There is a striking similarity between the FM-specific effects we have shown and those for AM shown by Wojtczak and Viemeister (2005): the size of the effect, temporal characteristics, and the modulation frequency selectivity are similar. A possible account for the present data is similar to that we suggested for AM forward masking: there are modulation frequency-selective neural circuits/modules that adapt in the presence of FM and recover their sensitivity after a relatively brief postexposure interval. There are physiological data suggesting that in cortex there is such a phenomenon that occurs for AM (Bartlett and Wang 2007). We know of no evidence that tuned, adaptable "detectors" exist for FM.

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Chapter 10
Electrophysiological Correlates of Intensity Resolution Under Forward Masking

Daniel Oberfeld

Abstract Nonsimultaneous masking can severely impair auditory intensity resolution, but the effect strongly depends on the stimulus configuration. For example, an intense forward masker causes a pronounced impairment in intensity resolution for standards presented at intermediate levels, but not for standards presented at low and high levels, resulting in a midlevel hump pattern (Zeng et al., Hear Res 55:223–230, 1991). Several aspects of the phenomenon cannot be explained by mechanisms in the auditory periphery. For instance, backward maskers cause midlevel humps at least as large as the humps caused by forward maskers. The present experiment was aimed at studying the relation between the effects of forward maskers on intensity resolution and on the slow components N1 and P2 of the auditory evoked potential. The EEG was recorded while listeners performed a one-interval intensity discrimination task in quiet and under forward masking. The 90-dB SPL masker caused a stronger reduction in sensitivity for a 60-dB SPL than for a 30-dB SPL standard, reflecting the midlevel hump. The effect of the masker on the N1 and the P2 amplitude paralleled the behavioral effects. The amplitude reduction caused by the masker was stronger for the 60-dB SPL than for the 30-dB SPL standard, thus also following a midlevel hump pattern. Listeners who showed a strong N1 midlevel hump tended to also exhibit a strong midlevel hump in sensitivity.

Keywords Auditory intensity discrimination • Forward masking • Signal detection theory • Auditory evoked potentials • N1 • P2

10.1 Introduction

Zeng et al. (1991) were the first to demonstrate that an intense forward masker (e.g., 90 dB SPL) causes strongly elevated intensity-difference limens (DLs) for a midlevel pure-tone standard, relative to the DL in quiet. On the other hand, there is

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only a small effect of the masker on the DLs for standards presented at low and high levels, resulting in the so-called *midlevel hump in intensity discrimination*, which is observed for masker-target intervals up to 400 ms (Zeng and Turner 1992). Although several explanations for the effects have been suggested, none of them is capable of accounting for the complete range of findings (Oberfeld 2008, 2009). Zeng et al. (1991) proposed that the effect was due to adaptation of low spontaneous-rate (SR) auditory nerve neurons showing slower recovery from prior stimulation than high-SR neurons (Relkin and Doucet 1991). However, subsequent experiments provided evidence for a contribution of more central mechanisms. In this context, two important findings are the midlevel hump caused by backward maskers, and the influence of the masker-target similarity on the masker-induced reduction in intensity resolution.

The fact that the midlevel hump is observed with backward maskers (Plack and Viemeister 1992) places a rather strong constraint on the potential physiological origins. For instance, if the neural response to the target persisted longer than 100 ms, then a backward masker presented 100 ms after target offset could interfere with this neural activity by terminating or reducing it. At the level of the auditory nerve (Harris and Dallos 1979), the cochlear nuclei (Rhode 1991), or the inferior colliculus (Nuding et al. 1999), no evidence for persistence over an interval of 100 ms has been reported, however. On the other hand, neuronal activity has been observed at up to 500 ms after signal offset in the medial geniculate body (Aitkin and Dunlop 1969) and in the auditory cortex (Brosch et al. 1999). A second potential explanation for the effect of a backward masker on intensity resolution would be that the masker presented in the first observation interval produces adaptation or inhibition, and therefore reduces the neural response to the target presented in the second interval. However, the two observation intervals were separated by more than 500 ms in the relevant experiments. Thus, to account for a midlevel hump at least as strong with backward maskers as with forward maskers (Plack and Viemeister 1992), it would be necessary to identify neuronal elements for which the adaptation by preceding stimulation is equally strong at a 100 ms masker-target interval (as with forward maskers) and at a 500-ms interval (as with backward maskers). Such a characteristic has not been observed at early processing stages (e.g., Aitkin and Dunlop 1969; Shore 1995). However, recovery times of several hundred milliseconds were found for neurons in the auditory cortex (e.g., Schreiner et al. 1997; Wehr and Zador 2005). Thus, both in terms of persistence and inhibition, the primary auditory cortex seems to be the first structure in the ascending auditory pathway that has physiological properties compatible with the midlevel hump caused by backward maskers (cf. Brosch et al. 1998).

