

Research report

Age and experience-related improvements in gap detection in the rat

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Accepted 2 June 2004

Available online 22 July 2004

Abstract

The ability to accurately process brief, successive acoustic signals rapidly presented to the central nervous system is believed to underlie successful language development. The limits of temporal resolution of the auditory system, often assessed using gap detection tasks, has been widely studied in relation to developing and decoding speech. In the present study, a reflex modification paradigm was used to investigate potential shifts in gap detection thresholds in rats across development, with test sessions beginning on postnatal day (P) 15, P35 and P64. We found that thresholds decreased over the course of development. These thresholds were determined to lie between 10 and 20 ms for the P15 and P35 groups, and between 5 and 10 ms for the P64 group. Moreover, we observed improvements in gap detection thresholds in all age groups over 5 days of testing, including the youngest age group (P15). These later results suggest that experience-dependent plasticity mechanisms at the level of sensory processing are operational and observable both very early in development, and also in adult animals. The present findings also demonstrate maturational improvements in silent gap detection using a pre-pulse inhibition paradigm.

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Theme: Development and regeneration

Topic: Sensory systems

Keywords: Auditory; Gap detection; Development; Experience; Plasticity

1. Introduction

It is thought that fine auditory acuity, including the ability to detect brief silent gaps, is critical for accurate decoding of the speech stream. Moreover, the ability to process brief, successive and rapidly changing stimuli is

believed to underlie the timely acquisition of early language. Slowed or inaccurate auditory processing may cause essential information to be missed, resulting in difficulty deciphering the speech stream. Individuals with auditory processing difficulties may thus exhibit deficits in phonological, syntactic and/or grammatical processing, and indeed, there is accumulating evidence that impaired auditory processing is characteristic of developmental language delays and impairments (for reviews, see Refs. [23,38]).

One of the most widely used paradigms in the study of auditory temporal acuity is gap detection, classically defined as the ability to detect a brief silent period in otherwise continuous auditory background (typically white noise). Gap detection is an accepted and reliable behavioral

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¹ This research was conducted in accordance with the principles stated in the Guide for the Care and Use of Laboratory Animals, National Research Council, National Academy Press, 1996, and the Animal Welfare Act of 1966, as amended. The views of the authors do not purport or reflect the position of the Department of the Army or the Department of Defense (para. 4-3, AR 360-5).

measure of auditory temporal resolution, and various gap detection tasks have been devised to test the limits of auditory acuity (i.e., to determine gap detection thresholds) across different species (human [16], rat [22], chinchilla [13], zebra finch [28], as well as clinically identified populations [4,26]), and even over the course of development (human [35,36,37] and rat [8]). Taking these findings a step further, the relationship between gap detection abilities and longitudinal language outcome in humans has also been investigated by several groups.

For example, Benasich and Tallal (1996) examined a sample of infants with a family history of language impairment (FH+), thus at an elevated risk of developing a language impairment themselves, along with matched controls in a prospective longitudinal study [5,34]. The authors found that infant auditory processing thresholds, defined as the shortest detectable gap between two complex tones, strongly predicted language outcome at 16, 24 and 36 months of age in both groups [1,2]. Similarly in a retrospective study, Trehub and Henderson (1996) found that infants who performed above the median on an auditory gap detection task at age 6.5 or 12 months had more sophisticated language skills at 16–29 months of age, including larger expressive vocabularies and longer, more complex sentence production. These convergent findings support the use of infant auditory processing measures to predict later language outcome.

Studies of age-related changes in gap detection abilities in normally developing infants have shown that infants have higher (i.e., poorer) thresholds than adults [36,37], and young children diagnosed with developmental language disorders (e.g., Specific Language Impairment, or SLI) exhibit higher gap detection thresholds as compared to controls [24]. This is notable since adults with a related form of language disability (developmental dyslexia) perform as well as controls in gap detection tasks [25], even though these same dyslexics show clear evidence of deficits in processing more demanding auditory stimuli comprised of rapidly changing elements (see Ref. [10] for review). Convergent data thus suggest the existence of a developmental progression in the ability to perceive silent gaps embedded in otherwise continuous auditory stimuli, even within clinically impaired populations.

