The relative detectability for mice of gaps having different ramp durations at their onset and offset boundaries

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The effect on gap detectability of varying noise fall time (FT) and rise time (RT) of the gap boundary ramps was examined in mice using reflex modification audiometry, measuring inhibition of acoustic startle reflexes by variously shaped gaps just preceding reflex expression. In experiment 1 (n = 12) inhibition increased up to near-asymptotic values with longer FT (0, 1, 2, 3, 5, or 10 ms) and QT (quiet time, 0 to 13 ms), with a 2:1 trade-off between FT and QT. In experiment 2 (n = 24) inhibition increased for any RT above 0 ms (2, 3, 5, or 7 ms) if QT = 1 ms, but diminished with increased RT when QT = 3 or 8 ms. Enhanced detectability for subthreshold gaps by longer ramps results from their extending the apparent gap duration. The negative effect of increased RT for threshold gaps suggests the importance for gap detection of the stronger neural responses to sharp edges at the end of the gap shown previously in the mouse inferior colliculus. These effects are specific to gaps: inhibition for fixed (70-dB SPL) or varied level pulses (30 to 60 dB) was unaffected by varying the ramped edges (experiments 3 and 4, n = 9). © 2002 Acoustical Society of America.

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I. INTRODUCTION

The ability to detect brief, temporal decrements in a background noise provides a simple, convenient, and useful experimental paradigm for studying in both humans and in laboratory animals the acoustic variables and the characteristics of the listener that may be important in the temporal processing of more complex acoustic signals (see, for example, Michelsen, 1985). Many investigators have analyzed the effects on gap detection of individual differences between subjects, such as age and degree of hearing impairment (Florentine and Buus, 1984; Irwin and McAuley, 1987; McCroskey and Kidder, 1980; Salvi and Arehole, 1985; Snell, 1997; Trehub et al., 1995; Walton et al., 1997; and others), and the acoustical characteristics of the gap carrier and the gap itself, including the spectral composition, the bandwidth, and the level of the carrier, and the depth of a partially filled gap (for example, Buus and Florentine, 1985; Eddins et al., 1992; Ison et al., 1998; Forrest and Green, 1987; Penner, 1975; Snell et al., 1994). With rare exception, all of these experiments on gap detection in both laboratory animals and human listeners have used gaps with near-instantaneous onsets and offsets. Such abrupt transitions must characterize very few natural sounds, and at least for this reason alone, besides their intrinsic interest, further study of the effects of variation in onset and offset ramps is warranted. In the present experiments we varied the rise and fall time of brief gaps embedded in noise, using the method of reflex modification audiometry (Young and Fechter, 1983) to measure the behavioral effects of gaps in noise presented at subthreshold and suprathreshold gap durations.

There are but three published experiments describing the effects on gap detection of varying the temporal details of the envelope of a gap in a noise carrier, these appearing in very different experimental paradigms. Leitner et al. (1993) used reflex modification audiometry to study gap detection in rats, in an experiment in which gaps having different durations of quiet time (QT: 0 to 10 ms) and different rise–fall times (linear RT/FT: 0.25 to 2.5 ms) were used as the probe stimuli, to show that adding ramps to small gaps increased their inhibitory effect on startle behavior. Allen et al. (2002) provided psychophysical evidence in humans for the beneficial effect of adding different rise or fall times (linear RT or FT: 2 to 8 ms) to brief gaps (QT: 1 to 4 ms), which enhanced detection probability and reaction speeds. Barsz et al. (1998) measured neural activity in single units of the central nucleus of the inferior colliculus (IC) of mice in response to gaps having different onset and offset ramps (cosine-squared RT and FT: 0.5 to 16 ms) to find that adding a brief ramp to a brief gap increased its effect, while longer ramps of 8 and 16 ms led to reduced responses at the end of the gap and increased neural gap thresholds. These diverse sets of data are in general agreement for the positive effects of brief gaps and brief ramps, but the psychophysical data obtained in humans by Allen et al. (2002) provided no indication that longer values of FT or RT had any detrimental effect on gap detection.

