

Reactivation of a Dormant Representation of an Auditory Stimulus Feature

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Abstract

■ Research with the mismatch negativity component of event-related potentials has uncovered a system that detects change in the acoustic environment on an automatic basis. The system is considered to compare incoming stimuli to representations of the past and to emit an MMN if change is detected. Previous investigations have shown that the relevant memory of the

past can become dormant and then be reactivated by a reminder stimulus. It is unclear, however, whether what is reactivated is an holistic representation of stimuli or separate representations of features of stimuli. The present study provides data that supports the latter possibility but leaves open the former one. ■

INTRODUCTION

Research with the mismatch negativity (MMN) component of event-related potentials (ERPs) has revealed a system that detects changes in the acoustic environment in an automatic manner (Näätänen, 1992). This deviance detection system is known because it emits an electrical signal (the MMN) when a change in previously repeating stimuli is detected. The signal has been found to be generated in the primary or immediately adjacent auditory cortex (Alho, 1995). For the system to detect change it must be able to compare current stimuli with representations of the past. Two of the questions that have been asked about this system are how long the memory it uses lasts and whether the system operates on acoustic features or gestalt representations of stimuli.

Current evidence indicates that the memory in question lasts about 10 sec (Cowan, Winkler, Teder, & Näätänen, 1993; Sams, Hari, Rif, & Knuutila, 1993). Because the duration of the memory is in the range of estimates of the duration of sensory memory (Cowan, 1984), it has been generally assumed that the deviance detection system obtains its information about the acoustic environment from sensory memory. However, Cowan et al. (1993) and Winkler, Cowan, Csépe, Czigler, and Näätänen (1996) also found that the system uses representations that have long-term memory characteristics. Specifically, they found that representations of

the past that are used to ascertain the occurrence of change can become deactivated and later reactivated (however, there are several interpretations of the concept of “activation,” as explained in Cowan et al. and the present discussion).

A number of studies have shown that the deviance detection system operates on both acoustic features analyzed separately and on specific combinations of features, possibly even including gestalt representations of the acoustic stimulus (for a review, see Ritter, Deacon, Gomes, Javitt, & Vaughan, 1995). For example, Gomes, Ritter, and Vaughan (1995) found that a MMN was elicited by infrequent changes in the duration of tones, even though the tones varied widely from trial to trial in intensity and frequency. In other words, the system tracked the duration of the tones while the combination of other features of the tones constantly changed (cf. Aulanko, Hari, Lounasmaa, Näätänen, & Sams, 1993; Huotilainen et al., 1993; Winkler et al., 1990). On the other hand, Gomes, Bernstein, Ritter, Vaughan, and Miller (1997) and Sussman, Gomes, Nousak, Ritter, and Vaughan (in press) found that the system tracks combinations of the features of stimuli, emitting an MMN when there is a change in the conjunction of features. In Gomes et al., three tones (termed *standards*) occurred frequently, each of which had a different combination of intensity and frequency. One tone (termed the *deviant*), which occurred infrequently, had the intensity of one of the

standards and the frequency of one of the other standards. The deviant, which had a combination of intensity and frequency not present in any of the standards, elicited an MMN. In Sussman et al., the combination of frequency and location were similarly manipulated. In addition, Czigler and Winkler (1996) found that a deviant would only elicit one MMN if it differed from previously repeating stimuli on two features, if the analysis of one of the two features is completed before the analysis of the other feature. This was accomplished by having the deviant differ from the standard in frequency and duration. The duration of the deviant was arranged such that the MMN based on duration peaked about 75 msec later than the MMN based on frequency. If the representation of the frequency and duration of the standard were only maintained separately, one would expect two MMNs, given that other studies (Levänen, Hari, McEvoy, & Sams, 1993; Schröger, 1995) have shown that two MMNs can be elicited by one deviant that differs from the standard on two features, when the two MMNs have approximately the same latency. The results of Gomes et al., Sussman et al., and Czigler and Winkler are consistent with gestalt representations of acoustic information.

In the studies that showed that the deviance detection system operates on individual features as well as holistic representations of features, the memory used by the system was considered to be transient in nature. In the experiments that showed long-term memory characteristics of the representations used by the system (Cowan et al., 1993; Winkler, Cowan, Csépe, Czigler, & Näätänen, 1996), it was not possible to distinguish whether the information maintained in long-term memory was stored as independent representations of given features or as holistic representations from which specific features of preceding tones could be accessed. In the present investigation, we set out to establish whether separate representations of acoustic features are maintained in the long-term store, which appears to occur in the transient store. To this end, the present study contained a condition similar to one used in Cowan et al. (1993), with one critical difference. A review of the conceptualization and experimental design of Cowan et al. may facilitate understanding the present study.