Developmental changes in gap detection in the rat have also been examined [8]. Dean and colleagues report that gap detection thresholds change as a function of age, as well as experience (repeated daily testing), from infancy through adulthood. These results were obtained using a pre-pulse inhibition paradigm (acoustic startle reflex modification). However, in this paradigm, the startle-eliciting stimulus (SES) was presented at fixed intervals, introducing the possible confound of interval-based habituation (i.e., anticipation of the SES). In addition, repeated testing was only conducted over 3 days, although it has been shown in adult rats that startle responses do not reach asymptotic levels until the fifth or sixth day of repeated testing [7]. In the

present study, we attempted to more clearly delineate a developmental progression in the ability to perceive silent gaps within background noise by eliminating these caveats and others.

The goal of the present experiment was to investigate potential developmental changes in gap detection in rats, working from prior investigations of auditory processing with this model [6,11]. Specifically, we sought to characterize developmental shifts in gap detection using three different age groups: postnatal day (P) 15 (juvenile), P35 (adolescent) and P64 (adult). We hypothesized that developmental shifts in gap detection thresholds would be found and that these may be differentially affected by repeated testing experience as a function of age.

2. Methods

2.1. Subjects

Time-mated female Wistar rats (Charles River Laboratories, Wilmington, MA) were received at the University of Connecticut by RHF. One day after birth, each litter was culled to 10 pups (6 males and 4 females, total $n=60$ males).²

Pups were housed with their mother until weaning occurred on P22. Thereafter, male littermates were housed in pairs. One pair of subjects from each litter was tested beginning on P15, P35 or P64, respectively ($n=20$ for each age group). In this way, one littermate pair was included in each cross-sectional age group (total of six subjects from each litter). This experimental design was used to control for cross-litter variability, and to allow Age to be used as a within-subjects variable in the data analysis (based on demonstrated littermate correlations). Subjects were maintained on a 12-h light/dark cycle and all testing occurred during the light phase of the cycle. Food and water were available ad libitum, except during daily testing (35–100 min).

2.2. Testing apparatus and stimuli

A reflex modification paradigm was used based on the mammalian acoustic startle reflex (ASR). The ASR is a sudden reflexive contraction of the flexor muscles, resulting in a momentary crouching posture, in response to an

² The animals used in this experiment were part of a larger study investigating the effects of induced cerebrocortical microgyria on rapid auditory processing. Thus, male pups were randomly designated to receive either a bilateral sham or freezing lesion, balanced within each litter. On P1, focal necrotic lesions were induced using a modified technique employed by Dvorák and Feit [9], which is explained in detail elsewhere [14]. There were 10 lesions and 10 shams in each age group (one littermate pair per age group). It has been shown elsewhere that animals with microgyric lesions and sham littermates perform similarly on the present gap detection 0–100-ms task (see also Refs. [6,30]).

unexpected, intense sound [21]. In rats, the ASR emerges around P12, concurrent with the onset of hearing [32]. The magnitude of the startle response can be both attenuated and enhanced through various experimental manipulations, and thus the ASR has been widely used in studies of sensorimotor information processing and plasticity (e.g., Ref. [31]). The ASR is significantly reduced when a detectable non-startling stimulus (a cue) is presented 30–500 ms before the onset of a startle eliciting stimulus (SES). This well-known type of reflex modification is called pre-pulse inhibition (PPI [20]). In the rat, PPI emerges between P13 and P16 [29].

For the current experiment, each subject was placed in an open-ended, opaque polypropylene cylindrical confine, appropriate for body size, atop a Stoelting movement transducer platform (model EAM #31404, Stoelting, Chicago, IL). Five platforms were used simultaneously to test five subjects in a quiet room. The output voltages from the platform were band-pass filtered (1000–1 Hz) and passed into a Biopac MP100WS Acquisition system (Biopac Systems, Santa Barbara, CA), which was connected to a Power Macintosh 7200/120. There the output signals were rectified on-line. The Biopac system acquired the incoming signal at a sampling rate of 1000 samples/s. This combined apparatus recorded the amplitude of the subjects' whole-body ASR. The epoch of interest was 150 ms long, beginning with the onset of the SES. The extracted peak value of an epoch served as a subject's response amplitude for a given trial.