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as had been found by Barsz et al. (1998) for neural thresholds in mice. To the contrary, both stimulus detection and response speeds in humans were enhanced by adding long as well as brief ramps to the terminal boundary of periods of quiet within the gap.

Thus, at present the overall generality and theoretical significance of these data depicting the effects of temporal variation at the boundary edges of gaps in noise on gap detection across the several research domains are uncertain. The present experiments followed the general procedures of Leitner et al. (1993), save that here mice rather than rats were used as subjects. Following Allen et al. (2002), we varied RT and FT independently over a range that included the short ramp durations that had positive effects in all of the research reported to date as well as the longer durations that had negative consequences in the work of Barsz et al. (1998). Reflex modification audiometry is an especially appropriate method to examine the potential correspondence of behavioral psychophysical measures in animals and IC electrophysiology. The phenomenon on which it is based, namely, the inhibition of the ASR by immediately prior acoustic events, depends on the integrity of the IC (Leitner and Cohen, 1985), and electrical stimulation of the IC inhibits the acoustic startle reflex (ASR) with a time course consistent with the idea that the inhibitory pathway has an obligatory passage through the IC (Li et al., 1998). Thus, if the effect of varied gap envelopes on neuronal activity in the IC of the mouse has a direct correspondence in mouse behavior, then it would be most likely to appear in experiments concerned with the inhibitory effect of gaps on the acoustic startle reflex. Two pulse experiments were also conducted in order to determine whether the behavioral effect of ramps in gap envelopes would be the same or greater than that of ramped noise pulses: Barsz et al. (1998) had reported that ramps in the gap envelope had a greater neural effect than ramps in the envelope of a noise pulse.

II. METHODS

A. Subjects

The subjects for the two gap experiments were 24 mice (14 male, 10 female), the F1 hybrid offspring of CBA/CaJ males and C57BL/6J females, approximately 10 weeks of age. Twelve mice were tested in the first experiment, while all 24 were tested in the second. The subjects for the two subsequent pulse experiments were 14 mice (11 male, 3 female), all of the CBA/CaJ strain, approximately 4 months of age. Four mice were tested in both experiments, the others used in only one experiment, for a count of 9 in each. All were group housed in the University of Rochester vivarium in a constant climate and a 12/12 h normal L/D cycle, and were tested in the daytime. Food and water were available ad libitum save during the test session. All procedures were approved by the University of Rochester Committee on Animal Resources.

B. Apparatus

A mouse was confined for testing in an acrylic plastic cage, 5 cm wide, 7 cm long, and 4 cm high, with slotted sides and roof for free sound penetration. The cage was mounted on a suspended acrylic platform to which an accelerometer was attached, and placed in an anechoic chamber (Eckel Corp., Cambridge, MA, model number 555-250-3) housed within a sound-attenuating room (IAC, Bronx, NY), one mouse being tested at a time. The startle stimulus was a 110-dB (peak-to-peak, SPL linear scale), 20 ms duration noise burst provided by a white-noise generator, gated through an electronic switch with <0.2 ms rise and fall times, then amplified and delivered through a high-frequency tweeter with maximum output at 16 kHz and a 5-dB/octave roll-off. The gap carrier (rms 70-dB SPL, linear scale) in the first two experiments and the prepulse in the last two was provided by the same white-noise generator, gated through a second electronic switch with variable rise and fall times, and then amplified and delivered through a Panasonic high-frequency leaf tweeter that varied by no more than ±6 dB over a range of 2 to 100 kHz. The ambient noise level in the chamber was less than 25 dB SPL for all frequencies above 125 Hz. Sound levels were measured with a 1-in. Bruel and Kjaer microphone, model 4135, connecting to a measuring amplifier, Bruel and Kjaer, model 2610.

