The effect of spatial separation of signal and noise on masking in the free field as a function of signal frequency and age in the mouse

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Masking of low- (4 kHz) and high-frequency (25 kHz) signals by one-octave bandpass maskers either spatially coincident with the signal or contralateral to it was examined in mice, 4–6 and 20–22 months of age, in the free field. Signals were presented 120 ms prior to a startle stimulus and differences in their inhibition of the startle reflex, relative to startle stimulus alone trials, were used to measure the severity of masking. Inhibition was reduced or eliminated by spatially coincident noise for weak but not for relatively intense signals, providing the type of “loudness recruitment” effect characteristic of human listeners in similar stimulus conditions. The spatial separation of the signal and its masker relieved this maskingleike effect for the high-frequency pair in both young and old mice. In contrast there was no beneficial effect of the shift in spatial location for the low-frequency pair at either age. This finding of masking release for high- but not low-frequency stimuli supports the hypothesis that the sound shadow provided by the head and pinna would yield a favorable signal-to-noise level difference for a contralateral masker and an ipsilateral signal only at very high frequencies in the mouse. The presence of masking release in these old mice, a first generation hybrid strain with near-normal high-frequency hearing in ABR measures, agrees with reports that the masking release resulting from a similar manipulation in aged human listeners with minimal high-frequency hearing loss is the equal of that obtained in the young listener. © 1998 Acoustical Society of America. [S0001-4966(98)07008-8]

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INTRODUCTION

The purpose of the present experiment was to determine whether the masking of a tonal signal by noise would be relieved by their spatial separation in mice, and whether either the degree of masking or the degree of masking relief afforded by the shift in location would be affected by the frequency of the signal or by the age of the mouse. The experiment was performed under free field conditions using the methods of reflex modification audiometry (Young and Fechter, 1983). These methods have been used in human listeners, both those with normal hearing and the hearing impaired, to provide objective behavioral evidence for the masking of weak signals by noise, and for loudness recruitment at high signal levels under masking conditions (Reiter and Ison, 1979) and they are readily adapted to study similar problems in laboratory animals (Hoffman and Ison, 1991). One rationale for examining this sensory phenomenon in the mouse follows from the observation that the many inbred strains of mice and their hybrid offspring provide animal models that capture various types of age-related hearing loss [see especially Willott (1996) for a recent review of this work and its implications]. The neural substrates of age-related hearing loss as well as the genetics of hearing loss are being vigorously investigated in the C57BL/6J strain, often contrasted with the CBA strain. In the present research we used the first generation (F1) hybrid mouse of a C57 × CBA pairing, which yields offspring with minimal individual differences within a group and a relative minor hearing loss with age, as the first generation hybrid offspring have better hearing than either of the parent strains (for example, Erway et al., 1993; Henry and Chole, 1980; Li and Borg, 1991). The study of masking and masking release in this mouse may provide a useful vehicle for subsequent physiological analyses, and add to our general understanding of these phenomena as they appear in different groups of human listeners.

There are many studies of the beneficial effects for stimulus detection of varying the spatial location (or laterality) of signals and maskers in human listeners, with the general outcome that the hearing impaired and the elderly profit less from the spatial separation of signal and masker in either the free field (Colburn et al., 1982; Duquesnoy, 1983; Warren et al., 1978) or under earphones (Grose et al., 1994; Pichora-Fuller and Schneider, 1991). These findings are consistent with other data showing the elderly to be less successful in sound localization than young normal listeners (Colburn, 1982; Colburn et al., 1987; Tonnig, 1975). However, some data indicate that the benefit of spatial separation of signals from maskers is lost not with age alone, but only when age is combined with hearing impairment, so that, e.g., the advantage provided by this manipulation for elderly listeners with minimal hearing impairment is the same as that seen in young listeners under free field conditions, both groups doing better that aged listeners with severe mid- and high-frequency hearing loss (Gelfand et al., 1988). This last report indicates that the critical cues which the elderly human listeners use in this task are those provided by high-
frequency components of the signal and the masker: An impo-

