An electrophysiological index of stimulus unfamiliarity

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Abstract

This study investigated the functional significance of the N2 response to novel stimuli. In one condition, background, target, and deviant stimuli were simple geometric figures. In a second condition, all stimulus types were unfamiliar/unusual figures. In a third condition, background and target stimuli were unusual figures and deviant stimuli were simple shapes. Unusual figures, whether they were deviant, target, or background stimuli, evoked larger N2 responses than their simple, familiar counterparts. N2 elicited by an unusual background stimulus was larger than that evoked by simple, deviant stimuli, a pattern opposite that exhibited by the subsequent P3. Deviance from immediate context had limited influence over N2 amplitude. The results suggest that novelty N2 and novelty P3 reflect the processing of different aspects of “novel” visual stimuli. The novelty P3 is particularly sensitive to deviation from immediate context. In contrast, the novelty N2 is sensitive to deviation from long-term context that renders a stimulus unfamiliar and difficult to encode.

Descriptors: ERPs, Novelty processing, Stimulus unfamiliarity, Stimulus deviance, N2, P3

The mammalian brain has evolved to meet the formidable challenge of being able to rapidly process different aspects of novelty. Something can be novel with respect to deviation from a person’s recent experience (e.g., within the context of an experiment) or total experience (e.g., determined by events prior to the experiment). The existence of distinct electrophysiological markers of the processing of these various aspects of novelty has yet to be determined.

The most commonly studied event-related brain potential (ERP) response to novel stimuli is the “novelty P3.” The novelty P3 (sometimes designated as the P3a) is evoked in all three of the primary sensory modalities in response to infrequent, “novel” stimuli that deviate from background (Courchesne, Hillyard, & Galambos, 1975; Knight, 1984, 1997; Knight & Nakada, 1998; Knight & Scabini, 1998; Yamaguchi & Knight, 1991). It has been distinguished from the target P3 (P3b), which tends to have a more posterior scalp distribution, longer latency, and a sensitivity to stimuli that a subject must detect and either respond to or count (Hillyard & Picton, 1987; Picton, 1992; Squires, Squires, & Hillyard, 1975). Typically, the novelty P3 is preceded by a large, anteriorly distributed negative wave in the 180–325 ms temporal window that is presumed to be part of the “family” of wave forms designated as the N2. The current study investigated the functional significance of the N2 (or N200) response to novel visual stimuli, the primary emphasis being on how this component differs from the subsequent novelty P3.

Like the P3, the N2 has not been viewed typically as a unitary brain potential, but instead has been characterized as representing various subcomponents, with different functions and underlying cerebral sources (Naatanen & Picton, 1986; Pritchard, Shappell, & Brandt, 1991). For example, in the auditory modality, the N2a (or mismatch negativity) is elicited automatically, without conscious perception of the evoking stimuli and tends to have a frontocentral maximum, whereas in the visual modality, the N2a is described as “semiautomatic,” evoked by task-irrelevant stimuli in an attended channel, and tends to have a lateral-posterior distribution (Freedman, Roth, & Kopell, 1976; Naatanen & Gaillard, 1983; Naatanen & Picton, 1986; Naatanen, Simpson, & Loveless, 1982; Ritter, Simson, & Vaughan, 1983; Squires et al., 1975). The N2a is extremely sensitive to stimuli that deviate physically from the immediately preceding context (Sams, Alho, & Naatanen, 1983, 1984; Ullsperger, Gille, & Pfeifer, 1985). The N2b, on the other hand, requires conscious perception of the stimulus and is particularly sensitive to low stimulus probability (Naatanen & Gaillard, 1983; Naatanen et al., 1982; Sams et al., 1984; Squires et al., 1975). The N2b tends to be centered around Cz in both the auditory and visual modalities (Freedman et al., 1976; Sams et al., 1983; Simson, Vaughan, & Ritter, 1976; Squires et al., 1975). The N2c also requires conscious perception of the stimulus and in addition requires that the...
stimulus be designated as a target (Naatanen & Picton, 1986; Ritter, Simson, & Friedman, 1979; Ritter et al., 1983; Ritter, Simson, & Vaughn, 1982; Sams et al., 1983). In the auditory modality, the N2c tends to have a frontocentral distribution and in the visual modality a lateral-posterior distribution (Breton, Ritter, Simson, & Vaughn, 1988; Lovrich, Simson, Vaughn, & Ritter, 1986; Pritchard et al., 1991). It has been suggested that the N2c may reflect an early stage of “controlled processing,” involving stimulus identification or categorization, while the parietaled distributed P3b that follows it reflects the process of updating working memory about events in the environment designated as significant (Donchin, 1981; Donchin & Coles, 1988).

