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Habituation of the orienting response as reflected by the skin conductance response and by endogenous event-related brain potentials

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Abstract

The paper is concerned with the question of whether endogenous components of the auditory event-related brain potential (ERP) qualify for showing habituation of the orienting response (OR). Although response decrements have been found in nearly every ERP component, this question is still of current concern because a true selective response inhibition proving habituation of the OR is still lacking. The question has been tackled using single-trial ERP measurements in classical variants of the repetition/change paradigm commonly used in the traditional OR research on autonomous responses such as the skin conductance response (SCR). Results on 120 adults indicate that at least two endogenous components of the ERP, an anterior slow negative wave and a posterior slow positive wave, meet essential requirements of habituation: like the exemplary OR component, the SCR, both slow waves declined systematically with repeated stimulations and, more than that, recovered in response to fundamental changes. In the same way, an anterior positivity resembling the novelty P3 levelled off systematically with the stimulations, but without showing recovery. Thus, in so far as habituation of the OR is conceptualised as a selective inhibitory central nervous system process which can be assumed to have taken place only if a systematic (usually exponential) response decrement is followed by a recovery, the generalised decrement of the P3 cannot be equated with habituation, whereas the selective response diminution of both slow waves would have to be regarded as typical of habituation.

Keywords: Habituation; Novelty P3; Orienting response; Recovery; SCR; Slow waves

1. Introduction

In an attempt to clarify a serious matter concerning the orienting response (OR) research, the paper deals with the question of whether prominent endogenous waves of the event-related brain potential (ERP), well established and defined by others as novelty P3 and orienting wave components, meet essential requirements to qualify as indicators of the OR. That is to say, it investigates experimentally whether they show the triggering and, particularly, the habituation of the OR. This was done by analysing individual trials of classical variants of the repetition/change paradigm typical of the study of the autonomic nervous system (ANS) OR and by appraising results with reference to an exemplary ANS component of the OR, the skin conductance response (SCR).

The OR is predominantly conceptualised as a fundamental biological mechanism responding to novel, unexpected or unpredictable stimuli (Sokolov, 1963). It essentially functions as a "What-is-it?" detector (Pavlov, 1927, p. 12) involuntarily capturing attention (Graham and Hackley, 1991) and improving the perception of stimuli (Pavlov, 1927; Sokolov, 1963). In the broader sense, OR is a term for quite a number of organismic changes including inhibition of ongoing activity, autonomic changes, postural adjustments and an increase in sensitivity of sensory organs (Lynn, 1966). In any case, as soon as the OR releasing stimuli lose their novelty or unpredictability, the OR vanishes as a result of habituation. Habituation is therefore its hallmark or distinctive feature and any indicator of the OR must, accordingly, reflect this process, which is

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supposed to happen automatically as a result of repeated stimulations. It is generally agreed that the response inhibition process referred to as habituation is distinguishable from other inhibition processes by its selective nature. If we repeatedly present a subject with a stimulus, the magnitude of the OR will decrease exponentially up to some asymptotic base level (Barry, 1996, p. 470). But even a slightly different stimulus will bring about a recovery of the OR. Strictly speaking, habituation of the OR, conceptualised as a selective and inhibitory central nervous system (CNS) process (e.g., Sokolov, 1960, 1963; Voronin and Sokolov, 1960), can thus be assumed to have taken place only if a systematic (i.e., usually exponential) response decrement with stimulus repetition (labelled: response habituation) is followed by its recovery in response to a distinguishable stimulus deviance (labelled: response recovery). A generalised decremental process such as fatigue (for other examples, cf. Stephenson and Siddle, 1983, p. 183) is incommensurate with this recovery. Furthermore, Sokolov (1963, p. 286) demonstrated that the selective character or filter function of habituation is not merely a result of simple local changes in analyser excitability and he introduced the concept of the "neuronal model of the stimulus" to explain the selective nature of habituation.

By neuronal model, Sokolov (1963, p. 286) meant "a certain cell system whereby the information is stored concerning the properties of a stimulus". This information includes not only simple physical and temporal characteristics of past stimulation but also complex characteristics such as the sequence and patterning of stimuli (cf. pp. 286–289). According to Sokolov's (1960) OR theory (Voronin and Sokolov, 1960), a mismatch between stimulus and model triggers the OR. Habituation, on the other hand, is the result of active inhibition of the OR by the neuronal model of the stimulus. Each occurrence of a redundant event increases the precision of the model and, with increasing precision, this (selective) inhibition is enhanced, while the occurrence of a discordant stimulus will again trigger an OR. The greater the stimulus change, i.e., the difference between the new stimulus and the old stimuli, the larger the recovery. If only one and the same stimulus is presented in a habituation procedure, then a recovery of the response may be observed already when the new stimulus differs from the standard one by a value approximating the difference threshold. If non-redundant events are applied, habituation proceeds in a generalised manner and covers a range of related stimuli (Voronin and Sokolov, 1960, p. 338). The degree of this "habituation generalisation" increases with the repetition of presentations of various stimuli. Response recovery by a novel change is thus said to be the combined consequence of incomplete habituation generalisation and of neuronal mismatch. The concept of the neuronal model is, according to Sokolov (1963), closely connected with the "extrapolating properties of the nervous system". The nervous system thus "elaborates a forecast of future stimuli as a result of repeated stimulation and compares these forecasts with the stimuli actually in operation" (Sokolov, 1963, p. 287). When there is a lack of coincidence between an actual event and its forecast, an OR develops. The extrapolatory nature of the modelling process was emphasised also in Sokolov's (1966, 1969) subsequent work. The neuronal model operative at any particular point in time accordingly represents a contextual forecast rather than simply a template of the stimuli presented up to that point. At any moment, it thus reflects the most probable sequence of future events.

As Sokolov (1963) emphasised in his *unitary* conception of the OR, the effects of repetition and change should appear in all output parameters or components of the OR in a comparable manner. That is to say, for physiological measures to be considered components of Sokolov's single response system evoked by orienting stimuli, they should behave in a uniform manner, showing the same systematic decrement with repeated stimulations followed by a similar recovery in response to a mismatch. It is therefore a commonly held view that these components of the unitary response are interchangeable indices of the OR. Any component of the OR may thus be used as an indicator of its occurrence and habituation.

Consequently, endogenous components of the ERP meet the essential criteria of an indicator or a component of Sokolov's unitary OR, if they initially respond to orienting stimuli but subsequently show habituation, i.e., decline systematically and in a selective fashion with the repetition of these stimuli, and if they do this in the exact same manner as the SCR—the exemplary indicator of the unitary OR. As proof of its selectivity, the reduced component amplitude should recover in response to a fundamental change. As physiological measures vary with their susceptibility to measurement artefacts, a close covariation of measures (the third criterion) is not seldom considered a dispensable restriction imposed on possible indicators of the OR, but there is a clear agreement among experts that these indicators must, nevertheless, necessarily meet the remaining criteria one and two.

Although in the meantime some response decrement has been found in nearly every endogenous component of the ERP, like in the novelty P3 (Knight and Scabini, 1998; Friedman et al., 2001; Sambeth et al., 2004) or in the slow negative wave component of the orienting wave (Rohrbaugh, 1984; Zimmer and Demmel, 2000), a true selective response inhibition proving habituation of the OR is still lacking in the ERP domain. To this gap, in our knowledge about functional CNS components, the rationale of the current study is thus addressed. A positive proof of habituation calls for particular paradigms, which place emphasis, not on the averaging procedure, commonly used in ERP research–it would obscure rapid changes in response amplitude across repeated stimulations–but on single-trial analyses, such as those used in the repetition/change paradigm typical of the traditional OR research on ANS responses like the SCR. As a rule, paradigms

appropriate for investigation of OR habituation use low stimulus presentation frequencies and interstimulus intervals long enough to avoid refractory-like effects and to restrain preparatory activity. Only by means of these paradigms, habituation, conceptualised as a selective CNS process, can be verified unambiguously and thus distinguished from other central nervous or peripheral processes resulting, not in a selective, but in a generalised response diminution.