Cowan et al. (1993) reasoned that if it could be shown that a memory had become inactive or dormant, and that it could be reactivated by a single “reminder” stimulus, it would be reasonable to consider that long-term storage was involved. The basic experimental design consisted of the delivery of trains of nine tones (one tone every 610 msec) interspersed with 11 to 15 sec of silence. Within a train, all of the tones were of the same frequency or one of the tones (termed a *deviant*) differed in frequency from the other tones. The eight or nine tones of any given train that were identical (depending on whether or not a deviant was included) were termed *standards*. When a deviant was delivered, it randomly

appeared in either the first, second, fourth, sixth or eighth position of a given train. As in most studies that have examined the deviance detection system, subjects ignored the stimuli and read material of their own choosing.

Cowan et al. (1993) used two conditions. The purpose of the first condition was to establish how many standards need to be delivered in order for a deviant to elicit an MMN. In the *roving-standard* condition, the frequency of the standards differed from one train to the next, varying randomly among nine different frequencies. It was found that the first tone of the trains, which always differed in frequency from the standards of the immediately preceding train, did not elicit an MMN. Normally, an MMN would occur if there had not been an 11- to 15-sec interval of silence between the trains. A deviant presented in the second position (i.e., a tone that differed in frequency from that of the first tone) also did not elicit an MMN, but deviants presented in the fourth and later positions did elicit MMNs. The absence of an MMN to a deviant in the second position of a roving-standard condition was replicated in Winkler et al. (1996). Thus it was concluded that at least two or three standards must be delivered before a deviant can elicit an MMN. A related result was found by Winkler (1993), who presented pairs of tones, the first tone varying in frequency from one pair to another. The second tone of each pair was randomly identical to the first or differed from it in frequency. No MMN was elicited by the second tones that differed from the first tones, again indicating that more than one standard must be presented before a deviant tone can elicit an MMN.

The purpose of the second condition of Cowan et al. (1993) was to establish whether the memory for the standards of preceding trains had been saved in a form that had become inactive and could be reactivated by a reminder tone. In the *constant-standard* condition, the stimuli were delivered in the same way as just described, except that the frequency of the standards was constant across all trains. Deviants in the first position did not elicit an MMN, a finding that was attributed to an inactivation of the representation of the standards of the preceding train due to the interposition of an 11- to 15-sec period of silence. However, deviants in the second and later positions did elicit MMNs. In contrast to the roving-standard condition, then, presentation of only one standard in the current train was sufficient for a deviant to elicit an MMN. The key finding of the study was that a deviant in the second position did not elicit an MMN in the roving-standard condition but did in the constant-standard condition. As mentioned above, the absence of an MMN to a deviant in the second position of the roving-standard condition was attributed to the necessity of presenting two or three standards before an MMN could be elicited. The presence of an MMN to a deviant in the second position of the constant-standard condition after only one standard was attributed to a reactiva-

tion of the memory of the standards of the previous train or trains (all of which had the same frequency). The presentation of the first standard was deemed to function as a reminder of the representation of the previous standards. Evidence that the memory was in a dormant state at the beginning of each train was that deviants delivered in the first position of a train did not elicit an MMN. Additional evidence that the memory of the standard was in a dormant state was reported by Winkler, Cowan, et al. (1996). They replicated the result of the constant-standard condition, adding six interfering tones to the end of each train that varied among frequencies different from those of either the standard or deviant. The interfering tones rendered it unlikely that a viable representation of the standards was present in sensory memory at the onset of the next train. Because the relevant acoustic information could become dormant and subsequently be reactivated, this suggested to the authors that the information had been maintained in long-term memory while in the deactivated state.

Cowan et al. (1993) pointed out that the advantage of the constant-standard condition over the roving-standard one in eliciting an MMN to a deviant in the second position “indicates that the absolute pitch information itself must be held at least 11–15 sec in memory” (p. 918). The reason given was because “even a single presentation of the standard was sufficient to reactivate the representation of the standard tone” (p. 918). What is not clear from the extant data is whether the absolute frequency of the standard was maintained by itself while in the dormant state (i.e., in a separate representation from other features that might have been maintained), whether a representation based on feature integration was maintained that could be accessed to retrieve the absolute frequency of the standards, or perhaps that both kinds of representations were maintained.

The modification that we introduced into the design of Cowan et al. (1993) in the present study stemmed from the studies described above that indicated that the deviance detection system can operate on the basis of features. In the roving-standard condition of Cowan et al. (1993), the frequency of the standards of the trains was varied among nine different levels. A frequency deviant in the second position of this condition did not elicit an MMN. However, other features of the standards, such as their intensity, duration, and location, were constant across trains. The question we therefore examined was whether a tone in the second position that differed from the standards with regard to a feature that was held constant across trains would elicit an MMN, despite the variation in other features of the standards across trains. Accordingly, we used a design that was identical to the roving-standard condition except that deviants differed from the standards in intensity and only occurred in the second position. (Scherg, Vajsar, and Picton, 1989, have shown that the MMN is not affected by whether stimuli are presented in a random or nonrandom manner.) We,

therefore, had a roving-standard (or roving feature) condition with respect to frequency but a constant-standard (or constant feature) condition with respect to intensity. If an intensity deviant in the second position elicited an MMN, this would indicate that a long-term memory of the intensity of the standards of the previous train(s) had been maintained and was reactivated by the first tone of the train. That is, the first tone of a train would serve as a reminder of the intensity of the standards of the previous train(s). We also thought that an MMN elicited by an intensity deviant in the second position of our design would indicate that what had been reactivated was a separate representation of the intensity of the standards of the previous train(s). Were a tone to reactivate a holistic representation of the standards of the previous train, that is, a representation based on feature integration, it might be expected to serve as a reminder of all of its features. However, a finding that a given tone delivered in a similar stimulus environment would reactivate the representation of one feature (intensity in this instance) while not doing so for another feature (frequency in Cowan et al., 1993) would seem to support independent representation of acoustic features in the long-term storage (but have no bearing on holistic storage).

