

Processing Spatial and Temporal Discontinuities: Electrophysiological Indicators

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Abstract In a series of four experiments measuring behavioral performance and event-related brain potentials (“ERPs”) in a texture segmentation task, we investigated whether there is evidence that texture stimuli containing a local discontinuity (“D-textures”) are conceptually different from homogeneous stimuli (“H-textures”). Stimuli were presented in an oddball design, with relative frequency of D-textures and H-textures being varied between experiments. It was found that these stimuli are not interchangeable in an oddball situation, as rare D-textures in a context of frequent H-textures give rise to the typical N2b–P3b effects, whereas rare H-textures in a context of frequent D-textures do not. This asymmetry arose because D-textures always elicited enlarged P3b components regardless of their relative frequency. It was concluded that the spatial discontinuity in D-textures adds a feature of “targetness” to these stimuli. Moreover, it was found that a posterior negative-going shift in the N2b latency range (“pN2b”) was mainly modulated by visual stimulus features. This result confirms and extends earlier findings demonstrating the sensitivity of the posterior N2b to physical stimulus characteristics.

Introduction

Discontinuities in the environment are of potential relevance to living organisms. They represent cues for organizing the sensory input into perceptual objects and create the informational basis for categorizing stimuli into different stimulus classes such as figure vs. ground or target vs. nontarget. Our sensory systems are specialized in detecting such discontinuities so that they are often registered even if we do not consciously intend to detect them. For example, in audition we may unintentionally become aware of distortions from isochronous presentation of tones (e. g., Näätänen, 1992; Schröger, 1997). Similarly, in vision object clusters may appear to “pop-out” from their background if they can be grouped on the basis of a common orientation that is different from the orientation of the surrounding elements (e. g., Julesz, 1981; Nothdurft, 1991).

Spatial Discontinuities in Texture Segmentation Tasks

Our ability to detect discontinuities in the environment has been investigated in a large number of studies. One paradigmatic approach to clarifying this issue in vision is research on texture segmentation (for overviews, see, among others, Bergen, 1991; Sagi, 1995). In these studies, participants are typically asked to discriminate displays containing a small region of disparate or discontinuous texture elements embedded in a larger region of homogeneous texture elements (“D-textures”) from displays consisting of homogeneous texture elements only (“H-textures”). The detection of D-textures is said to be – under particular circumstances – effortless or preattentive (Julesz, 1981; Wolfe, 1992), resulting in the apparently spontaneous segmentation of the image in figure and ground. Much of the work in texture segmentation research has been aimed at identifying and characterizing those features of texture stimuli that allow for this spontaneous segmentation.

In a typical task, participants are required to indicate whether a briefly presented texture was completely homogeneous or contained a discontinuity. It is then investigated whether discrimination performance is influenced by varying, for example, texture size, form of texture elements, similarity between background elements and discontinuous elements, presentation duration, and so on. It has been found that only certain combinations of visual features allow for effortless texture segmentation (Nothdurft, 1992, 1993), that discrimination performance improves with practice (Karni & Sagi, 1991, 1993; Shiu & Pashler, 1992; for an overview, see Sagi & Tanne, 1994), but that there is only a limited transfer of learning to new conditions (Karni & Sagi, 1991; Shiu & Pashler, 1992; Ahissar & Hochstein, 1997). Additionally, it has been shown that discrimination performance depends on presentation time as well as on retinal eccentricity of the discontinuity, with some types of textures, it reaches its maximum if discontinuities are presented foveally, and decreases with increasing retinal eccentricity of the discontinuity (Saarinen, Rovamo, & Virsu, 1987; Meinecke, 1989). However, with textures consisting of lines of different orientation, discrimination performance reaches its maximum if discontinuities are presented at an eccentricity of about 4° – 6° of visual angle, and decreases both when retinal eccentricity is decreased and when it is increased, a phenomenon known as “central performance drop” (CPD) (Kehrer, 1987, 1989; Meinecke & Kehrer, 1994; Joffe & Scialfa, 1995; Gurnsey, Pearson, & Day, 1996).

In recent years, a number of studies have examined electrophysiological correlates of texture segmentation, investigating whether different kinds of texture stimuli elicit systematically different patterns of brain activity (e. g., Bach & Meigen, 1992, 1997; Srebro, Oguz, & Purdy, 1994; Regan & He, 1995). However, the more basic question – whether there is a fundamental difference between the neural processes involved in the perception of D-textures and the neural processes involved in the perception of H-textures – has as yet not been addressed directly. Are D-textures and H-textures just perceived as being physically different stimuli, or are they perceived as being different *types* of stimuli? We stated above that our ability to detect discontinuities in the environment is of biological significance because it provides the informational basis for distinguishing between targets (objects that potentially require some sort of response) and nontargets (objects that do not seem to require any response).^{*} Therefore, it seems reasonable

to assume that D-textures are not only *perceptually*, but also *conceptually* different from H-textures. Intuitively, the subjective impression of a D-texture consisting of figure and ground seems to support this assumption. More importantly, experimental evidence has been reported that discontinuous regions in D-textures are processed preferentially compared to homogeneous regions (Scialfa & Joffe, 1995). Consequently, one might speculate that the discontinuity in D-textures is perceived as a “target,” even if there is no explicit instruction to do so. H-textures, on the other hand, might lack this inherent “targetness.” In a series of four experiments, this hypothesis was tested with the measurement of behavioral discrimination performance and the recording of event-related brain potentials (ERPs) in an oddball paradigm.

Temporal Discontinuities in Oddball Tasks

ERP components that are of potential relevance in studying the brain’s differential processing of discontinuous vs. continuous stimuli are the N2b and P3b. These components are known to be modulated by differences in stimulus categorization rather than by differences in physical stimulus attributes. The N2b is a fronto-centrally distributed negative deflection occurring between 200 and 300 ms relative to stimulus onset, and the P3b a broadly distributed component with a parietal maximum that has a peak latency of about 300 to 700 ms relative to stimulus onset. Both components have been successfully measured for studying the processing of discontinuities in serial stimulation (oddball paradigms), and in the context of discrimination between two classes of stimuli (e. g., target vs. nontarget).

The N2b and P3b components are particularly sensitive to stimulus probability in oddball paradigms, where infrequent “deviant” stimuli represent a discontinuity in an otherwise homogeneous train of “standard” stimuli. These disruptions of a serial presentation can be thought of as *discontinuities in the temporal domain*, where a repetitive sequence (“S S S S . . .”) is occasionally interrupted by an infrequent and unexpected event (“S S S D S . . .”). It is usually found that the infrequent stimuli elicit enlarged N2b and P3b components relative to those elicited by frequent stimuli. These effects are further modulated by factors such as stimulus complexity, ease of stimulus discrimination, and attention. Although the functional significance of these components is not yet finally settled, it is widely accepted that they reflect pro-

^{*} Throughout this paper, the terms “target” and “nontarget” are used in the rather loose sense of “response-relevant stimulus” (i. e., a stimulus potentially requiring the execution of a specific kind of action) vs. “response-irrelevant stimulus.” They will not be used in the more specific sense of “embedded discontinuity” vs. “embedding context,” as is often the case in the texture segmentation literature, or in the sense of “rare stimulus” vs. “frequent stimulus” as is often the case in the oddball literature.

cesses concerned with the detection and evaluation of task-relevant information, and that their amplitudes and latencies are often correlated with behavioral performance measures (e. g., Donchin, 1981; Verleger, 1997; for reviews see, e. g., Picton & Hillyard, 1988; Ritter & Ruchkin, 1992). It has been argued above that there is a functional similarity between the processing of temporal (serial) discontinuities and the processing of spatial (texture) discontinuities, as both reflect the identification and differential processing of stimuli that are of particular biological relevance. One thus might speculate that the N2b and P3b components could also be sensitive to *discontinuities in the spatial domain* (e. g., when the discontinuity is characterized as differential orientation of a subset of texture elements in a particular area of the texture).