Taking this into account, the present study tested two independent groups of subjects for habituation using the SCR and non-averaged but corrected and low-pass filtered EEG data as basis for the analyses. One group (*identity group*) was confronted with a typical repetition/change paradigm. It was made up of the repeated verbal presentation of a standard stimulus, a monadic digit, followed, at the test trial (trial seven), by a physical or identity change. The other group (*regularity group*) was tested with a variant thereof (cf. Unger, 1964). It is especially suitable for the study of the postulated extrapolating properties of the modelling process Sokolov (1963, 1966, 1969) held responsible for habituation of the OR. Here subjects received a sequence of six different monadic digits presented verbally in an ascending order. This was followed by a violation of that order to establish an anomaly in a rule-governed sequence, i.e., to evoke a kind of conceptual mismatch or schema discrepancy. Hence, the different numerical series of these two groups were suitable to test two different kinds of change for their effect on the dependent variables. A third independent group of subjects (*random group*) was used as a control group. It received no extra experimental change condition in the test trial, as in the previous six trials neither identity nor regularity were established. The three groups thus varied in the composition of the habituation series, but they did not with respect to the stimulus (another monadic digit) presented at the test trial. Nevertheless, three levels of change in all–a physical identity change, a conceptual change and no extra change–were induced by the conditions applied to the groups in order to test for a *selectivity of response recovery*, which in this case is a recovery to the physical identity change and to the conceptual change but not in response to mere chance (cf. random group).

Thus, according to Sokolov's (1963) OR theory, the activation of a gradually proceeding selective inhibition process leading to the typical behavioural weakening or *response habituation* and–by virtue of a change–to a *response recovery* was expected for the two experimental groups confronted with a repetition/change condition (identity and regularity group) and for *every* dependent variable qualifying as OR indicator candidate. In the random group, response habituation was expected as well, however, not primarily on grounds of well-founded "physical" (as in the identity group) or "cognitive" (as in the regularity group) factors of influence on the formation of a neuronal model, but rather on the basis of invariables this group had in common with the other groups such as the external context. For lack of a remarkable change, recovery must however be absent in the responses of the random group. Beyond that, due to presentations of various stimuli, a slight weakening of the selectivity of the habituation process, i.e., habituation generalisation, might be expected to occur both in the random and in the regularity group. With respect to the size or *rate of response habituation*, no clear prediction can be derived from the literature (cf., e.g., Zimny et al., 1969). While it might be expected from Sokolov's OR theory (1963) that the rate of habituation would be greatest for a series of identical stimuli, next greatest for stimuli presented in serial order and slowest for stimuli presented in random order, Zimny et al. (1969) actually found no differential effects of these three conditions on the amount of SCR habituation. Ex post it is a bold venture to reconcile these findings with the predictions derived from the theory, even if habituation should eventually relate to the elaboration of a forecast about the most probable sequence of future events only. It is, however, absolutely plausible to explain them with pre-experimental experience of such strength that the particular sequence of stimuli did not produce substantial modifications to the neuronal model of numerical sequences (cf. Zimny et al., 1969, p. 171). But it cannot be as simple as that either, as the fact that Zimny et al. (1969) found a change effect or recovery of the SCR only to their test stimulus representing the identity change (but cf. also Yaremko et al., 1970; Yaremko and Keleman, 1972; Zimmer, 2002) calls for an explanation, too. Concerning strength of recovery, one aspect of this explanation could perhaps be the degree of habituation generalisation, which is thought to increase with the repetition of varying stimuli. Nevertheless, both the theory and the last-mentioned findings foreshadow a *response recovery* in the two groups confronted with an experimental change (physical identity change or conceptual change) the magnitude of which should at all events relate to the rate of habituation, i.e., to the strength of the neuronal model at this point. Moreover, a *selectivity of response recovery*, i.e., a recovery to both changes but not in response to mere chance, was expected, too.

2. Methods

2.1. Participants

Participants were 120 (44 male, 76 female) volunteers (mean age: 24 years, median: 23, S.D.: 4.8, range: 19–43 years) who reported no history of hearing loss or hearing difficulties and who were paid (5 € an hour) for their services. They were randomly assigned to the experimental between-subjects conditions, with a roughly balanced distribution of gender being aimed at, however. Most of the participants (90%) were university students. About half the participants (17 male, 46 female) were students of psychology. The conditions did not differ appreciably in age, gender

and social affiliation of the participants. Informed consent was obtained from all participants prior to the start of the experiment.

2.2. Stimuli, apparatus and procedure

As stimuli, soft-spoken digits were digitised and played-back by a commercial PC sound card (AV-510, PCI 8338 chip). They were presented through loudspeakers at an interstimulus interval of constant 15 s in sequences consisting of seven stimulus presentations. Intensity of these natural stimuli was near 60 dB SPL (re: 0.0002 dyn/cm^2) at the headrest of the subject's chair. Three different numerical series were utilized (cf. Section 2.4).

After a 6-min pre-experimental rest period, participants were truthfully informed (cf. Zimny et al., 1969) that a sequence of digits would be acoustically presented in a little while (about 2 min later) and that they should relax without using common relaxation techniques. In addition, they were given an easy task. The task was given in order to make sure that the participants take notice of the stimulus sequences (cf. Section 2.4). They were further asked to avoid excessive movement and to look towards a fixation spot in front of them located directly at the horizontal line of vision. In order to ensure that physiological measurements were not contaminated by movement artefacts, yawning or nodding, the participants were monitored by a hidden camera.

2.3. Physiological recording and treatment of raw data

A unipolar electroencephalogram (EEG) was recorded (at 250 Hz, gain: 10,000, time constant: 30 s, upper cut-off frequency: 30 Hz) from frontal (Fz), central (Cz) and parietal (Pz) scalp sites, according to the international 10–20 electrode system, using a commercial tool kit of Falk Minow Services (based in Munich, Germany) consisting of an electrolyte (abralyt light, purchase order number V18), sintered Ag/AgCl standard cup electrodes and an electrode cap system (easy-cap). Reference was measured from linked earlobes with sintered Ag/AgCl electrode clips and the EEG electrolyte. In order to control for ocular artifacts in the EEG, the horizontal and the vertical electrooculogram was recorded using sintered Ag/AgCl electrodes and a commercial electrode gel. Horizontal eye movements were recorded from the skin surface adjacent to the outer canthus of each eye, eye blinks and vertical eye movements at the superior and inferior orbital ridges, directly above and below the subject's right pupil. Electrode impedances were kept below 5000 Ω at all loci and the differences of impedances of homologous sites were usually within 500 Ω. The subject was grounded at the position AFz.

EEG raw data were corrected off-line by application of the regression method suggested by Gratton et al. (1983). Subsequently, these corrected data were additionally low-pass filtered by means of a fast Fourier transform method (cut-off frequency: 8 Hz).

Recording of electrodermal activity was accomplished using sintered Ag/AgCl electrodes (1 cm in diameter) filled with 0.05 M NaCl electrolyte. The electrodes were placed on the thenar and hypothenar eminences of the subject's left hand using electrode adhesive collars. Skin conductance (SC) was detected by a constant voltage (0.5 V) SC coupler (for details, cf. Zimmer and Demmel, 2000). Resolution of SC data was 0.01 μS.

The recording took place in a sound-attenuated, electrically shielded, air-conditioned and dimly illuminated IAC chamber (Type 3277) with subjects seated in a semi-reclining chair. Air-conditioning maintained a constant room temperature of 23 °C and a relative humidity of atmosphere of around 40%.