Each subject was tested on the gap detection task for 5 days, with one test session per day. Auditory stimuli were generated on a Macintosh Quadra 700 and were played free field via speakers located approximately 75 cm above the animals. A continuous background stimulus (broad band white noise) was presented at 75 dB. A trial consisted of the presentation of a variable duration silent gap 50 ms before the presentation of the SES. The SES was a 50-ms "burst" of white noise presented at 105 dB with a 0-ms rise/fall time (Fig. 1, from Ref. [6]) and was presented repeatedly with a variable intertrial interval (16, 18, 22 or 24 s) to reduce anticipation [22]. Silent gaps were 0, 2, 5, 10, 20, 30, 40, 50, 75 or 100 ms in duration. Each of these 10 conditions was

randomly presented 30 times for a total of 300 trials per session. The 0-ms (uncued) condition provided a baseline measure of the ASR.

3. Results

3.1. Statistical analyses

Mean startle amplitudes in millivolts were computed for each subject at each of the 10 gap durations (including 0 ms or uncued). Grand means were then computed for all subjects at each age (P15, 35 or 64). Attenuated response values (calculated as a percentage of baseline startle response) were derived for each subject by dividing the cued response at each condition (2, 5, 10, 20, 30, 40, 50, 75 or 100 ms) by the uncued response (0 ms) and multiplying the quotient by 100. Values not significantly different from 100% indicate equivalency in startle amplitudes for cued and uncued trials, and hence no detection. A mixed factor repeated measures analysis of variance (ANOVAs) was performed using attenuated response values as the dependent measures. Day (five levels) and gap duration (nine levels, since the 0-ms condition converts to 100%) were within subjects factors, and treatment (two levels) was a between subjects factor. Each age group was analyzed separately. In a separate set of ANOVAs, the effect of litter was examined, with gap and day as within subjects factors. It was determined that there were no significant effects of litter or treatment at any age or gap duration, so the data were pooled for all further analysis (see absolute startle amplitude analyses below). Gap duration did not meet the assumption of sphericity, so the Greenhouse–Geisser correction was used. Finally, attenuated response amplitudes were analyzed across all three age groups using a mixed factor repeated measures ANOVA. Age (three levels) was a between subject variable, and day and gap duration were within subject variables. For this analysis, gap duration and day did not meet the assumption of sphericity, so the Greenhouse–Geisser correction was used.

Using the absolute startle amplitude values, a mixed model repeated measures analysis of variance (ANOVA) was performed with within factors gap duration and day for each age group. For the P64 and P35 groups, gap duration did not meet the assumption of sphericity in the absolute startle response analyses, so the Greenhouse–Geisser correction was used. In order to determine the gap durations that produced significant startle inhibition, pairwise comparisons (paired *t*-tests) of mean startle amplitude on cued (2–100 ms) versus uncued (0 ms) trials were performed. These comparisons were done with averaged ASR responses (over all 5 days of testing), as well as on each day for each age group. These results were compared to specifically evaluate the effects of repeated testing. Significant reduction of startle amplitude indicates detection of the pre-pulse stimulus.

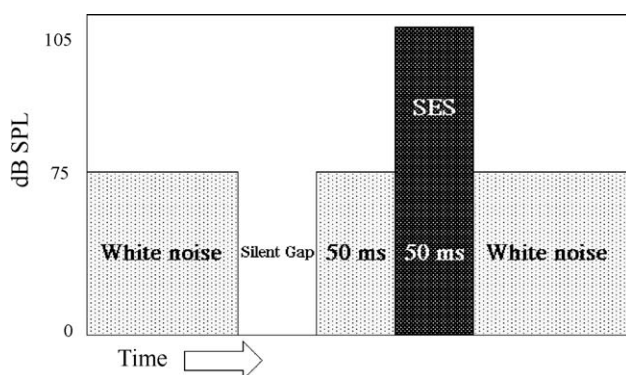


Fig. 1. Stimulus presentation protocol for silent gap detection.

Both absolute and attenuated response measures are reported in order to evaluate different aspects of performance. For example, the absolute response amplitudes are useful for determining gap detection thresholds at each age by comparing differences between startle responses at various gap durations. However, absolute response amplitudes cannot be used for across-age comparisons due to variations in the animals' body weights at the different ages tested. Attenuated response, which is a percentage of baseline measurement, allows for across-age comparisons because this ratio measure assumes equal proportionality across the scale of measurement.