It is not clear which, if any, of these N2 components is the one that is evoked in response to novel stimuli. Infrequently presented, nontarget stimuli, in the auditory, tactile and visual modalities elicit an anteriorly distributed negative wave that, as noted, is typically followed by a novelty P3 response (Baudena, Halgren, Heit, & Clarke, 1995; Courchesne, 1978; Courchesne et al., 1975; Daffner et al., 1998; Halgren et al., 1995a; Knight, 1984; Knight & Nakada, 1998; Knight & Scabini, 1998; Snyder & Hillyard, 1976; Squires et al., 1975). In fact, the tight association between the N2 and P3 has led some researchers to describe the novelty N2-P3a waveform as a unified complex that reflects the CNS involvement in the orienting response (e.g., Halgren et al., 1995a; Knight, 1984; Naatanen & Gaillard, 1983; Snyder & Hillyard, 1976). It is unclear from published reports the extent to which the two components of this wave complex index the same underlying processes or reflect separate, but related functions.

Much of the research on the N2-P3a has been in the auditory modality (e.g., Baudena et al., 1995; Halgren et al., 1995a, 1995b; Ritter, Vaughan, & Costa, 1968; Roth, 1973; Snyder & Hillyard, 1976; Squires et al., 1975). However, a similar pattern has been noted in the visual modality (Courchesne et al., 1975; Daffner et al., 1998; Daffner et al., 2000; Knight, 1997). Often, the deviant stimuli used involve verbal material (e.g., letters, numbers, or symbols) that differ from repetitive background and rare target stimuli (e.g., Baudena et al., 1995; Halgren et al., 1995a, 1995b). Of particular interest is the work of Courchesne and colleagues (1975), whose novel visual stimuli consisted of nonverbal material. They reported that infrequently presented unrecognizable, quasirandom color patterns evoked a large frontally distributed N2 followed by a P3. In a recent study, we reported results consistent with Courchesne et al.’s observations (Daffner et al., 1998). As with Courchesne et al.’s experiment, the novel stimuli were unfamiliar or unusual visual patterns presented in an infrequent, unpredictable fashion, while the background stimulus was a simple, familiar line drawing that appeared repetitively.

The deviant stimuli presented in Courchesne et al.’s and our study were “novel” in several different ways. First, they were unusual in the sense of appearing rarely and unpredictably. Second, they deviated from the immediate context of the experiment (physical changes in a repetitive stream of stimuli). Third, they also deviated from long-term contexts (i.e., patterns that have not been encountered previously as determined by events prior to the experiment). As noted by Courchesne et al., such stimuli are difficult to recognize and encode and are viewed as unusual or unfamiliar.

In the current study, we investigated which of these factors that contribute to the novelty of a visual stimulus has the greatest impact on generating the N2 response. Subjects participated in three tasks whose presentation order was counterbalanced. All of the tasks contained infrequent, deviant stimuli that differed from frequently presented repetitive background stimuli. In each task, the deviant stimuli occurred with the same degree of low probability and unpredictability of appearance. The major difference among the tasks was the relationship between the background and deviant stimuli, which, depending on the task, were selected either from a set of simple, easily recognizable geometric figures or a set of unusual/unfamiliar line drawings. By using the same strategy, we recently demonstrated (Daffner et al., 2000) that the novelty P3 (as measured from the preceding N2 peak) is extremely sensitive to stimuli that deviate from immediate context and that this electrophysiological response is large even when the deviant stimuli are simple, familiar shapes and the background stimulus is a highly unusual figure. Here, our data are analyzed to determine if the N2 response follows the same pattern or if it reflects somewhat different, but related processes.

The available literature on the N2 supports the prediction that deviant stimuli should evoke a larger N2 than repetitive background stimuli. We further hypothesized that deviant stimuli that were more unusual would elicit a larger N2 than deviant stimuli that were simple and easily recognized. Such a finding would imply that this component of the N2 indexes more than just deviation from the immediately preceding context, presumably being held in a short-term buffer (Naatanen, 1992), but also involves access to additional information about stimulus familiarity, recognizability, and/or complexity. To examine this issue, we compared the N2 to a repetitive background stimulus that was a highly unusual shape (i.e., it deviated from long-term context) with the N2 to infrequent deviant stimuli that were easily recognizable, simple geometric figures. A larger N2 to such a background stimulus would differentiate the N2 from the novelty P3, which did not exhibit this pattern. Such a pattern would be consistent with the hypothesis that the brain generates a differential response to various aspects of stimulus novelty, with the novelty P3 being more sensitive to deviation from immediate context and the “novelty” N2 being more sensitive to deviation from long-term experience (i.e., unfamiliarity).

Methods

Subjects

Twenty-four right-handed native English speaking undergraduates (mean age = 21 ± 1 years, 15 women) participated in the present study. None had known neurological problems or learning disabilities. Written informed consent was obtained from all subjects before the study. Subjects were paid for their time.

Experimental Tasks

There were three experimental tasks, whose order was counterbalanced across subjects. Each task included three categories of visual stimuli: (a) a repetitive background stimulus (probability 0.7), (b) an infrequent target stimulus (probability 0.15), and (c) infrequent deviant stimuli (probability 0.15), consisting of a set of unique figures, each shown only once during the experiments. All stimuli came either from a set of simple geometric figures or a set of unusual/unfamiliar figures (e.g., fragmented or “impossible” objects), many of which were from the collection of drawings used by Kosslyn et al. (1994) and Kroll and Potter (1984). The particular stimuli assigned to each task were chosen randomly from the two sets of figures noted above.