As far as we can determine, there are no published be-
havioral analyses of sensory processing in laboratory animals
that have examined the relationship between auditory masking
and the relative locations of signals and their maskers
with age or with hearing impairment. Heffner and Donnell
(1993) have studied the related problem of auditory spatial
location in the C57 strain, finding that old mice were less
sensitive to differences in spatial location than younger mice.
The authors attributed this deficit to the age-related high-

The conceptual problem is that as a binaural phenomenon, is appropriate for describing the auditory performance of any species which has an audiogram restricted to the very high frequencies, and for which changes in signal location must be coded by interaural differences in signal level. (And this question is also relevant for the human listener when level differences are manipulated independently of temporal differences under artificial earphone conditions.) The conceptual problem is that as a high-frequency signal moves away from the spatial location of the noise masker then it necessarily moves away from one ear and toward the other. Depending in detail on the head-related transfer function across frequency (Shaw, 1974, for humans; McFadden and Willott, 1994a, for mice), then it can be expected that the level of the signal must increase at one ear and decrease at the other; and if the masker is fixed in position, then the signal-to-noise ratio must necessarily increase at one ear and must necessarily decrease at the other. Thus when relative signal-to-noise interaural level differences are provided by shifts in the relative locations of signal and noise any beneficial effect this might have on the severity of masking is “binaural” only in the sense that the binaural listener has one ear for which the signal-to-noise ratio has necessarily improved; and the listener must differentially weight this ear over the other.

For this reason, a demonstration in the mouse that the severity of masking is reduced when a signal is moved away from a masker is an instance of “binaural unmasking” only in the sense that the data demand that the mouse can differentiate between the inputs at the two ears and be more responsive to the ear that provides the better signal-to-noise ratio. (This analysis for the mouse is exactly that proposed for the human listener by Bronkhorst and Plomp, 1988, when isolated level differences were used to indicate the spatial locations of signals and maskers. Listeners with asymmetric high-frequency hearing losses were shown not to benefit from shifts in spatial location when the more favorable signal-to-noise ratio was presented to the impaired ear.) It is of considerable interest that McFadden and Willott (1994b) have recently provided electrophysiological evidence for “location unmasking” of this sort in young anesthetized C57 mice. Tone-evoked single unit activity in the inferior colliculus contralateral to the signal increased when a masker was moved away from the signal, showing thus a physiological analogue of the binaural masking level difference. This unmasking-like effect was not evident in older mice with a high-frequency hearing loss, which is consistent with the deficit in spatial location ability described by Heffner and Donnell (1993). However, the physiological effects provided by McFadden and Willott do not necessarily imply that a similar unmasking phenomenon can be demonstrated in a behavioral analysis. In their experiment the experimenters (not surprisingly) chose to measure activity in the inferior colliculus contralateral to the signal; but if they had measured activity on the side ipsilateral to the signal they would have surely found more masking, not less masking, as the masker was moved away from the signal, because the masker would then be moving to the more favorable contralateral position. In order for a similar unmasking effect to appear in a behavioral experiment, we must assume that the mouse is also able to selectively use just that part of the central auditory system contralateral to the signal that provides the better signal-to-noise ratio.

In the present experiment we masked high (25 kHz) and low (4 kHz) tonal signals in one-octave bandpass noise centered on the signal, with masker and noise either spatially coincident or separated by 180 degrees, left and right. The subjects were first generation offspring of C57BL/6J and CBA/CaJ mice. They have the typical high-frequency hearing of mice and show “hybrid vigor” compared to their parents, having minimal high-frequency hearing loss with age (Erway et al., 1993). Two independent hypotheses were tested. First, if release from masking does occur in the mouse, then it should be evident only for the high-frequency signal. Second, if the older mice have no high-frequency hearing impairment, then they should also have no age-related decline in the strength of masking release that is
found following a shift in the relative spatial locations of signal and masker in young mice.