3.2. Gap detection results

3.2.1. Attenuated response analyses

The attenuated response analyses revealed a significant main effect of gap duration (P15: $F_{8,144}=24.16$; P35: $F_{2,14,38.58}=83.21$; P64: $F_{2,46,44.25}=101.44$; $p<0.0001$ for all) and day (P15: $F_{4,72}=6.87$; P35: $F_{4,72}=28.13$; P64: $F_{4,72}=30.73$, $p<0.0001$ for all) at each age. There was also a significant day \times gap duration interaction at each age (P15: $F_{32,576}=5.19$; P35: $F_{9,39,169.01}=14.10$; P64: $F_{9,85,177.31}=14.68$; $p<0.0001$ for all). These data are presented in Fig. 2a–c. There was no significant main effect or interaction of treatment at any age (P15: $F_{1,18}=0.19$; P35: $F_{1,18}=0.03$; P64: $F_{1,18}=0.01$; ns for all). There was also no significant main effect or interaction for Litter at any age (P15: $F_{9,10}=1.85$; P35: $F_{9,10}=0.92$; P64: $F_{9,10}=0.71$; ns for all). Based on these findings, the data were pooled for all further analyses (Fig. 3).

Results of an attenuated response across age ANOVA revealed a significant main effect of age ($F_{2,57}=19.9$, $p<0.0001$), day ($F_{3,33,189.85}=52.28$, $p<0.0001$) and gap duration ($F_{3,28}=184.4$, $p<0.0001$), as well as an age \times gap duration interaction ($F_{6,56,186.8}=20.35$, $p<0.0001$), a day \times gap duration interaction ($F_{17,31,986.49}=21.79$, $p<0.0001$) and a three-way age \times day \times gap duration interaction ($F_{34,61,986.49}=4.67$, $p<0.0001$). Examination of the simple effects for the day \times gap duration interaction showed that across all ages, there is a significant effect of repeated testing for all gaps *except* 2 and 5 ms ($p<0.05$ for 10, 20, 30, 40, 50, 75 and 100 ms gaps). Looking at the simple effects of the age \times gap duration interaction revealed a significant effect of age at all gap durations except 2 and 5 ms ($p<0.05$ for 10, 20, 30, 40, 50, 75 and 100 ms gaps), suggesting that at gaps of 10 ms and greater, age influences the attenuated response amplitude when averaged across all 5 days of testing. These findings are presented in Fig. 4. The three-way age \times day \times gap duration interaction reflects the fact that day effects (i.e., experience) were clearly greater at the older two ages for salient gaps.

3.2.2. Absolute response analyses

For the absolute response amplitude analysis, there was a significant main effect of gap duration within each age group