Figure 1 provides examples of the stimuli used in each task. In one task, background, target, and deviant stimuli all came from the set of simple, easily recognizable, geometric figures (“all simple task”). In another task, background, target, and deviant stimuli all
came from the set of unusual/unfamiliar stimuli ("all unusual task"), and in a third task, the background stimulus and the target stimulus were from the set of unusual figures, while the deviant stimuli came from the set of simple, recognizable, geometric figures ("mixed stimuli task").

Each task presented 250 line drawings, white on black background displayed on a 16-inch color monitor. Each figure subtended a visual angle of approximately 2.5° along its longest dimension. These stimuli appeared within a fixation box subtending a visual angle of approximately 3.5° × 3.5°, that remained on the screen at all times. Stimuli were presented in pseudorandom order with the additional constraints that no more than two deviant stimuli were presented consecutively, and that each block of 50 stimuli had the same number of background stimuli and approximately the same number of target and deviant stimuli.

**Procedure**

Subjects were introduced to the laboratory setting and following electrode placement (see below) were seated in front of a computer monitor in a sound-attenuated room. Subjects were told that the experiment involved the study of brain wave responses as they looked at different kinds of pictures. They were informed that they would be viewing a set of pictures and that they could look at each picture for however long or short they liked. They controlled the viewing duration by a button press that triggered the onset of the next stimulus. All stimuli were displayed for a minimum duration of 600 ms. The interval between the offset of one stimulus and the onset of the next stimulus ranged between 800 and 1,200 ms, and was determined randomly. Subjects also were asked to respond to the designated target stimulus by pressing a foot pedal (ipsilateral to the button press). The target figure for each task was introduced to the subjects by showing it for 30 s immediately before the start of the task. The 250 stimuli for each task were presented in five blocks of 50 stimuli each, with a brief break between each block. Longer breaks were taken between each task. The laterality of the responding hand and foot was counterbalanced across subjects.

**ERP Recordings**

An electrode cap (Electro-Cap International) was used to hold the 13 active electrodes to the scalp, including three midline sites (Fz, Cz, and Pz) and 10 lateral sites (O1, O2, P3, P4, C3, C4, F3, F4, F7, and F8) based on the international 10-20 system locations (see Figure 2A). These sites were all referenced to the left mastoid and the impedance between each recording site and the reference was reduced to less than 5 kΩ. Two electrodes (left mastoid reference) were placed to monitor eye artifacts: one beneath the left eye (to check for eye blinks and vertical eye movements) and the other to the right of the subject’s right eye (to check for lateral eye movements). A final electrode was placed over the right mastoid (referenced to the left) to monitor asymmetric mastoid activity. (None was found.)

The electroencephalogram (EEG) was amplified by a Grass Model 12 Neurodata Acquisition system (~3 dB cutoffs of 0.01 and 100 Hz) and continuously digitized (200 Hz) by an IBM AT compatible microcomputer yielding 1,280 ms of data from each electrode site, beginning 100 ms before stimulus onset.

**Data Analysis**

A continuous record of the raw EEG was stored on hard disk. EEG epochs for the three stimulus types (background, target, deviant) were averaged separately offline to form the ERPs for each respective condition. Trials with eye blinks (>50 µV peak-to-peak amplitude in the channel below the left eye), eye movements (>50 µV peak-to-peak amplitude in the channel next to the right eye), or amplifier blocking were excluded from data analysis. The temporal intervals used for defining N2 and P3 in each task were determined after reviewing the individual ERP plots for all subjects. The N2 amplitude was defined as the peak negative ampli-

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**Figure 1.** Examples of the repetitive background stimulus (70% frequency), target stimulus (15% frequency), and deviant stimuli (15% frequency) from the (A) all simple task, (B) all unusual task, and (C) mixed stimuli task.
Figure 2. (A) Montage illustrating the location of electrode sites based on the international 10-20 system. (B–D) Grand-average event-related potential plots in response to background stimuli (dotted lines), target stimuli (dashed lines), and deviant stimuli (thick lines) for the (B) all simple task, (C) all unusual task, and (D) mixed stimuli task. For illustrative purposes, in (C), the arrowhead marks the N2 wave at the Fz electrode site, the straight arrow marks the N2 wave at the Cz electrode site, and the curved arrow marks the P3 wave at the Cz electrode site in response to deviant stimuli.
tude occurring 200–325 ms after stimulus onset. N2 latency was defined in terms of the timepoint of the N2 wave at the Fz electrode site. The P3 latency was found to be earlier for the all simple task than the other two tasks. For the all simple task, P3 was defined as the peak positive amplitude occurring 300–525 ms after stimulus onset, whereas for the all unusual and mixed stimuli tasks, the P3 was the peak positive amplitude occurring 325–525 ms after stimulus onset. Peak amplitudes were measured with respect to the average of the 100 ms prestimulus baseline.