I. METHOD

A. Subjects

The subjects were 12 male mice, the F1 hybrid offspring of CBA/CaJ males and C57BL/6J females. The original breeding stock was obtained from Jackson Laboratories. Six mice were 4 months of age at the beginning of testing, and 6 were 20 months of age. They were group housed in the University of Rochester vivarium under constant climate control and a 12/12 hour normal light/dark cycle, and tested in the daylight hours. Food and water were available ad libitum.

B. Apparatus

The subject was confined for testing in a movable frame made up of six pairs of vertical wire rods (0.125 cm diameter, 1 cm apart), which were brought up lightly alongside the torso from the hind end to just short of the ears. The subject’s head was fixed in place by cementing a wooden Q-tip to the skin on the top of the head, this projecting slightly downward from a fastener to run along the back of the mouse. The head was not held absolutely rigid by this device, but in the lightly tranquilized mouse any movement of the head was minimal. The holding apparatus was secured on top of a suspended acrylic platform that had been covered with a sound absorbent material, and was mounted directly over an attached accelerometer (model SA-2-300, Statham Laboratories, Beverly Hills, CA). This assembly was placed in a double walled sound-attenuating room (inside dimensions approximately 2 m on a side), constructed by the Industrial Acoustics Company, Bronx, NY. White noise that was used for the startle stimulus was provided by a white noise generator, then shaped by an electronic switch and attenuated by a programmable attenuator, all constructed at the University of Rochester. This stimulus was amplified on one channel of a wide band stereo amplifier then delivered through a high-frequency speaker (model 075-105C, JBL Sound Inc., Los Angeles, CA), placed vertically directly over the subject’s head, at a distance of 32 cm. The startle stimulus was 25 ms in duration, with 5-ms rise/decay times, and was set at 115 dB SPL (linear scale). On a Bruel & Kjaer sound-level meter (model 2203, Naerum, Denmark) the startle stimulus varied by no more than ±3 dB at octave bands centered at 4–16 kHz, dropping by 10 dB at 32 kHz.

Thirty cm and 90 degrees off the midline to the left and to the right of the subject were two Sony MDR-004 head phone speakers, 180 degrees apart. The left speaker was used to present a sinusoidal prepulse of 4 kHz or 25 kHz which had a total duration of 40 ms including 15-ms rise/decay times. This signal was generated by a Krohn-Hite model 4400A function generator, gated through a electronic switch, then amplified. Its level was set by a second programmable attenuator constructed at the University of Rochester, and varied between 30 and 80 dB SPL, in 10-dB steps. Bandpass noise was presented on some trials, with the noise source passed through a 1-octave bandpass filter centered at the signal frequency, and then to an attenuator to create the two 50-dB bandpass maskers, 1-octave wide. The masker was either mixed with the signal and presented through the left speaker, or was directed to the right hand speaker. Signal and masker levels were measured using the external filter of the B&K sound level meter and a ¼-in. microphone.

On the recording side of the experiment, the force of the animal’s response to the intense noise burst was detected by the accelerometer. The output of the accelerometer was passed through a bridge amplifier and integrated over a 100-ms period beginning with the onset of the startle stimulus. Stimulus presentation and response recording were under computer control.

C. Procedure

In this experiment it was important that the head of the animal be fixed in place so that the stimuli would be presented at a consistent spatial location. For this reason the subjects were lightly sedated for testing, using chlorpromazine (‘‘Tardaxen’’), a neuroleptic dopamine antagonist that at higher doses is in common use to tranquilize awake animals for electrophysiological experiments (e.g., Walton et al., 1997). The dose was titrated across animals and across days to be sufficient to maintain the animal in a quiet posture during testing, without eliminating startle behavior. Initially the animals were injected with about 0.3 mg/kg (IM) and the dose was progressively increased by as much as 0.1 mg/kg as the subjects developed higher levels of tolerance over the course of the experiment. The subjects were placed in a quiet environment for 45 min after the injection to allow the drug to take effect, and sometimes a supplementary dose was given at the end of this rest period. If the startle reflex was strongly depressed or if the animal began to move then testing was discontinued for that day.

