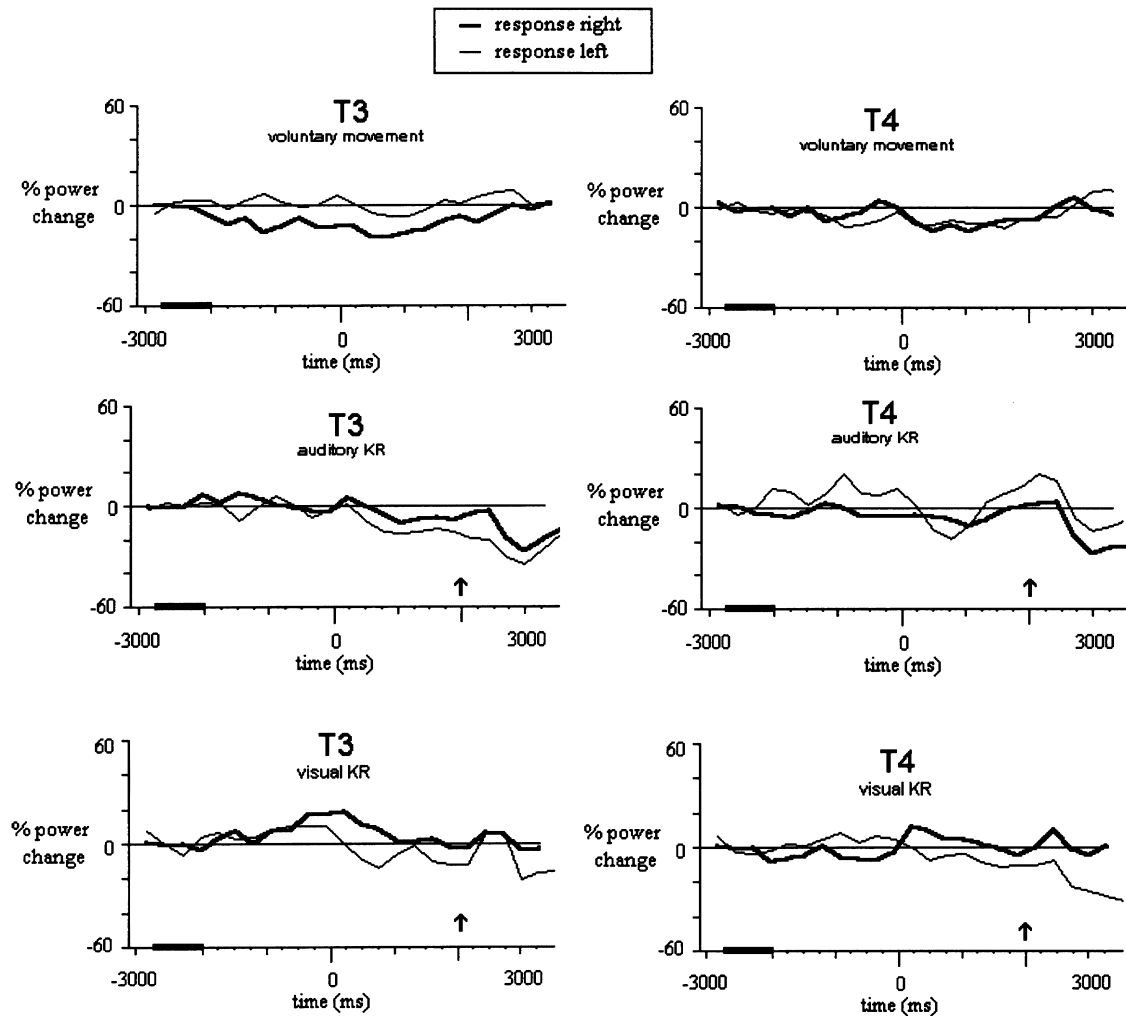


Fig. 3. ERD/ERS time courses on non-subtracted data, for left- and right-hand responses at temporal channels. The 8–10 Hz frequency band is displayed, because this is the band in which ERD is most consistently significant according to the *t*-tests (see Table 3). Legends as indicated in Fig. 1.

neither a clear response side * hemisphere interaction (only an intricate 5th order interaction), nor any significant effects at central electrode positions. Thus, any condition effects in the subtracted data can only be attributed to the anticipation of the KR stimulus.