Data were analyzed using repeated-measures analyses of variance (ANOVAs). Midline and lateral sites were analyzed separately. There were three levels of stimulus type (background, target, novel) and three levels of task (all simple, all unusual, mixed stimuli tasks). For ERP measures, there were three midline electrode sites (Fz, Cz, Pz), four lateral electrode sites (01/2, P3/4, C3/4, F3/4), each with two levels, one for each hemisphere. Between-task analyses that yielded a significant main effect or interaction involving the task variable were followed up with planned contrasts between the levels of the task variable (e.g., all simple task vs. all unusual task vs. mixed stimuli task). Follow-up analyses on Task × Stimulus type interactions contrasted the three stimulus types for each task separately. Background stimuli that, on average, had 35 trials per block, were analyzed for differences across blocks, for which there were five levels. In looking at scalp site interactions with other variables, the data were normalized using a z score technique (Kounios & Holcomb, 1994) similar to the method recommended by McCarthy and Wood (1985) to avoid problems associated with using ANOVA to assess site by factor interactions. Only electrode site interactions that remained significant after normalizing the data are reported. The Geisser–Greenhouse correction (Geisser & Greenhouse, 1959) was applied for all repeated measures with more than 1 degree of freedom.

Results

Description of the Wave Forms

As can be seen in Figure 2B–D, in all of the tasks, each stimulus type produced an early, anteriorly distributed negative-going component that peaked around 100 ms (N1). At the most posterior sites, especially 01 and 02, the ERPs were of the opposite polarity (P1) in the same latency range. Following the N1, there was a positive-going P2 between 100 and 200 ms that was centrally distributed. Posteriorly (01/2), in the same temporal range, there was a deflection in the opposite (negative) polarity, followed by a positive wave. In the 200–325-ms temporal window, stimuli evoked an anteriorly distributed negative-going wave (N2). In the all unusual and mixed stimuli tasks, the N2 to deviant and target stimuli was followed at lateral frontal sites (especially F7/8) by a prolonged negativity that lasted until 600–700 ms. At other locations, the N2 was followed by a P3 wave. After the P3, there was a broad posteriorly distributed positive slow wave, which for deviant and target stimuli lasted until 800–900 ms, and for background stimuli lasted until around 500 ms. At central-frontal midline sites, target stimuli also elicited a broad negative wave beginning between 600 and 700 ms.

Table 1. Summary of the Analysis of Variance Performed on the N2 Amplitude at Midline and Lateral Sites

<table>
<thead>
<tr>
<th>Source</th>
<th>Midline sites</th>
<th>Lateral sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Task (T)</td>
<td>(2.46)</td>
<td>27.97</td>
</tr>
<tr>
<td>Stimulus type (ST)</td>
<td>(2.46)</td>
<td>0.56</td>
</tr>
<tr>
<td>Electrode site (ES)</td>
<td>(2.46)</td>
<td>52.14</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>T × ST</td>
<td>(4.92)</td>
<td>5.24</td>
</tr>
<tr>
<td>T × ES</td>
<td>(4.92)</td>
<td>2.76</td>
</tr>
<tr>
<td>ST × ES</td>
<td>(4.92)</td>
<td>8.98</td>
</tr>
<tr>
<td>T × ST × ES</td>
<td>(8.148)</td>
<td>4.28</td>
</tr>
<tr>
<td>T × H</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>ES × H</td>
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<td>ST × H</td>
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<td>T × ST × ES × H</td>
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</table>
Electrode site interaction, $F(2,46) = 50.44, p < .00005, \eta^2 = 0.67$. The N2 amplitude to the deviant stimuli was larger than to the simple deviant stimuli of the all simple task or the mixed stimulus task. This effect was observed across all midline sites to a similar degree, main effect of task for deviant stimuli: $F(2,46) = 12.25, p < .0003, \eta^2 = 0.83$, with no electrode site by task interaction ($p > .18$) and at frontocentral sites laterally, Task $\times$ Electrode site interaction, $F(6,138) = 15.94, p < .00005, \eta^2 = 0.55$. N2 values for deviant stimuli in the mixed stimulus were larger than in the all simple task across all midline sites, $F(1,23) = 11.37, p < .003$, and at frontocentral sites laterally, Task $\times$ Electrode site interaction, $F(3,69) = 5.1, p < .02, \eta^2 = 0.52$.

A similar pattern emerged for the target stimuli. N2 amplitude was larger in response to the unusual targets of the all unusual task and mixed stimulus task than the simple targets of the all simple task at anterior sites, Task $\times$ Electrode site interaction, midline: $F(4,92) = 3.67, p < .03, \eta^2 = 0.62$; lateral: $F(6,138) = 13.09, p < .00005, \eta^2 = 0.49$. However, unlike background stimuli, there were no differences between the all unusual and mixed stimulus task.