Outline of the Present Experiments

The present study used a combination of the oddball situation with a texture segmentation task as the basic experimental design. Categorization of D- and H-textures was investigated by varying the relative probability of D- and H-textures. This manipulation enabled us to employ a specific type of preattentively performed categorization – the categorization of frequent and infrequent types of stimuli, which results in a well-known pattern of ERP effects – as a measure for the equivalence or nonequivalence of D- and H-textures; it was reasoned that if D-textures possess an inherent feature of targetness, while H-textures do not, then there should be a clear asymmetry in the ERP effects depending on whether D-textures or H-textures were presented infrequently. More specifically, rare D-textures in a context of frequent H-textures were expected to elicit enlarged N2b and P3b components (“normal” oddball effects), because in this situation, spatial discontinuities and temporal discontinuities will act in parallel. This was tested in Experiment 1. Rare H-textures in a context of frequent D-textures, however, should not elicit normal oddball effects, because this situation creates a conflict between spatial discontinuities and temporal discontinuities. This was tested in the remaining experiments. If under both conditions similar ERP patterns were observed (i. e., enlarged N2b and P3b components elicited by rare stimuli), then this would have to be regarded as indicating that there is no fundamental conceptual difference between D-textures and H-textures.

Texture stimuli either consisted of oblique lines that all had the same orientation (H-textures), or they contained a small array of differently oriented lines in one out of three locations (D-textures). The subjects’ task was, by pressing one out of two response buttons, to indicate whether they had perceived an H-texture or one

of the D-textures. Discontinuities in D-textures were located either foveally or peripherally. It was expected to replicate the typical CPD results, i. e., a discrimination advantage for peripherally presented discontinuities compared with foveally presented discontinuities. Moreover, effects of eccentricity were expected to occur in the ERPs too. The time course and distribution of these ERP effects may yield information about when and where eccentricity modulates texture segmentation.

General Method

Stimuli and Apparatus

Examples of the stimuli employed in the four experiments are depicted in Figure 1. Texture stimuli consisted of a matrix of 31×21 evenly spaced elements, subtending a visual angle of $19^\circ \times 13^\circ$. Elements were oblique lines, tilted 45° to the right or left, respectively. Each line was approximately 0.7° in length and approximately 0.1° in width. Elements subtended a visual angle of about 0.5° vertically and horizontally, and the distance between adjacent elements was approximately 0.6° horizontally and vertically, measured from center to center.

Texture stimuli were either homogeneous (consisting of leftward-tilted or rightward-tilted elements only; “H-textures”), or nonhomogeneous. Non-homogeneous texture stimuli contained an array of 3×3 elements, subtending a visual angle of approximately $1.8^\circ \times 1.8^\circ$, which consisted of lines tilted to the direction opposite to the surrounding elements. This discontinuity appeared either in the center of the texture (“Dc-textures”), or was horizontally displaced to a location 4.5° to the left or right of fixation (measured from the center of the discontinuity: “Dp-textures”). Textures composed of leftward-tilted or rightward-tilted context elements appeared with equal probability throughout the experiment. Masking stimuli were constructed by superimposing a leftward-tilted and a rightward-tilted H-texture upon one another, thus resulting in a 31×21 array of “X”-like elements.

In addition to the texture stimuli, a “ready sign” (a question mark subtending a visual angle of approximately $0.7^\circ \times 0.5^\circ$) and a fixation point (subtending a visual angle of approximately $0.1^\circ \times 0.1^\circ$) were presented. Stimuli were presented on a 17" low-emission computer screen and appeared in black on a light-grey background (luminance about 37 cd/m^2).

Participants

There were eight participants in each experiment. Participants were paid volunteers, none of whom took part in

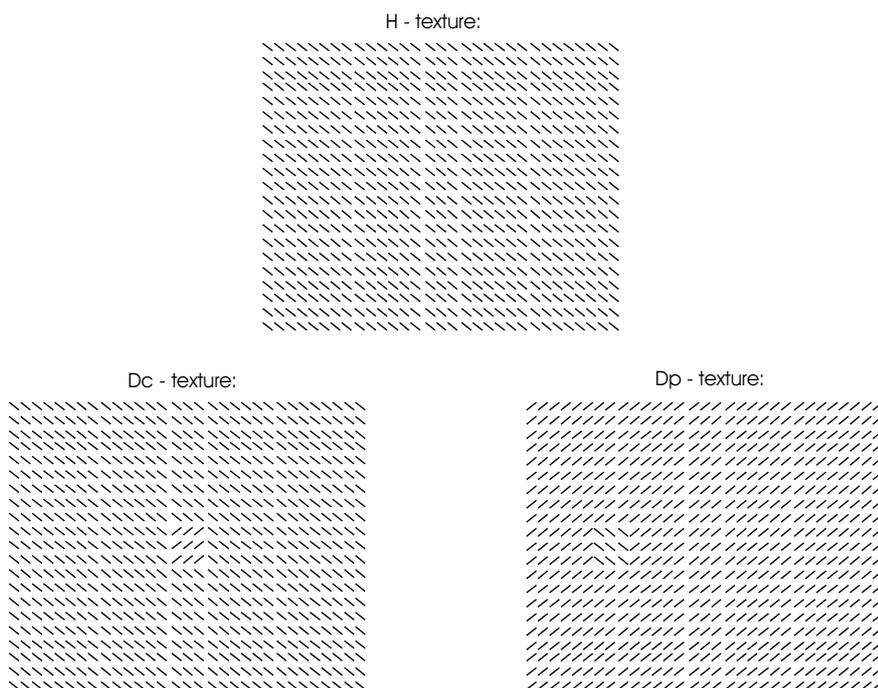


Figure 1 Example of the texture stimuli used in Experiments 1–4. *Top*: Homogeneous texture (H-texture), consisting of lines of one orientation only. *Bottom*: Nonhomogeneous textures (D-textures), containing an array of lines with a different orientation, presented either centrally (Dc-texture, bottom left), or peripherally (Dp-texture, bottom right). Note that in all experiments, textures consisting mainly (D-textures) or exclusively (H-textures) of leftward tilted elements and textures consisting mainly or exclusively of rightward tilted elements appeared with equal probability.

more than two of the experiments. All participants were right-handed and had normal or corrected-to-normal vision.

Procedure

Participants were seated in a comfortable chair in a dimly lit, electrically shielded and sound attenuated chamber, with response buttons under their left and right index fingers. A computer screen was placed 60 cm in front of the participant's eyes, carefully positioned so that the stimuli occurred in the center of the horizontal straight-ahead line of sight.

At the beginning of the experiment, a training block of 48 trials was delivered. Experimental blocks consisted of 100 trials on average (see below for details). Each trial began with the presentation of the ready sign at the center of the screen. Participants initiated the trial whenever they felt ready to do so by pressing both response buttons simultaneously. After this, the ready sign was immediately replaced by the fixation point, which in turn was replaced by a texture stimulus after 700 ms. The relative frequency of H-textures and D-textures was varied between experiments, but each of the three D-textures (left, right, and central discontinuity) was delivered with equal probability. After 100 ms, the texture stimulus was replaced by the mask, which remained visible until a response was given by pressing one of the two response buttons. Half of the participants had to press the right button in response to a D-texture and the left button in response to an H-texture; for the other half this stimulus-

response mapping was reversed. After a response had been delivered, the masking stimulus was replaced by the ready sign, and the next trial could be initiated. Participants were requested to maintain central eye fixation, to avoid eyeblinks after they had initiated a trial, and to respond as quickly and accurately as possible. Moreover, they were encouraged not to wait too long before initiating the next trial.