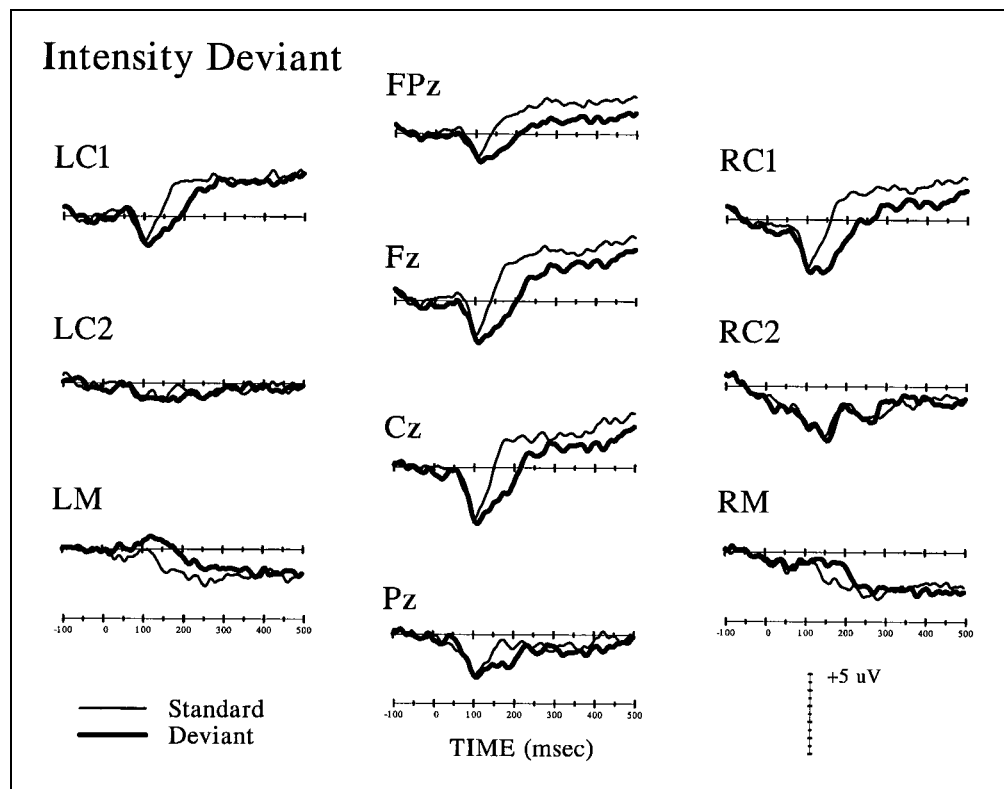
To extend the investigation to another feature, a second condition was employed in which intensity of the standards varied from train to train but with the standard frequency held constant across trains and with frequency deviants occurring in the second position of the trains. In this way, it could be determined whether the same deviant feature (frequency) that did not elicit an MMN in the second position of trains in the roving-standard condition of Cowan et al. (1993) would do so in the present design, in which intensity roves but frequency is held constant across trains.

RESULTS

Intensity Deviant Condition

In this condition the standards of the trains roved in frequency from train to train, and intensity deviants were presented in the second position of the trains. The grand mean ERPs across subjects for the standard (thin lines) and deviant tones (thick lines) in the second position of the trains are shown in Figure 1. At Fz the ERPs elicited by the deviant tones separated from those elicited by the standard tones at a latency of about 100 msec, being more negative for the deviants than the standards. Figure 2 depicts the grand mean difference waveforms customarily used to delineate the MMN by subtracting the ERPs elicited by the standards from the ERPs elicited by the deviants. The MMN peaked at about 170 msec, displaying a topography typically reported for an intensity deviant, being largest fronto-centrally, absent at LC2 and RC2, and inverted in polarity at the mastoids. Table 1 presents the

Figure 1. Grand mean ERPs elicited by the standards (thin curves) and deviants (thick curves) in the Intensity Deviant condition. In this and subsequent figures, stimuli were delivered at time zero.



mean amplitude across subjects of the voltage for the standard and deviant ERPs in the latency region of the MMN. The values were significantly different at Fpz, Fz, Cz, Pz, LC1, RC1, LM, and RM. At LC2 and RC2, where the MMN is usually not seen, a nonsignificant result was obtained.