Regarding background stimuli, the N2 amplitude to the simple background stimulus in the all simple task was smaller than to the unusual background stimulus in the all unusual or the mixed stimulus tasks, main effect of task, midline sites: $F(2,46) = 34.67, p < .00005, \eta^2 = 0.94$; lateral sites: $F(2,46) = 12.34, p < .0002, \eta^2 = 0.91$. This diminished amplitude was most salient at frontocentral sites, Task $\times$ Electrode site interaction, midline sites: $F(4,92) = 7.83, p < .003, \eta^2 = 0.73$; lateral sites: $F(6,138) = 27.1, p < .00005, \eta^2 = 0.55$. The N2 response to the background stimulus in the mixed stimulus task was significantly larger than in the all unusual task, midline sites: $F(1,23) = 15.31, p < .0008$; lateral sites: $F(1,23) = 8.53, p < .008$, especially at frontocentral locations, Electrode $\times$ Task interaction, midline: $F(2,46) = 12.25, p < .0004, \eta^2 = 0.77$; lateral: $F(3,69) = 13.75, p < .00005, \eta^2 = 0.60$. Of further interest was whether the size of the N2 to unusual background stimuli diminished in association with repeated presentations. (A block analysis of the background stimuli is possible because of the relatively larger number of this type of trial.) In fact, no significant decline was found in N2 amplitude to unusual background stimuli across blocks in the all unusual or mixed stimulus tasks.

### N2 Latency

There was no overall differences in N2 latency across tasks ($p > .7$). There was a main effect of stimulus type, $F(2,46) = 7.19, p < .003, \eta^2 = 0.83$, because the N2 to background stimuli peaked earlier than to deviant stimuli. N2 latency in response to the different stimulus types varied across tasks, Stimulus type $\times$ Task interaction, $F(4,92) = 3.04, p < .04, \eta^2 = 0.72$. Follow-up analyses revealed that in the all simple task, no differences were found in N2 latency among stimulus types. However, in the all unusual task, the background stimulus had an earlier N2 peak than the target and deviant stimuli, $F(2,46) = 5.63, p < .008, \eta^2 = 0.96$, whereas in the mixed stimulus task, the N2 to the background and target stimuli peaked earlier than the deviant stimuli, $F(2,46) = 5.79, p < .007, \eta^2 = 0.96$.

### Summary of P3 Amplitude

Figure 4 illustrates the P3 amplitude at the Pz site for each stimulus type across all of the tasks, which was the site of maximal amplitude at midline sites, main effect of electrode site, $F(2,46) = 179.1, p < .00005, \eta^2 = 0.78$. P3 amplitude varied across stimulus types, main effect of stimulus type, midline sites: $F(2,46) = 47.41, p < .00005$; lateral sites: $F(2,46) = 50.0, p < .00005$, with P3 response to target stimuli being larger than to deviant stimuli, which in turn was larger than to background stimuli. This pattern was observed within each task (i.e., no Stimulus type $\times$ Task interaction).

Thus, in the mixed stimulus task, the simple deviant stimuli evoked a larger P3 response than the unusual background stimulus, midline $F(1,23) = 18.06, p < .0004$; lateral $F(1,23) = 13.12, p < .002$.

There was a significant Stimulus type $\times$ Electrode site $\times$ Task interaction at lateral sites only, $F(12,276) = 4.92, p < .0007, \eta^2 = 0.39$. For background stimuli, there were no significant differences across tasks except at frontal sites, Task $\times$ Electrode site interaction, $F(6,138) = 5.70, p < .003, \eta^2 = 0.45$. Here the P3 amplitude to background stimuli in the mixed stimulus task was smaller than in the all simple or all unusual task. P3 response to target stimuli at parietal sites did not differ across tasks. For deviant stimuli, P3 was smaller in the all unusual and mixed stimulus task than in the all simple task, main effect of task, $F(2,46) = 5.23, p < .02$, especially at frontal sites, Task $\times$ Electrode site interaction, $F(6,138) = 11.66, p < .00005, \eta^2 = 0.42$. This result may have reflected the impact on P3 amplitude of a larger N2 response to deviant stimuli in the all unusual and mixed stimulus tasks.

### Viewing Durations

Viewing durations on the different stimulus types varied across tasks, Task $\times$ Stimulus type interaction, $F(4,92) = 22.09, p < .00005, \eta^2 = 0.34$. As shown in Figure 5, viewing durations on the unusual deviant stimuli in the all unusual task were significantly longer than on the simple deviant stimuli in the all simple task, $F(1,23) = 26.48, p < .00005$, or the mixed stimuli task, $F(1,23) = 18.70, p < .004$. There were no significant differences in viewing durations on the simple deviant stimuli of the latter two tasks. However, subjects looked at deviant stimuli longer than the repetitive background stimulus in each task, main effect of stimulus type, $F(1,23) = 32.14, p < .00005$, including the mixed stimuli task, $F(1,23) = 13.37, p < .002$. Viewing durations were shorter...
on the simple background stimuli in the all simple task than on the unusual background stimuli in the mixed stimuli task, $F(1,23) = 13.47$, $p < .002$, or the all unusual task, $p < .06$. Viewing durations also were shorter on the simple target stimuli in the all simple task than the unusual targets in the all unusual, $F(1,23) = 10.40$, $p < .004$, or mixed stimuli task, $F(1,23) = 18.06$, $p < .004$. Subjects looked at the unusual target stimuli in the mixed stimuli task longer than in the all unusual task, $F(1,23) = 4.77$, $p < .04$.