The acoustic startle reflex in rodents consists of a rapid sequence of rostral to caudal movements beginning with eye and pinna responses and a brief extension of the limbs, followed by a generalized flexion response that brings the body together in a compact hunched posture (Davis, 1984; Horl-lington, 1968). The response is usually quantified in rodents by the force it exerts on the floor of the housing cage, which is detected by the accelerometer attached to its substrate. The onset latency of the response measured in the EMG can be as brief as 5 to 7 ms (Ison et al., 1973) in the rat, while in the present apparatus the onset of the recorded response is typically 10 to 14 ms after the onset of the eliciting noise burst. Figure 1 shows schematics of two stimulus conditions at the top, a control “no-gap” condition on the left, and a gap condition on the right. The lower functions show the traces of the resulting two responses. (See the legend for details.) Stimulus presentation and response measurements were under computer control.

C. Procedure

All experimental tests began with the mouse being placed in the chamber for a 5 min period, in background noise (experiments 1 and 2), or in quiet (experiments 3 and 4). For the gap experiments the mice then received trials in which the startle stimulus was presented in the presence of an uninterrupted noise to provide a control baseline response, and other trials in which the startle stimulus followed a brief gap in the noise. Twelve subjects received 8 test days (those mice tested in experiments 1 and 2), and 12 received 6 test days. At least one rest day intervened between each test. For the pulse experiments the startle stimuli were presented in quiet, sometimes alone, sometimes following a brief noise burst. Five mice received just 1 test day, for the first pulse experiment; 5 mice received 2 test days, for the second pulse experiment; and 4 mice received 3 test days total, for both experiments. The various stimulus conditions were always given in 11 randomized blocks of trials, in which each con-
dation was presented before any condition was repeated, and the intertrial intervals averaged 20 s (15 to 27 s).

The major graphic and statistical analyses of variance (ANOVA) of the data used mean relative levels of inhibition, in which each subject’s mean response for any particular stimulus condition (ASR<sub>c</sub>) was expressed as the complement of its amplitude relative to that of its mean control response (ASR<sub>c</sub>), that is (1 – ASR<sub>c</sub> / ASR<sub>n</sub>), given as “1-%C” in the figures. The first block of trials was not used in the analyses but was presented to allow adaptation to the experimental conditions. The probability levels associated with the F values were calculated using the Huynh–Feldt adjustments for degrees of freedom in repeated measures designs.

D. Experimental designs

1. Pretraining for gap detection

The inhibitory effect of weak prestimuli given at lead times beyond about 30 ms increases in rodents with experience with the testing conditions (Crofton <em>et al.</em>, 1990; Ison and Bowen, 2000), and for this reason the main gap experiments in this report were preceded by two series of preliminary tests, following the procedures previously used in rats to provide experience with gap detection. All mice first received 3 test days in which a startle stimulus was given alone, or preceded by a gap in a 70-dB noise of 10-ms duration and RFT of 0 ms (actual ~0.2 ms) having various lead times, 10, 15, 20, 30, 40, 60, 110, 160, and 210 ms, gap onset to startle onset. They then received a fourth pretraining day in which the startle stimulus was given alone, or preceded by a gap with varying durations, 1, 2, 3, 4, 6, 8, 10, and 15 ms, RT/FT = 0 ms, the gap ending 50 ms prior to the onset of the startle stimulus.

2. Effect of variation in noise FT at gap onset on reflex inhibition

This experiment examined the effect of variation in noise FT at the start of the gap with the noise RT at the end of the gap fixed at 0 ms (see Fig. 1). The startle stimulus was presented 50 ms after the end of the gap. The subjects (<em>n</em> = 12) were tested over 2 days. There were 13 different stimulus conditions: one in which the startle stimulus was presented alone (i.e., gap duration = 0 ms, this condition given twice as often as any other to provide a more reliable control baseline); four conditions in which the gaps had rise and fall times both set at a nominal 0 ms, and their QT = 1, 2, 3, or 13 ms; three conditions in which the total gap duration was 3 ms, made up of QT = 0, 1, or 2 ms, paired with FT = 3, 2, and 1 ms; and five conditions in which QT = 3 ms, and FT = 1, 2, 3, 5, or 7 ms (and thus the total gap duration was 4, 5, 6, 8, or 10 ms). An additional “no-stimulus” control condition was given in each block, in which the accelerometer output was integrated over a 100-ms period without a preceding stimulus to provide an activity baseline.