Frequency Deviant Condition

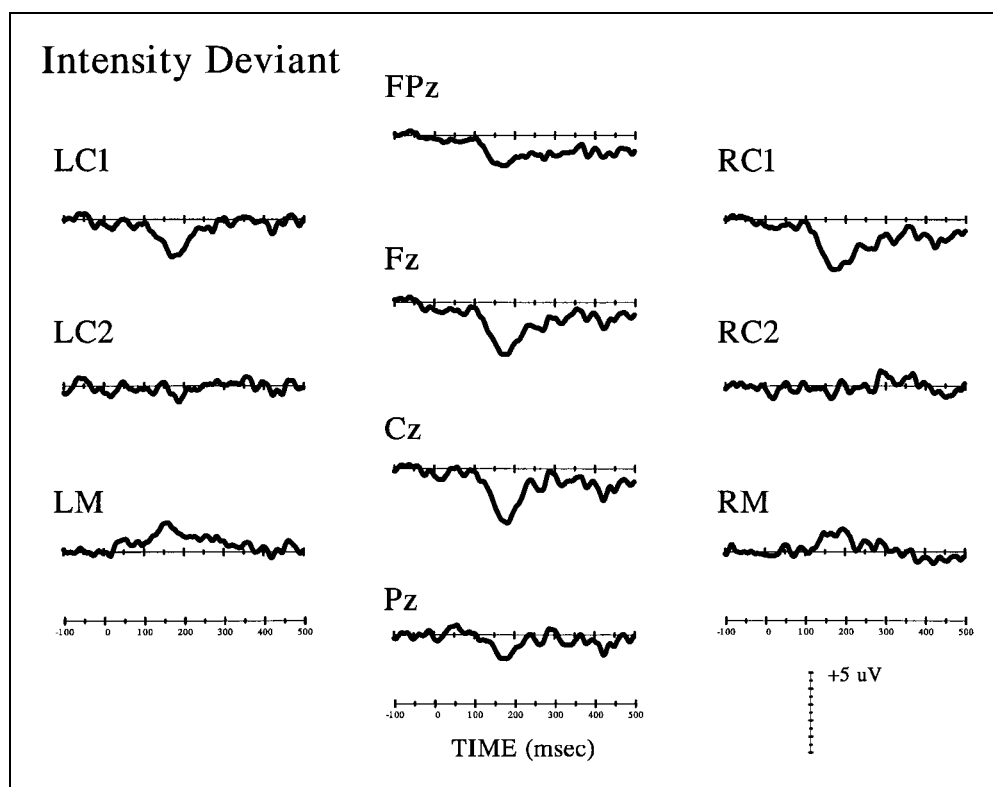
In this condition the standards of the trains roved in intensity from train to train and frequency deviants were presented in the second position of the trains. The grand mean ERPs across subjects for the standard (thin lines) and deviant tones (thick lines) in the second position of the trains are shown in Figure 3. The ERPs elicited by the deviant tones separated from those elicited by the standard tones at a latency of about 100 msec, being more negative for the deviants than the standards. Figure 4 depicts the grand mean difference waveforms used to delineate the MMN. As can be seen, the MMN was smaller and earlier than in the Intensity Deviant condition. The MMN peaked at about 130 msec, displaying a topography typical for a frequency deviant. Table 2 presents the mean amplitude across subjects of the voltage for the standard and deviant ERPs in the latency region of the MMN. The values were significantly different at Fpz, Fz, Cz, RC1, LC1, and LM. At LC2 and RC2, where the MMN is usually not seen, a nonsignificant result was obtained.

DISCUSSION

Taken together, the results of the two conditions indicate different states of affairs for the representation of the frequency and intensity of the standards at the time of the first position of the trains. In the Intensity Deviant condition, the representation of the frequency of the standard began *de novo* because of the periods of silence between trains and the variation in the frequency of the standards among the preceding trains. A representation of the frequency of the standards of the immediately preceding train might have been maintained in a dormant state in a longer-term memory, but this representation could not have been reactivated by the first tone of the next train because it differed in frequency from that of the standards of the preceding train. For intensity, the representation appears not to have begun *de novo* but, instead, to be associated with a reactivation of the long-term memory of the intensity of the standards of the preceding train(s), making it possible for a deviant in the second position to elicit an MMN. On this view, the long-term representation of the intensity of the preceding standards was reactivated independently of whatever long-term representation of the frequency of preceding standards persisted, suggesting that the representations of frequency and intensity were stored independently. Similar considerations apply to the Frequency Deviant condition, reversing the inferences made for the representations of intensity and frequency.