During the training block, error feedback was given on each trial: In case the incorrect response key had been pressed, the masking stimulus was replaced by the texture stimulus delivered in the current trial. This feedback stimulus remained visible for 1000 ms. If the correct key had been pressed, the mask was immediately replaced by the next ready sign. During the experimental blocks, no feedback was given. At the end of each block, participants were informed about their number of correct and incorrect responses and about their reaction times. There was a short break of several seconds up to approximately one minute after each block.

Data Recording

EEG was recorded with Ag-AgCl electrodes (5 mm in diameter) from Fz, Cz, Pz, O1, and O2 (according to the international 10–20 system), as well as from left and right central scalp sites (C3' and C4', located 1 cm in front of C3 and C4, respectively). All electrodes were referenced to the nose. Electrode impedance was kept below 5 kOhm. In addition, horizontal and vertical EOG were recorded from the outer canthi of the eyes and from

above the right eyebrow, respectively. For EOG electrodes, impedance was kept below 10 kOhm. Amplifier bandpass was 0.10–70 Hz. EEG was sampled online with a frequency of 256 Hz. Reaction times and correctness of response were recorded for each trial.

Data Analysis

EEG was averaged offline for epochs of 800 ms, starting 100 ms prior to stimulus onset and ending 700 ms afterwards. Prior to analysis, EEG was filtered with a 20 Hz/24 dB per octave low-pass filter in order to remove high-frequency noise. Trials containing saccadic eye movement or eyeblinks (indicated by HEOG or VEOG voltage exceeding $\pm 50 \mu\text{V}$) or muscular artefacts (indicated by any voltage exceeding $\pm 70 \mu\text{V}$) were excluded from analysis. EEG was averaged for correct trials only, separately for H-texture trials, trials containing a central discontinuity (“Dc trials”), trials containing a left discontinuity, and trials containing a right discontinuity.

After visual inspection of the data, N2b latency range was determined as 250 ms–350 ms after texture onset, and P3b latency range was determined as 325 ms–525 ms after texture onset. N2b and P3b were quantified as the peak amplitude values within the respective time windows.* For the N2b component, visual inspection of the ERP waveforms revealed substantial differences between anterior electrode sites (Fz, Cz, C3', and C4') and posterior sites (Pz, O1, and O2). In order to capture these differences between anterior N2b (“aN2b”) and posterior N2b (“pN2b”), analyses were performed separately for anterior sites and for posterior sites. P3b was analyzed for midline electrodes (Fz, Cz, and Pz).

An initial series of repeated measures analyses of variance (ANOVAs) was performed on D-texture ERPs for each of the amplitude values to test for the possibility of further reducing the data. First, ANOVAs were conducted for the factors PERIPHERALLOCATION (left discontinuity, right discontinuity) and ELECTRODE (Fz, Cz, C3', C4' for the aN2b; Pz, O1, O2 for the pN2b; Fz, Cz, and Pz for the P3b). No difference between ERPs elicited by left and right discontinuities was found. Consequently, ERPs elicited by peripheral discontinuities were grouped together (“Dp”-ERPs). Second, ANOVAs were conducted for the factors LOCATION (central, peripheral) and ELECTRODE. Neither aN2b nor P3b were influenced by the location of the discontinuity. For these components, therefore, ERP values were averaged across both conditions (“D”-ERPs),

and subsequent analyses were performed with the factors STIMULUS TYPE (D-texture, H-texture) and ELECTRODE. The pN2b, however, was influenced by the location of the discontinuity (central vs. peripheral) in three out of four experiments. Consequently, Dp-values and Dc-values were not averaged for this component, and in subsequent analyses of the pN2b the factor STIMULUS TYPE consisted of three levels (Dp-texture, Dc-texture, and H-textures). Additional ANOVAs were conducted for this component comparing each of the three stimulus pairings separately. In all analyses, Greenhouse-Geisser adjustments to the degrees of freedom (indicated in the results sections by ϵ) were performed where appropriate.

Mean correct response rate and mean RTs were determined separately for H-texture trials, Dc-texture trials, and Dp-texture trials. Standard deviations of RTs were determined for each block separately, and only those trials where RTs did not exceed the range of ± 3 standard deviations from mean RT of the given block are reported in the results section. Preliminary analyses revealed a robust CPD that was not affected by the experimental manipulation (peripheral discontinuities: 92.7% correct, 463 ms; central discontinuities: 78.0% correct, 509 ms; both $F(1,28) > 4.89$, both $P < .036$; interactions of CPD with experimental group: both $F(3,28) < 0.6$, both $P > .67$). This replicates the CPD findings typically observed in texture segmentation tasks using line orientation as the relevant feature (e. g., Gurnsey et al., 1996; Joffe & Scialfa, 1995; Kehler, 1987, 1989). Since behavioral performance is only of marginal interest for the scope of the present paper, the respective effects will not be reported for each experiment separately. Additional analyses, however, comparing D-textures response with H-texture responses, revealed a significant interaction of stimulus type and experimental group for reaction times ($F(3,28) = 11.91$, $P < .001$). Therefore, these results will be reported separately for each experiment, using paired *t*-tests to compare correct response rates and reaction times for D-textures and H-textures.

Experiment 1: H-Textures Presented Frequently (75%), D-Textures Presented Infrequently (25%)

The main purpose of this experiment was to establish that D-textures and H-textures will elicit the same ERP pattern typically found in oddball situations if these stimuli

* As can be seen from Figures 2 to 5, enlarged pN2b components caused major negative-going shifts at posterior electrode sites. This might have led to an artificial reduction in P3b amplitude. To test for this hypothesis, P3b was requantified as a peak-to-peak value (i. e., as the difference between the negative peak amplitude in the N2b latency range and the positive peak amplitude in the P3b latency range). Statistical analyses of these data revealed essentially the same pattern of P3b effects in all four experiments as did the baseline-to-peak analyses.