The mice received trials in which the startle stimulus was delivered alone or preceded by the tonal prepulse, presented at a lead time of 120 ms (signal onset to startle onset), with the signal variously set at 30, 40, 50, 60, 70, or 80 dB SPL. Trials were given in blocks of eight trials, each block containing two control startle alone trials and one each of the signal levels, these given in random order. There were six different types of blocks, resulting from the 2×3 factorial design of two types of signal (4 kHz and 25 kHz, presented on the left) and three masking conditions (no masker, masker on left, and masker on right). On every day of testing the subjects were presented at least once with all six test conditions in random order, allowing for their even representation at a subject’s level of sedation across all conditions. If sedation continued after running the first set of conditions, the subject continued to be tested through another set of testing conditions. If the sedation wore off before completing a full set either the mouse received additional sedative and was retested on all conditions in that set, or was allowed to rest and started at the beginning of that set of test conditions on the next scheduled test day. This experiment was carried out over a course of 2 months, with at least 2 full days between test days. A total of nine sets of each blocked condition was completed for each subject.
The analysis of these data used a relative response transformation of the response amplitude scores. For each block of trials the amplitude score (in voltage units) for each condition was normalized, that is, expressed as a proportion of the total amount of responding in that block, in order to equate the contribution of each block of trials to the total, as the amplitude of the reflex across days may have been affected variously by the levels of drug effective at the time. Then a mean for each condition was taken from the nine sets of normalized scores, and then the mean of each of the prepulse conditions was expressed as a proportion relative to the mean of the control condition. This proportion was then subtracted from 1.0 to give the value of the strength of reflex inhibition provided by each prepulse level, relative to the size of the control response. These resulting data were subjected to repeated measures analyses of variance (ANOVA). The probability values associated with the F-values were calculated using the Huynh–Feldt adjustments for degrees of freedom.

At the end of the behavioral experiment the hearing of the two groups of mice was tested using standard brain stem evoked response audiometry (see Ison et al., 1997, for procedural details). ABR audiograms were provided using tone bursts presented at 11/s having 5-ms durations, 1-ms cosine shaped rise–fall times (10%–90%), and center frequencies of 4, 8, 10, 12, 16, 24, and 36 kHz. Each averaged response was comprised of 300–500 stimulus presentations, with the ABR recorded over a time epoch of 10 ms. The stimulus level was lowered in 10 dB SPL and then 5-dB steps to below the threshold of the most prominent wave, typically wave 4/5, appearing at about 5 ms. The data were analyzed by repeated measures ANOVA, again using the Huynh–Feldt adjustments.

II. RESULTS

A. Masking and the effects of spatial location

Figure 1 displays the mean inhibitory effects of the high- and low-frequency signals on the acoustic startle reflex under the several masking conditions, the younger mice in the upper portion of the figure, the older mice in the lower. Increasing the level of the signal increased its inhibitory effect (as seen in the open symbols), which is a basic finding in experiments on reflex inhibition (see Hoffman and Ison, 1980). The overall effect of the noise on reflex inhibition was identical to those seen previously in human subjects run under similar conditions (Reiter and Ison, 1979) in that the masking effect of the noise was maximal with weak signals and then declined and finally disappeared with stronger signals (as seen in the comparison of solid and open symbols). In both subject populations, humans and mice, increasing the level of the signal provided a “recruitment” type of effect on reflex inhibition similar to that shown for loudness judgments in the psychophysical data presented in the classic report of Steinberg and Gardner (1937). The degree of masking was reduced when the 25-kHz signal and its high-frequency masker were presented from different locations, the signal on the left and the masker moved 180 degrees to the right (seen in the comparison of the two sets of solid symbols at the right of Fig. 1), while there was no systematic difference between the two locations of the low-frequency masker for the 4-kHz signals (seen on the left side the figure). To the extent that age effects were present in the data depicted in Fig. 1, they were seen as a slight overall decrement in inhibition in older mice, and, if anything, a slight increase in “release from masking” provided by the shift in the location of the high-frequency masker.