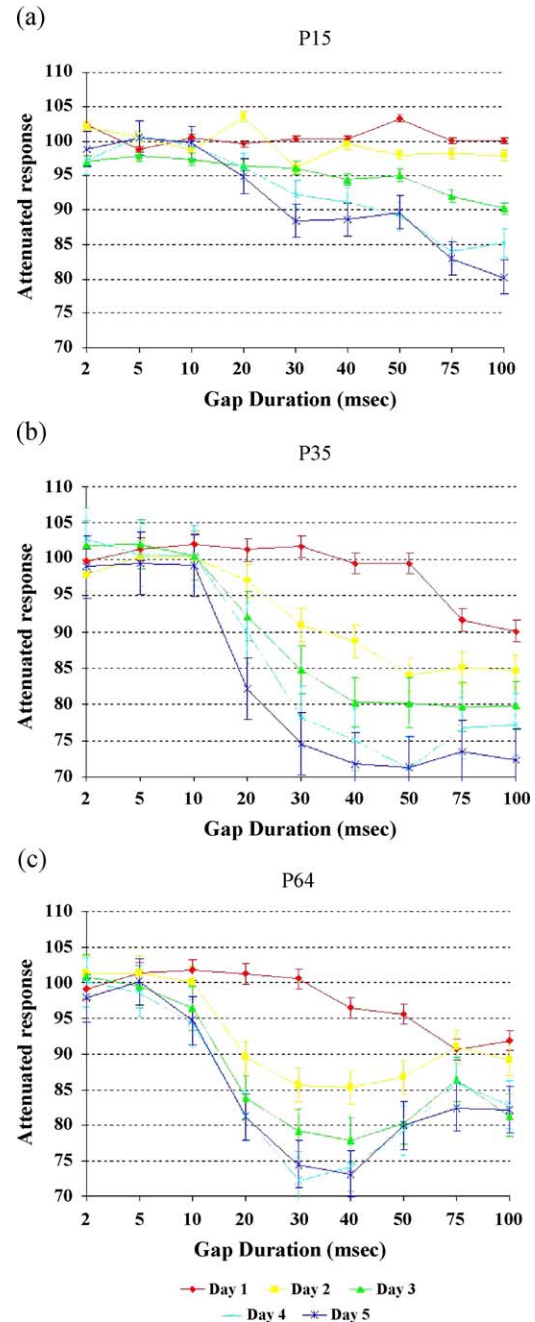


Fig. 2. Percent of baseline startle response (attenuated response) is plotted as a function of gap duration for all subjects in each age group: (a) P15, (b) P35 and (c) P64.

(P15: $F_{4,87, 92.51}=25.37$; P35: $F_{2,18,41.47}=85.26$; P64: $F_{2,17,41.24}=108.08$; $p<0.0001$ for all). Gap detection thresholds for each age group were determined from pairwise comparisons of absolute startle amplitudes at each gap duration (2, 4, 10, 20, 30, 40, 50, 75 and 100 ms) to the 0-ms condition. Threshold was inferred to lie between the smallest gap that differed significantly from zero and the next gap, which was not significantly different from zero, at the 0.05 α level. P15 and P35 thresholds were determined to lie between 10 and 20 ms, while the P64 threshold was between 5 and 10 ms.

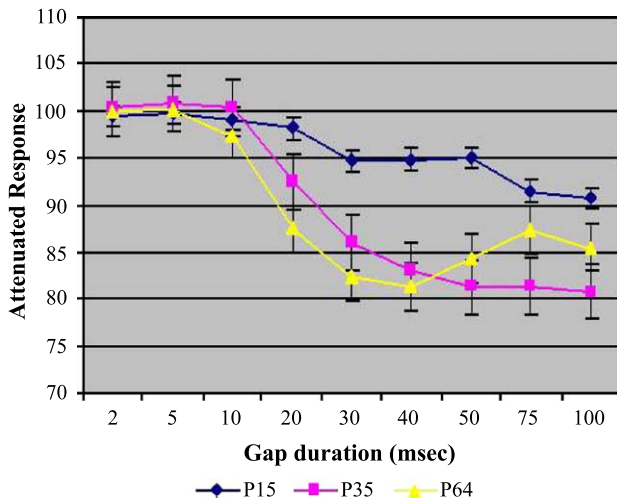


Fig. 3. The averaged attenuated responses over 5 days of testing are presented for each age group. Note that the steepest increase in inhibition between 5 and 10 ms (noted by a decrease in attenuated response score) is exhibited by the P64 subjects, and a similar increase in inhibition between 10 and 20 ms is seen for the P35 subjects. The poorest attenuation is exhibited by the P15 group.

There was a significant effect of repeated testing (day) for the two younger age groups (P15: $F_{4,76}=10.44, p<0.001$; P35: $F_{4,76}=19.68, p<0.001$; P64: $F_{4,76}=0.635, ns$). This reflects higher response amplitudes on day 1 and lower response amplitudes on day 5 (i.e., improved detection with ongoing experience). These results are shown in Fig. 4(a–c). There were also significant day \times gap duration interactions at each age (P15: $F_{11.02,209.48}=5.82$; P35: $F_{9.18,174.47}=15.17$; P64: $F_{9.92,188.41}=16.82$; $p<0.001$ for all). Because of this, we examined gap detection thresholds for each age group on *each day* of testing using pairwise comparisons. These results are summarized in Table 1(a–c). All groups displayed improvement (i.e., decrease in threshold) with repeated testing, with the greatest improvement between days 1 and 3. On day 1, adults (P64 group) exhibited the best performance (threshold between 30 and 40 ms), followed by the P35 group (threshold between 75 and 100 ms). The P15 group showed no evidence of detection for any gap duration until day 3. The P64 and P35 groups continued to improve in gap acuity through days 2 and 3. The ‘best’ gap thresholds were achieved by day 3 in all groups, with thresholds between 10 and 20 ms for the P15 and P35 groups, and between 5 and 10 ms for the P64 group.