Another finding suggesting central processing stages as the origin of the midlevel hump is *similarity effects* (for a review see Oberfeld 2008). For instance, Schlauch et al. (1997) found that adding a 4.133-kHz "cue tone" to a 1-kHz forward masker strongly reduced the size of the midlevel hump for a 1-kHz standard, presumably by helping the listeners to differentiate between the masker and the standard. A related finding is that a 10-ms forward masker causes a stronger DL elevation for a midlevel 10-ms standard than does a 250-ms masker (Schlauch et al. 1997).

The latter result is incompatible with adaptation in the auditory nerve that *increases* with the duration of the masker (e.g., Harris and Dallos 1979). Instead, the two findings suggest an effect of the *perceptual similarity* of masker and standard, akin to the well-established effects of the target-distractor similarity in auditory perception and other domains (e.g., Baddeley 1966; Duncan and Humphreys 1989; Kidd et al. 2002). Oberfeld (2008) also discussed whether the midlevel hump *per se* could be a similarity effect. In earlier experiments, a fixed-level, intense masker had been combined with various standard levels, so that the *masker-standard level difference* and the standard level were correlated. For a low-level standard, the level difference was always larger than for a medium-level standard. Thus, the different DL elevations at different standard levels could have been due to the variation in the masker-standard level difference rather than to the variation in standard level, as previous studies assumed. The data by Oberfeld (2008) showed, however, that the effect of a forward-masker is stronger at midlevels even if the masker-standard level difference is controlled, thus providing an even stronger definition of the midlevel hump. To account for the similarity effects, Oberfeld (2008) proposed a model based on the loudness enhancement hypothesis (Carlyon and Beveridge 1993), which assumes a relation between the masker-induced impairment in intensity resolution and masker-induced changes in target loudness (Oberfeld 2007).

Motivated by the evidence for central origins of the midlevel hump, the present combined psychoacoustic and event-related potentials (ERP) experiment for the first time studied the effect of forward maskers on sensitivity in an intensity discrimination task and on the long-latency component waveforms N1 and P2 of the auditory evoked potential (AEP; cf. Picton et al. 1974). The EEG was recorded while the listeners actively performed a one-interval intensity discrimination task (Oberfeld 2006). The N1 is evoked by a relatively abrupt change in acoustic energy at a given frequency and peaks approximately 100 ms after stimulus onset (cf. Näätänen and Picton 1987). It is in part generated by an auditory-specific supratemporal source located in primary auditory cortex. There are at least two other sources contributing to the N1, one located in the lateral temporal lobe, and one unknown source probably located in the frontal lobe (e.g., Giard et al. 1994). The supratemporal subcomponent appears as a positive deflection at the mastoids if the nose is used as the reference (Näätänen and Picton 1987). According to the concept by Näätänen and Winkler (1999), the N1 indexes the storage and the processing of a stimulus in auditory sensory memory and represents a *sensory feature trace* (Durlach and Braida 1969; Massaro 1975; Cowan 1984). At this point, it should be noted that in more general terms, the effects of backward maskers and the influence of the masker-target similarity can be viewed as effects on the *memory representation* of target intensity (Plack and Viemeister 1992; Carlyon and Beveridge 1993; Oberfeld 2008). In this line of thinking, we expected the N1 to reflect the behavioral consequences of a forward masker in an intensity discrimination task. Note, however, that for our stimuli, the N1 amplitude is unlikely to be a direct correlate of the target level presented on a given trial, that is, to be higher if the standard-plus-increment rather than the standard is presented. This is because the N1 is a response to sound onset and is correlated with the overall sound pressure level (e.g., Mulert et al. 2005), so that the rather small level difference between the standard and the standard-plus-increment (e.g., 60 dB SPL versus 65 dB SPL) should have only a very small effect on the N1 amplitude (Tanis 1971). Rather, we assume that the N1 amplitude reflects the precision of the sensory trace representation of intensity.