The increase in reflex inhibition provided by the increase in signal level led to a significant main effect in the ANOVA: for signal level, \( F(6/60) = 127.70, p < 0.01 \); and the decrement in reflex inhibition in the presence of the masking noise led to a second significant main effect: for masking condition: \( F(2/20) = 60.56, p < 0.01 \). This effect of masking condition interacted with signal frequency, \( F(2/20) = 6.72, p < 0.01 \), with signal level, \( F(12/120) = 16.48 \), and with their interaction, for MC×SF×SL, \( F(12/120) = 6.11, p < 0.01 \). The older mice were less inhibited that the younger mice overall, \( F(1/10) = 12.84, p < 0.01 \), and this effect of age interacted with the interaction of frequency level and signal level, \( F(6/60) = 2.89, p = 0.02 \), but not with masking condition (\( p > 0.30 \)).

A subsequent ANOVA compared the inhibitory effects of the nonmasked signal against that of the masked signal with the masker at the same location. The deleterious effect of the masker on the signal was significant, \( F(1/10) = 101.63, p < 0.01 \), but this masking effect was reduced at the higher signal levels, for the MC×SL interaction, \( F(6/60) = 21.87, p < 0.01 \). It is noteworthy that this masking effect of the noise did not vary with age or with signal fre-
frequency, $F_s < 0.01$. Other ANOVA examined the effect that shifting the location of the masking noise had on the severity of masking, in comparisons of the two masked functions having solid symbols in Fig. 1. Here the most important outcome was that the reduction in the masking effect produced by changing the location of the masker depended on the frequency of the signal, for the masker location by SF interaction, $F(1/10) = 11.00, p < 0.01$; and separate ANOVA for each frequency alone showed that the relief from masking provided by shifting the location of the masker contralateral to the signal was significant for the high-frequency signal, $F(1/10) = 31.10, p < 0.01$, but not for the low-frequency signal, $p > 0.25$. In general there was no significant effect of age on either the severity of masking or on the degree of masking release in this set of comparisons, for interactions of A×L, all $p > 0.10$. Age effects were apparent only in their interaction with signal level for the 4-kHz signal, for A×SL, $F(6/60) = 7.19, p < 0.01$, perhaps reflecting the observation that older mice appeared to show less inhibition than the young mice for the highest signal level, at 80 dB, $F(1/10) = 16.66, p < 0.01$, but were not different at lower signal levels, $F < 1$.

B. ABR measures of threshold in young and old mice

Figure 2 provides the mean thresholds from 4 kHz to 36 kHz in the two groups of mice. The old mice had higher thresholds than the younger mice, but their loss occurred primarily at the lower frequencies, below 16 kHz. The ANOVA of these data showed an age effect, $F(1/10) = 9.38, p < 0.02$, which interacted with the significant frequency effect, $F(8/80) = 4.84, p < 0.01$. Subsequent ANOVA showed that there was no significant age effect for 24 kHz and above ($p = 0.1$), whereas there was significant loss of sensitivity for frequencies in the older mice below 16 kHz, $F(1/10) = 12.54, p < 0.01$. These data are unusual as most age-related hearing loss in the mouse is apparent first for high-frequency signals, as in the C57BL/6J parent, or is a relatively flat loss, as in the CBA parent, for example. However, the findings are consistent with those reported by Erway et al. (1993) for this particular hybrid mouse. In the ABR data provided by Erway et al. the hybrid offspring of the C57 and CBA strains showed no loss in click thresholds from 12 months of age at least up to 23 months, indicating that they must have a substantial band of frequencies for which there was no loss in hearing; but their 23 month old mice had a significant greater loss at low frequencies coupled with significant greater sensitivity at high frequencies in comparison to the old CBA parent. It will be noted that in the data of Erway et al. and in the present data the age-related loss of threshold sensitivity in the ABR was greatest for the 4-kHz frequency. This is the signal condition in the behavioral data showing less inhibition in the old mice compared to the young mice, although they were not significantly different in the severity of masking at either frequency.