However, when we consider differences between conditions in the time interval preceding the KR stimulus, the *t* tests and the ANOVA on the non-subtracted data show differential power. The ANOVA does not reveal any condition effects, whereas the *t* tests indicate two differences between conditions.

First, the *t* tests reveal a significant ERD on occipital electrode positions preceding a visual KR stimulus that is not present in the voluntary movement and auditory KR conditions. This condition effect is consistently present only in the 12–16 Hz band before subtraction, whereas the *t* tests on the subtracted data reveal that the effect is present in the 10–12 Hz band as well. The condition effect is also present in the ANOVA on the subtracted data, which supports the notion that the ERD preceding a visual KR is partially masked by post-movement ERS before subtraction.

It should be noted that on the basis of the ANOVA on the subtracted data, we should conclude that the scalp distribution of the ERD preceding a visual KR stimulus is flat, since there are no interactions with the factor 'electrode position'. However, if we consider the *t* test results on the subtracted data (see Tables 2 and 3) and Fig. 4(c,d) it is clear that the ERD preceding a visual KR stimulus was indeed restricted to posterior electrode positions. This is in accordance with the corresponding hypothesis formulated in the introduction. The observed ERD preceding a visual KR is modality-specific, in the sense that it is only present in the visual KR condition.

Second, the *t* tests before subtraction reveal a significant ERD on T3 from 8 to 10 Hz preceding an auditory KR, but only when the subjects responded with the left hand. In order for this effect to be modality-specific, we would expect it to be absent preceding a visual KR. In the latter condition however, both T3 and T4 show similar effects. Moreover, the effect is rather inconsistent, and together with the fact that after subtraction the *t* tests indicate that this condition effect has largely disappeared, we conclude that