Although the P2 has often been treated as unitary with the N1 (e.g., Davis and Zerlin 1966), there is growing evidence that the P2 represents an independent component (Crowley and Colrain 2004). The functional significance is less clear than for N1, but it has been suggested that positive deflections in the AEP occurring around 200 ms after sound onset might be related to stimulus classification and discrimination (Novak et al. 1992).

10.2 Method

Eleven normal-hearing listeners participated in the experiment. One of them was the author, the others were volunteers who received partial course credit or payment and provided written informed consent according to the Declaration of Helsinki. Due to a poor EEG data quality, the data of two subjects were excluded from the analyses. The remaining nine participants (two men) were between 21- and 35-year-old and right-handed.

The stimuli were generated digitally, played back via an RME ADI/S digital-to-analog converter (f_S=44.1 kHz), attenuated (TDT PA5), buffered (TDT HB7), and presented to both ears via Sennheiser HDA 200 headphones. EEG was recorded with a NeuroScan SynAmps system.

A one-interval, two-alternative forced-choice intensity discrimination task was used (absolute identification; Braida and Durlach 1972). On each trial, a pure-tone standard with a frequency of 1 kHz and a duration of 50 ms (including 5-ms ramps) was presented. A level increment was added to the standard with an a-priori probability of 0.5. The task was to decide whether the softer tone (standard) or the louder tone (standard-plus-increment) had been presented. The level increment was fixed within each block. A 30-dB SPL and a 60-dB SPL standard were presented in quiet, and combined with a 90-dB SPL forward masker. The forward masker was a 1-kHz sinusoid with a duration of 100 ms (including ramps). The silent interval between masker offset and standard onset was 120 ms.

The experiment consisted of six sessions in which only behavioral data were collected (termed *psychoacoustics sessions* in the following), followed by one session in which EEG was recorded while the listeners performed the same identification task. Visual trial-by-trial feedback was provided in the psychoacoustics sessions but not in the EEG session, in order to avoid visually evoked potentials.

Sessions 1 and 2 were practice sessions. In session 3, an individual level increment was selected, which was used in the main experiment. Intensity resolution was measured for a 60-dB standard in quiet, and for a 30-dB SPL and 60-dB SPL standard combined with a 90-dB SPL forward masker. On the basis of the resolution-per-dB ($\delta = d'/\Delta L$) per listener and condition (Durlach and Braida 1969), one individual level increment ΔL_i was selected, so that the arithmetic mean of the sensitivity in the easiest and in the most difficult condition could be expected to be $d'=1.6$. This increment was used in the subsequent sessions constituting the main experiment. ΔL_i ranged from 2.9 to 9.0 dB (M=5.0 dB, SD=1.97 dB). In each of the sessions 4–6, three 120-trial blocks were presented for each of the four masker/standard level combinations, with ΔL fixed to the individually selected value. In session 7, in which EEG was recorded, the same stimuli and the same task as in sessions 4–6 were used. Three 46-trial blocks were run for each masker/standard level combination.

For each block, the sensitivity (d') was calculated on the basis of a signal detection theory (SDT) model assuming equal-variance Gaussian distributions (Green and Swets 1966). The "log-linear correction" for extreme proportions was used (cf. Hautus 1995).

The EEG was recorded at 21 electrode sites compatible with the 10–20 system (Fp1, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, O2, and mastoids LM and RM), using the nose as reference. Vertical and horizontal electro-oculograms (EOGs) were also recorded. Impedances were kept below 5 kΩ. The sampling frequency was 500 Hz. The EEG was filtered online with a 70-Hz low pass, and offline with a 1–20 Hz band pass. For artifact rejection, a standard deviation criterion of 30 μV in a 200-ms window for electrode Fz and the vertical and horizontal EOG was used. AEPs were analyzed in 750-ms epochs with a prestimulus baseline of 200 ms. The valid epochs were averaged for each subject and experimental condition separately, namely for each combination of standard level (30, 60 dB SPL), masker level (in quiet, 90 dB SPL), and target type (standard, standard-plus-increment), and then averaged across all subjects to obtain the grand mean waveforms. As can be seen in Fig. 10.2, the 100-ms masker started at 0 ms, followed by the 50-ms target after a silent interval of 120 ms. The N1 and P2 amplitudes were calculated as the mean voltage in the 40-ms period centered at the peak in the grand average waveform. In quiet and in forward masking, the N1-component peaked at 90 ms and 104 ms after target onset, respectively. The peak of the P2-component occurred at 176 ms and 190 ms after target onset in quiet and in forward masking, respectively. The channels Fz and Cz, where the largest responses were obtained (Näätänen and Picton 1987; Crowley and Colrain 2004), were pooled for the statistical analysis.

