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Anticipatory attention to verbal and non-verbal stimuli is reflected in a modality-specific SPN

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Abstract The time estimation paradigm allows the recording of anticipatory attention for an upcoming stimulus unconfounded by any anticipatory motor activity. Three seconds after a warning signal (WS) subjects have to press a button. A button press within a time window from 2,850 ms to 3,150 ms after the WS is considered ‘correct’, a movement prior to 2,850 ms after the WS is labelled ‘too early’ and a movement after 3,150 ms is labelled ‘too late’. Two seconds after the button press a Knowledge of Results (KR) stimulus is presented, informing the subject about the correctness of the response. Stimulus Preceding Negativity (SPN) is a slow wave which is recorded prior to the presentation of the KR stimulus. The SPN has a right hemisphere preponderance and is based upon activity in a network in which prefrontal cortex, the insula Reili and the parietal cortex are crucial. In the present study we asked two questions: (1) does the SPN show modality specificity and (2) does the use of verbal KR stimuli influence the right hemisphere preponderance? Auditory and visual stimuli were presented, in a verbal mode and in a non-verbal mode. SPN amplitudes prior to visual stimuli were larger over the visual cortex than prior to auditory stimuli. SPN amplitudes prior to auditory stimuli were larger over the frontal areas than prior to visual stimuli. The use of verbal stimuli did not influence the right hemisphere preponderance. We concluded that apart from the supramodal effect of KR stimuli in general, there is (first) a modality-specific activation of the relevant sensory cortical areas. The supramodal network underlying the attention for and the use of KR information is activated either from different sensory areas or from language processing cortical areas.

Keywords Stimulus preceding negativity · SPN · Anticipatory attention · Anticipatory activation of sensory cortex · Modality specificity

Introduction

In the present paper we describe an experiment in which anticipatory processes are investigated in the sensory domain. The continuous stream of information reaching our senses is so abundant that selection is necessary to maintain order in our relation to the environment. Attention realizes the selection of relevant stimuli. Although the relevance of a stimulus goes beyond the modality in which that stimulus is presented, the latter can only reach the CNS via one of the sense organs. Thus whatever the behavioral level at which the stimulus plays its role, anticipatory attention aimed at that stimulus is directed at a certain modality. Under experimental conditions attention is called upon by instructing subjects or by presenting them a cue, suggesting which aspect of the upcoming stimulus is crucial. This results in a decrease in error rate or a faster reaction time. Thus, these changes in behavior become manifest *after* the presentation of the crucial stimulus. The same holds for the psychophysiological indices of attention. Yet the crucial processes must have taken place *before* the stimulus arrives.

Anticipatory processes may influence all stages of information processing between perception and action. This implies that all brain areas involved in the information processing from input to output are “set” in order to facilitate the future behavior (Brunia 1999). Setting is a manifestation of a top-down organization, in which the prefrontal cortex plays an essential role (Fuster 1997). From there different brain areas can be activated. Facilitation of perceptual processes can be realized by shifting the membrane potentials of neurons in the sensory brain areas of the different modalities towards the firing threshold. A similar process in motoric brain structures can realize facilitation of response speed or accuracy. Facilitation of so-called “higher” psychological functions can be

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realized by a comparable process in relevant brain structures. The psychophysiological reflection of these anticipatory processes can be investigated by recording event-related slow potentials.

Slow potentials preceding an event reflect the increasing activation of groups of neurons in cortical areas, which are part of a network underlying some future behavioral activity. Mostly the event is the presentation of a stimulus, which has to be processed in a cognitive task, and which leads to some kind of motor activity. The event can also be a self-paced movement. From a physiological point of view there is no difference between anticipatory processes in the sensory domain and in the motor domain (Brunia 1999). In both cases a circumscribed excitation has to be built up in crucial groups of neurons, which leads finally to their discharge. Thus the difference is not in the *nature*, but in the *localization*, of the process in the brain. The latter determines its behavioral consequences.