III. DISCUSSION

In this experiment the graded reduction in reflex inhibition obtained by presenting the signals at varying levels against a noise background shown here in the mouse is the same as that seen in a similar behavioral experiment with human subjects (Reiter and Ison, 1979), and both sets of data capture the characteristic “loudness recruitment” effect found for masked tones varying in level in psychophysical measures of loudness (Steinberg and Gardner, 1937). Our older mice had a modest impairment in threshold sensitivity as measured in the ABR, particularly at the lower frequency, and a similar slight decrement in reflex inhibition. We did not find that overall the masking effect of the noise background was more severe in our older mice, whereas this is the typical finding in the older human listener (Patterson et al., 1982). We do note, however, that the age-related difference in masking is relatively small in listeners with minimal hearing impairment (Gelfand et al., 1988), and perhaps the present experiment did not have sufficient power to detect what might be expected to be a small effect. It is also possible that the failure to find an increase in masking with age is in part a result of the age-related loss of inhibition for the less intense unmasked signals apparent in Fig. 1. The level of inhibition for the unmasked signals provides the baseline against which masking is assessed, and the lower baseline in the older mice, plus the fact that masking was very strong even in young mice at the low and moderate signal levels, may have resulted in a “floor effect” for masking at these levels. There is some hint that masking was more severe in the older mice for higher signal levels, at which not only did the older mice show reasonably high levels of baseline inhibition but, also, masking was reduced for the young mice. For these values, at 70 dB and 80 dB, the greater difference for old compared to young animals between the inhibition scores provided by the unmasked signal and those provided by the signal coincident with the masker was of marginal significance, $t(10) = 2.05, p < 0.05, 1$-tail.

There is a very small but consistent literature on changes in the ability to locate sound objects in space in aged or in hearing impaired laboratory animals. Brown (1984) and Harrison (1981) both found a loss of discrimination between spatial locations in aged rats, and Heffner and Donnal (1993) showing a similar effect in the C57BL mouse. The data of Heffner and Donnal (1993) must clearly be attributed to age-related hearing impairment rather than age alone, but the meaning of the effects obtained with aged rats is not certain as they may be more heterogeneous in their sensory impair-
ments than the inbred strains of mice. The one study of the changes in neural activity in the inferior colliculus that varied the spatial location of masker and signal (McFadden and Willott, 1994b) provided neurophysiological data generally consistent with the findings of Heffner and Donnal in their showing that the “masking release” associated with a change in the relative location of the masker was greater in the young C57BL mouse compared to the old mouse, although they also report evidence for masking release with relatively low-frequency signals that would not be expected to provide significant interaural level differences. It is generally thought that only interaural intensity differences are available to very small mammals such as mice (e.g., Brown, 1994), because the small interaural distance across their heads, approximately 3 cm, provides only slight interaural timing cues at onset, and the phase locking that provides interaural phase differences for larger mammals with low-frequency hearing are therefore not available to them. Indeed, the brain stem nuclei presumed to be sensitive to interaural phase relations in large mammals are poorly represented in small mammals (Heffner and Masterton, 1990). The behavioral data provided in the present experiment are consistent with this line of reasoning in their showing that moving the masker away from the signal reduced the severity of masking for the high-frequency but not the low-frequency masker, which, by hypothesis, could not provide interaural differences in signal versus masker level: but the data of McFadden and Willott raise the interesting possibility that under some conditions the mouse may have a second cue to spatial location.