10.3 Results and Discussion

10.3.1 *Sensitivity*

Mean sensitivity in the psychoacoustics sessions is shown in panel A of Fig. 10.1. In quiet, the sensitivity was higher for the 60-dB SPL than for the 30-dB SPL standard, $t(8)=4.79$, $p=0.001$ (two-tailed), reflecting the near-miss to Weber's law.

Paired-samples *t*-tests indicated that the masker-induced decrease in sensitivity was significant at the 30-dB SPL standard level, $t(8)=5.01$, $p=0.001$ (two-tailed), as well as at the 60-dB SPL standard level, $t(8)=8.38$, $p=0.001$ (two-tailed). In previous experiments using an adaptive procedure, the midlevel hump was defined as a stronger masker-induced elevation of the intensity DL (relative to the DL in quiet) for a midlevel standard than for a low-level or high-level standard (Zeng and Shannon 1995). The DLs measured via an adaptive procedure correspond to a fixed level of sensitivity, d' can be assumed to be proportional to ΔL (e.g., Jesteadt et al. 2003), and in the present experiment, a constant level increment was used for a given listener in all conditions. Therefore, we expected the 90-dB SPL masker to cause a stronger decrease in d' at the 60-dB SPL than at the 30-dB SPL standard level, compatible with the midlevel hump. The sensitivity was analyzed via a repeated-measures analysis-of-variance (ANOVA) based on a univariate approach. The two within-subjects factors were masker level and standard level. Partial η^2 is reported as a measure of effect. There was a significant Masker Level × Standard Level interaction, $F(1, 8)=49.46$, $p<0.001$, $\eta^2=0.86$, compatible with a midlevel hump. The effect of standard level and the effect of masker level was also significant [$F(1, 8)=10.46$, $p=0.012$, $\eta^2=0.57$ and $F(1, 8)=48.89$, $p<0.001$, $\eta^2=0.86$, respectively].

In order to check whether the stronger masker-induced reduction in d' at the 60-dB SPL standard level could be due to a floor effect, a test by Marascuilo (1970) was used to determine whether d' was significantly higher than 0 for a given listener and masker/standard level combination. The hits and false alarms were pooled across the three blocks obtained per condition. For two listeners, d' was not significantly higher than 0 ($p>0.05$, one-tailed) in the forward masking conditions. With the data from these two listeners excluded, a Masker Level × Standard Level repeated-measures ANOVA again showed a significant Masker Level × Standard Level interaction, $F(1, 6)=57.91$, $p<0.001$, $\eta^2=0.91$. Thus, the stronger masker-induced reduction in sensitivity at the 60-dB SPL than at the 30-dB SPL standard level cannot be attributed to a floor effect.

Sensitivity in the EEG session, which is not displayed due to space limitations, showed a pattern very similar to sensitivity in the psychoacoustic sessions, apart from a general reduction in sensitivity that was likely due to the absence of trial-by-trial feedback.

10.3.2 Auditory-Evoked Potentials

The grand-mean AEPs in quiet are shown by the dashed lines in Fig. 10.2, averaged for standard and standard-plus-increment (see below). The AEPs are depicted for the most informative electrodes Fz and Cz, and the left mastoid (LM). As can be seen by the confidence intervals in panels B and C of Fig. 10.1, all tones elicited a significant N1 and P2 component. At the mastoids, the characteristic polarity inversion was observed (Näätänen and Picton 1987). A Standard Level × Target Type