2.4. Experimental manipulations

Presentation of the stimuli followed a between-subjects design consisting of three acoustically presented numerical series. Series 1 was a typical repetition/change sequence build up by the sextuple presentation of a single stimulus (digit 1, *identity group*) followed by an acoustically deviant stimulus (digit 8). Thus, in order of presentation, the digits 1, 1, 1, 1, 1, 1 and 8 established series 1. Series 2 was build by the digits 1, 2, 3, 4, 5, 6 and 8, presented in this specified order, i.e., up to digit 6 it was an orderly ascending sequence (*regularity group*) followed by the out-of-sequence digit 8. The digits 9, 2, 4, 5, 3, 6 and 8 constituted series 3, i.e., a random sequence (*random group*). All series were identical with regard to trial 7. However, in case of series 2, the digit on trial 7 followed a changed but still ascending order, whereas in case of series 1 it terminated repetition and in case of series 3 it was merely part of a random sequence.

Accordingly, the trials 1–6 were defined as the habituation trials or as the levels of the repeated measures variable habituation trial, whereas trial 7 was suitable as a test or, in two cases (in the identity and the regularity group), as a recovery trial. These trials were thus utilized to look for the criteria of a true selective response inhibition proving habituation of the OR, response habituation (cf. Section 3.2) and response recovery (cf. Section 3.3), as a function of the specified between-subjects factors order (levels: *identity*, *regularity*, *random*) and change (levels: *physical identity change*, *conceptual change*, *no extra change*) as they were implemented by presentation of the three numerical series differing with regard to the composition of the habituation trials.

The task, given to make sure that the participants take notice of the stimulus sequences, was suggested by grouping factor task instruction. One half of each group was instructed to listen to the numerical series and silently count the number of occurrences of digits greater than 9 in order to report it at the end of the series. Essentially, these digits never occurred and thus the instruction resulted in a passive

attend procedure. The other half was instructed to listen to the numerical series and silently count the number of occurrences of digits smaller than 10, in order to report it at the end of the series. Essentially, every digit presentation had to be counted and thus the instruction resulted in an active attend procedure.

2.5. Dependent variables

The dependent variables of the CNS activity were the amplitudes of promising endogenous ERP components measured as average event-related voltage activity from defined post-stimulus epochs with the average activity of the last second of the pre-event EEG trace serving as baseline. The time slots used for quantification of ERP components were: 320–400 ms for the mid-line *P3*, 500–580 ms for the frontal *SNW1* and parietal *SPW*, 600–2000 ms for the frontal and fronto-central *SNW2*, and 600–1000 ms for a spatial and temporal more localised SNW2 (A/Ncz/800, according to Courchesne et al., 1984; cf. also Zimmer, 2002; below named "transient vertex SNW2" or $tSNW2_c$). The abbreviations SNW1, SPW and SNW2 go back to Rohrbaugh (1984, pp. 356–357). They denote a frontal negative and parietal positive slow wave (SNW1 and SPW, respectively), which is, in each case, followed by yet another slow wave, a uniform negative wave which tends to be predominant at frontal and central sites and is labelled slow negative wave 2 (SNW2). Together, these slow waves constitute a wave which was formerly labelled "orienting wave" (Loveless and Sanford, 1974a,b). The utilized time slots are visualised in Fig. 1 as bold type lines. In giving prominence to waveform features (latency, polarity, shape) only, this figure is merely a preliminary description of the ERP components dealt with. In later sections (above all Section 3.1), they will be further characterized by means of two additional sources of variance—spatial (topographical patterns) and condition (experimental effects). It should be noted that the present study does not pursue the aim of detecting and defining new components of the ERP. Quite to the contrary, it is solely concerned with the question of whether prominent ERP waves or deflections, which have been well established and defined by others as components of the ERP, and were measured in this study by the traditional method of taking their amplitude in approved latency windows, meet essential requirements of OR indicator.

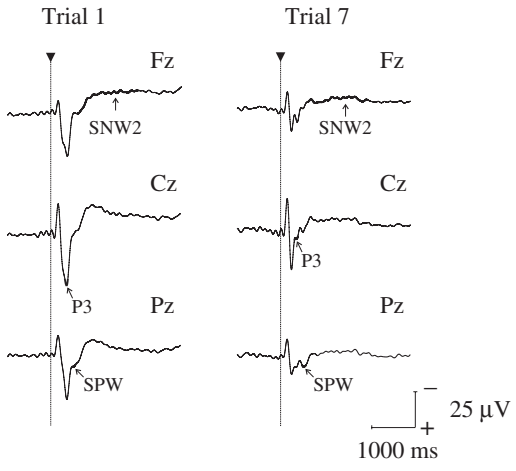

Fig. 1. Time slots of the extracted and analysed auditory ERP components visualised on averaged mid-line records of two trials (the first trial of the habituation series and the test or selective recovery trial) as bold type lines. The ERPs depicted are the result of an averaging across all subjects. Arrows and vertical lines mark the point in time of stimulus onset. Negativity is upward.

Dependent variable of the ANS activity was the amplitude of the *SCR*, i.e., the difference between the minimum (occurring in a latency window of 1.0 s to 3.0 s post-stimulus) and the first maximum of the evoked SC increment. In the following, this exemplary component of the OR will be treated as a standard of comparison for the appraisal of the results on the ERP components.

2.6. Data analysis and statistical evaluation

Response habituation was analysed on the basis of the trials 1–6. *Response recovery* was measured as the difference between the response to the test trial (trial 7) and the averaged response to the second half of the habituations trials (trials 4–6). *Selectivity of response recovery* would then result in an effect of the numerical series (the experimental groups) on the response recovery measure, that is, it would consist of a recovery in series 1 (to the physical identity change) and 2 (to the conceptual change) but not in series 3 (to mere chance).

With respect to response habituation, the repeated measures effect over the trials 1–6 was additionally decomposed into its linear and its quadratic orthogonal polynomial components. This restriction to only two major trends is justified by theoretical assumptions linking the habituation process to a negative exponential function (cf., e.g., Vossel and Zimmer, 1989, p. 142). Accordingly, a significant repeated measures effect, due to a diminution of response strength, together with a significant linear as well as quadratic trend across the trials, may be accepted as indication of an exponential function typical of habituation.

When statistically significant effects were obtained for the repeated measures factor (habituation trial), the probability of error (P) was readjusted using the Greenhouse–Geisser epsilon correction procedure; in these cases, the original (uncorrected) degrees of freedom are still presented, but along with the respective epsilon value (ϵ) and the significance level reached by the readjusted P value. P values smaller than .05 were considered statistically significant.

3. Results[1]

3.1. Description of ERP components

The observed *auditory P3* had an anterior scalp distribution and was strongest at the vertex (cf. Fig. 1). The maximum amplitude of its average waveform peaked at about 340–380 ms, which is typical of an auditory P3 to orienting stimuli. Significant differences on the first trial between the electrode sites Fz, Cz and Pz (F[2,228]=15.34, P<.01, ϵ=.845) gave proof of its observable anteriorly oriented distribution. This scalp topography is consistent with the scalp focus of a P3, which has been labelled "novels P3" or "novelty P3" (Courchesne et al., 1975; Fabiani and Friedman, 1995; Friedman et al., 2001; Grillon et al., 1990).[2]

In addition, as would be expected from a *novelty P3* (cf. Friedman et al., 2001, p. 362) levelling off with a reduction of stimulus novelty, i.e., with repeated stimulations, the maximum size of the P3 moved, across the habituation trials, from a central or centro-frontal to a parietal scalp focus (cf. already Courchesne et al., 1975, p. 140). This statistically confirmed interaction (F[10,1140]=6.41, P<.01, ϵ=.715) of the mid-sagittal (Fz, Cz, Pz) electrode sites with the habituation trials is shown in Fig. 2. It indicates that the reduction in P3 amplitude from the first to the sixth stimulus event was more marked for an anterior than for a posterior part of the P3.