Two very well known slow potentials are the CNV (Walter et al. 1964) and the Readiness Potential (RP; Kornhuber and Deecke 1965). The size and potential distribution of the CNV late wave is for a large part determined by motor preparation (Rohrbaugh and Gaillard 1983). Yet there is a relatively small number of papers in which a non-motor contribution to the late wave has been advocated (e.g. Donchin et al. 1972; Simons et al. 1979; Klorman and Ryan 1980; Larbig et al. 1982; Macar and Besson 1985; Ruchkin et al. 1986; McCallum 1988). In the classic CNV motor preparation and anticipatory attention for the response stimulus are confounded, in contrast to the time estimation task. Here both processes are separated in time: the RP, accompanying preparation of the movement is followed by a Stimulus-Preceding Negativity (SPN) accompanying anticipatory attention to the Fb stimulus (Brunia 1988; Damen and Brunia 1987; Brunia and Damen 1988). Apart from the latter studies the pre-feedback SPN has been recorded in different theoretical settings (Stuss and Picton 1978; Grünewald and Grünewald-Zuberbier 1983; Chwilla and Brunia 1991; Rösler and Heil 1991).

In a series of experiments we investigated the SPN recorded prior to a Knowledge of Results (KR) stimulus in a time estimation task. The KR stimulus was presented after a movement, which mostly had to be carried 3 or 4 s after a warning stimulus within a time window of 300 or 400 ms, respectively. It was used to inform subjects about the correctness of their time estimation. We found a sustained negativity over the prefrontal cortex and a sharply increasing negativity over the parietal cortex (Brunia and Damen 1988; Damen and Brunia 1994). In a dipole modeling study of the SPN, Böcker et al. (1994) found a bilateral frontotemporal dipole, probably localized in the insula Reili. This suggested to us the existence of an underlying network in which the prefrontal cortex, the parietal cortex and the insula Reili were the crucial nodes. A recent PET study, which tested this hypothesis, showed indeed an activation of these cortical areas (Brunia et al. 2000). Taken together, there is a reasonable amount of evidence for the notion that presenting KR about a recent

performance is based upon activity in a network in which the prefrontal cortex, the parietal cortex and the insula Reili play a crucial role. In earlier studies of Grünewald and Grünewald-Zuberbier (1983) and of Grünewald et al. (1984), in which the authors presented KR about performance in a positioning or aiming task, the SPN was also found. This suggests that information about timing of a movement and about positioning of a movement activates a comparable network. Since the KR function as such is supramodal we wondered whether the underlying network could be activated via different sensory modalities. Rohrbaugh and Gaillard (1983) have refuted the existence of modality-specific anticipation in the CNV late wave, in our opinion only because of the large influence of the movement-related activity. We like to demonstrate that the SPN distribution is different for different modalities, just as the RP distribution is different for finger and foot movements (Brunia and Vingerhoets 1981). Should we be able to show that, we have an argument in favor of a comparable selection mechanism in the sensory domain and in the motor domain. Thus, the first question we asked is: is the anticipatory activity prior to the perception of a relevant stimulus selective, i.e. does it depend upon the stimulus modality?

A well-known marker of incoming information in sensory cortical areas is the N1, a negative exogenous evoked potential (EP), which becomes manifest about 100 ms after stimulus onset. It has a widespread distribution over the skull. The visual N1 has largest amplitudes over the occipital areas and the auditory N1 over frontocentral areas. In line with earlier suggestions (Vaughan and Ritter 1970; Wood and Wolpaw 1982), Näätänen and Picton (1987) interpreted the latter finding as resulting from the orientation of the dipoles in the supratemporal cortex. Selective attention to an auditory stimulus is reflected by an enhancement of the N1 amplitude. This extra (endogenous) negativity has been termed Negative Difference (Nd) wave by Hillyard et al. (1973) and Processing Negativity by Näätänen (1982). Notwithstanding this contrast in interpretation of the underlying process, there is no doubt that selective attention evokes an endogenous negativity around the time the N1 appears. Apart from this temporal coincidence there is also a spatial coincidence: Mäkelä and Hari (1990) demonstrated that the early Nd is generated in the supratemporal gyrus, an area supposed to be the origin of the auditory N1. For the visual modality the picture is different. Attention effects become manifest at a later point in time than in the auditory modality, and probably not in the primary cortex, but in the extrastriate cortex (Heinze et al. 1994). In line with these results Gratton (1997) confirmed with his optical imaging technique that early attention effects become manifest around 100 ms after stimulus presentation, not in the primary cortex, but in the extrastriate cortex (see also Näätänen and Alho 1995). Given the potential distribution of the exogenous and early endogenous components around the N1, our first question can be phrased as follows: does the SPN prior to an auditory KR stimulus show largest amplitudes over the

frontal areas and prior to a visual KR stimulus over the occipital areas?