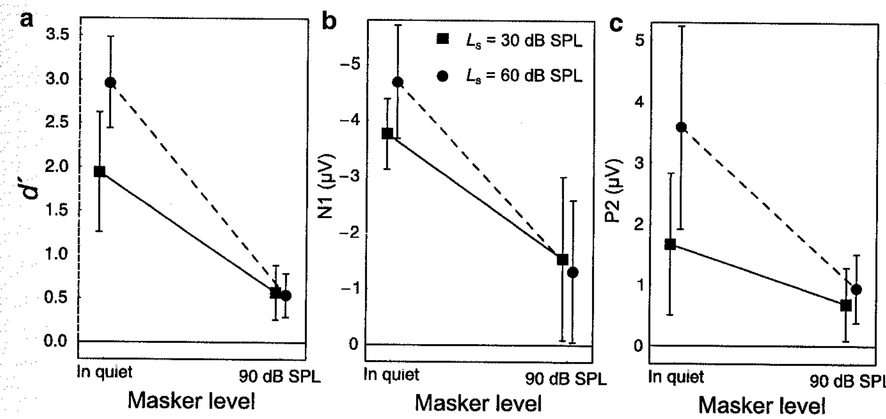

Fig. 10.1 Panel **a**: Mean sensitivity (d') in the absolute intensity identification task as a function of masker level and standard level (L_S). The level increment was individually selected and constant across all masker/standard level combinations. *Squares*: 30-dB SPL standard. *Circles*: 60-dB SPL standard. Panels **b** and **c**: Mean N1 and P2 amplitudes in response to the target. Pooled channels Fz and Cz; responses to standard and standard-plus-increment averaged. *Error bars* show 95% confidence intervals

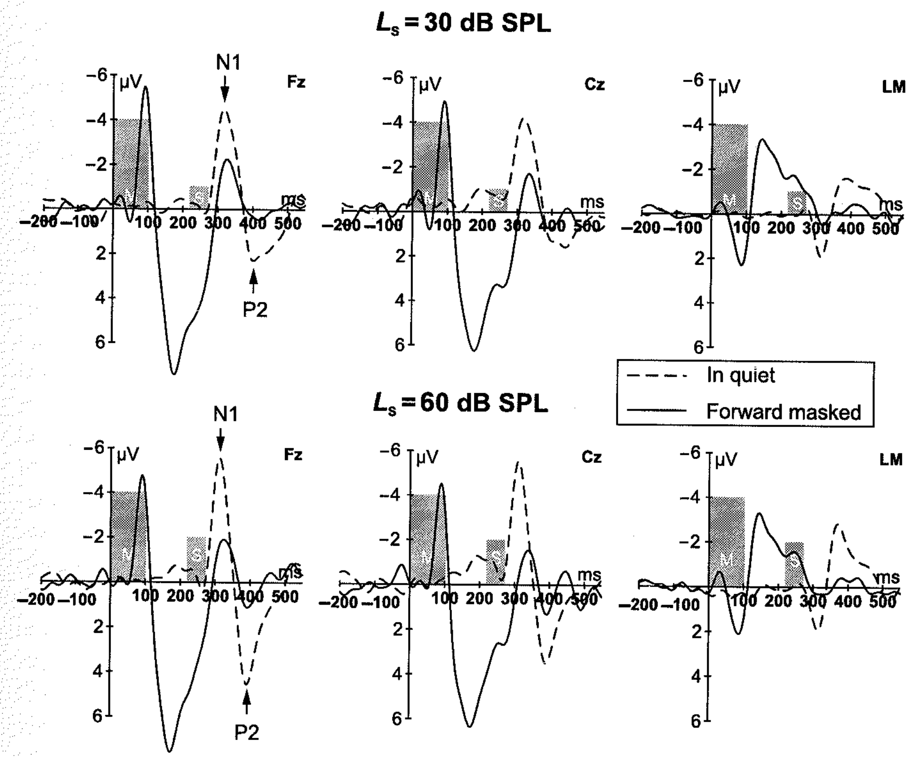

Fig. 10.2 Grand mean event-related potentials at electrode positions Fz, Cz, and LM. *Dashed curves*: target tone presented in quiet. *Solid curves*: with 90-dB SPL forward masker. *Upper row*: 30-dB SPL standard. *Lower row*: 60-dB SPL standard. The *gray rectangles* indicate the temporal positions of masker (*M*) and standard (*S*). In the in quiet condition, the masker was omitted

(standard, standard-plus-increment) repeated-measures ANOVA conducted on the N1 amplitude at pooled electrodes Fz and Cz showed a marginally significant increase with standard level, $F(1, 8)=4.81$, $p=0.060$, $\eta^2=0.39$, compatible with previous findings concerning the intensity dependence of the N1 (e.g., Adler and Adler 1989; Mulert et al. 2005). The N1 amplitude in response to the standard-plus-increment was not significantly higher than in response to the standard, $F(1, 8)=0.17$, $p=0.70$. This result is compatible with data by Tanis (1971); see above. The Standard Level × Target Type interaction was not significant, either, $F(1, 8)=0.40$, $p=0.55$.