3. Effect of variation in noise RT at gap offset on inhibition

This experiment examined the effects of varied noise RT at the end of the gap, and all gap conditions were run with a 0-ms noise FT at the beginning of the gap. A schematic of a gap with a particular nonzero rise time would look like the right-hand upper graph in Fig. 1, save that the gap would begin with an abrupt noise offset and end with a ramped noise onset. The startle stimulus was presented 50 ms after the beginning of the ramped noise onset at the end of the gap. The subjects (<em>n</em> = 24, 12 of which had served in the preceding experiment) were tested on 2 days. This experiment included 15 stimulus conditions: one in which the startle stimulus was presented alone (again twice as frequently as the other conditions); four conditions in which the gaps had RT = 0 ms and QT = 1, 3, 8, or 15 ms; four conditions in which QT = 1 ms, and RT = 2, 3, 5, or 7 ms (and the total gap was thus 3, 4, 6, or 8 ms); two conditions in which QT = 3 ms, and RT = 5 or 7 ms (total gap times of 8 or 10 ms); and four conditions in which QT = 8 ms, and RT = 2, 3, 5, or 7 ms (total gap times of 10, 11, 13, or 15 ms). Spontaneous activity was integrated over a 100-ms period without a preceding startle stimulus once in each block to provide the activity baseline.

4. Effect of variation in noise pulse RT/FT on inhibition

The preliminary stimulus was a 70-dB noise pulse, with onset and offset ramps of 0, 5, or 10 ms. The total duration of the prepulse with the 0-ms RT/FT was 20 ms, but the total duration of the prepulse with the 5-ms RT/FT was 25 ms and the prepulse with the 10-ms RT/FT had a duration of 30 ms. Variation in total duration was intended to equate acoustic energy in each pulse. The interval between the onset of the prepulse and the onset of the startle stimulus was maintained at 50 ms. The procedures were the same as used above for
the gap experiments save that no pretraining was thought to be necessary in experiment 3 for the 70-dB prepulse.

5. Effect of variation in noise pulse RT/FT and noise pulse level on inhibition

The preliminary stimulus was a noise pulse. Its RT/FT had two values, 0 and 10 ms, each presented at four levels, namely, 30, 40, 50, and 60 dB. Because weak prepulses were used, 2 test days were run for this experiment. All other procedures were the same as those described above.

III. RESULTS

A. Preliminary test for gap detection

Figure 2 shows the mean relative response and the standard error of the mean (M±SEM) to the startle stimulus when preceded by gaps of varied duration. These data are similar to those obtained in the rat (Ison and Bowen, 2000) and in human listeners run under similar conditions (Ison and Pinckney, 1983), especially in their reaching a near-asymptotic level of inhibition of about 50% in relative inhibition units at about 4 ms. The mean gap threshold in these data was 2.46 (±0.27) ms, this value defined for each mouse as the minimal gap duration at which inhibition was at least 50% of its maximum. This value is just slightly greater than the mean threshold of 2.03 ms found in phasic on-neurons in the mouse IC by Walton et al. (1997).

B. Effect of variation in noise FT at gap onset on inhibition

Figure 3 shows the mean values for the inhibitory effects of gaps having QT of 0 to 13 ms and FT varying overall from 0 to 10 ms. The main gap function obtained with the FT set at 0 ms approximated that shown in Fig. 2, with the strength of inhibition rising rapidly as QT increased from 0 to 3 ms, and then showing a small additional increase with a QT of 13 ms: overall $F(3/33) = 15.96, p < 0.01$. Increasing the FT at the beginning of gaps having any particular QT strengthened their inhibitory effect, especially for relatively small gap durations: thus, compared to gaps with FT of 0 ms and QT of 0, 1, or 2 ms, comparable gaps with the same QT but FT of 3, 2, or 1 ms, respectively, in each case had a significantly stronger effect, $p < 0.05$, for Bonferroni multiple comparison $t$-tests following a significant overall ANOVA. These data agree with those of Allen et al. (2002) in human listeners in their showing that adding a nonzero FT to a subthreshold or near-threshold QT increased its salience. They show also that substituting an FT for some portion of QT in these relatively brief gaps had the expected opposite effect of diminishing inhibition: thus, for a series of gaps with a total gap duration (QT+FT) of 3 ms, the effect of a gap with the QT of 3 ms was greater than that a gap with a QT of 1 ms and FT of 2 ms, which in turn was more inhibitory than a gap with a QT of 0 ms and FT of 3 ms (all $p < 0.05$). The effect of adding FT to gaps with a QT of 3 ms was generally positive, though modest in size: the ANOVA of the apparent stronger inhibitory effect of FT for gaps with QT of 3 ms provided a significant linear increasing effect on inhibition, $F(1/11) = 8.06, p < 0.05$.