A second issue investigated in the present experiment is the right hemisphere preponderance of the SPN in the time estimation paradigm. In most of our studies a movement had to be made in a well-defined time window, 2 s after which a KR stimulus was presented. In all studies in which left and right hand responses were investigated, an interaction between response side and hemisphere was found (Brunia and Damen 1988; Damen and Brunia 1987, 1994; Grünewald and Grünewald-Zuberbier 1983; Grünewald et al. 1984). The right hemisphere preponderance recorded prior to a left-sided movement remained present during the interval between movement and KR stimulus presentation. The left hemisphere preponderance prior to a right-sided movement changed during that same interval into a right-sided preponderance of the SPN. The existence of a right hemisphere preponderance was demonstrated beyond doubt in an experiment in which physically identical stimuli were used as instruction stimuli at trial onset, and as KR stimuli at trial offset (for details see: Damen and Brunia 1994). The SPN prior to KR stimuli showed a clear right hemisphere preponderance, which was later confirmed in a PET study (Brunia et al. 2000). Again a right-sided activation was found in prefrontal area BA45, the junction of the posterior insula with the temporal transverse gyrus and the posterior parietal cortex. Thus the right hemisphere preponderance of the KR network is beyond doubt. This does not mean that we understand its cause. In our experiment subjects were attending the KR stimuli, in order to apply their message to the next trial. Interestingly, Mesulam (1981) has suggested a specific role of the right hemisphere in directed attention.

Notwithstanding the large number of clinical and neuropsychological studies suggesting a left hemisphere involvement in language, only a few CNV studies exist aimed at laterality effects during expectant attention for verbal information (Rebert and Low 1980; Butler et al. 1981; for a review see McCallum 1988). Since confounding of attention with motor preparation is almost inevitable in CNV studies (see, however, Ruchkin et al. 1986), we reasoned that the time estimation paradigm would give us a better chance to record lateralized anticipatory potentials preceding verbal stimuli. Therefore the second question we asked was: Is the right hemisphere preponderance of the SPN affected by the use of verbal KR? The KR function as such is supramodal. Therefore it is implausible that the right hemisphere preponderance will be affected by modality. This is also the provisional conclusion from the available literature. Yet one would expect that the setting of the sensory areas as such would be measurable. For language stimuli it is not in advance evident that the right hemisphere preponderance is vulnerable to language stimuli.

Summarizing, we investigated in this study the effects of modality of KR stimuli. Within one group of subjects we compared the visual and auditory KR stimuli, both in the verbal and non-verbal mode. On the basis of our earlier

work (Brunia 1988), we formulated the following hypotheses:

1. There is a modality specific potential distribution of the SPN, comparable to the different RP distribution prior to hand and foot movements.
2. There is no effect of modality upon the right hemisphere preponderance of the SPN.
3. The right hemisphere preponderance will be partly vulnerable to the use of verbal stimuli at the utmost.

Materials and methods

Participants

Twenty right-handed subjects, ten female and ten male, aged between 19 and 28 years (mean 22.1, SD 2.06) participated in this experiment. Handedness was determined with a modified version of the Edinburgh Inventory (Oldfield 1971). Participants were paid for completing the experiment. They had normal or corrected-to-normal vision and hearing. An informed consent was obtained from all subjects.

Apparatus and procedure

Participants were seated in a comfortable armchair placed in a dimly illuminated, sound attenuating, and electrically shielded chamber. A computer monitor was placed in an adjacent, similarly shielded room. It was visible to the participants at a distance of about 1.5 m at eye level. The participants fixed their gaze on the screen throughout the experiment. Response keys were mounted at the end of both armrests. The task for the participants was to press one of the keys exactly 3 s after an auditory starting stimulus (1,000 Hz, 70 dB, 100 ms) that was produced via a speaker placed behind the subject at a distance of about 0.5 m. The participants received knowledge of results (KR) about the accuracy of their timing at 2 s after the button press. A correct response was defined as a key press issued within the range of 3,850–4,150 ms after the starting stimulus.