The N1 was followed in time by the P2. There was a significant effect of standard level on the P2 amplitude, $F(1, 8)=45.1$, $p<0.001$, $\eta^2=0.85$. The effect of target type and the Standard Level × Target Type interaction failed to reach significance, $F(1, 8)=1.17$, $p=0.31$, and $F(1, 8)=3.17$, $p=0.113$, respectively. Because there were no effects involving target type, neither for N1 nor for P2, the amplitudes of the responses to the standard and to the standard-plus-increment were averaged in all further analyses.

The solid lines in Fig. 10.2 show the AEPs in the masking conditions. As can be seen in Fig. 10.1, panels B and C, the forward-masked N1 and P2 amplitudes to the target tones were small but significantly different from 0 μV. The N1 and P2 amplitudes followed a similar pattern as the sensitivity (Fig. 10.1). The forward maskers caused a decrease in both the N1 and the P2 amplitude, at the 30-dB SPL standard level [N1: $t(8)=2.83$, $p=0.022$ (two-tailed); P2: $t(8)=2.11$, $p=0.068$ (two-tailed)] as well as at the 60-dB SPL standard level [N1: $t(8)=4.41$, $p=0.002$ (two-tailed); P2: $t(8)=3.60$, $p=0.007$ (two-tailed)]. The reduction in the N1 and in the P2 amplitude caused by the forward masker was stronger for the 60-dB SPL than for the 30-dB SPL standard, just as the reduction in sensitivity was stronger for the midlevel standard. Thus, the N1 and P2 amplitudes showed a pattern compatible with the midlevel hump. This observation was partially confirmed by two Masker Level × Standard Level repeated-measures ANOVAs conducted separately for the N1 and the P2 amplitudes. For the N1, the Masker Level × Standard Level interaction was marginally significant, $F(1, 8)=3.74$, $p=0.089$, $\eta^2=0.32$. The effect of masker level was also significant, $F(1, 8)=15.41$, $p=0.004$, $\eta^2=0.66$. The standard level had no significant effect on the N1-amplitude, $F(1, 8)=1.53$, $p=0.25$, $\eta^2=0.16$. In the P2 time window, there was a significant Masker Level × Standard Level interaction, $F(1, 8)=7.76$, $p=0.024$, $\eta^2=0.49$. The effects of standard level and masker level were also significant, $F(1, 8)=58.51$, $p<0.001$, $\eta^2=0.88$, and $F(1, 8)=11.30$, $p=0.01$, $\eta^2=0.59$, respectively.

At this point, it should be noted that contamination of the response to the target by residual activity resulting from the forward masker presents a potential problem for the interpretation of the data. However, exactly the same 90-dB SPL masker preceded the 30-dB SPL and the 60-dB SPL target tone at exactly the same ISI. Therefore, under the usual assumption of linear additivity of the EEG responses (e.g., Hansen 1983), it is valid to compare the two conditions with respect to the masker-induced amplitude reduction. Consequently, the conclusion that the amplitude reduction caused by the 90-dB SPL masker was

stronger at the intermediate standard level is unchallenged by potential residual activation. Could the different amounts of reduction in the N1 amplitude caused by the masker at the two different standard levels be due to the refractoriness of the N1 (e.g., Budd et al. 1998)? As the N1 subcomponents have refractory periods of 3–10 s (Näätänen and Picton 1987), a forward masker identical in frequency to the target can reduce the amplitude of the N1 to the target because the time interval between the target and the sound preceding it is considerably shorter than in quiet. However, in the present experiment, the temporal configuration was identical at the two standard levels. Therefore, it is unlikely that refractoriness caused the stronger N1 amplitude reduction at the intermediate standard level.