As could be expected from findings of Courchesne et al. (1981, 1984), an early part of the SNW2 (latency window: 600–1000 ms post-stimulus), a transient SNW2 (tSNW2), was, like the P3, strongest at the vertex. A significant main effect on the first trial, brought out by a comparison of the electrode sites Fz, Cz and Pz (F[2,228]=27.46, P<.01, ϵ=.805), indicated this scalp topography phenomenon statistically. The maximum size of this chiefly centrally pronounced slow negative wave was in the temporal window Courchesne et al. (1984) used for determining the vertex "A/Ncz/800". Below (Sections 3.2–3.3), it will be labelled $tSNW2_c$ and any further analysis of this slow wave will therefore–and for an improved comparability with the study of Zimmer (2002)–be restricted to its dominant site of appearance, the vertex. By comparison to this temporary SNW, the classical and rather long-lasting *SNW2* evinced, as could be expected (cf., e.g., Zimmer and Demmel, 2000), a high profile at the frontal as well as at the central site (see Fig. 1), which clearly characterized it as typical late component of the orienting wave (Rohrbaugh, 1984). Correspondingly, it showed on the first trial, for example, an effect of the electrode sites (F[2,228]=38.72, P<.01, ϵ=.859).

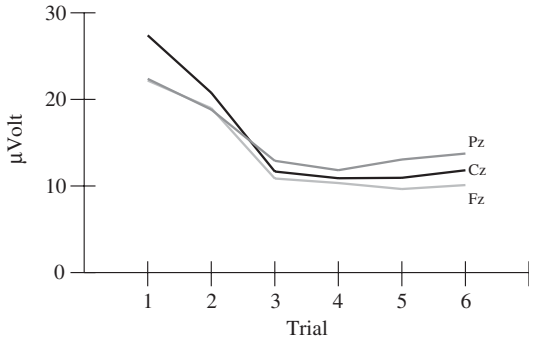

Fig. 2. Decline of the average P3 amplitude across the six habituation trials, depicted as a function of the electrode sites (Fz, Cz, Pz).

In addition, as could be expected from its scalp topography in response to the first stimulus presentation, the *SNW2* amplitude declined (in absolute values) from the first habituation trial (Fz: −10.11 μV, Cz: −12.07 μV, Pz: −4.65 μV) to the average of the remaining ones (Fz: −1.85 μV, Cz: −3.00 μV, Pz: −0.86 μV) at all electrode sites but particularly at the afore-dominated scalp sites. Its fronto-central scalp focus nevertheless survived. Statistically, this topographical phenomenon appeared as a significant interaction of the electrode sites with the just mentioned repeated measures factor (F[2,228]=18.38, P<.01, ϵ=.886) or with the original repeated measures factor habituation trial (F[10,1140]=5.55, P<.01, ϵ=.738). The scalp distribution of the *tSNW2*, showing initially (to the first stimulus) a noticeable central dominance (Fz: −5.94 μV, Cz: −11.35 μV, Pz: −4.16 μV), also changed significantly (F[2,228]=10.55, P<.01, ϵ=.827) from the first trial to the average of the remaining ones (Fz: −1.41 μV, Cz: −2.98 μV, Pz: +0.18 μV; averaged over these latter trials) and across the single habituation trials (F[10,1140]=6.03, P<.01, ϵ=.729).

With regard to the early component of the orienting wave, neither Fig. 1 nor any further information on the course of the curve provided evidence of a substantial frontal *SNW1*. But its positive counterpart (cf. Rohr-

[1] All statistical analyses were carried out with the additional grouping factor task instruction (cf. Section 2.4), but results did not depend noticeably on this variable.

[2] Although Courchesne et al. (1975) claimed that their *novelty P3* was different from the *P3a* reported by Squires et al. (1975), some researchers have labelled the P3 elicited by novel stimuli as P3a (Katayama and Polich, 1998, p. 24). After application of factor analysis and multiple regression analysis to the two sets of ERP waveforms, Simons et al. (2001) suggest that these components are very similar, potentially the same and "shift the burden of proof back to those who wish to continue a case for distinction" (p. 216). In the present study, this case must consequently not be made and the discovered type of P3 with a vertex or more anterior scalp distribution than a typical target P3 is for the present referred to as *novelty P3*—not only for descriptive simplicity. Particularly, it should be noted that the novelty P3 is not only elicited by highly novel or complex unrecognizable visual (as, e.g., Courchesne et al., 1975, p. 140, originally thought) or acoustic stimuli (e.g., Courchesne et al., 1984; Fabiani and Friedman, 1995) but also by simple, familiar shapes (e.g. Daffner et al., 2000c) and–as used in the present study–by simple and relatively familiar auditory stimuli (e.g., Katayama and Polich, 1998), and that it is observed under both passive and active attention conditions (cf., e.g., Gaeta et al., 2003; Jeon and Polich, 2001; Simons et al., 2001, p. 215; Woods, 1990; Debener et al., 2005).

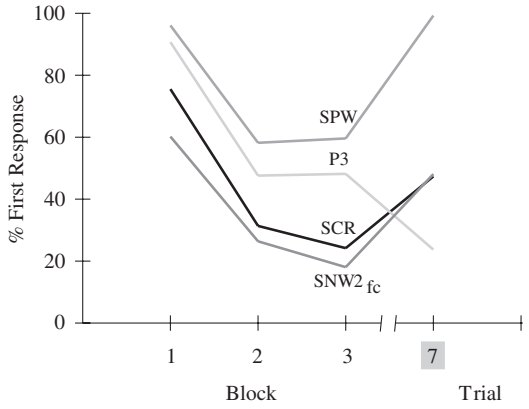

Fig. 3. Exemplary illustration of response habituation and recovery in four dependent variables (SCR, mid-line P3, parietal SPW and fronto-central SNW2). To simplify matters, the course of response habituation is depicted across three blocks of two trials at a time. The marked trial (7) on the abscissa is the test trial. The measures are displayed in relation to their respective first response (as percentage change).

baugh et al., 1978, 1979), the parietal *SPW*, was easily identifiable, particularly in the seventh trial, the test trial, with the aid of its latency, polarity and shape, as well as its typical posterior scalp distribution (cf., e.g., Zimmer and Demmel, 2000).

3.2. Response habituation

As regards *response habituation*, i.e., a systematic (usually exponential) response decrement with repeated stimulation, which must be considered the *first criterion* of habituation as a selective CNS inhibition process, most dependent variables behaved in correspondence with Sokolov's (1963, 1975) OR theory.

A significant repeated measures effect of factor habituation trial appeared in the SCR ($F[5,570]=129.88$, $P<.01$, $\epsilon=.502$), P3 ($F[5,570]=31.45$, $P<.01$, $\epsilon=.830$), SPW ($F[5,570]=2.60$, $P<.05$, $\epsilon=.878$), $SNW2_f$ ($F[5,570]=11.01$, $P<.01$, $\epsilon=.859$), $SNW2_{fc}$ ($F[5,570]=13.41$, $P<.01$, $\epsilon=.859$) and in the $tSNW2_c$ ($F[5,570]=12.63$, $P<.01$, $\epsilon=.834$). It could be traced back to a significant *linear* (SCR: $F[1,114]=191.67$, $P<.01$; P3: $F[1,114]=73.73$, $P<.01$; SPW: $F[1,114]=5.62$, $P<.05$; $SNW2_f$: $F[1,114]=17.75$, $P<.01$; $SNW2_{fc}$: $F[1,114]=24.72$, $P<.01$; $tSNW2_c$: $F[1,114]=21.71$, $P<.01$) and for