Experiment 1: H-textures 75%, D-textures 25%

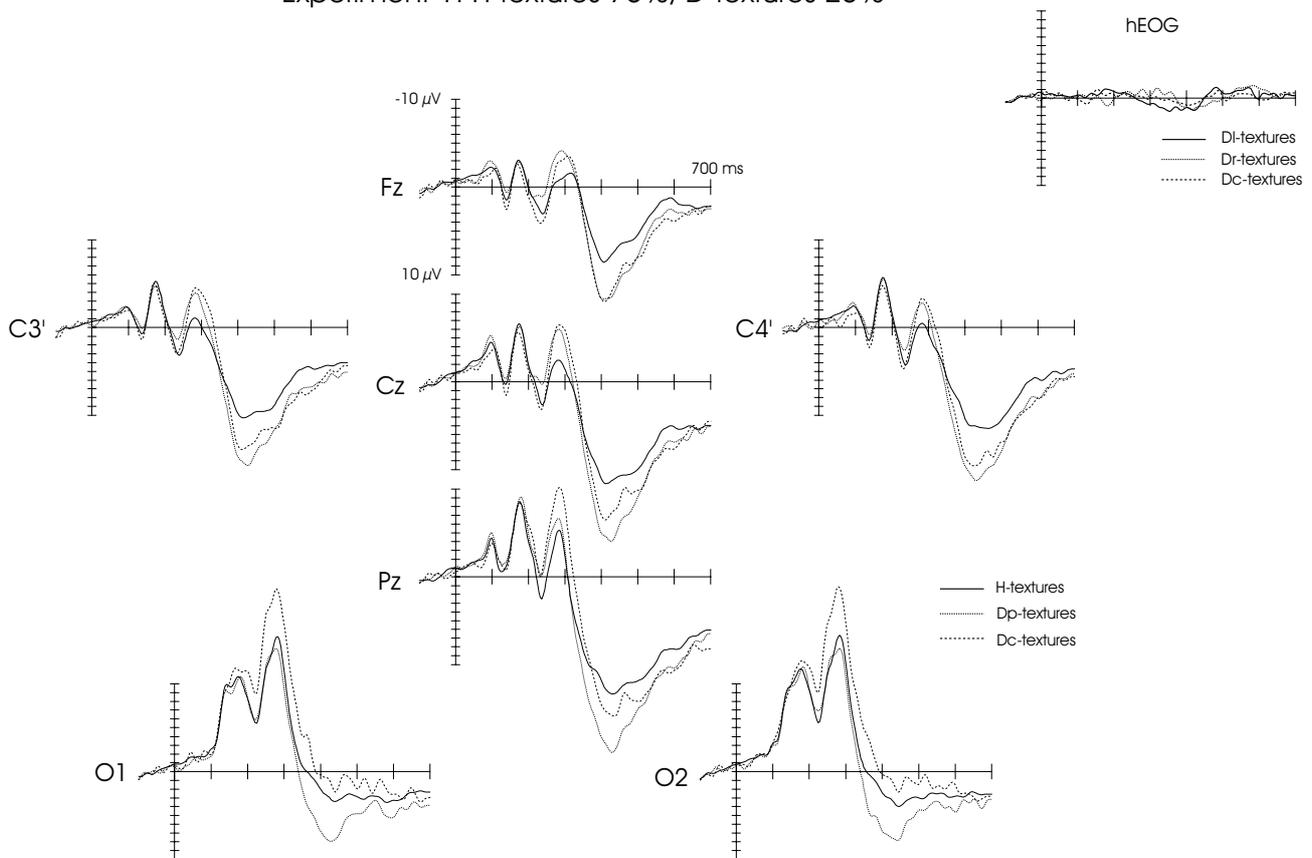


Figure 2 Experiment 1, H-textures presented on 75% of all trials, D-textures presented on 25% of all trials: Grand mean average ERP waveforms elicited by H-textures (homogeneous texture; solid line), Dc-textures (central discontinuity; broken line), and Dp-textures (peripheral discontinuity; dotted line). Upper right panel: Horizontal EOG in response to peripheral discontinuities appearing to the left of fixation (DI-textures; solid line), to the right of fixation (Dr-textures; dotted line), and at fixation (Dc-textures; broken line). Note that in this and in all subsequent figures, negative-going deflections are plotted upward.

are presented with different relative probabilities. In 75% of all trials an H-texture was presented, while in 25% of all trials a D-texture was presented. It was assumed that rare stimuli would elicit an enlarged N2b-component as well as an enlarged P3b-component, compared to the ERPs elicited by frequent stimuli (e. g., Ritter, Simson, Vaughan, & Friedman, 1979; Ritter, Simson, Vaughan, & Macht, 1982).

Method

Participants were 20–45 years old (mean age: 26 years), two were male. *Stimuli, apparatus and procedure* were as described above. The experiment consisted of eight blocks, containing 96 trials each, 72 of which consisted of H-textures, 8 consisted of Dc-textures, 8 consisted of left Dp-textures, and 8 consisted of right Dp-textures. *Data recording and data analysis* were as described above.

Results and Discussion

Behavioral Performance

Correct response rate was higher for H-responses than for D-responses (98.4% vs. 92.6%; $t(7) = 3.09$, $P < .018$), and correct responses were executed faster for H-textures than for D-textures (395 ms vs. 456 ms; $t(7) = 4.01$, $P < .005$).

Electrophysiological Data

As can be seen from Figure 2, D-textures elicited both an enlarged aN2b and an enlarged P3b compared to H-textures ($F(1,7) = 11.92$, $P < .011$; and $F(1,7) = 6.44$, $P < .039$, respectively), thus exhibiting the typical pattern of oddball effects, with the infrequently presented stimuli eliciting larger N2b and P3b components than the frequently presented stimuli. However, only Dc-textures, but not Dp-textures, elicited an enlarged pN2b compared to H-textures ($F(1,7) = 14.89$, $P < .006$; and $F(1,7) =$

0.19, n.s., respectively), also reflected in a significant difference between Dc-pN2b and Dp-pN2b ($F(1,7) = 7.49, P < .029$). From the present data it is unclear whether this difference in pN2b effects is due to an enhancement of the pN2b elicited by central discontinuities, or to a reduction of the pN2b elicited by peripheral discontinuities. One could assume, for example, that the onset of the P3b component elicited by Dp-textures reduced the amplitude of the preceding N2b component. However, Figure 2 indicates that there was no latency difference between Dc-P3b and Dp-P3b, and post-hoc analyses revealed no correlation between pN2b amplitude and P3b amplitude at posterior electrode sites, thus giving no statistical support to this assumption.

In sum, the present results show that it is possible to obtain systematic ERP differences between homogeneous and nonhomogeneous texture stimuli in an odd-ball situation. Both N2b and P3b turned out to be sensitive to the experimental manipulation. Moreover, there was some indication that the N2b component recorded at anterior sites may reflect different processes than the

negative-going deflection recorded at posterior sites within the same latency window. However, since D-textures were presented infrequently, one cannot distinguish between ERP effects based on the specific processing of temporal discontinuities and ERP effects based on the specific processing of spatial discontinuities. The following experiment was designed to disentangle these factors.

Experiment 2: H-Textures and D-Textures Presented with Equal Probability (50%)

This experiment tested whether it is possible to obtain differences between D-texture ERPs and H-texture ERPs without the aid of an additional distinguishing stimulus attribute such as relative stimulus frequency. To this end, D-textures and H-textures were presented