In summary, this experiment found that adding noise-offset ramps to the beginning of gaps provided a graded increase in their inhibitory effect according to the duration of the ramp, and never weakened gap inhibition even for suprathreshold gap durations. The overall pattern in these data is similar to that reported for human gap detection by Allen et al. (2002).

C. Effect of variation in noise RT at gap offset on inhibition

Figure 4 shows the mean values for the inhibitory effects of gaps having QT of 0 to 15 ms, and RT of 0 to 7 ms. The gap duration function for gaps with RT of 0 ms again approximates those shown in Figs. 2 and 3 in its rapid increase in inhibition from 0 to 3 ms and a slow increase thereafter: $F(4/92) = 91.21, p < 0.01$. For gaps with QT of 1 ms, increasing RT from 0 ms to values ranging from 2 to 7 ms...
increased their inhibitory effect, $F(4/92) = 7.46, p < 0.01$. Subsequent *t*-tests using Dunnett’s method for comparisons having a common control value showed that all gaps having a nonzero RT differed from the gap with RT of 0 ms, $p < 0.01$, but, as is evident in Fig. 4, none of these gaps with a nonzero RT differed from each other, $F < 1$. In contrast to this positive outcome of increasing RT when QT was equal to 1 ms, inspection of the data obtained with gaps having QT of 3 or 8 ms reveals that increasing the RT above 0 ms in these conditions had the opposite effect of reducing the strength of inhibition. The ANOVA of the effect of RT on gaps having QT = 3 ms provided a significant decreasing linear trend for RT, $F(1/23) = 5.29, p < 0.05$, as well as a significant effect overall, $F(2/46) = 3.79, p < 0.05$. The gap with an RT of 7 ms, and, thus, a total gap duration of 10 ms, provided significantly less inhibition than the gap with an RT of 0 ms and a total gap duration of just 3 ms, $p < 0.05$. An ANOVA of all gaps with a QT of 8 ms also provided a significant linear decreasing trend in inhibition with increased RT, $F(1/23) = 7.55, p < 0.05$, and there were significant differences between gaps with RT of 5 and 7 ms contrasted with the gap with an RT of 0 ms, $p = 0.05$.

In summary, this experiment found that when a ramped noise onset was added to the end of a subthreshold quiet period then gap inhibition was increased, but by a fixed amount regardless of the RT; in contrast, when the same RT was added to the end of a longer threshold or suprathreshold gap, then inhibition was reduced. The overall pattern in these data is similar to that provided by Barsz et al. (1998) in their study of neural activity in the mouse IC.

**D. A comparison of the inhibitory effects of adding RT and FT to a fixed quiet period**

Allen et al. (2002) found that for human listeners the increment in either response speed or the probability of detection produced by increasing the duration of an onset or offset ramp at the beginning or end of the gap was precisely matched by increasing the duration of absolute quiet by one-half that value, and that the functions for RT and FT overlapped throughout their entire range. Figure 5 shows the data of both of the present gap experiments aligned along a common dimension of “equivalent quiet gap time,” which was calculated by adding one-half of the RT or FT to the duration of quiet within the gap. The solid lines describe the mean levels of inhibition for the two sets of control gaps with 0-ms ramped onsets and offsets across gap duration, which generally lie within 1 SEM of each other. The dotted lines describe the mean levels of inhibition for gaps with either ramped noise offset at their beginning (FT > 0 ms, open circles) or ramped noise onset at their end (RT > 0 ms, open diamonds). The 2:1 trade-off function between ramp time and quiet time to determine an equivalent quiet time provides a good fit between the FT functions (solid versus open circles), but not for the RT functions (solid versus open diamonds). Ramps placed at the beginning of the gap and those placed at its end have very different effects, with the disadvantage in relative inhibitory strength for the noise onset ramp placed at the end of the gap beginning at the 2-ms equivalent quiet time.