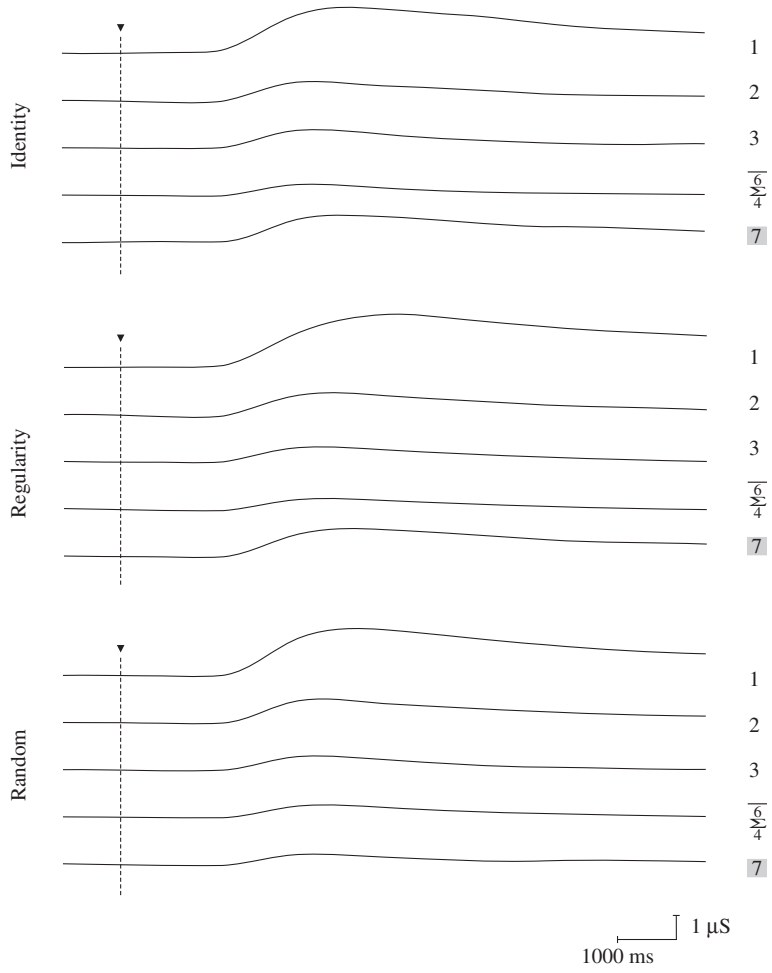

Fig. 4. Event-related electrodermal activity dependent on the groups (identity, regularity, random), the habituation trials 1, 2, 3, 4–6 (average activity), and the test trial (marked 7). Arrows and vertical lines mark the point in time of stimulus onset.

the most part additionally to a *quadratic* trend (SCR: $F[1,114]=134.78$, $P<.01$; P3: $F[1,114]=42.17$, $P<.01$; SPW: $F[1,114]=0.00$, n.s.; $SNW2_f$: $F[1,114]=13.29$, $P<.01$; $SNW2_{fc}$: $F[1,114]=19.42$, $P<.01$; $tSNW2_c$: $F[1,114]=18.07$, $P<.01$) across the trials. These results indicate a systematic decline of response strength across the habituation trials that shares features with a negative exponential function (cf. Fig. 3), with the one exception of the SPW showing also a systematic (cf. linear trend) but not a flawless exponential decline (a significant quadratic trend failed to appear in addition to the significant linear trend). The indices f and c, affixed to the SNW2 and tSNW2, denote the scalp sites Fz and Cz. Note, in the time domain of the frontal SNW1, neither a marked negativity, typical of the SNW1, nor a regular decline of its response strength occurred across the habituation trials. On the contrary, the putative "SNW1" showed a rather artificial (linear) increase across these trials as indicated by a repeated measures effect ($F[5,570]=5.40$, $P<.01$, $\epsilon=.815$) and a linear trend ($F[1,114]=12.89$, $P<.01$) that essentially could arise from a decreasing influence of the posterior SPW on the frontal site. Dependent on the groups, the response habituation of the event-related electrodermal activity and of the event-related brain potential is shown in Figs. 4 and 5, respectively. Above changes across the habituation trials did not, however, interact significantly with the groups.

3.3. Response recovery

As regards the *second criterion* of habituation as a selective CNS inhibition process, i.e., the selectivity of response habituation indicated by *response recovery* to a distinguishable change in stimulation, recovery effects were found in the amplitude of the SCR ($F[1,114]=48.21$, $P<.01$) as well as in the amplitudes of the SPW ($F[1,114]=4.68$, $P<.05$), $SNW2_f$ ($F[1,114]=9.91$, $P<.01$), $SNW2_{fc}$

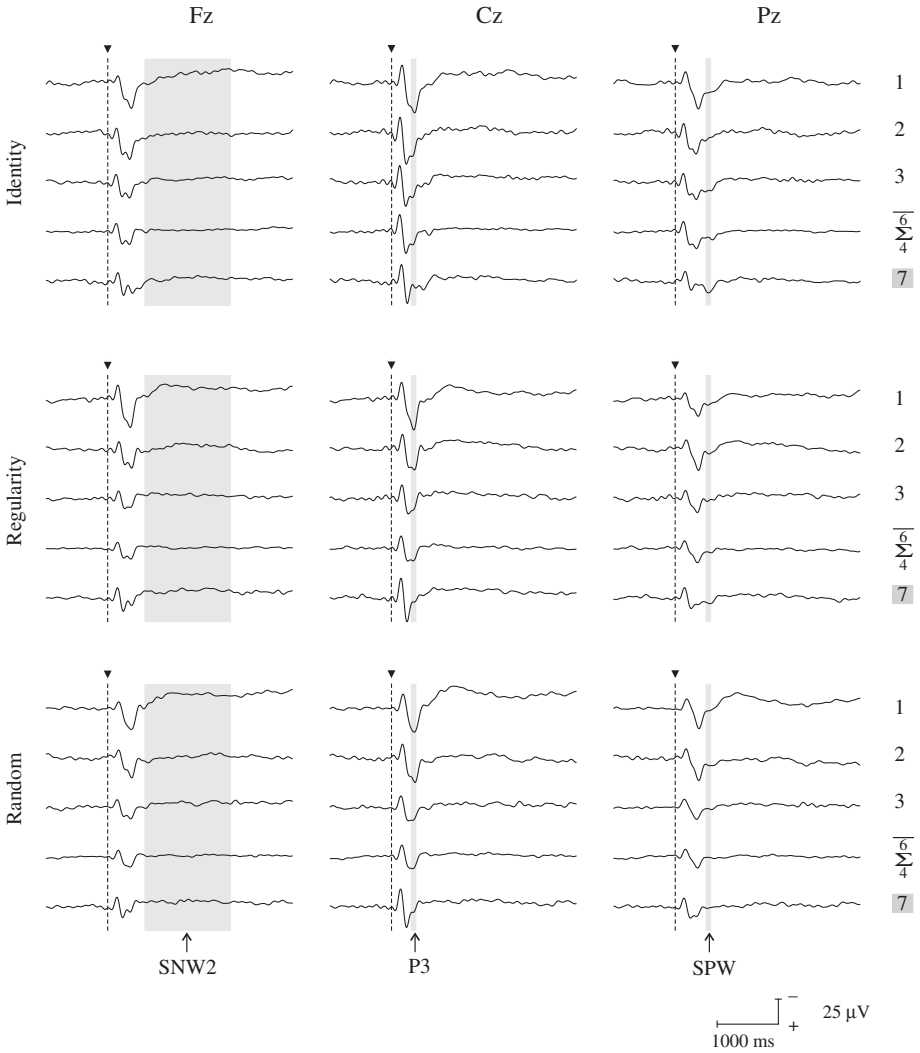

Fig. 5. Event-related brain potential dependent on the groups (identity, regularity, random), the electrode sites (Fz, Cz, Pz), the habituation trials 1, 2, 3, 4–6 (average potential), and the test trial (7). Arrows and vertical lines mark the point in time of stimulus onset. The time slots used for quantification of the three endogenous ERP components (labelled as: P3, SPW and SNW2) are visualised on selected electrode sites as marked area. Negativity is upward.

(F[1,114]=8.09, P<.01) and tSNW2$_c$ (F[1,114]=4.80, P<.05). Not only no recovery but the opposite effect, a further decline of the response amplitude, was found for the P3 (F[1,114]=19.97, P<.01) and, non-significantly, for the putative SNW1 (F[1,114]=2.08, P=.15). Figs. 3–5 picture the effects.[3] Recovery effects were almost independent of their statistical evaluation. When, different from above and also from Fig. 3, not all but only the two experimental change conditions were recruited for analysis of recovery, the effects were as follows: SCR (F[1,76]=64.97, P<.01), SPW (F[1,76]=4.49, P<.05), SNW2$_f$ (F[1,76]=6.03, P<.05), SNW2$_{fc}$ (F[1,76]=5.27, P<.05) and tSNW2$_c$ (F[1,76]=3.42, P<.10). Again, no recovery but the opposite effect occurred in the P3 (F[1,76]=15.74, P<.01) and in the putative SNW1 (F[1,76]=4.14, P<.05). In addition, in all variables showing a recovery, the two fundamental changes had no differential effect.