The modality (visual, auditory) and nature (nonverbal, verbal) of the KR stimulus constituted the experimental conditions. The visual nonverbal stimuli (duration 100 ms) were a horizontal line, a vertical line or a plus sign, respectively, for too early, correct or too late responses. The auditory nonverbal stimuli were tones of different pitch (respectively, 500, 1,000, 2,000 Hz, 70 dB, 100 ms duration). For verbal KR the Dutch equivalent of the words 'too short', 'correct' or 'too long' were used, presented either on the monitor or via the speaker. The four conditions were run twice, once with left hand responses and once with key presses with the right hand. There were thus eight blocks, the order of presentation of which was counterbalanced over participants. Each block consisted of 60 trials.

Recording and data analysis

Brain potentials were recorded with 8-mm Ag-AgCl electrodes affixed to the scalp with electrode cream (Grass EC2) at F3, F4, C3, C4, P3, P4, O1, O2, T3' and T4'. T3' and T4' were located midway between T3 and C3 on the left side, and between T4 and C4 on the right side. Linked mastoids served as a reference. The interelectrode impedance was always less than 3 k Ω . Three pairs of 2-mm Ag-AgCl electrodes monitored eye movements. They were placed above and below both eyes, and on the lateral sides of both eyes. The signals were recorded with a 14-channel Nihon Kohden 4314F machine with a modified 30-s time constant. Low pass filtering was at 35 Hz (roll off 6 dB/octave). Signals were digitized (12 bit) on-line from 1 s prior to the starting signal until 1 s following the key

press at a rate of 128 Hz. The single trial signals were then corrected off-line for eye movements using the method described by Van den Berg-Lenssen et al. (1989), and checked for other artifacts by passing the corrected data through a window of 80 μ V. The single trials were then averaged, time locked to the key press, separately for each of the eight blocks, and only the data from 1,700 ms prior to the key press to 500 ms after the presentation of the KR stimulus were analysed. The amplitude of the MPN was defined as the mean amplitude over the last 100 ms preceding the key press. The amplitude of the SPN was defined as the mean amplitude recorded over the last 100 ms prior to the presentation of the KR stimulus. The interval of 1,700–1,500 preceding the key press or prior to the KR was used as a baseline for the MPN and the SPN, respectively. Amplitude measures were subjected to MANOVA with the within-subjects factors Language (verbal/nonverbal), Modality (visual/auditory), Movement Side (left/right), Hemisphere (left/right), and Electrode Position (F, C, P, T' and O). For trend analyses on the SPN, we used six successive intervals of 100 ms each up to the presentation of the KR. This analysis used the same baseline and within-subjects factors as above.

Results

Performance

The percentage of correct trials was 47.0%, averaged over modality, language, and hands. The overall percentage of too early responses was 21.9% and there were 31.1% overshoots. The effect of presenting KR on performance becomes apparent when sequential trials are considered. Of all trials immediately following early responses, only 6.0% were also too early, whereas 9.6% were correct and 6.3% were too late. That is, 76% of all early responses were later on the subsequent trial. For late responses, 13.3% were correct on the following trial, and 6.9% were too early. Only 10.9% of late responses were also late on the subsequent trial. That is, 65% of late responses were followed by a shorter response. Finally, the 47% correct responses were followed by 24.2% correct responses, 8.5% too early and 14.3% too late trials. Thus, the majority (52%) of the correct responses remained correct on the subsequent trial. Altogether, these are clear indications of the beneficial effect of presenting KR, also confirmed by statistical testing ($F_{(4,16)} = 8.89$, $p < 0.001$). Modality and language did not affect performance in any way (all $F < 1$).