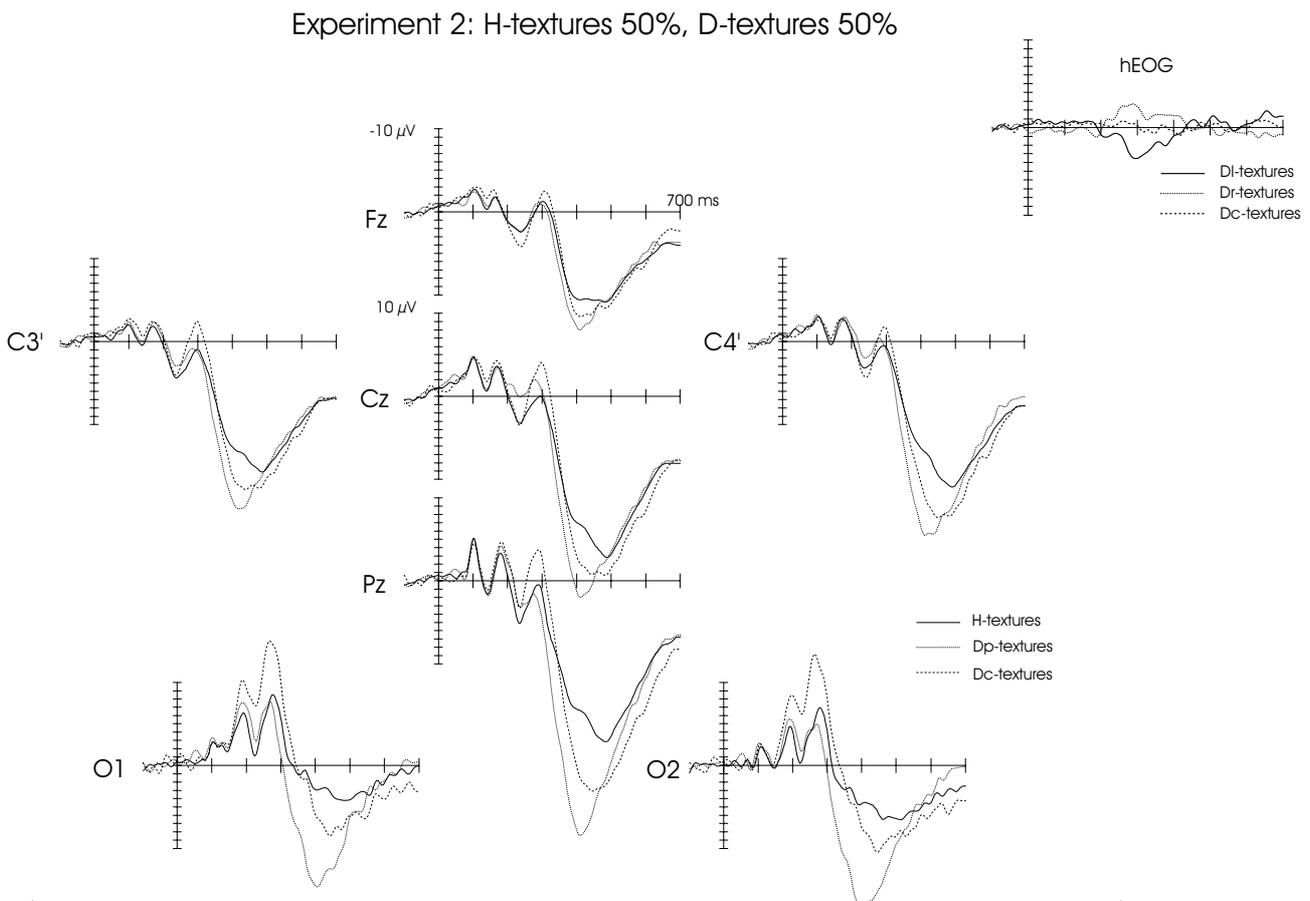


Figure 3 Experiment 2, H-textures presented on 50% of all trials, D-textures presented on 50% of all trials: Grand mean average ERP waveforms elicited by H-textures (homogeneous texture; solid line), Dc-textures (central discontinuity; broken line), and Dp-textures (peripheral discontinuity; dotted line). Upper right panel: Horizontal EOG in response to peripheral discontinuities appearing to the left of fixation (DI-textures; solid line), to the right of fixation (Dr-textures; dotted line), and at fixation (Dc-textures; broken line).

with equal probability. If the effects observed in the previous experiment were exclusively the result of brain processes associated with the detection of discontinuities in the temporal domain, then one would expect no differences between H-texture ERPs and D-texture ERPs in the present experiment. If, on the other hand, the ERP effects described above are also in part the result of brain processes associated with the detection of a discontinuity in the spatial domain, then in the present experiment ERP effects should be observed which more purely reflect processing of discontinuities in the spatial domain.

Method

Participants were 21–38 years old (mean age: 27.3 years), four were male. *Stimuli, apparatus and procedure* were as described above. The experiment consisted of five blocks, containing 96 trials each. *Data recording and data analysis* were as described above.

Results and Discussion

Behavioral Performance

Although correct response rate was again higher for H-responses than for D-responses (96.7% vs. 88.5%), this effect failed to reach significance ($t(7) = 1.44, P > .19$). Moreover, there was no appreciable difference between correct D-response RT and correct H-response RT (491 ms and 487 ms, respectively; $t(7) < 0.15, P > .89$). The probability manipulation therefore affected RTs, as the RT advantage for H-textures observed in the previous experiment was no longer present in this experiment. This finding indicates that the RT distribution observed in the previous experiment can be regarded as reflecting the fact that RTs are generally shorter in response to a relatively more frequent stimulus (“stimulus probability effect,” e. g., Miller & Pachella, 1973), rather than as reflecting some genuine processing advantage of H-textures as compared to D-textures.

Electrophysiological Data

Although Figure 3 suggests that D-textures elicited larger aN2b components than H-textures, this difference failed to reach significance ($F(1,7) = 2.26, P > .13$). This absence of a reliable aN2b effect in the present experiment indicates that the effect observed in the previous experiment reflected detection of a temporal discontinuity rather than detection of a spatial discontinuity. More

specifically, it indicates that the aN2b is sensitive to the relative frequency of stimulus *categories* (D-texture vs. H-texture, or stimuli requiring a left-hand response vs. stimuli requiring a right-hand response) rather than to relative stimulus frequency per se. Note that, although overall D-texture frequency was 50%, each individual type of D-texture (left, right, and central) was presented on only 16.67% of all trials. Thus, if the enlargement of the aN2b observed before had been due to detecting an infrequent stimulus, D-textures should still elicit larger aN2b components than H-textures.

With respect to the pN2b component, the results of the previous experiment were replicated: Dc-textures, but not Dp-textures, elicited an enlarged pN2b compared to H-textures ($F(1,7) = 20.49, P < .003$; and $F(1,7) = 0.22, n.s.$, respectively), and the difference between Dp-pN2b and Dc-pN2b was again significant ($F(1,7) = 16.92, P < .004$). This result further supports the assumption that the pN2b is sensitive to the location of a spatial discontinuity.

Most interestingly, D-textures still elicited an enlarged P3b compared to H-textures ($F(1,7) = 9.16, P < .019$). This effect was larger at posterior sites than at anterior sites, as evidenced by a significant STIMULUS TYPE \times ELECTRODE interaction ($F(1,7) = 6.05, P < .031, \epsilon = .639$). This finding indicates that the P3b is modulated not only by discontinuities in the temporal domain, but also by discontinuities in the spatial domain. Since the P3b is known to be sensitive to the significance or “targetness” of a stimulus (e. g., Duncan-Johnson & Donchin, 1977; Squires, Donchin, Herning, & McCarthy, 1977; Johnson & Donchin, 1980; for a review, see Picton & Hillyard, 1988), one might take this finding as evidence that the discontinuity embedded in D-textures renders these stimuli more “target-like” than H-textures even under conditions of equal stimulus and response frequencies.

There is, however, an alternative interpretation that has to be considered carefully: Since each individual type of D-texture was presented on only 16.67% of all trials, the enlarged P3b elicited by D-textures might as well indicate that this component is sensitive to the relative frequency of individual stimulus types. If this hypothesis holds, then presenting each individual stimulus type with equal probability should result in larger P3b components triggered by H-textures than by D-textures, because of a group of equiprobable stimuli those which require the less frequent response are known to elicit the larger P3b component (Karlin & Martz, 1973). If, on the other hand, the “targetness” hypothesis holds, then even under these conditions D-textures should elicit P3b components which are at least as large as those elicited by H-textures. This will be tested in the following experiment.

Experiment 3: D-Textures Presented Frequently (75%), H-Textures Presented Infrequently (25%)

In the present experiment, H-textures, Dc-textures, left Dp-textures, and right Dp-textures were presented with a probability of 25% each, resulting in a total probability of 75% for D-textures. In all other respects, the experimental design was similar to Experiments 1 and 2. In the discussion of the previous experiment, it was assumed that the aN2b is primarily sensitive to differences in the relative frequency of stimulus categories, but is not influenced by the presence or absence of a spatial discontinuity. If this assumption is correct, then in the present experiment H-textures should elicit an enlarged aN2b component compared to D-textures. Furthermore, it was reasoned that if the P3b effect in Experiment 2 was due to differences in the relative frequency of left, right, and central D-textures as compared to H-textures,

then in the present experiment, this effect should be reversed (i. e., H-textures should elicit a larger P3b than D-textures); under conditions where all stimuli are equiprobable, but one of them requires a less frequent response than the others, this stimulus is known to elicit the largest P3b (Karlín & Martz, 1973). If, however, the enlarged D-texture P3b does reflect processing of the “targetness” of the embedded spatial discontinuity, then no such reversal of the P3b effect should be found.

Method

Participants were 21–38 years old (mean age: 30.3 years), four were male. Stimuli, apparatus and procedure were as described above. The experiment consisted of eight blocks, containing 96 trials each. Data recording and data analysis were as described above.