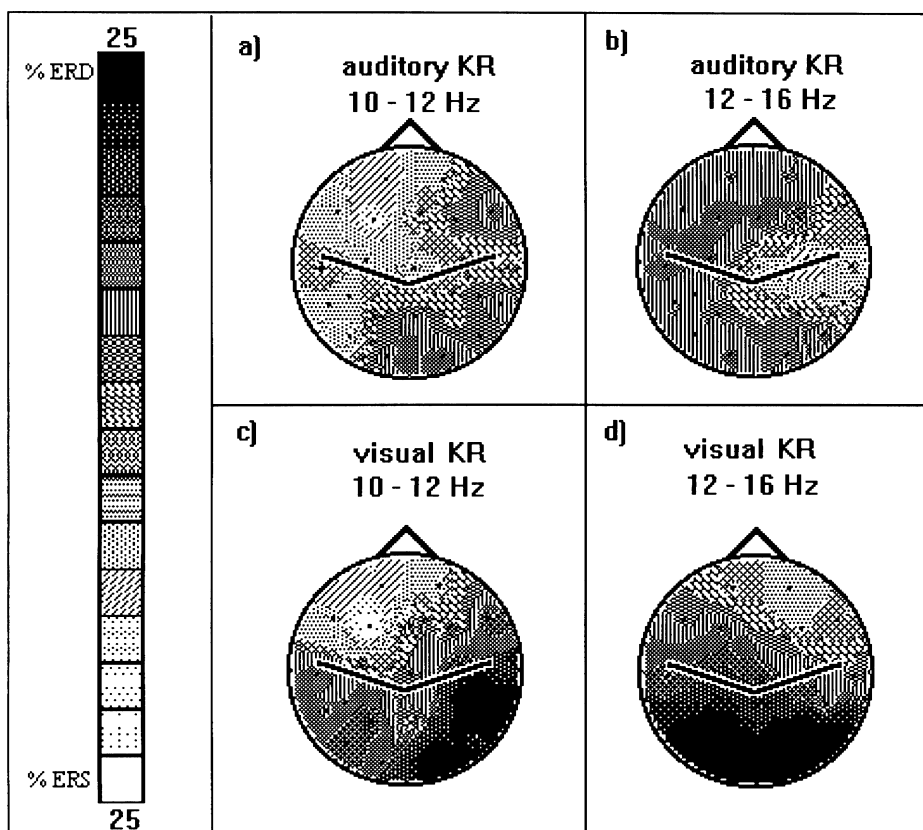


Fig. 4. ERD maps after subtraction of the voluntary movement condition from the auditory and visual KR conditions in two different frequency bands, in the time interval from 250 to 0 ms preceding the KR. Note that (1) the ERD preceding a visual KR is localized to posterior electrode positions and (2) the post-movement central ERS has disappeared as a result of the subtraction. Data are from right-hand responses.

the effect is too inconsistent to be reliable. Thus, no indications of modality-specific desynchronization were found at all in the auditory modality, contrary to the corresponding hypothesis formulated in the introduction.

We did not find any ERD components that could be related to activity in the *Insulae Reili*, contrary to hypothesis (5) formulated in the introduction. This is in contrast with a dipole model of the SPN that was based on the same data set as has been used in the present experiment (Böcker et al., 1994c). Together with the fact that we found no right hemisphere dominance in the ERD as opposed to what is usually reported for the SPN, this could suggest that ERD is less sensitive to the anticipation of an affective-motivational event than its slow potential analogy, which would make ERD an excellent candidate for identifying modality-specific, visual anticipatory attention.

In conclusion, the present study provides evidence of the primary motor cortex being in a preparatory state prior to movement execution, and of the primary visual cortex being in a preparatory state preceding the presentation of a visual KR stimulus. However, preceding an auditory KR we do not find any indications of preparatory activity in primary auditory cortex.

The present data are also relevant with respect to a model of intermodal selective attention that has been proposed by

Skinner and Yingling (1976, 1977); Yingling and Skinner, 1977). This so-called gating model describes a thalamocortical gating mechanism, in which the thalamus, which itself is in turn controlled by the frontal cortex, serves as a gate in the regulation of the transmission of information from subcortical sensory and motor structures to the primary sensory and motor cortices (for a detailed description of the model, see Brunia, 1993b, 1997). As proposed by Brunia (1993b, 1997), the gating model, which was initially developed to describe intermodal selective attention, could also provide an explanation (in functional and structural terms) of motor preparation and anticipatory attention. It would predict a correspondence between slow potentials and ERD during motor preparation and anticipatory attention. According to the model, these preparatory processes should be reflected both by negative slow waves and ERD that are maximal over the respective primary sensory cortex when a stimulus is anticipated, and over the pre- and post-central cortex when a movement is prepared for.

The predictions based on the gating model are confirmed both by slow potential data and by ERD data as far as motor preparation is concerned: there is a close correspondence between the two measures in a voluntary movement paradigm. However, it is unclear why both measures display a different lateralization. This suggests that the thalamo-cor-

tical gating circuit might not be the only, and maybe not even the principle circuit through which motor preparation is realized.

As we pointed out in the introduction, slow potential research has consistently failed to find correlates of modality-specific anticipatory attention (with the exception of Lang et al., 1984). The present experiment, directed at identifying patterns of ERD related to anticipatory attention, has been at least partially successful in this respect (i.e. in the visual modality, not in the auditory). However, there is a lack of a correspondence between ERD and slow potentials in the present study. A possible explanation for this may lie in the fact that the time estimation paradigm is not adequate for isolating the relevant preparatory process: the affective-emotional value of presenting a KR stimulus might be masking the slow potential correlate of the pure anticipatory attention, whereas ERD might be less sensitive to the anticipation of an affective-motivational event, as has been suggested above.

In future research, other paradigms, such as employing probe and instruction stimuli should also be studied with the ERD technique. Furthermore, event-related power changes in the higher frequency bands must be considered as well (e.g. the 40 Hz band, see Pfurtscheller et al., 1993, 1994), in order to have a complete picture of synchronization and desynchronization patterns in the entire frequency spectrum of the EEG, which ranges from 0 to 60 Hz.

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