Selectivity of response recovery (cf. also Figs. 4 and 5), which, in the case in point, consists in a response recovery in series 1 (to the physical identity change) and 2 (to the conceptual change) but not in series 3 (to mere chance), proved significant only in the amplitude of the SCR (F[2,114]=15.50, P<.01). On series 1 and 2, the SCR increased (in size: 0.672 μS and 0.719 μS, respectively), whereas on series 3 it slightly decreased (in size: −0.059 μS).

4. Discussion

The present study was undertaken to address the question of whether prominent endogenous components of the ERP qualify for indicating habituation, which is the characteristic or distinctive feature of an OR. The results suggest that at least some of these components show signs of habituation and thus behave like a promising indicator or a component of Sokolov's (1963) unitary OR, while exactly one, presumably a novelty P3 component, clearly underachieves and thus fails the test. However, only one response, the "antique" SCR, fulfils all requirements of an OR indicator without any qualification. Again the SCR turns out to be an exemplary component of the unitary OR. Other than the novelty P3, the SCR and, with certain reservations (see below: selectivity of response recovery), the investigated slow waves (SPW and variations of the SNW2) indicated habituation in the human brain. That is to say, they responded with a systematically diminishing response amplitude to repeated stimulations and, more than that, the underlying inhibitory process–according to Sokolov (1963, 1975) a common inhibitory brain process for the SCR and other OR components–proved to be selective, because this decrement or response habituation was consequently followed by a recovery in response to fundamental changes regarding the information of stimulation. Selectivity of response recovery, on the other hand, that is a recovery to fundamental changes but not in response to mere chance appeared solely in the SCR (see below). In the same way, the novelty P3 levelled off systematically with the stimulations, but then showed definitely no recovery. In so far as habituation of the OR is conceptualised as a selective CNS inhibition process which can be assumed to have taken place solely if a systematical response decrement, particularly an exponential decline, is followed by a recovery, the generalised decrement of the novelty P3 cannot be equated with habituation. Only a recovery unequivocally argues for the assumption that a diminution of response strength, shown in response to stimulus reiterations, is stringently attributable to no factors other than a selective inhibition process. On this account, the above mentioned restraints regarding the functional significance of the systematic diminution found in the amplitudes of the slow waves could, for want of evidence as regards selectivity of their recovery, also sound a note of caution.

Contrary to expectations as well as to findings in the SCR, the recovery of the ERP slow wave components turned out not to be selective, i.e., the slow waves did not respond more strongly to the experimentally implemented changes, physical identity change and conceptual change, than to the random change at the end of a sequence of changes. Therefore, it cannot be definitively ruled out that the test stimulus–for incomprehensible reasons–brought about a recovery anyway. Such an argumentation, however, is in conflict with the selective recovery of the SCR, simply because the different kinds of stimulus sequences either allow for a selective recovery to the test stimulus or not. So, either the slow waves generally recover to something other than the experimentally implemented changes, while the SCR does solely reflect these changes, or the partly unexpected finding is to due to nothing but errors of measurement. Given the verisimilitude that the SCR is not a quarter as susceptible to measurement artefacts as single-trial ERP components, it would–on second thoughts about the unexpected data from the relative small-sized control group that merely consisted of 40 people–be unjustified to conclude that the slow waves do on no account reflect habituation, especially as their considerable decline with the repeated stimulations as well as their reappearance to the experimental changes was exemplary, even if selectivity of recovery could not be proven (cf. with Fig. 5). However, a variable that does not reliably represent all the essential characteristics of inferred processes is but of limited use as an indicator of them. Therefore, some reservation might at this point still be in order. Not rejecting a hypothesis cannot, as a matter of course, be equated with considering it true.

[3] Fig. 5 moreover shows, particularly on the test trial and in any case preceding the P3, a conspicuous negative-going potential of an anterior scalp topography, which Polich (1985) regarded as a N2 component reflecting "violations of complex similarities and dissimilarities" (p. 363). Due to the further P3 diminution on the test trial, it may here alternatively be regarded as a pure "withdrawal from P2 to baseline". Above all, a missing selectivity to the change conditions questions its interpretation with reference to Polich.

Among the two experimental change conditions, a differentiable recovery was not found, i.e., the amount of recovery was independent of the kind of change (physical identity change or conceptual change). This finding is–ex post facto–no surprise, because it is in line with the absence of a difference in the rate of habituation. It empirically contravenes, in one respect, the results of Zimny et al. (1969), who found a recovery of the SCR only to their test stimulus representing an identity change, but it agrees, on the other hand, with the results of Yaremko et al. (1970), Yaremko and Keleman (1972) and Zimmer (2002), who found the SCR quite sensitive to a conceptual change. Accordingly, the overall pattern of results still appears to be most parsimoniously explained with the aid of Sokolov's (1963) OR theory. A comparable response habituation among the experimental groups would then index the establishment of an abstract rule—such that participants could anticipate the stimuli of the numerical series correctly as belonging to an identical, a regular or a random series. A response recovery would, accordingly, index the violation of the respective rule. The pattern of results is thus compatible with the extrapolatory nature of the modelling process as emphasised in Sokolov's (1963, 1966, 1969) neuronal model conception. The neuronal model operative at any particular point in time consequently represents a contextual forecast rather than simply a template of the stimuli presented up to that point. Nonetheless, with respect to the response behaviour shown in response to the different kinds of change, not even the exemplary indicator of the OR, the SCR, reflected another assumption that could legitimately be drawn from Sokolov's theory: that a differing response recovery is the result of the different degree of habituation generalisation. Thus, either his theory contains misleading statements and generalisation should for incomprehensible reasons be regarded negligible, or even the SCR encounters difficulties in showing these differences clearly enough. Provided that the SCR reflected all OR phenomena very well, the response habituation arising with equal strength among the different experimental groups of the current study could, a posteriori, be reduced to similarities regarding the gradual formation of a comparable neuronal model. This model would take into consideration not only the known stimulus category and the features of the familiar stimuli including their initially uncertain time of appearance, but also the specific kind of already well-known numerical series, as well as their identical external context. The independence of response recovery from the kind of change (physical identity change, conceptual change), on the other hand, could be due to a non-existent or at least trifling generalisation of habituation and, particularly, to a comparable forecast error or neuronal mismatch. After careful consideration of results, the contribution of habituation generalisation to response recovery must have been negligible; otherwise, at least weak effects of the differing series would have had to crop up, since the other actually unknown variables, such as the external context of the stimuli, the time of their appearance, as well as the features of the female voice with which the numerals were presented, remained unchanged within the series and therefore probably exerted their equalising influence on the habituation of the OR.

An early, frontal SNW1 component of the orienting wave did not crop up or was completely superposed by an irradiation of the posterior SPW. This current finding is in agreement with data of Zimmer (2002) and might be due to the type of auditory stimulation used, i.e., natural speech stimuli. For others (e.g., Rohrbaugh et al., 1978, 1979; Spencer et al., 2001; Zimmer and Demmel, 2000) clearly have found a SNW1 to acoustic stimulation by single (unpaired) tone pips. In any case, the present finding may just be another piece of evidence for the independent variation of the anterior negative and posterior positive aspects of the early part of the orienting wave (cf. Friedman, 1984; Loveless et al., 1987; Rohrbaugh and Gaillard, 1983). It should, however, be noted that, instead of addressing this issue at stake, a single longer-latency posterior positivity, in the latency range of the wave here labelled–under the influence of Rohrbaugh (1984)–early posterior part of the orienting wave or SPW, is more often than not defined as $P3_2$ (e.g., Cycowicz and Friedman, 1998) or P3b (recently, e.g., by Debener et al., 2005 or Gaeta et al., 2003). Others (e.g., Ruchkin and Sutton, 1983), in turn, distinguish the SPW or "P4" from an earlier P3b with approximately the same latency as the novelty P3. In so far as it responded to the change conditions, this late positivity is in all probability a component or part of the orienting response and thus connected with processes related to novelty detection and evaluation. Assuming that the conceptual change as well as the identity change of the current study can both be regarded as examples of violations in rule-governed sequences, such a change sensitive late posterior positivity could, according to Núñez-Peña and Honrubia-Serrano (2004), belong to a "family" of late positive waves which are thought to index "detection for any anomaly in rule-governed sequences" (p. 130). In keeping with the concept of ERP components proposed by Donchin et al. (1978), it is important to emphasize that this late novelty wave, i.e., the SPW, does not correspond however with the novelty P3 but is yet another ERP component. For, as found in the current study, these two waves differ considerably with respect to their morphology, scalp distribution and sensitivity to experimental manipulations.