Movement-preceding negativity

The paradigm used in this study allowed the temporal separation of Movement- and Stimulus-Preceding Negativity. Because this paper was aimed at investigating influences upon the SPN, we only will briefly discuss the MPN. The MPN (RP) was recorded prior to the button press in the prescribed time window. Its amplitude was largest over the central electrode positions (main effect for the factor Electrode Position, $F_{(4,16)} = 7.43$, $p < 0.01$). Left hand movements elicited a larger RP than right hand movements (Response Side $\times$ Electrode Position interaction: $F_{(4,16)} = 6.57$, $p < 0.01$). The RP was larger

Fig. 1 Averaged waveforms recorded in the time estimation task, aligned to the response (first vertical line) and the KR stimulus (second vertical line), separately for the auditory and visual modalities. The waveforms represent grand averages over the factors Movement Side, Language, and 20 subjects. The time interval between the two vertical lines is 2 s

contralateral to the movement side than ipsilateral to the movement side (Response Side $\times$ Hemisphere interaction: $F_{(1,19)} = 11.58$, $p < 0.01$). In other words we replicated our earlier findings, described in the “Introduction”.

Stimulus-preceding negativity

Figure 1 shows the SPN recorded in the four conditions for each response side. With left hand movements the right hemisphere lateralization is obvious, with right hand movements it is also present, but less pronounced, and only in the last few hundreds of milliseconds.

Overall analysis

The SPN exhibited the largest amplitudes over the parietal area and smallest amplitudes over the frontal area (main effect for the factor Electrode Position, $F_{(4,16)} = 3.40$, $p < 0.05$). As in most of our earlier studies the SPN was larger over the right hemisphere than over the left hemisphere (main effect for the factor Hemisphere: $F_{(1,19)} = 17.5$, $p < 0.001$). Although this is the case over all electrode positions, the left-right differences were unequal for the different positions (Electrode Position $\times$ Hemisphere interaction, $F_{(4,16)} = 7.13$, $p < 0.005$, see Fig. 2). The largest difference was present over the temporal electrode positions, and the smallest amplitudes

Fig. 2 Means involved in the interaction between the factors Electrode Position and Hemisphere for the Stimulus-preceding Negativity. Error bars denote standard error of the mean

over the left temporal area. Prior to verbal KR the SPN amplitude was larger following a left hand movement than following a right hand movement. Prior to non-verbal KR the SPN was larger following a right hand movement than following a left hand movement (Response Side $\times$ Language interaction: $F_{(1,19)} = 4.73$, $p < 0.05$). In the verbal mode the SPN showed larger amplitudes prior to visual KR stimuli than prior to auditory KR stimuli. In the non-verbal mode larger SPN amplitudes were present prior to auditory than prior to visual KR stimuli (Language $\times$ Modality interaction: $F_{(1,19)} = 17.58$, $p < 0.001$). The largest SPN amplitude in the visual modality was present over the parietal and occipital electrode positions and the largest SPN amplitude in the auditory modality over the frontal area (Modality $\times$ Electrode Position interaction: $F_{(4,16)} = 5.16$, $p < 0.01$).

Modality

As illustrated in Fig. 3 there was a complete reversal in the modality effects between frontal and occipital electrode positions. Over the frontal cortex SPN amplitudes were larger prior to auditory KR stimuli ($-3.3 \mu V$) than prior to visual KR stimuli ($-1.7 \mu V$). Over the occipital cortex SPN amplitudes were larger prior to visual stimuli ($-4.8 \mu V$) than prior to auditory stimuli ($-3.3 \mu V$). Simple effects of Modality were significant both at frontal ($F_{(1,19)} = 12.99$, $p < 0.001$) and at occipital ($F_{(1,19)} = 5.53$, $p < 0.05$) electrodes.

Because we found a Language $\times$ Modality $\times$ Electrode Position interaction ($F_{(4,16)} = 5.17$, $p < 0.007$), we analysed the Modality $\times$ Electrode Position separately for the verbal and non-verbal conditions. In the *verbal condition* amplitudes were larger prior to visual stimuli ($-3.5 \mu V$) than prior to auditory stimuli ($-2.8 \mu V$). There was a nearly significant main effect for Modality ($F_{(1,19)} = 4.05$, $p < 0.06$). Next the SPN showed a clear modality-specific distribution over the occipital cortex. Amplitudes were larger prior to visual ($-5 \mu V$) than prior to auditory KR stimuli ($-3.1 \mu V$). Over the frontal cortex amplitudes were