Experiment 3: H-textures 25%, D-textures 75%

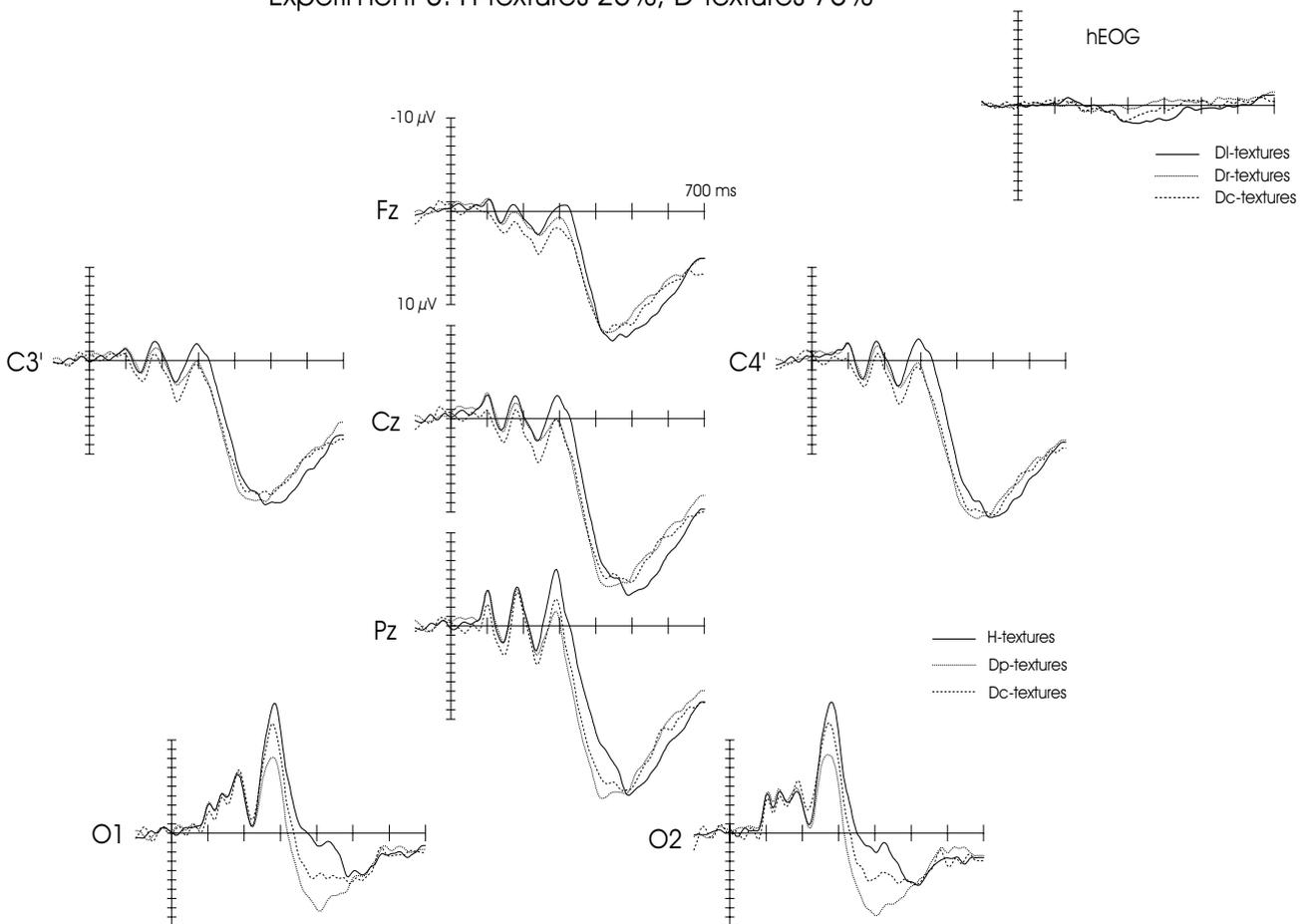


Figure 4 Experiment 3, H-textures presented on 25% of all trials, D-textures presented on 75% of all trials: Grand mean average ERP waveforms elicited by H-textures (homogeneous texture; solid line), Dc-textures (central discontinuity; broken line), and Dp-textures (peripheral discontinuity; dotted line). Upper right panel: Horizontal EOG in response to peripheral discontinuities appearing to the left of fixation (Dl-textures; solid line), to the right of fixation (Dr-textures; dotted line), and at fixation (Dc-textures; broken line).

Results and Discussion

Behavioral Performance

Again, correct response rate was higher for H-responses than for D-responses (93.0% vs. 85.7%), but again this effect failed to reach significance ($t(7) < 0.8$, $P > .45$). Contrary to both previous experiment, and in accordance with the “stimulus probability effect” (Miller & Pachella, 1973), H-response RTs were slower than D-response RTs (561 ms vs. 473 ms; $t(7) = 3.42$, $P < .011$).

Electrophysiological Data

Figure 4 indicates that, as expected, H-textures elicited a larger aN2b than D-textures. This difference approached significance in the two-sided test ($F(1,7) = 5.55$, $P < .051$). This finding supports the notion that the aN2b is primarily (although perhaps not exclusively) modulated by relative frequency of stimulus category (infrequent H-texture/H-responses vs. frequent D-texture/D-responses), rather than by relative frequency of stimulus type (25% each). In contrast to both previous experiments, D-textures elicited smaller pN2b components than H-textures ($F(1,7) = 9.51$, $P < .018$ for Dc-textures; and $F(1,7) = 5.27$, $P < .055$ for Dp-textures). Although Figure 4 indicates that, as before, Dc-textures tended to elicit larger pN2b components than Dp-textures, this difference failed to reach significance ($F(1,7) = 2.35$, $P > .16$).

Of special importance to the present study is the finding that the P3b elicited by D-textures was still not smaller than the P3b elicited by H-textures ($F(1,7) < 0.09$, n.s.). In the discussion of Experiment 2 it was argued that D-textures had elicited larger P3b components than H-textures perhaps because each of the three types of D-texture was delivered on only 16.67% of all trials, while H-textures were delivered on 50% of the trials. It was reasoned that the P3b component might be sensitive to these differences in relative frequency of individual stimulus types rather than to the spatial discontinuity embedded in D-textures. In the light of the present results, however, this interpretation does not hold; since all stimuli were equiprobable, only those stimuli that required the less frequent response (i. e., H-textures) should have elicited an enlarged P3b (Karlin & Martz, 1973). This was clearly not the case.

Thus, the results of the present experiment again show a dissociation of aN2b effects and P3b effects. In the previous experiment, this dissociation occurred because no aN2b effect was observed (in accordance with the equal distribution of H-textures and D-textures), while a P3b effect was present in the form of an enlarged P3b elicited by D-textures. In the present experiment, the reverse was true: An aN2b effect was present (reflecting

the unequal distribution of H-textures and D-textures), but no P3b effect. Taken together, this pattern of results supports the assumption that the aN2b is sensitive mainly to discontinuities in the temporal domain (relative frequency of stimulus categories), while the P3b is sensitive to discontinuities in the temporal as well as in the spatial domain. In particular, the finding of a large P3b triggered by D-textures irrespective of relative stimulus and/or response frequency clearly supports the idea that the discontinuity embedded in D-textures represents a “target,” i. e., an event of special relevance (see above). If this conclusion is correct, then it should be virtually impossible to obtain “normal” oddball effects with D-textures as frequent stimuli and H-textures as rare stimuli even if the differences in relative frequency are rather extreme. This was tested in Experiment 4.

Experiment 4: D-Textures Presented Frequently (90%), H-Textures Presented Infrequently (10%)

D-texture stimuli were presented with a probability of 90% (i. e., 30% for each individual type of D-texture), while H-textures were presented with a probability of only 10%. In all other respects, the experimental design was similar to Experiments 1 to 3. It was expected that similar results as in Experiment 3 should be obtained, i. e., infrequent H-textures were expected to elicit an enlarged aN2b component, while both H-textures and D-textures were expected to elicit large P3b components – H-textures because they are rare and require an infrequent response, and D-textures because the embedded spatial discontinuity adds an inherent element of “targetness” to the stimulus.