The results of the present experiment cannot be in-

Figure 2. Grand mean differences waveforms (deviant minus standard ERPs) obtained in the Intensity Deviant condition.



interpreted as due to reactivation of holistic representations of the standards of the preceding train maintained in long-term storage. The tones in the first position always had a different combination of values for its features than the standards of the preceding train. This was because the frequency of the standards in the Intensity Deviant condition and the intensity of the standards in the Frequency condition varied from train to train. It

would not be expected that a tone would reactivate holistic representations of previous standards if it had a different combination of features. However, this does not rule out the possibility that holistic representations are also maintained in the long-term store. In the constant-standard condition of Cowan et al. (1993) and Winkler, Cowan, et al. (1996), the combination of features of the tones in the first position *was* identical to that of the

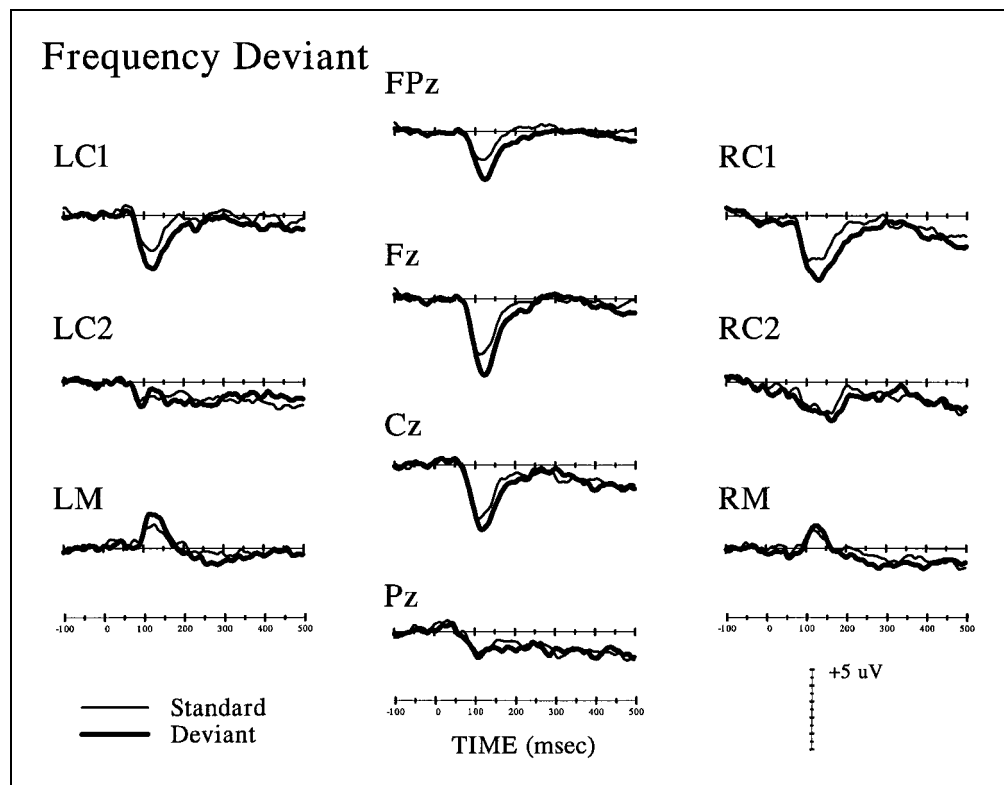
Table 1. Mean Amplitude (and Standard Deviation) in μV Across Subjects in the Intensity Deviant Condition of the Standard and Deviant ERPs, and the Difference Between Them, in the Latency Region of the MMN

Electrode	Standard	Deviant	Difference	F
Fpz	1.0 (2.2)	-0.7 (1.6)	-1.7 (2.6)	13.4 ^a
Fz	2.0 (2.3)	-0.9 (2.2)	-2.9 (2.3)	40.0 ^a
Cz	1.4 (2.2)	-1.6 (3.2)	-3.0 (2.8)	41.2 ^a
Pz	-0.6 (2.6)	-1.9 (2.5)	-1.3 (2.3)	7.5 ^a
RC1	0.8 (2.6)	-2.1 (1.6)	-2.9 (2.2)	37.9 ^a
RC2	-1.9 (2.5)	-2.1 (1.9)	-0.3 (2.2)	0.3
RM	-1.9 (1.7)	-0.7 (1.7)	1.2 (1.4)	6.2 ^b
LC1	1.8 (2.6)	-0.3 (2.2)	-2.1 (2.4)	19.8 ^a
LC2	-0.4 (2.0)	-1.0 (1.4)	-0.5 (2.1)	1.4
LM	-1.3 (1.6)	0.1 (1.4)	1.4 (1.0)	9.0 ^a

^a $p < 0.01$.

^b $p < 0.05$.

Figure 3. Grand mean ERPs elicited by the standards (thin curves) and deviants (thick curves) in the Frequency Deviant condition.



standards of the preceding trains. Therefore, it is ambiguous whether the first tones of the trains in their study reactivated an holistic representation of the preceding standards, a separate representation of the frequency of the preceding tones, or both.

Our results, along with those of Cowan et al. (1993) and Winkler, Cowan, et al. (1996), show that long-term memories are made concerning the acoustic properties dealt with by the deviance detection system. Questions pertaining to these results concern how it comes about that these memories are stored in a longer form as well as where in the flow of information they are stored. It seems unlikely that representations of the acoustic past, relevant to the deviance detection system, reach a more durable form simply because they have occurred. Instead, a more reasonable possibility is that the original representations of sensory input are altered or transformed by the system such that they enter a long-term state. This possibility may best be understood in the context of considering that the system itself constructs memories.