**E. Effect of varied RT/FT on inhibition by noise pulses**

Figure 6 (top panel) shows the inhibiting effects of 70-dB noise pulses presented 50 ms before a startle stimulus, the pulses having RT/FT of 0, 5, or 10 ms. These prestimuli inhibited the response on average by about 75%, their SEM overlapped, and the ANOVA of the effect of RT/FT on inhibition provided an $F < 1$. Noise pulses provided more inhibition of startle than did gaps for a carrier of the same intensity. This finding suggested that the examination of RT/FT in pulses should be extended to lower pulse intensities that would have inhibitory effects approximating those of gaps, and perhaps also a similar degree of sensitivity to variation in RT/FT. The lower portion of Fig. 6 shows the effect of varying the RT/FT of the prepulse, at 0 and 10 ms, across
different pulse intensities, from 30 to 60 dB SPL. Inhibition increased with level as anticipated, $F(3/24) = 59.87, p < 0.01$. There was a small difference in inhibition in six of the nine mice favoring the 0-ms RT/FT for the moderate 40- and 50-dB prepulse levels that provided approximately the same inhibition values as the asymptotic gaps, but for the group as a whole this difference was not significant, and the overall effect of RT/FT provided $F < 1$.

The purpose of these two experiments was to determine if the effects on reflex inhibition of varying RT and FT at the boundaries of a gap in noise background would be duplicated if the inhibiting stimulus was a noise pulse in a quiet background. Barsz et al. (1998) reported that responsivity of onset cells in the IC of the mouse was sensitive to noise-burst rise time, but that increasing the RT of the noise marking the end of the gap had a more profound effect than variation in the RT of a noise burst presented in quiet. Varying the RT/FT of a noise pulse does not affect reflex inhibition in rats (Ison, 1978), but the present experiments were necessary to extend these findings to the mouse. In summary, neither of these experiments found that varying the RT/FT of noise pulses had a significant effect on the strength of reflex inhibition in mice.

**IV. DISCUSSION**

The present set of data confirms the general conclusion apparent in the small number of prior publications on this problem, that variation in the temporal structure of gap envelopes provided by changing the durations of the noise offset and onset ramps at its boundaries affects both threshold detection and the salience of suprathreshold gaps (Allen et al., 2002; Barsz et al., 1998; Leitner et al., 1993). Lengthening the duration of the noise offset ramp at the start of gaps consistently strengthened its inhibitory effect on startle behavior in the mouse for a range of near-threshold quiet periods, entirely in accord with the increased probability of detection of gaps and increased response speed in the similar condition reported for human listeners by Allen et al. (2002).

In the human psychophysical data, the terms of the 2:1 trade-off between quiet gap duration and ramp time indicated that the underlying variable determining the effect of FT on gap salience was the magnitude of the dip in the acoustic energy integrated across the duration of the gap, and the same effect for FT was seen here for reflex inhibition in the mouse. These FT data are consistent with the reports of Forrest and Green (1987) in human listeners and Ison et al. (1998) in mice, both showing that directly manipulating the amplitude of this dip by varying the noise floor within the gap systematically varied its detectability, and are consistent also with a loudness-detector model of gap detection developed by Florentine et al. (1999). Further, in the present experiment the expected complement to this effect was also demonstrated, in the data showing that a gap is a less effective stimulus if the noise offset ramp is not added to the gap, but instead extends into its quiet period.