10.3.3 *Relation Between the Behavioral and Electrophysiological Consequences of Forward Masking*

The mean data displayed in Fig. 10.1 show a similar pattern for sensitivity and for the N1 and P2 amplitudes, and the statistical analyses confirmed this similarity. But was the relation between the behavioral and the electrophysiological consequences of a forward masker suggested by these data also present at the level of the individual? Imagine a listener for whom the masker had a stronger effect on sensitivity than for the 30-dB SPL standard. Does such a listener showing a strong "behavioral" midlevel hump also exhibit a strong "AEP" midlevel hump in the sense that the masker has a stronger effect on the N1 amplitude at the 60-dB SPL than at the 30-dB SPL standard level? To answer this question, we first computed the masker-induced reduction in sensitivity, $\Delta d' = d'(\text{quiet}) - d'(\text{masked})$, for each subject and standard level. The difference between the reduction in d' at the 60-dB SPL and the 30-dB SPL standard level ($\Delta d'_{60} - \Delta d'_{30}$) is a measure for the behavioral midlevel hump. Similarly, the difference between the N1 amplitude reduction at the two standard levels ($\Delta N1_{60} - \Delta N1_{30}$) is a measure for the AEP midlevel hump. As can be seen in Fig. 10.3, these two differences were positively correlated, Spearman rank correlation coefficient $r_s=0.63$, $p=0.034$ (one-tailed), $N=9$. For the P2, the correlations between the difference in the d' reduction between the two standard levels and the difference in the amplitude reduction were not significant ($r_s=-0.017$). As Fig. 10.3 shows, the masker had a stronger effect on d' at the 60-dB SPL than at the 30-dB SPL standard level for all listeners, while for the N1, there were three listeners showing the opposite pattern, evident by negative values on the x-axis. These data are of course at odds with the assumed correlation between the d' and the N1 midlevel hump. Inspection of the individual data indicated, however, that two of the negative values on the x-axis seem to be due to problems with the EEG data, because for one of the three listeners, the N1 amplitude was *positive* at the 30-dB SPL standard level under masking, and for another listener, the N1 amplitude at the 60-dB SPL standard level was higher under masking than in quiet.

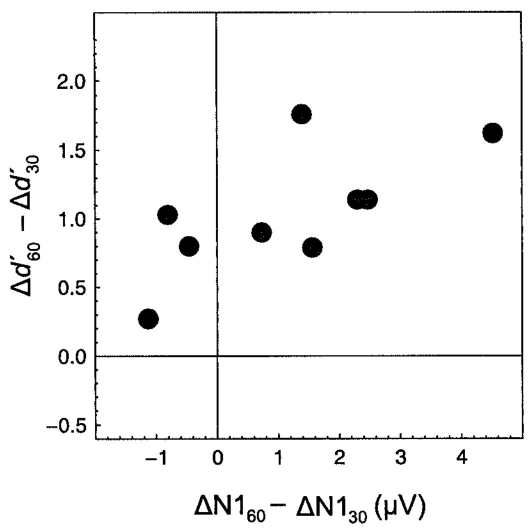

Fig. 10.3 Relation between the midlevel humps in sensitivity and in the N1 amplitudes. *Horizontal axis*: difference between the reduction in the N1 amplitude at the 60-dB SPL and the 30-dB SPL standard level ($\Delta N1_{60} - \Delta N1_{30}$), which is a measure for the N1 midlevel hump. *Vertical axis*: difference between the reduction in d' at the 60-dB SPL and the 30-dB SPL standard level ($\Delta d'_{60} - \Delta d'_{30}$), which is a measure for the behavioral midlevel hump. Each *data point* represents one listener

10.4 Summary

The experiment studied the effects of forward masking on intensity resolution and on the cortical auditory evoked potentials N1 and P2 to the target. The effects of the forward maskers on the N1 and P2 amplitudes paralleled the behavioral reduction in sensitivity because all showed a midlevel hump pattern. At the level of the individual, we found a relation between the masker-induced sensitivity reduction and the reduction in the N1 amplitude. Thus, the N1 represents an electrophysiological correlate of the effects of nonsimultaneous masking on intensity resolution. This finding is compatible with suggestions that the masker-induced reduction in sensitivity can be understood in terms of effects on the memory representation of target intensity (cf. Oberfeld 2008) because the N1 indexes the processing in auditory sensory memory (Näätänen and Winkler 1999). For the P2, the relation to the behavioral effects was less clear cut.