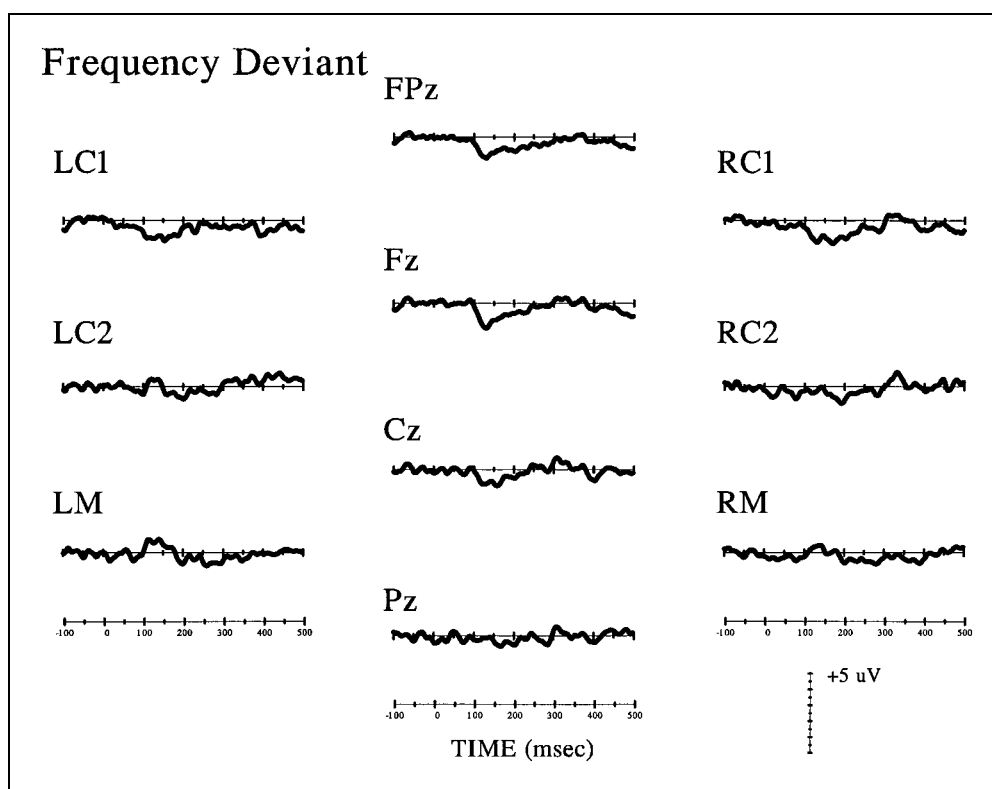
It has been shown that at least two standards must be delivered before a deviant elicits an MMN (Winkler, Cowan, et al., 1996). Cowan et al. (1993) suggested that the reason for this is that the deviance detection system must develop a norm or invariance concerning the acoustic environment for it to detect deviance. Schröger (1997) has proposed that the encoding of the relevant acoustic input may be characterized in terms of “the actual stimulus input” (termed *R*) and “invariants inher-

ent in the recent stimulation” (termed *R'*). For convenience, we will adopt the *R* and *R'* notation.

Schröger (1997) has shown that *R'* encoding requires a period of time. Trains of 4 or 11 tones that consisted of all standards or standards followed by a deviant. The two sets of trains had constant stimulus onset asynchronies (SOAs) of 40 or 200 msec. The amount of time that elapsed between the onset of the first tone and the onset of the deviant in a given train, therefore, was either 120, 400, 600 or 2000 msec. MMNs were elicited by deviants for the latter three periods of time but not for the 120 msec amount of time. Consequently, the time to encode *R'* is somewhere between 120 and 400 msec.

One of the most important developments in investigations of the deviance detection system is the demonstration of the more complex kinds of *R'* encoding that the system is capable of establishing. Whereas early studies indicated that the system identified invariances pertaining to simple features, such as frequency, intensity, and the like, more recent investigations have shown that the system also detects invariances that span a series of sounds, such as sequential patterns (Schröger, Näätänen, & Paavilainen, 1992) and even abstract relations (Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992). In Tervaniemi, Maury, and Näätänen, (1994) most tones decreased in frequency from one trial to another, and infrequently a tone was either the same frequency or was higher in frequency than the preceding tone. In Saarinen et al. (1992), pairs of tones decreased in frequency from the first to the second tone of a pair most

Figure 4. Grand mean difference waveforms (deviant minus standard ERPs) obtained in the Frequency Deviant condition.



of the time, and infrequent pairs increased in frequency from the first to the second tone. In addition, the absolute frequencies of the pairs of tones were randomly varied across several levels. The MMNs elicited by the infrequent events in these two experiments indicate that the system identifies patterns of acoustic events of an abstract nature. Note that what is identified as an invariance is not contained in sensory memory's initial (R) record of recent acoustic events but, rather, is formulated

on the basis of an analysis of what is contained in that record.