Correlations Between ERP Amplitude and Viewing Duration
Collapsing across tasks and stimulus types, the amplitude of the P3 response evoked by stimuli correlated with viewing duration (Spearman’s $\rho = 0.3$, $p < .0001$). In contrast, there was no correlation between N2 amplitude and viewing duration, $p > .6$.

Discussion
The major purpose of this study was to better understand the functional significance of the N2 evoked by novel visual stimuli and to delineate ways the N2 may differ from the novelty P3. The experiment was constructed so that the main difference among the three tasks was the relationship between background and deviant stimuli, which, depending on the task, either came from a set of simple, easily recognizable geometric shapes or a set of highly unusual, unfamiliar drawings.

Four major findings emerged, which can be summarized as follows: (1) deviance from long-term experience (unfamiliar/unrecognizable stimuli) had a marked impact on the visual N2 amplitude; (2) deviance from immediate context had a limited impact on the visual N2 amplitude; (3) frequency of stimulus presentation had little influence on the visual N2 amplitude; and (4) designated target stimuli had a limited effect on the visual N2 amplitude. The evidence for each of these observations is reviewed below.

First, deviance from long-term experience (unfamiliar/unrecognizable stimuli) was found to have a strong impact on visual N2 amplitude. Data supporting this conclusion include the following: Unusual deviants of the all unusual task evoked a larger N2 than simple deviants of the all simple and mixed stimuli tasks. The N2s

![Figure 4](image-url)

**Figure 4.** P3 amplitude in microvolts (mean ± SEM) at the Pz electrode site for each stimulus type across all three tasks.

![Figure 5](image-url)

**Figure 5.** Viewing duration in milliseconds (mean ± SEM) for each stimulus type across all three tasks.
evoked by unusual backgrounds and unusual targets of the all
unalusual and mixed stimuli tasks were larger than the N2s evoked
by simple backgrounds and simple targets of the all simple task.
Perhaps the most convincing evidence for this effect is that in
the mixed stimuli task, the N2 elicited by an unusual background
stimulus was larger than that evoked by simple deviant stimuli.
Germane to the issue of whether the novelty N2 and P3 are func-
tionally independent is the finding that this latter pattern of re-
sponse for the N2 is the opposite of that exhibited by the subsequent
P3, which was larger to the simple deviant stimuli than to the
unalusual background stimulus.
Second, whereas the study found that deviance from immediate
context had an impact on the visual N2 amplitude, this effect was
limited. The strongest evidence in support of the N2’s role in
responding to contextual deviance is that at midline sites in the all
unalusual task, unusual deviant stimuli evoked a larger N2 than the
unalusual background stimuli. However, in the all simple task, the
N2 was not larger for deviant than background stimuli. Moreover,
in the mixed stimuli task, simple deviant stimuli evoked an N2 that
was smaller than that evoked by the unusual background stimulus.
The limited impact of contextual deviance on N2 amplitude in this
study may have been due to the fact that the deviant stimuli oc-
curred at a higher probability than in many other studies in the
literature (i.e., $p = .15$ vs. .10–.12). However, this explanation
appears to be inadequate, because the probabilities used were suffi-
cient to evoke significantly larger P3 waves to deviant than to
background stimuli.

Third, frequency of stimulus presentation had little influence
over the visual N2 amplitude. In the all simple task, infrequent
deviants and infrequent targets did not evoke larger N2s than the
frequent backgrounds. In the all unusual task, the N2 amplitude of
infrequent targets was no larger than the frequent backgrounds.
Finally, in the mixed stimuli task, the frequent (unalusual) back-
ground stimulus elicited a larger N2 response than the infrequent
(simple) deviants.

Fourth, the study found that stimuli that were designated as
targets did not tend to augment the visual N2 amplitude. Evidence
for this interpretation includes the fact that in the all simple task,
the target stimuli did not elicit a larger N2 than the background
stimuli. Similarly, in the all unusual task, the N2 amplitude evoked
by the target stimuli was not larger than the N2 evoked by back-
ground stimuli.

In short, the central finding of the study is the major role that
unfamiliarity or unrecognizability (deviation from long-term ex-
perience) has on generating the visual N2. Several observations
require further comment, as they do not neatly fit the interpretation
being developed, and support the view that factors other than
unfamiliarity also contribute to the amplitude of the negative wave
between 200 and 325 ms. The findings in question tend to involve
the mixed stimuli task. The unusual background stimulus in the
mixed stimuli task evoked a larger N2 than the unusual back-
ground stimulus in the all unusual task. Similarly, the simple de-
viant stimuli of the mixed stimuli task elicited a larger N2 than the
simple deviant stimuli of the all simple task.