Method

Participants were 21–40 years old (mean age: 30 years), four were male. *Stimuli, apparatus and procedure* were as described above. The experiment consisted of five blocks, containing 120 trials each. *Data recording and data analysis* were as described above.

Results

Behavioral Performance

Overall discrimination performance was considerably lower than in the previous experiments, and did not differ between H-texture responses (78.8% correct) and D-texture responses (74.7% correct; $t(7) < 0.42$, $P > .69$). As

Experiment 4: H-textures 10%, D-textures 90%

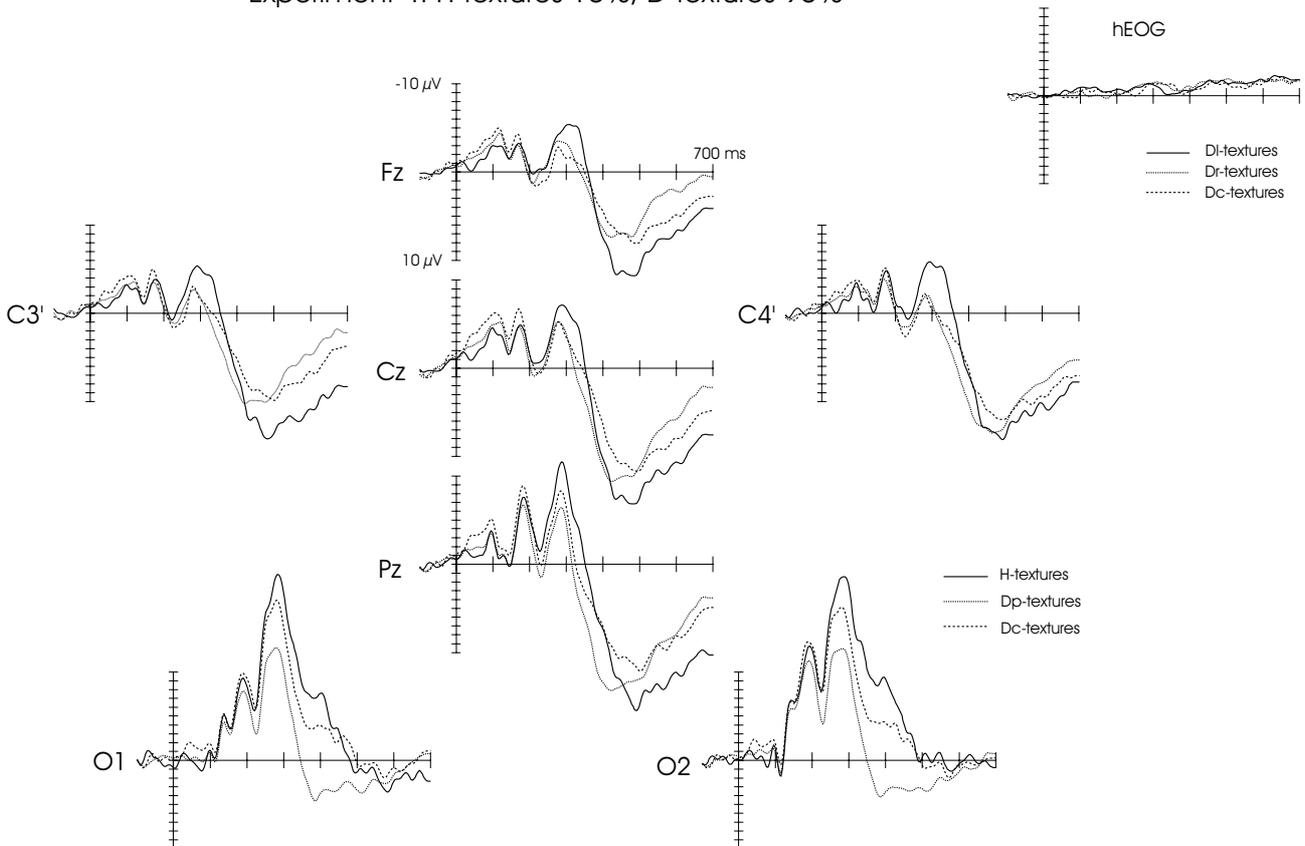


Figure 5 Experiment 4, H-textures presented on 10% of all trials, D-textures presented on 90% of all trials: Grand mean average ERP waveforms elicited by H-textures (homogeneous texture; solid line), Dc-textures (central discontinuity; broken line), and Dp-textures (peripheral discontinuity; dotted line). Upper right panel: Horizontal EOG in response to peripheral discontinuities appearing to the left of fixation (DI-textures; solid line), to the right of fixation (Dr-textures; dotted line), and at fixation (Dc-textures; broken line).

in Experiment 3, RT to correctly identified H-textures was slower than RT to correctly identified D-textures (626 ms vs. 524 ms; $t(7) = 4.56$, $P < .003$).

Electrophysiological Data

Although Figure 5 indicates that H-textures elicited an enlarged aN2b component compared to D-textures, this effect was not statistically significant ($F = 1.8$, n.s.).* As in Experiment 3, Dp-textures elicited a smaller pN2b component than H-textures ($F(1,7) = 10.26$, $P < .015$) and Dc-textures ($F(1,7) = 7.21$, $P < .031$), while the difference between pN2b components elicited by Dc-textures and pN2b components elicited by H-textures failed to reach statistical significance ($F(1,7) = 4.48$, $P > .07$).

Importantly, although there was a numerical tendency for D-textures to elicit larger P3b components than H-textures, this difference still failed to reach significance ($F(1,7) = 3.54$, $P > .101$). This confirms the assumption that temporal discontinuities (rare stimuli) and spatial discontinuities (D-textures) both possess a feature of “targetness,” which enables them to elicit an enhanced P3b component. Therefore, no standard oddball design can be constructed with infrequent H-textures in a context of frequent D-textures, as this results in a conflicting distribution of the “targetness” feature; temporal discontinuities are represented by spatially homogeneous stimuli (i. e., H-textures), while spatial discontinuities represent temporally homogeneous (i. e., frequently repeated) stimuli.**

* Detailed inspection of the data revealed that while six out of eight participants showed a substantially enlarged aN2b component elicited by H-textures, two participants showed a reversed aN2b effect, i. e., D-textures elicited a larger aN2b component than H-texture. Since this effect did not correlate with identification performance, and was not observed for any participants in the previous experiment, it cannot be explained at present.

** The conflicting distribution of the “targetness” feature might even account for the rather low identification performance observed in the present experiment. The high error rate for H-responses was expected given that 90% of all trials required a D-texture response, and only 10% required an H-texture response, inducing a strong response-bias toward D-texture responses. However, the high error rate for D-textures

General Discussion

In texture segmentation tasks, participants are required to indicate whether a briefly presented texture was completely homogeneous (“H-textures”) or contained a small region of discontinuous elements (“D-textures”). When textures are composed of short line segments, identification of D-textures is usually better for discontinuities presented at a retinal eccentricity of about 4°–6° visual angle than for discontinuities presented foveally (“CPD,” Kehler 1987, 1989). Although the electrophysiological correlates of texture segmentation have been investigated in several studies (e. g., Bach & Meigen, 1992, 1997; Regan & He, 1995; Srebro et al., 1994), we are not aware that the question whether there is a fundamental difference between the neural processes involved in the perception of D-textures and those involved in the perception of H-textures has ever been addressed directly. The main goal of the present study was to investigate this issue. Specifically, the aim was to test the hypothesis that D- and H-textures are categorized as two nonequivalent classes of stimuli. It seems reasonable to assume that because of the special biological significance of discontinuities in the environment, the discontinuity embedded in D-textures might add a feature of “targetness” to these stimuli which would be lacking for H-textures. Consequently, D-textures and H-textures should be regarded as conceptually dissimilar stimuli (i. e., “targets” and “nontargets”), rather than as physically dissimilar, but conceptually equivalent stimuli.