There are two basic ways in which R could be accessed in order to formulate R'. One way would be for the system to examine what is contained in sensory memory each time a stimulus occurs, reformulating all the various invariances it is capable of identifying on the basis of the information contained in that particular scan. This would mean that the system would need to refor-

Table 2. Mean Amplitude (and Standard Deviation) in μV Across Subjects in the Frequency Deviant Condition of the Standard and Deviant ERPs, and the Difference Between Them, in the Latency Region of the MMN

<i>Electrode</i>	<i>Standard</i>	<i>Deviant</i>	<i>Difference</i>	<i>F</i>
Fpz	-1.4 (1.1)	-2.5 (1.5)	-1.1 (0.7)	11.7 ^a
Fz	-2.9 (1.9)	-4.1 (2.6)	-1.2 (1.1)	15.4 ^a
Cz	-2.6 (2.4)	-3.4 (3.0)	-0.8 (1.4)	6.7 ^b
Pz	-1.0 (1.9)	-1.2 (2.4)	-0.2 (1.0)	0.5
RC1	-2.6 (1.7)	-3.7 (2.5)	-1.1 (1.1)	12.2 ^a
RC2	-1.6 (1.9)	-1.9 (2.4)	-0.3 (0.9)	0.6
RM	0.8 (0.7)	1.1 (1.2)	0.3 (0.9)	0.7
LC1	-1.8 (2.0)	-2.8 (2.3)	-1.0 (2.2)	12.4 ^b
LC2	-0.9 (1.1)	-0.7 (1.5)	-0.3 (0.8)	0.7
LM	1.2 (1.0)	1.9 (1.1)	0.7 (1.4)	4.8 ^b

^a < 0.01 .

^b < 0.05 .

mulate all the various invariances it is capable of identifying each time a new event occurs. Another way would be for the system to make representations of the invariances extracted from sensory memory and store them in memory for a set period of time. In this way, the inefficiency of reestablishing invariances that continue to apply each time a new stimulus occurs would be eliminated.

A reason for believing that the R' encodings are maintained in memory pertains to the finding that the memory that underlies the system persists for about 10 sec (Cowan et al., 1993; Sams et al., 1993). Consider a situation in which the memory in question has a duration of 10 sec and tones are delivered at the rate of one every 8 sec. Assume, also, that for this situation two presentations of a standard are needed for a deviant to elicit an MMN (as in Winkler, Cowan, et al., 1996). The first standard tone is delivered at time zero, the second at time 8 sec, and a deviant that differs from the standard in frequency is presented at time 16 sec. If the system operates by reformulating R' each time a new stimulus occurs, it could not determine that an invariance applies with respect to the deviant at time 16 sec because the representation of the first standard would no longer be in memory. However, if the system operates by storing R' in memory, it would establish the invariance concerning frequency associated with the standard on its second presentation and store that in memory for, say, 10 sec. Because the deviant follows the establishment of R' at time 8 sec by 8 sec, it should be capable of eliciting an MMN at time 16 sec. Because it is known that the MMN can be elicited with interstimulus intervals of 8 and more sec (Böttcher-Gandor & Ullsperger, 1992; Czigler, Csibra, & Csontos, 1992; Sams et al., 1993; Gomes et al., in press), the data favor the view that the system stores the R' representations for a period of time. This view is compatible with the hypothesis of Winkler, Karmos, and Näätänen (1996) and Näätänen and Winkler (submitted) that the system maintains a constantly updated model of the recent acoustic environment across trials and makes (pre-attentive) inferences about future events.

There is evidence that when the system makes an R' representation, it does so abruptly rather than gradually and that after a passage of time it deactivates the memory abruptly. Cowan et al. (1993) found that the amplitude of the MMN elicited in position 4 of their roving-standard condition was as large as the amplitude of the MMNs elicited by deviants in all subsequent positions. The roving-standard condition is the best method devised to date to investigate the construction of invariances because the system may be considered to begin anew in constructing representations of the standard with each train of stimuli. On the other hand, whereas in studies of the duration of the memory underlying the system the MMN is not observed at intervals greater than about 10 sec (Cowan et al., 1993; Sams et al., 1993), a

uniform finding is that there is no decrease in the amplitude of the MMN (when it is obtained) as the interval is increased (Böttcher-Gandor & Ullsperger, 1992; Czigler, Csibra, & Csontos, 1992; Gomes et al., in press; Mäntysalo & Näätänen, 1987; Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1987; Sams et al., 1993; Schröger, 1996; Schröger & Winkler, 1995). Thus, it appears that if a curve were constructed of the amplitude of the MMN as a function of time alone, it would onset abruptly, maintain a constant amplitude, and then offset abruptly. This suggests the activation, maintenance, and deactivation of R' representations by the deviance detection system.

Part of the answer to the question of how a longer-term representation is made with respect to the record of the recent acoustic past, then, is that the deviance detection system transforms the R record into R' representations, which are stored in memory. It is not clear, however, whether all R' representations take on the more durable duration observed in this and other studies, in the sense of being capable of being reactivated after becoming dormant (Cowan et al., 1993; Winkler, Cowan, et al., 1996) or whether R' representations require additional reinforcement before they do so. In all three of the studies just mentioned, the constant-standard (or constant-feature-standard) condition was the only condition delivered in a given session. Consequently, it is not known whether these long-term memory representations were based on the immediately preceding train or on some accumulation of many preceding trains. However, the creation of R' does appear to be an essential step.