Unlike other ERP components, like the SNW2 and the SPW (cf. already Loveless, 1979, 1983), the presumable novelty P3 definitely cannot act as an adequate indicator for the entire novelty response referred to as unitary OR. But to what did this P3 respond in the present case, if it were not the typical novelty antecedents of an OR? The very fact that a distinct positive deflection, typical of the novelty P3, appeared particularly in response to the first stimulus of each series (cf. also Sambeth et al., 2004), at least argues for the involvement of this P3 in *an involuntary interrupt*

procedure being inherent in the function of the OR in our real world (cf., e.g., Lynn, 1966; Pavlov, 1927; Waters et al., 1977). Whether this interruption is synonymous with the involuntary capture of attention attributed to orienting (Kahneman, 1973) and to a frontal aspect of the novelty P3 (Friedman et al., 2001) remains to be seen. If it were so, the present study would make a good point of showing that the involuntary capture of attention is not necessarily elicited by contextual novelty or surprising events (out of context stimuli), as would be expected from contemporary theories of orienting and attention (cf., e.g., Graham and Hackley, 1991), but only by events–even relatively simple and familiar stimuli like the used numerals–that effectively call for a transitory interruption of concurrent operations or mental processes and thus give rise to a passively initiated process of unspecific "re-orienting" of attention to input. Otherwise, it would be difficult to understand, why a novelty P3 was triggered by the first stimulus of the series, which terminated the boring and fatiguing rest, and not by the test trial stimulus (belonging to the task and attended to anyway, due to the instruction), which actually involved uncovering a forecast error or neuronal mismatch. That is to say, it seems that a passive interruption associated with a passively initiated re-orienting or altering of behavioural modes, but not novelty per se, results in a novelty P3. Consequently, even if novelty detection should by any possibility participate in elicitation of a novelty P3, an emergency or, respectively, the lack of coincidence between an actual event and a forecast built up in the course of repeated stimulation by a system reflecting the most probable sequence of future events (Sokolov, 1963, p. 287) is definitely not the crucial event that can account for the novelty P3. In other words, the novelty P3 does not reflect the detection of a deviant event per se. Moreover, this even seems to be independent of the kind of deviation. In any case, in the present study, neither a physical nor a conceptual change resulted in a novelty P3. In imitation of Posner and Peterson (1990), this P3 could rather, at least in the present case, originate from neural sources related to an alerting and, above all, initial attention allocation.

According to a conception put forward by Lindsley (1982), both functions, the interruption as well as the re-orienting, may mainly stem from one system, *a brain-stem-hypothalamic-hippocampal system*. It is involved in "orienting responses, arousal, alerting and attentive states, scanning for information, investigatory behaviors, motivation, discrimination and information registry, learning and memory consolidation, voluntary behaviors and response inhibition" (Lindsley, 1982, p. 365). But it appears to be mainly a neuromodulatory effect of this system that is instrumental in the kind of re-orienting of attention mentioned above (cf. also Posner and Peterson, 1990, pp. 37–38). This neuromodulation has its origin in the activation of the pontine nucleus locus coeruleus (LC). It is a fact that this nucleus is not only involved (cf. Pineda, 1995, pp. 143–145) in, for example, orienting, exploratory activity and the switching of attention, but that it is, most notably, instrumental in provoking the above mentioned re-orienting of attention to input (Foote and Morrison, 1987, p. 74). The LC even appears to play a significant role in the electrogenesis and modulation of P3-like events by changing the physiological context in which novel and relevant events are evaluated and processed (Pineda, 1995, p. 149; Pineda et al., 1989). The nature of this re-orienting and its promotion by the LC has been accurately described by Foote and Morrison (1987): "the function of LC could best be described as altering behavioral modes from internally oriented and generated states, such as sleep, grooming, and food consumption, to an externally oriented mode that involves active matching of appropriate behaviors with novel, stressful, or informative stimuli" (p. 74; cf. also Foote et al., 1991). It is obvious that this kind of re-orienting should accompany a stimulus bringing a boring and fatiguing rest abruptly to an end. Consequently, the involuntary interruption and re-orienting are conceptualised as being *not* dependent on a high level of general or unspecific activation, that is to say, their elicitation need not rely on an intensified vigilance and on an active involvement of attention in a sensory discrimination task, as might be the case with a distraction from the task and the elicitation of a concomitant anterior P3 (cf. Comerchero and Polich, 1998, 1999; Goldstein et al., 2002; Katayama and Polich, 1998; Schröger et al., 2000). Quite to the contrary, low vigilance levels even seem to promote this interruption and re-orienting.

Moreover, the above conception of an unspecific re-orienting to input (or in a more common language: the shift of attention to input) is different from the conception, delineated by Schröger and Wolff (1998), of another type of attention shift, a more controlled and rather specific redirection of attention, that is, a "re-orienting to the task set" (indicated by a RON, a fronto-central "re-orienting negativity" in the 480–550 ms latency range, following the P3 to a distraction). By the way, it is very interesting to see in the present data that–unlike the novelty P3–another late positive wave, the parietal SPW, occurring in the temporal window of the RON, seems to reflect quite strikingly the forecast error postulated by Sokolov (1963) in his neuronal model conception.

The above hypothesis of a brain-stem-hypothalamic-hippocampal system (Lindsley, 1982) being involved, for example, in the involuntary interrupt procedure of the OR and (Knight, 1996)[4] in the generation of both the scalp recorded anterior novelty P3 as well as the sympathetic SCR-OR, must, however, be extended by at least a *prefrontal control* (cf. already Lindsley, 1982, for a

[4] He showed that, in normal controls, the P3 elicited by novel auditory stimuli was accompanied by a SCR, whereas in patients with posterior hippocampal lesions the SCR as well as the frontal aspect of the P3 elicited by these stimuli was dramatically reduced.

reticulo-thalamo-orbitofrontal cortex system, exercising control functions in the regulation of arousal, vigilance, attention and orienting, that is even involved in the amplitude modulation of cortical potentials) in order to account for the missing recovery of the novelty P3 to the present change stimuli. Otherwise, it would be difficult to understand, why it was triggered by the first stimulus of the series and not by those later stimuli which were able to uncover a forecast error or neuronal mismatch. According to Knight and Scabini (1998), regions of the prefrontal cortex, particularly the dorsolateral source for the frontal scalp component of the novelty P3 (cf., e.g., Daffner et al., 2000a; Knight, 1984), form together with the posterior hippocampal source for the anterior novelty P3 (cf., e.g., Knight, 1996) a *prefrontal-hippocampal network* (cf. also Yamaguchi et al., 2004, for a recent proof of this neural system with functional magnetic resonance imaging) that is involved in the detection of perturbations in the environment. These or other related generator connections (cf. Baudena et al., 1995; Dien et al., 2003; Halgren et al., 1995a,b; Ranganath and Rainer, 2003; Yago et al., 2003) during novelty detection seem to be crucial in the determination of whether a novelty P3 needs to be generated or not.