It would be interesting to study electrophysiological responses from processing stages preceding or following the processing stage indexed by N1, in order to further narrow down the locus of the mechanisms causing the midlevel hump in intensity discrimination. For example, Näätänen and Winkler (1999) proposed that the auditory feature trace is transformed into a long lasting and partially analyzed auditory stimulus representation, which is indexed by the *mismatch negativity* (MMN; for a recent review see Näätänen et al. 2007). Many studies found that the MMN is closely related to psychophysical performance (cf. Näätänen and Alho 1997), to a greater extent than the N1. Thus, the MMN amplitude and latency can be expected to exhibit an even stronger correlation with intensity resolution than the N1.

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Chapter 11
Neuronal Measures of Threshold and Magnitude of Forward Masking in Primary Auditory Cortex

Ana Alves-Pinto, Sylvie Baudoux, Alan Palmer, and Christian J. Sumner

Abstract Psychophysical forward masking is an increase in the threshold of detection of a brief sound (probe) when preceded by another sound (masker). These effects are reminiscent of the reduction in physiological responses following prior stimulation. However, previous studies of the response of auditory nerve fibers (Relkin and Turner, 1988) found probe threshold shifts following stimulation that were considerably smaller than those found perceptually. Although such threshold shifts are larger in some units of the cochlear nucleus (Ingham et al., 2006), these are either inhibitory interneurons or project to inhibitory neurons. A better account is obtained at the level of the IC in the awake marmoset (Nelson et al., 2009).

In the present study, we measure responses of neurons in the primary auditory cortex of the anesthetised guinea pig to forward masked pure tones. Signal detection theory methods are used to infer probe detection thresholds. The objective is to determine whether forward masked thresholds in cortical neurons are higher than those of sub-cortical neurons.

Changes in the neurometric function (the computed % correct against probe level) due to prior stimulation are diverse: for some units the function is shifted towards higher probe levels; for others the slope of the function becomes shallower. Thresholds shifts (e.g., 50 dB for a 60-dB SPL masker) calculated for individual units are on average much larger than seen in sub-cortical nuclei. Across the population, the minimum thresholds are also larger than the thresholds observed psychophysically. There is little evidence that persistent activity in response to the masker is contributing to masking.

Keywords Forward masking • Primary auditory cortex • Guinea pig • Signal detection theory

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Preface

This volume contains the papers presented at the 15th International Symposium on Hearing (ISH), which was held at the Hotel Regio, Santa Marta de Tormes, Salamanca, Spain, between 1st and 5th June 2009.

Since its inception in 1969, this Symposium has been a forum of excellence for debating the neurophysiological basis of auditory perception, with computational models as tools to test and unify physiological and perceptual theories. Every paper in this symposium includes two of the following: auditory physiology, psychophysics or modeling. The topics range from cochlear physiology to auditory attention and learning. While the symposium is always hosted by European countries, participants come from all over the world and are among the leaders in their fields. The result is an outstanding symposium, which has been described by some as a "world summit of auditory research."

The current volume has a bottom-up structure from "simpler" physiological to more "complex" perceptual phenomena and follows the order of presentations at the meeting. Parts I to III are dedicated to information processing in the peripheral auditory system and its implications for auditory masking, spectral processing, and coding. Part IV focuses on the physiological bases of pitch and timbre perception. Part V is dedicated to binaural hearing. Parts VI and VII cover recent advances in understanding speech processing and perception and auditory scene analysis. Part VIII focuses on the neurophysiological bases of novelty detection, attention, and learning. Finally, Part IX describes novel results and ideas on hearing impairment. Some chapters have appended a written discussion by symposium participants; a form of online review that significantly enhances the quality of the content. In summary, the volume describes state-of-the-art knowledge on the most current topics of auditory science and will hopefully act as a valuable resource to stimulate further research.

It is not possible to organize a meeting of this size and importance without a considerable amount of help. We would like to express our most sincere thanks to the organizing team: Almudena Eustaquio-Martín, Jorge Martín Méndez, Patricia Pérez González, Peter T. Johannesen, and Christian Sánchez Belloso, whose expertise and willing help were essential to the smooth running of the meeting and preparation of this volume. Many thanks also to the staff of the Fundación General de la Universidad de Salamanca for their skillful and unconditional support with the administrative aspects of the organization. We are very grateful for the generosity