Concerning the question of where the dormant representations that are reactivated are stored, Cowan et al. (1993) suggested they are stored in long-term memory. A related question is where R' representations are stored when initially created. One possibility, which Schröger (1997) adopted, is that they are stored in the long phase of sensory memory. This is a reasonable inference because the duration of R' representations appears to be similar to those of the long phase of sensory memory (Cowan, 1984). Another possibility is that they are stored where they are created (i.e., in the deviance detection system). If that were the case, the R' representations that are in a deactivated state would reside in the same place as when they are in an activated state. Hence, deactivated R' representations would remain in the system and be readily available to it when a reminder stimulus occurs. This is consistent with the observations that led to the view described above that the deviance detection system is responsible for the activation, maintenance, and deactivation of R' representations.

Cowan et al. (1993) presented an alternative interpretation of their result that a deviant in the first position of the trains in the constant-standard condition did not elicit an MMN. The 11- to 15-sec period of silence between the trains could have distanced the deviant from

the preceding train of standards, thereby putting it out of context. This interpretation is similar to distinctiveness theories concerning recency effects (Crowder, 1993; Neath & Crowder, 1990) and short- and long-term modality effects (Glenberg, 1987). Were this view to be supported, it would mean that what is reactivated by the standard in the first position is the context within which the frequency or intensity of the standard of the preceding train(s) applied. In any case, it is not just the frequency or intensity of the standards of the preceding train(s) that is reactivated but the R' representation that the frequency or intensity is an invariance of the preceding train(s).

METHOD

Subjects

Ten young adults (eight women) were subjects in the first (intensity deviant) condition and ten young adults (three women) were subjects in the second (frequency deviant) condition. Two of the subjects participated in both conditions. All of the subjects were paid for their participation in the experiment.

Experimental Procedure

The subjects sat in a comfortable chair and ignored the stimuli, reading a book of their choice. The stimuli were pure tones of 100-msec duration (5% rise/fall times) presented binaurally via insert earphones. Each run included 36 trains of tones. Stimulus onset asynchrony within a train was 600 msec. The time between trains was 11, 12, 13, 14, or 15 sec, selected on a random basis without replacement. There were 12 runs in the experiment and a break between each run.

Intensity Deviant Condition

Within trains, all of the standard-tones had the same frequency, but the frequency of the standards differed from one train to another. The frequency of the standards was either 420, 465, 510, 555, 600, 645, 690, 735, or 780 Hz. There were four random orders of the nine standard-tone frequencies in a run. The intensity of the tones was 70 dB SPL except that, on alternate trains, the intensity of the second tone in a train (the deviant) was 60 dB SPL.

Frequency Deviant Condition

Within trains, all of the standard-tones had the same intensity, but the intensity of the standards differed from one train to another. The intensity of the standards was either 63, 66, 69, 72, 75, 78, 81, 84, or 87 dB SPL. There were four random orders of the nine standard-tone intensities in a run. The frequency of the tones was 600

Hz except that, on alternate trains, the frequency of the second tone in a train (the deviant) was 735 Hz.

ERP Recording

Brain electrical activity was recorded using dc-coupled amplifiers, with a low-pass filter setting of 40 Hz. Midline electrodes were placed at Fpz, Fz, Cz, and Pz. Lateral electrodes were placed along a coronal chain from Fz to each mastoid consisting of electrodes one-third of the distance from Fz to the mastoid (LC1 and RC1 for the left and right coronal chain, respectively), two-thirds of the distance from Fz to the mastoid (LC2 and RC2) and the left (LM) and right (RM) mastoids. The reference was the nose. Ocular potentials were monitored with bipolar electrodes placed at the outer canthi and above and below the left eye. Trials on which electrical activity exceeded $\pm 75\mu\text{V}$ at all but the horizontal EOG recordings were automatically rejected. All recordings were subsequently assessed visually for residual artifact. Recordings began 100 msec prior to stimulus onset and extended 500 msec poststimulus.

Data Analysis

The 12 runs in each condition were combined for each subject. Grand mean ERPs, averaged across subjects, were obtained for display purposes and were used to select a latency window for amplitude measurement of the MMN. The largest negativity at Fz between 100 and 200 msec in the grand mean difference waveforms (standard minus deviant waveforms) was designated the latency of the MMN. The latency selected for the Intensity Deviant condition was 170 msec and for the Frequency Deviant condition was 130 msec. For each subject and recording site, the mean voltage of the ERPs elicited by the standards and deviants in the second position was measured across a latency window from 25 msec before to 25 msec after the peak latency selected for each condition. To establish the presence of the MMN, planned comparisons (Hays, 1963) were calculated to determine whether the mean amplitude of the standards and deviants in the latency region of the MMN differed at each recording site. The mean square error terms used for these comparisons were calculated separately for each condition.

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