Fig. 3 Effect of stimulus modality on the Stimulus-preceding Negativity at frontal and occipital electrodes. Error bars denote standard error of the mean

larger prior to auditory ($-2.6 \mu V$) than prior to visual stimuli ($-2.1 \mu V$; Modality $\times$ Electrode Position interaction: $F_{(1,19)} = 8.84$, $p < 0.01$). In the *non-verbal condition* there was a main effect for Modality ($F_{(1,19)} = 6.98$, $p < 0.02$). The SPN showed again a modality-specific distribution. Over the occipital areas amplitudes were larger prior to visual stimuli ($4.6 \mu V$) than prior to auditory stimuli ($-3.5 \mu V$). Over the frontal areas amplitudes were larger prior to auditory stimuli ($-4.1 \mu V$) than prior to visual stimuli ($-2.8 \mu V$) (Modality $\times$ Electrode Position interaction: $F_{(1,19)} = 11.14$; $p < 0.01$).

Apart from analysing only the maximum SPN amplitude immediately before the KR, we also assessed the *time course* of the SPN over the last 500 ms by comparing amplitudes over five epochs of 100 ms using polynomial contrasts. This analysis confirmed the overall effects described above, but also indicated that SPN increased over the last 500 ms before the KR, and that the *increase* also differed between conditions. A linear effect of the factor Interval ($F_{\text{lin}(1,19)} = 15.94$, $p < 0.001$) reflected this overall increase of $-0.7 \mu V$. The increase was slightly greater for auditory than for visual KR (-0.8 vs $-0.6 \mu V$, $F_{\text{quad}(1,19)} = 9.35$, $p < 0.01$), and over the occipital as compared to the frontal electrodes (1.5 vs $0.1 \mu V$, $F_{\text{lin}(1,19)} = 12.83$, $p < 0.01$). A linear effect on the interaction between Modality and Position ($F_{\text{lin}(1,19)} = 6.15$, $p < 0.05$) indicated that the SPN over the frontal electrodes increased for auditory KR ($-0.4 \mu V$), but slightly *decreased* for visual KR ($-0.2 \mu V$), whereas the SPN over the occipital electrodes always increased (-1.1 and $-1.5 \mu V$ for auditory and visual KR, respectively).

Error-related SPN activity

In order to investigate a possible difference in SPN amplitude between correct and incorrect trials a MANOVA with factors Error (correct, incorrect), Hand (left, right), Language (verbal, non-verbal), Modality (visual, auditory), Electrode Position (FCTPO) and Hemisphere

(left, right) was carried out as well. By and large the same effects are found as in the overall analysis. There is neither a main effect for the factor Error, nor a simple interaction with one of the other factors. The size of the anticipatory activity does not indicate whether the correct or incorrect KR is expected.

Language

There was no significant Language $\times$ Hemisphere interaction. The right hemisphere lateralization of the SPN was present in both the verbal ($F_{(1,19)} = 8.83, p < 0.01$) and the non-verbal ($F_{(1,19)} = 8.48, p < 0.01$) conditions. Thus the use of verbal KR stimuli does not interfere with the functioning of the KR circuitry itself.

Because the interaction between the factors Language, Modality and Electrode Position was significant ($F_{(4,16)} = 5.17, p < 0.001$), we computed simple effects for verbal and non-verbal conditions separately. Figure 4 shows that the pattern of Fig. 3 remains essentially the same: the SPN is larger prior to visual stimuli over the occipital areas, and prior to auditory stimuli over the frontal cortex. However, the modality difference in SPN amplitude is larger over the occipital areas with verbal stimuli and over the frontal areas with non-verbal stimuli. Over both frontal and occipital areas visual SPN amplitudes increase and auditory SPN amplitudes decrease with verbal stimuli as compared to non-verbal stimuli.

All in all we do not see an argument in favor of a clear language-dependent effect over the left hemisphere.