These findings raise the possibility that the degree of contrast
between background and deviant stimuli within the context of an
individual task may influence N2 amplitude in response to both
types of stimuli. In the mixed stimuli task, there was greater con-
trast between (unalusual) background and (simple) deviant stimuli
than in the other two tasks in which background and deviant stim-
uli came from the same class of figures (i.e., either all unusual or
all simple). This contrast may have resulted in a larger N2 response
to the unusual background stimulus in the mixed stimuli task than
at the unusual background stimulus of the all unusual task. Sim-
ilarly, the contrast may have augmented the N2 response to simple
deviant stimuli in the mixed stimuli task relative to the simple
deviant stimuli of the all simple task. This explanation supports the
notion that although contextual deviance may not make the largest
contribution to N2 amplitude, it does play a role.

Within the mixed stimuli task, the N2 amplitude elicited by the
unalusual background stimulus was larger than that elicited by the
unalusual target stimuli. One would have predicted that when hold-
ing the degree of unfamiliarity between background and target
stimuli relatively equal, the low frequency stimuli designated as
targets would have generated a larger N2. One explanation for this
finding involves the possible impact of the P3 on the N2, which is
larger to target than background stimuli. Because the P3 overlaps
temporally with the N2, this overlap could have resulted in a
smaller N2 peak to target stimuli. However, if this were the case,
we would expect that this overlap would be most influential pos-
teriorly, where the target P3b is the largest. In fact, the difference
in N2 amplitude between target and background stimuli was seen
at frontocentral sites and not at parietal sites. Thus, an overlapping
P3 on N2 is unlikely to account for all of the findings of the N2
response to target stimuli. Rather, frequency and target designation
appear to have a limited influence over the visual N2.

In the examples cited, it is conceivable that the particular figure
chosen from the set of all possible unusual figures to be the back-
ground stimulus in the mixed stimuli task was “more unusual” than
the one chosen to be the target stimulus in the same task or the
background stimulus of the all unusual task. Although we think
this explanation is unlikely to be correct, it would be appropriate
to control for this factor in future studies by varying across sub-
jects the particular stimuli used as the unusual background and
target stimuli. Also of interest would be to study the impact of
varying the difficulty discriminating target from background stim-
uli across tasks. Recent work by Comerchero and Polich (1998,
1999) has suggested that a central determinant of the (novelty)
ERP response (at least in terms of P3) is not how unusual (novel)
the deviant stimulus is, but rather the degree of difficulty discrimi-
nating between targets and backgrounds. Tasks that are more dif-
ficult require increased attentional focus, which when disrupted by
deviant stimuli, generate a larger response. Our study did not sys-
tematically manipulate target discrimination difficulty, so whether
this factor played a role in the outcome is uncertain.

A careful review of our results has suggested that the negative
wave evoked in the 200–325 ms temporal window does not have
the typical features of traditional members of the N2 family, such
as marked sensitivity to physical deviance from immediate context
(i.e., N2a), low stimulus probability (i.e., N2b), or target designa-
tion (i.e., N2c) (Naatanen & Picton, 1986; Pritchard et al., 1991).
Rather, the amplitude of this visual N2 appears to be more strongly
linked to unfamiliarity or deviation from long-term experience.1

One possibility for why this observation has not been reported
previously is that most investigations of the N2 have been in the
auditory modality (e.g., Baudena et al., 1995; Halgren et al., 1995a,
1995b; Ritter et al., 1968; Roth, 1973; Snyder & Hillyard, 1976;
Squires et al., 1975). Although studies have been conducted in the

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1 It is possible that if the experiment had used more electrode sites, a
negative wave (e.g., in the lateral-posterior region) may have been detected
within the N2 temporal window, the properties of which might have been
more consistent with previously identified members of the N2 family of
wave forms.
auditory modality in which deviant stimuli were novel sounds (e.g., Grillon, Courchesne, Ameli, Elmasian, & Braff, 1990; Grillon, Courchesne, Ameli, Geyer, & Braff, 1990; Holdstock & Rugg, 1995; Rugg et al., 1993), we are unaware of any studies that have explicitly manipulated the degree of unusualness of the background stimuli relative to target or deviant stimuli or focused on the N2 component of this response. Future investigations will need to determine if there is a form of the auditory N2 that has similar functional properties to the N2 demonstrated in the visual modality in the present study. We suspect that the special features of the negative wave observed in the current study are linked to the processing of nonverbal, figural material in the visual modality. In this regard, the wave form reported here has many of the characteristics of what recently has been called the “picture N300” wave (Barrett & Rugg, 1990; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999) that has been observed in object decision and relatedness judgment priming tasks. In such experiments, picture primes are followed by a target picture. In one version of the task, the subject makes speeded decisions about whether the target is a real object and in another version, whether the target is related to the prime.