The beneficial effect of shifting the masker away from the high-frequency signal was at least as powerful in our old mice as it was in the young mice. If the ability to detect changes in the location of a sound source is assumed to be related to the “unmasking” provided by a relative shift in spatial location, then this finding appears contrary to the various reports showing age-related decrements in spatial localization in rats and mice. There are several possible explanations for this apparent conflict. One is that we had a single extreme measure of the effects of shifting spatial location, by 180 degrees, and perhaps smaller shifts in the angle between the masker and the signal would have revealed more subtle changes: but on the other hand, the loss of spatial discrimination noted in rats was obtained with just two locations 180 degrees apart. A second possibility is that this hybrid mouse represents an example of hybrid vigor along several auditory dimensions, including not only a resistance against age-related changes in threshold sensitivity as measured in the ABR, but also against deterioration at those central auditory sites important for computing the spatial location of sound objects. This is an interesting hypothesis to test in future research with the homozygous C57BL/6J and CBA parent strains. The third explanation depends on the reasonable assumption that the one essential acoustic cue associated with the change in the relative locations of the signal and the masker for these mice is the resulting interaural difference in their relative levels, a cue that can be present only for high frequencies but would be available in old mice with good high-frequency hearing. A relative reduction in the level of the high-frequency components of the now contralateral masker would be provided by the shadowing effect of the head and pinna at the ear ipsilateral to the signal, which would thus increase the signal-to-noise ratio at this ear, though, to be sure, the change in location would also result in an equivalent reduction in the signal-to-noise ratio at the ear contralateral to the signal. Assuming also that an old mouse, like the young mouse, is able to selectively respond to the ear with the better signal-to-noise ratio then the present results can be expected. The present outcome is very similar of that Gelfand et al. (1988), showing that aged human listeners with good high-frequency hearing benefit from the separation of signal and noise as much as do young listeners, and the acoustic cues available to our aged mice are likely to be those also available to the aged human.

IV. CONCLUDING REMARKS

The data on masking release presented here are not substantially different from those obtained under the more complicated conditions possible with aged human listeners, at least with the understanding that young human listeners use both temporal cues and level cues for determining spatial location, while the mouse has only the level cue. In humans the beneficial effect of shifts in spatial location are studied most often using earphone presentation of the stimuli, which, although they may assume configurations never obtained in the free field, allow complete control over both the temporal and the intensity cues that are important for humans in the free field. Pichora-Fuller and Schneider (1991) found no effects of age in “normal hearing” elderly versus young listeners when they compared masked thresholds for low-frequency tones in diotic masking conditions, but found that the elderly listeners showed less benefit from dichotic presentation, when the phase of either the noise or of the tonal signal was shifted by 180 degrees. Analogous effects were observed by Grose et al. (1994) for spondee recognition, again under earphone conditions with 180 degree shifts in the phase of the signal. These effects obtained in “normal hearing” aged humans seem different to those obtained in our “normal hearing” aged mouse, but the single cue to stimulus location in the human experiments was a difference in phase. These data strongly suggest that even “normal hearing” elderly humans have some difficulty in spatially locating the signal and the masker when only the temporal cue is available. Support for this idea is further provided in the data of Gelfand et al. (1988) who found no impairment in the benefit provided by a shift in the location of the signal relative to the masker in aged listeners with normal hearing in the free field, while they found a clear deficit in aged listeners with impaired hearing: the free field, in contrast to earphones, provides relative level information for signals and maskers at the two ears. These data, and our data as well, agree also with the report by Herman et al. (1977) that the ability to detect shifts in earphone lateralization for interaural level differences does not deteriorate with age. For the signals used in the present experiment, which had relatively long rise times so as to avoid a click at their onset, yet durations too brief to allow any orientation and subsequent “homing-in” on the signal as would be possible under com-
pletely natural conditions (for example, Ehret and Dreyer, 1984), only interaural differences in the relative levels of signal and masker could provide the cues to the changed location of the masker. We may hypothesize that in a similar behavioral experiment that used the hearing impaired C57BL/6J mouse as a subject the masking release attendant on the ability to separate masker and signal in space would diminish with age, unlike the persistence of this ability in their old F1 hybrid offspring, but in agreement with the perceptual effects shown by the impaired elderly listeners in the experiment of Gelfand et al. (1988): and, indeed, in agreement with the physiological data provided by McFadden and Willott (1994b).

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