Above it is argued that a change per se is not able to trigger a novelty P3 regardless of its novelty and regardless of a brain activity normally provoking this kind of P3. Only if an interruption of ongoing mental or behavioural activities (cf., e.g., Barceló et al., 2002; De Jong et al., 1990; Pfefferbaum et al., 1985; Pfefferbaum and Ford, 1988; Verleger and Berg, 1991), a distraction (cf., e.g., Escera et al., 1998; Grillon et al., 1990; Schröger, 1996; Schröger et al., 2000; Suwazono et al., 2000) or a shift of attention towards deviation (cf., e.g., Katayama and Polich, 1998; Näätänen, 1990, pp. 210–211; Näätänen et al., 1982; Woods, 1992) is in fact inevitable and will thus be realized, for example, in order to process a stimulus or deviant event properly and with a view to clarification of its behavioural significance, an anterior P3 highly resembling the novelty P3 of the modified (three-stimulus) oddball paradigm will be elicited. One but by far not the only reason for this may be that a preconscious mismatch detector activates an attention-switching mechanism. De Jong et al. (1990), for example, found a centro-frontal P3, which appeared to be directly related to the actual voluntary inhibition of a response, and Barceló et al. (2002) suggested a role of the frontally distributed P3 activity in the executive control of mental set shifting. But not even the detection of a mismatch is automatically answered by an attentional switch occurring with a concomitant P3 (cf., e.g., Lyytinen et al., 1992).

Taken together, the present data and their interpretation with reference to an interruption hypothesis regarding the functional significance of the novelty P3 are not only in general agreement with an attention shift account of the novelty P3 component that does not rely on a simple automatism between a registered mismatch and a shift of attention (cf., e.g., Lyytinen et al., 1992; Näätänen, 1990), but they also support the restoration of the novelty account by the prefrontal control (cf., e.g., Baudena et al., 1995, pp. 261–262; Knight, 1984; Knight and Scabini, 1998) dynamically regulating, for example, the subsequent allocation of attention to novel stimuli (cf. Daffner et al., 1998, 2000a,b, 2003). Daffner et al. (1998) found larger amplitudes of the N2–P3 response in frontal regions to be associated with longer viewing durations on novel (compared to background) stimuli, suggesting that the novelty P3 might reflect the activity of a neural system that serves to link attention to novel events. In addition, frontal lobe injury in humans markedly reduced the amplitude of the novelty P3 and attention to novel stimuli as measured by voluntarily controlled viewing duration (Daffner et al., 2000b, 2003). Damage to the human frontal lobes (particularly to the dorsolateral prefrontal cortex) selectively impaired the natural tendency to seek stimulation from novel and unusual stimuli (Daffner et al., 2000a). Thus, neural processes underlying the novelty P3 appear to regulate the allocation of attention and early exploratory behaviours, and disruption of these frontal lobe processes may prevent "the generation of a signal which indicates that a novel event in the environment requires additional attention due to its potential behavioural significance" (Daffner et al., 2000b, p. 927).

At present it is, however, not yet a settled matter of fact that the novelty P3 is directly linked with the production of an inhibition (cf. De Jong et al., 1990, pp. 177–178; Goldstein et al., 2002, p. 789). It is also possible that an anterior P3 does not reflect the trigger process for an inhibition, but merely the successful accomplishment of the interruption, which is, in case of the novelty P3, related to the initiation of an attention shift to the eliciting stimulus or to an unspecific re-orienting of attention to input. Pfefferbaum et al. (1985), for example, found by means of a Go/No-Go task the No-Go P3 to be certainly more anteriorly distributed than the Go P3 but showed also that an earlier ERP component, a frontal N2, was larger in the ERPs to No-Go than to Go stimuli (cf. also Bokura et al., 2001; Jodo and Kayama, 1992; Kok, 1986). Thus, although this kind of P3 modulation is generally considered to reflect an inhibitory mechanism, these and other related findings (cf., e.g., Falkenstein et al., 1999; Geczy et al., 1999; Pliszka et al., 2000) suggest that the No-Go N2 represents an inhibitory frontal lobe activity. While some authors (e.g., Falkenstein et al., 1999; Kopp et al., 1996) have doubted that a frontal inhibitory process is represented in the No-Go P3, others (Bruin et al., 2001) interpret the P3 Go/No-Go effect, but not the N2 Go/No-Go effect, in terms of inhibition (cf. also Suwazono et al., 2000). Bokura et al. (2001), on the other hand, suggest that the No-Go N2 and the No-Go P3 are likely "linked to different levels of inhibitory control" (p. 2231).

The observed change in scalp distribution of the P3 elicited by the auditory stimuli from anteriorly oriented early in the stimulus sequence to posteriorly focussed at the end of the habituation series is consistent with the results of several papers and with a decomposition of the scalp-

recorded novelty P3 into at least two functionally dissociated sub-components, an anterior aspect that shows reduction with stimulus repetition or time on task, and a posterior aspect that does not change in a consistent manner as subjects gain experience with auditory events (cf. Friedman et al., 2001, pp. 362–365). According to them, the anterior aspect of the novelty P3, i.e., the P3a, stems from a frontal lobe mechanism "that presumably serves to make the event available to consciousness and behavioral control" (p. 359), whereas the posterior aspect is assumed to reflect a rather "late, evaluative, stage of information processing" (p. 364) including, definitely, categorisation of the event and, possibly, "formation of a new representation in semantic memory" (p. 364; see also Barceló et al., 2002, p. 1891). The posterior aspect of the novelty P3 shows, however, features it has in common with the P3b elicited by rare target stimuli, so that it is quite possible that the posterior aspect of the novelty P3 is synonymous with the P3b. Friedman et al. (2001, p. 366) therefore concede the case for a co-activation of a frontally oriented P3a and a posteriorly oriented P3b being both elicited by novel stimuli (cf. also Debener et al., 2005; Gaeta et al., 2003; Goldstein et al., 2002; Spencer et al., 2001). In the present case, in particular, of a novelty P3 being elicited by significant stimuli (signals or attended stimuli), its posterior aspect is as likely as not mingled with or synonymous with the parieto-central target P3 or P3b, even though the observed changes with repetition resemble the topographical amplitude diminution and the rate of reduction of a novelty P3 elicited during an ignore condition more than these of a novelty P3 elicited during an attend condition (cf. Friedman et al., 1998).

In a nutshell, the present study, which was undertaken to address the question of whether endogenous single-trial components of the ERP qualify for showing habituation of the OR, suggests that at least two slow wave components of the ERP, the anterior SNW2[5] and the posterior SPW, meet essential requirements of habituation, while the preceding novelty P3, clearly fails to do so. Hence, the present data favour the assumption that these slow waves are, like the SCR but unlike the novelty P3, adequate components of Sokolov's (1963) unitary OR. The slow waves, however, differed from the SCR with regard to selectivity of recovery. Some uncertainty as to their legitimacy as components of the unitary OR thus remains. Yet, in so far as different signal-to-noise ratios might be responsible for this effect, the overall hypothesis need not be rejected. The novelty P3 presumably also reflects processes subserving orienting behaviour, most notably the transitory interruption of ongoing activity, but it does not adequately indicate the entire response pattern of the OR. According to an alternative interpretation of Sokolov's unitary OR theory put forward by Barry (1984, pp. 131–132), the novelty P3 would then merely be part of the unitary functional system and indicate solely a preliminary process involved in the OR elicitation, while Sokolov's components of the unitary OR, in the present case represented by the SCR and–with above reservation–the two slow waves (SPW and SNW2), would have to be considered indicators of the overall response (cf. also Rohrbaugh, 1984, pp. 326–328). While it is demanded of indicators of the OR that they each reliably reflect its characteristics, above all habituation, in a uniform manner, i.e., march lock-step, the physiological indicators of the different preliminary processes are allowed to fractionate, i.e., reflect differentially experimental manipulations of the processes involved in the OR.

[5] Irrespective of some well-established topographical restrictions and customary variations in the length of the temporal window used to quantify the SNW2 and, hence, also in line with Zimmer (2002).

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