The picture N300 has been defined as a frontally distributed negative wave in the 225–325 ms window that is largest in response to targets that are nonobjects or unidentifiable objects. Interestingly, such figures are similar to the set of unusual visual stimuli used in our experiment, and the electrophysiological response occurs in approximately the same temporal window as the visual N2 identified in the current study. The picture N300 also is evoked in response to unrelated real objects that deviate from expectations set up by the prime. However, the amplitude of this response is significantly smaller than that evoked by visual stimuli that deviate from long-term prior experience (i.e., in response to unidentifiable objects) (Holcomb & McPherson, 1994; McPherson & Holcomb, 1999). This negative wave seems to be specific to the processing of figural material. For example, an equivalent electrophysiological response has not been observed in analogous experiments using verbal material (i.e., priming experiments with unrelated or pseudowords as targets (Barrett & Rugg, 1990; Holcomb & Neville, 1990; McPherson & Holcomb, 1999).

Within the context of our experiment, the picture N300 wave or what we prefer to call the “visual novelty N2” wave may signal that a novel visual stimulus is not easily recognizable or encodable. This marker of unfamiliarity could indicate the likelihood that a stimulus has no readily available match in stored representations of known objects and thus deviates from long-term contexts. That a different response to unusual visual stimuli occurs within 325 ms after exposure suggests that the nervous system is capable of making a relatively rapid preliminary assessment that a visual image is unfamiliar, perhaps through a monitoring system that follows the output of a highly parallel search process. The anterior distribution of the visual N2 is consistent with the postulated role of the frontal networks in making decisions about novelty and familiarity (Metcalfe, 1993; Tulving, Markowitsch, Craik, Habib, & Houle, 1996; Tulving, Markowitsch, Kapur, Habib, & Houle, 1994).

Because the visual novelty N2 is sensitive to the nature of different kinds of stimuli, it seems unlikely to be simply registering the appearance of a visual stimulus (Stuss, Sarazin, Leech, & Picton, 1983). However, it is unclear whether the N2 is signaling that a novel visual stimulus requires additional processing to identify and make sense of it, or if the N2 represents the initiation of the processing itself. At frontal sites, the peak negative wave between 200 and 325 ms in response to unusual visual stimuli is followed by a prolonged negativity that persists until 600–700 ms. One possibility is that the novelty N2 reflects the categorization of a stimulus as unfamiliar. This function is in keeping with the role of some other members of the N2 family that are believed to be involved in the process of stimulus categorization (Naatanen & Picton, 1986; Pritchard et al., 1991; Ritter et al., 1979). The sustained anterior negativity that follows may index the activity of frontal systems that then serve to “look up” stored properties of objects that might contain elements of the difficult-to-identify figure (McPherson & Holcomb, 1999). Consistent with this notion are the findings of a positron emission tomography study investigating the processing of objects presented from noncanonical perspectives (Kosslyn et al., 1994). There was increased metabolic activity in the dorsolateral prefrontal cortex, which was interpreted as reflecting a top-down perceptual process of searching through stored data for potentially relevant visual information to interpret the presented stimulus.

The results of our study strongly suggest that stimulus unfamiliarity within the “local” context of an experiment is processed differently from stimulus unfamiliarity (unusualness) within the “global” context of a person’s prior experience (as represented in long-term stores). The novelty N2 wave identified in this study appears most sensitive to global, not local unfamiliarity. Supporting this interpretation, we found that the amplitude of the N2 response to unusual background stimuli did not decline across blocks, despite the fact that they were becoming increasingly familiar within the specific context of the experiment. Moreover, the N2 amplitude to these unusual background stimuli was larger than to simple stimuli that deviated from immediate context.

Although we suspect that the novelty N2 response is driven by unfamiliarity with a visual stimulus, the current experiment’s design cannot differentiate unfamiliarity from complexity. The unusual stimuli presented also tended to be more complex. In favor of the importance of unfamiliarity, previous investigations of the picture N300 have shown that the anterior negativity is larger in response to unidentifiable objects than unprimed real objects that exhibit a similar degree of complexity (Holcomb & McPherson, 1994; McPherson & Holcomb, 1999). One approach that could help disentangle the effects of complexity and unfamiliarity would be to compare the impact of deviant stimuli that were unfamiliar, but relatively simple (e.g., a distorted triangle) with deviant stimuli that were both unfamiliar and complex.

In summary, within the visual modality, the novelty N2 and the novelty P3 wave forms may reflect the processing of different aspects of “novel” visual stimuli. The novelty P3 is exquisitely sensitive to deviation from the immediate context in which a visual stimulus is presented. In contrast, although the novelty N2 can be enhanced by contextual deviance, it is exquisitely sensitive to deviation from long-term contexts that render a visual stimulus unusual and difficult to recognize. The complementary systems indexed by these electrophysiological responses allow an organism to process different dimensions of novelty, which may facilitate adaptive responses to a changing environment.

REFERENCES


(Received May 26, 1999; Accepted December 9, 1999)