To test this hypothesis, event-related brain potentials (ERPs) were measured, while stimuli were presented in the form of an oddball-paradigm, which has the advantages of (a) yielding a robust and well-investigated pattern of ERP effects and (b) allowing for the independent manipulation of the two relevant stimulus parameters (i. e., D-textures vs. H-textures, and frequent vs. infrequent stimuli). Relative stimulus frequency was varied between experiments: H-textures were presented in 75% of all trials in Experiment 1, in 50% of all trials in Experiment 2, in 25% of all trials in Experiment 3, and in 10% of all trials in Experiment 4. It was reasoned that if D-textures and H-textures were conceptually equivalent, rare D-textures in a context of frequently presented H-textures should elicit the same pattern of ERP effects as rare H-textures in a context of D-textures. If, on the other hand, D- and H-textures were nonequivalent, then a clear asymmetry in the ERP effects was expected depending on whether D-textures or H-textures were employed as rare stimuli.

ERP Correlates of Processing Homogeneous vs. Discontinuous Textures

Results indicate that D-textures and H-textures are not interchangeable in an oddball situation, as evidenced by a dissociation of (anterior) N2b effects and P3b effects. The aN2b component proved to be enhanced in response to temporal discontinuities. In Experiment 1, rare D-textures elicited a larger aN2b component than frequent H-textures, while in Experiments 3 and 4 rare H-textures – at least numerically – elicited a larger aN2b component than frequent D-textures. Results from Experiments 2 and 3 indicate that the aN2b is sensitive to temporal discontinuities with respect to stimulus categories (i. e., sets of stimulus types requiring the same response) rather than with respect to individual stimulus types per se: No difference between D-texture aN2b and H-texture aN2b was observed in Experiment 2, where D-texture responses and H-texture responses were equiprobable, while relative stimulus frequencies were 50% for H-textures and 16.67% for each of the three D-textures. In Experiment 3, on the other hand, where all four stimulus types appeared with equal probability (25%), while relative response frequencies were 75% for D-textures and 25% for H-textures, H-textures elicited a larger aN2b than D-textures.

A different pattern of results was obtained for the P3b component. If rare stimuli were D-textures (Experiment 1), the “normal” oddball effect occurred, i. e., rare stimuli elicited substantially larger P3b components than frequent stimuli. However, D-textures still elicited larger P3b components than H-textures in Experiment 2, where these stimuli were presented with equal probability. It was reasoned that this might be due to the fact that in this experiment each type of D-texture was presented only on 16.67% of all trials. If the P3b was sensitive to relative frequency of individual stimulus types (rather than to relative frequency of stimulus categories, as the aN2b), then presenting all four types of stimuli with equal probability (Experiment 3) should result in an enlarged P3b elicited by H-textures, because under this condition, H-textures require the less frequent response than D-textures (see Karlin & Martz, 1973). Presenting H-textures less frequently than each of the three D-textures (Experiment 4) should increase this effect. The results obtained in these two experiments do not support this hypothesis, as in both experiments, the P3b elicited by D-textures was about the same size as the P3b elicited by H-textures.

These findings cannot be explained in terms of the sensitivity of the P3b component to temporal discontinu-

seems at odds with this notion, and rather seems to reflect the existence of an opposite bias. Taken together, these behavioral results may be taken as evidence that in the present experiment participants found stimulus identification and/or selection of the appropriate response particularly difficult.

ities (i. e., infrequent events). Since in Experiment 4 H-textures were both rarer than D-textures and required the less frequent response, they should have elicited a substantially larger P3b component than D-textures under “normal” oddball conditions (i. e., under conditions where frequent and infrequent stimuli are otherwise equivalent). The fact that this result was not obtained indicates that in the present experiments, the P3b was enhanced not only in response to temporal discontinuities, but also in response to spatial discontinuities. Note that the missing P3b effect in experiments 3 and 4 was obviously not due to a failure of H-textures to elicit an enlarged P3b component, as the H-texture P3b in experiments 3 and 4 was substantially larger than that elicited in experiments 1 and 2. Rather, it was due to the fact that D-textures elicited an enlarged P3b component *as well*. It has been argued that it is the relevance of a stimulus that determines the amplitude of the P3b component (e. g., Berlad & Pratt, 1995; Donchin, 1981). One thus might conclude that the enhanced P3b in response to D-textures indicates their specific relevance in the present experiments. In other words, the spatial discontinuity seems to add a feature of “targetness” to D-textures, which is absent for H-textures, even though H-textures and D-textures were equally response relevant in the present experiments.

Taken together, the present results support the idea that, in addition to being perceptually different, D-textures and H-textures are also conceptually different. Spatial discontinuities in a homogeneous background seem to receive “special” processing, irrespective of whether or not they are presented infrequently or require an infrequent response. Homogeneous textures, on the other hand, do not receive this special processing. Consequently, D-textures presented infrequently in a context of frequent H-textures will elicit “normal” oddball effects (an enlarged aN2b followed by an enlarged P3b), while infrequent H-textures in a context of frequent D-textures do not, because this situation creates a conflict between detecting discontinuities in the temporal domain and detecting discontinuities in the spatial domain.

ERP Correlates of Processing Central vs. Peripheral Discontinuities

A secondary aim of the present study was to obtain electrophysiological correlates of the effects of retinal eccentricity on texture segmentation in order to obtain an additional measure of the processes underlying texture segmentation in a CPD-situation. Therefore, the discontinuous region in D-textures was presented either foveally or with a retinal eccentricity of 4.5° of visual angle. The prediction that discrimination performance

would be better for peripherally presented D-textures than for foveally presented D-textures was confirmed; a reliable CPD was found in all experiments, replicating the results of Kehler (1987, 1989). There was, however, no corresponding “oddball-like” effect in the ERPs, as neither the aN2b component nor the P3b component were more enlarged by less frequently identified central discontinuities than by more frequently identified peripheral discontinuities.

At posterior electrode sites, however, an interesting and rather unexpected effect of eccentricity on the ERP was observed: A negative-going shift in the N2b latency range (“pN2b”) was found to be larger for Dc-textures than for Dp-textures. (This effect was visible in all experiments, although it failed to reach significance in Experiment 3.) One might argue that this difference in pN2b amplitude is due to an artificial reduction of the Dp-pN2b, resulting from averaging across ERPs elicited by left and right Dp-textures; laterally presented discontinuities might activate brain areas that, to some extent, are oppositely oriented, resulting in some cancellation of their fields, while this is not the case for centrally presented discontinuities. For the present data, however, this interpretation does not hold; comparison of ERPs elicited by left and right Dp-textures did not reveal any differences between these waveforms, indicating that the pN2b effect is not caused by an artificially induced reduction of the Dp-pN2b.

In particular, Dp-textures did not elicit a N2pc component. This contralateral subcomponent of the target-related posterior N2 wave is assumed to reflect attentional processes relevant to the selection of task-relevant stimuli or the filtering out of irrelevant stimuli (Luck & Hillyard, 1994a,b; Eimer, 1996). Therefore, the absence of a N2pc in the present experiments might be taken as further evidence that detection of a spatial discontinuity in a texture segmentation task is achieved by a preattentional process.

To our knowledge, this is the first description of a modulation of a posterior N2-like component outside the literature on visual attention. It would be interesting to determine further the relationship between the pN2b and previously described posterior negativities such as the “occipital N230” (Wijers et al., 1987) and the “occipital N180” (Wijers et al., 1989), which seem to be sensitive to elementary stimulus features rather than to attentional factors; (the early part of) the “posterior selection negativity” (Michie et al., 1999; Smid, Jacob, & Heinze, 1999), which responds to changes in the discriminability of relevant stimuli; the N2pc as described by Luck and Hillyard (1994a,b; see also Eimer, 1996), which is elicited by pop-out targets; and the “posterior N2” as described by O’Donnell et al. (1997), which is sensitive to stimulus features like orientation, spatial frequency, and location.

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