N100

The N100 following the KR stimulus was largest over the frontocentral and smallest over the occipital electrodes (Electrode Position: $F_{(4,16)} = 21.78, p < 0.001$). It showed a significant main effect for the factor Modality ($F_{(1,19)} = 97.83, p < 0.001$), revealing that the amplitudes following auditory stimuli ($-7.5 \mu\text{V}$) were larger than following

Fig. 4 Interaction between the factors Language, Modality and Electrode Position for the Stimulus-preceding Negativity. Error bars denote standard error of the mean

Fig. 5 The difference in modality between frontal and occipital electrodes is the same for the SPN and the N100. Error bars denote standard error of the mean

visual stimuli ($-4.1 \mu\text{V}$). The significant main effect for the factor Language ($F_{(1,19)} = 27.28, p < 0.001$) showed that amplitudes following non-verbal stimuli were larger ($-6.3 \mu\text{V}$) than following verbal stimuli ($-5.3 \mu\text{V}$). The significant Modality $\times$ Position interaction ($F_{(4,16)} = 26.18, p < 0.001$) revealed that in the visual condition amplitudes were largest over the central ($-9.2 \mu\text{V}$) and frontal ($-8.4 \mu\text{V}$) areas, whereas amplitudes in the visual condition were largest over the occipital area ($-6.3 \mu\text{V}$). In the visual condition amplitudes recorded over the temporal ($-3.0 \mu\text{V}$) positions were smallest. A comparison with the Modality $\times$ Position interaction of the SPN, which was discussed earlier, is illustrated in Fig. 5, in which the mean amplitudes of SPN and N1 are represented together. Over the frontal cortex the auditory SPN is larger than the visual SPN, and the same holds for the N1. Over the occipital cortex the inverse picture is present: now the visual SPN is larger than the auditory SPN, while the same holds for the N1. This supports the notion that the SPN recorded over the frontal areas indeed reflects an anticipatory activation of the areas from where the auditory N1 is generated. Taken together the present results suggest that there is a modality-specific activation of the sensory areas, before these areas are confronted with the stimuli, evoking the N1.

Discussion

We investigated whether anticipatory attention for a KR stimulus is modality specific. We used the time estimation paradigm, because it allows separating in time movement preparation from the attention to the impending stimulus. We will not go into the details of the motor preparatory processes, because the results confirmed those reported in earlier studies (Böcker et al. 1994; Brunia and Damen 1988; Chwilla and Brunia 1991; Damen and Brunia 1987, 1994; Brunia et al. 2000). Also the KR circuitry itself is not our main concern, because the ongoing information in that circuitry is supramodal. Rather we wanted to know whether the SPN would show a different distribution over

the cortex when using stimuli in the visual or auditory modality. The present recordings do not permit conclusions about the sources whose activity is reflected in the SPN. It is a reasonable assumption, however, that pitch perception is a function of the primary auditory cortex. Moreover, Hubel and Wiesel (1959) have demonstrated that cells in the primary visual cortex in the cat are able to detect straight lines, so both the visual and auditory stimuli used in the present study can activate the primary cortex without having them broken down into more elementary parts. Since these stimuli have ecological value a further processing in secondary and higher cortices is necessary, though. Therefore there is no warrant for the suggestion that the anticipatory activity is restricted to or even present in the primary cortex. We found larger SPN amplitudes over the frontal cortex prior to auditory than prior to visual KR stimuli, and larger SPN amplitudes over the occipital cortex prior to visual than prior to auditory KR stimuli. This was the case for both verbal and non-verbal stimulus material. Thus, we conclude that the first hypothesis is confirmed: *the SPN does show a modality-specific distribution*. In other words: anticipatory attention to stimuli of different modalities does indeed increase local activity in the relevant cortices before the stimulus arrives. This might but need not be the case in the primary cortex already.

The results of our study are in contrast to those of Böcker et al. (1994), who also used auditory and visual stimuli. These authors did not find an indication of a modality-specific distribution. That study was also exceptional in that it did not show the right hemisphere preponderance, we almost always record. Compared to the auditory SPN, Böcker et al. (1994) hardly found a visual SPN. In contrast to the visual stimuli used in our study, Böcker et al. (1994) used stimulus duration in both modalities as the crucial variable. Up to now it has been the only study in which stimulus duration was used to inform subjects about their performance. Its possible importance should be studied in further experiments.