For human listeners, increasing FT and RT provided precisely the same beneficial effect on the detectability of gaps having a set QT, but in the present study FT and RT had different effects: an increase in FT was always beneficial, while an increase in RT increased inhibition for a gap with a subthreshold QT, but diminished the inhibitory effect of gaps with threshold or suprathreshold QT. While the observed effect of increasing RT depended on the duration of the quiet period, the pattern obtained in these data indicates that variation in RT always had two opposing effects, the difference in their expression reflecting the diminished importance of an increased quiet duration for longer gaps, given the compressive nonlinearity of the function relating gap detection to gap duration. For gaps having a brief quiet period, any gradual noise-onset ramp was more effective than the abrupt noise onset, but the strength of inhibition did not then increase with the longer RT values, as it did for longer FT values. This difference suggests that the positive and negative consequences of increasing RT beyond the abrupt offset condition were balanced in strength even when the beneficial effect of increasing the duration of the relative quiet period was near its peak. These data for RT are consistent with the physiological data collected by Barsz et al. (1998), showing that neural gap thresholds increased with longer RT/FT. They are contrary to the psychophysical data of Allen et al. (2002) collected in human listeners who demonstrated increased salience for gaps ending with a longer noise RT, and, overall, equivalent effects of variation in the duration of onset and offset ramp durations.

**FIG. 6.** Means ($\pm$SEM) for relative inhibition plotted against rise/fall time of a noise prepulse (experiment 3) or against level of a noise prepulse with rise/fall time as a parameter (experiment 4). Note that RFT has little effect on inhibition by noise pulses.
V. CONCLUSIONS

The effect obtained by Barsz et al. (1998) in the physiological experiment was attributed to the reduction in the strength of the onset response in phasic cells of the inferior colliculus with increased duration of the ramped noise onset at the end of the gap. The fact that increasing RT diminishes gap detectability agrees with the theoretical description of gap detection provided by Plomp (1964), as being determined by the vigor of the onset response at the end of the gap. He applied this model to the results of psychophysical experiments in human listeners in which gap duration and the level of the noise marker at the end of the gap were manipulated, but given the neural onset data of Barsz et al. (1998) obtained in the mouse IC, plus the understanding that the inhibition of the startle reflex by preceding acoustic events depends on IC activity (Leitner and Cohen, 1985; Li et al., 1998), his model also provides one possible account of the present finding of diminished behavioral effects for gaps having longer duration onset ramps at their end. These data obtained in mice are consistent also with a suggestion by Florentine et al. (1999) that gap detection is primarily based on detecting a loudness perturbation at the output of an auditory filter for brief gaps, but benefits as well from the neural response to noise onset at the end of the gap, especially for suprathreshold gaps and for noise onsets with a short rise time.

The question then remains why the behavioral data we obtain here with mice do not agree with those provided by human listeners working with similar stimuli, as reported by Allen et al. (2002). The answer may lie in differences in the methodological details of these experiments or in species differences in the way that rise time is encoded at the neural level, but it is important to point out that there were striking similarities between the data sets, despite these differences in species and methods. First, adding a ramped noise offset to the beginning of a quiet period increased the detectability of gaps and their suprathreshold salience, as indicated by a greater strength of reflex inhibition in mice, and by an increased probability of detection and increased response speed in humans. Second, the general shape of the functions relating performance to the “effective quiet period” were similar across the experiments and the trade-off for combining the noise-offset ramp duration with actual quiet time was identical. Third, lengthening the duration of the noise-onset ramp at the end of the gap did have a positive effect in both studies: in fact, the single difference in outcome was that this last manipulation had only a positive effect for human listeners, but an additional negative effect on gap salience in the behavior of the mouse that had no counterpart for human gap detection.

It is possible that the critical difference between the two sets of data is that reflex inhibition appears to depend heavily on the responsivity of cells in the inferior colliculus, and that the neural effects of gaps at this level of the IC (but not pulses presented in quiet, which affect many types of cells) are particularly dependent on there being a rapid rise in the carrier level at the end of the gap. In contrast, one may speculate that the detection responses of human listeners must depend on the results of additional processing at higher neuronal levels that might assign a greater weight to other features of the gap, for example, its effective quiet time. It would be interesting then to see if reflex modification audiometry applied to the human listener (as in Ison and Pinckney, 1983) might reveal the same decrement in the inhibitory effect of a gap that ended with a slowly rising noise onset as seen here in the mouse.

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