The right hemisphere dominance of the SPN was present prior to auditory and visual KR stimuli. This result confirms the second hypothesis: *there is no effect of modality upon the right hemisphere preponderance of the SPN*. There are two major functions that might play a role in this right hemisphere effect: attention and emotion. Directing attention upon a desirable object seems to be a function of the right hemisphere (Mesulam 1981). In line with that, Lang et al. (1984) described a Directed Attention potential with a right hemisphere preponderance. However, KR stimuli have also a motivational or emotional value. Kolb and Wishaw (1990) suggest that “the right hemisphere is more involved than the left in all aspects of emotional behavior” (loc. cit. p. 628). So both attention and emotion could have provoked the right hemisphere preponderance.

Neuropsychological studies suggest that processing of words might be a function of the left rather than of the right hemisphere. Passive listening to words or looking at words activates areas in the posterior part of the left

hemisphere, as can be demonstrated by PET and ERP studies (Posner and Raichle 1994; Snyder et al. 1995). This is the case both in the visual and in the auditory modality. We used verbal KR stimuli because we wanted to influence the right hemisphere preponderance by presenting stimulus material that is supposed to activate the left hemisphere rather than the right hemisphere. The Language $\times$ Modality $\times$ Electrode Position interaction made us separate the verbal and non-verbal conditions. The presentation of simple tones results in much larger SPN amplitudes over the frontal cortex than the presentation of words. This suggests an activation of auditory areas, which is different for verbal and non-verbal information. In the visual modality it is the other way around: The presentation of simple lines results in smaller SPN amplitudes than the presentation of words, not only over the occipital areas but also over the frontal areas. Taken together, the data suggest different ways of processing verbal and non-verbal information in both modalities. Yet the use of verbal KR stimuli did not affect the right hemisphere preponderance. This confirms our third hypothesis: *the right hemisphere preponderance is not vulnerable to the use of verbal stimuli*. The network underlying the KR function can be activated from different sensory areas and seems to be independent of the supramodal (verbal or non-verbal) type of feedback.

The next issue to be discussed is that of specificity. We found an SPN over the occipital areas prior to auditory stimuli, and over the temporal cortex prior to visual stimuli. This could be the consequence of volume conduction from the areas really activated, but it could also imply that the slow wave preceding the KR stimuli is non-selective. We consider our data a support for the selectivity hypothesis. Exogenous potentials like the N1 reflect the modality-specific response from circumscribed cortical areas upon stimuli reaching the brain from the environment. Processing negativity, showing up after the presentation of an attended stimulus, has also some modality-specificity (Näätänen and Michie 1978). This endogenous potential reflects voluntary attention to and further processing of relevant stimuli. Anticipatory attention is also a form of voluntary attention. We consider it a manifestation of the top-down organization of the brain. It goes along with the SPN. Its underlying physiological process is a systematic increasing activation of structures in which the post-stimulus attentional processes are going to take place, reflected in the processing negativity. We found indeed: (1) larger N1 amplitudes over the frontal cortex following auditory stimuli than following visual stimuli, and (2) larger N1 amplitudes over the visual cortex following visual than following auditory stimuli. We consider the comparable potential distribution of the visual SPN and the visual N1 on the one hand, and the comparable potential distribution the auditory SPN and the auditory N1 on the other hand, as support for the hypothesis that there is indeed a modality-specific anticipatory activation of sensory brain areas.

Such a process would have its analogue in the motor system, in which the RP reflects the setting of structures

that will be involved in the impinging execution of the movement, and which shows a limb-specific potential distribution, i.e. a distribution which is different for finger and foot movements (Brunia 1980; Brunia and Vingerhoets 1981). To clearly demonstrate *anticipatory* modality-specificity, the time estimation paradigm with KR is a better tool than the warned RT task, because the last 1.5 s of the 2-s waiting interval is not contaminated by movement-preceding activity. Given the fact that area-specific or modular cortical activation has been described *during* (cognitive) task performance (Birbaumer et al. 1992; Rösler et al. 1997), it is interesting that the modality specificity of the SPN suggests that a specific activation of a well-defined cortical area starts *prior to stimulus presentation*. If one considers the RP specific, there is no reason to have another opinion about the SPN.

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