In both the attenuated (Fig. 2a–c) and absolute (Fig. 4a–c) response analyses, in the P35 group on days 4 and 5, the greatest startle inhibition is seen around 40–50 ms. In the P64 group, a similar trend is observed on days 2 through 5 where maximal pre-pulse inhibition occurs between 30 and 40 ms. This may reflect a psychophysical phenomenon related to a transition point in a central auditory processing mechanism around a 30–40-ms gap. This mechanism may be influenced by development, since the greatest startle reducing gap duration differs between the P35 and P64

groups. Experience also appears to have an effect, since changes over the course of 5 days of testing in the 30–50 ms range are observable within both age groups. Based on the

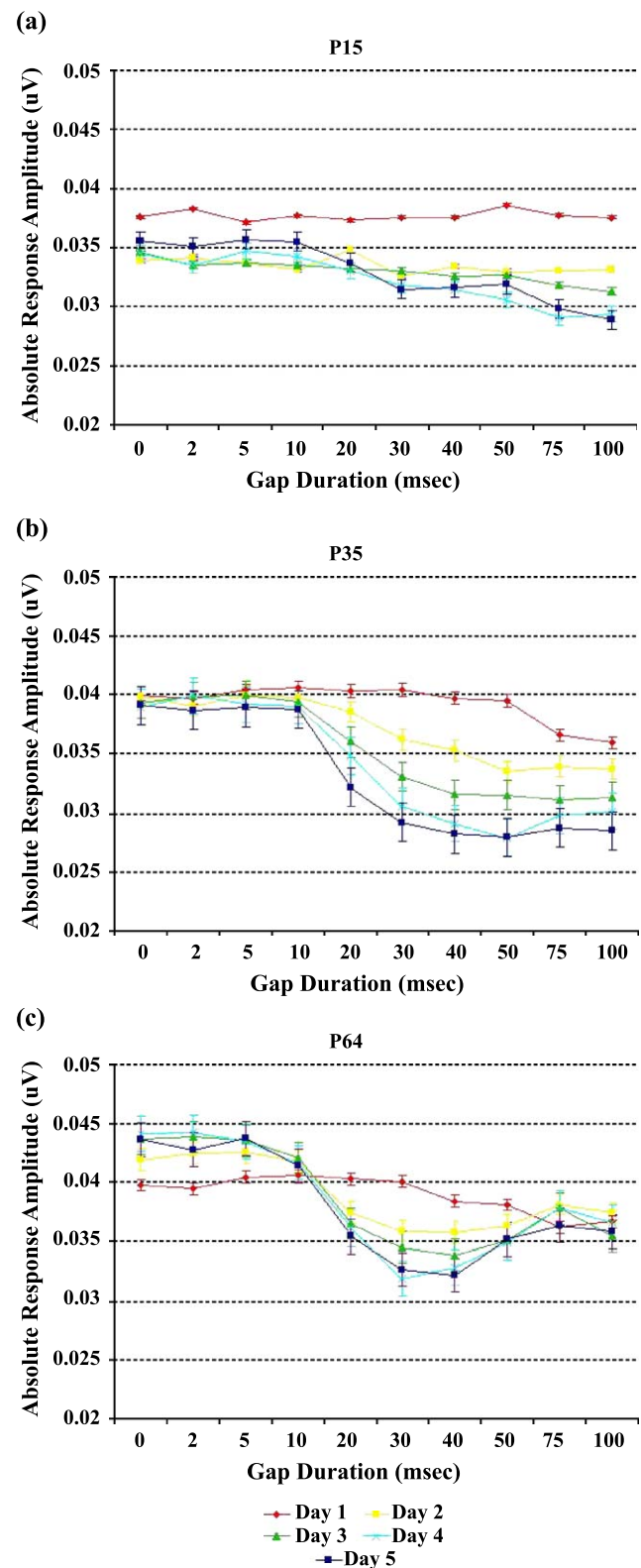


Fig. 4. Absolute startle response amplitude is plotted a function of gap duration for all subjects in each age group: (a) P15, (b) P35 and (c) P64.

Table 1
Shifts in gap detection threshold over 5 days of testing

	Day 1	Day 2	Day 3	Day 4	Day 5
<i>(a) P15</i>					
100×0	–	–	*	*	*
75×0	–	–	*	*	*
50×0	–	–	*	*	*
40×0	–	–	*	*	*
30×0	–	–	*	*	*
20×0	–	–	*	*	*
10×0	–	–	–	–	–
5×0	–	–	–	–	–
2×0	–	–	–	–	–
<i>(b) P35</i>					
100×0	*	*	*	*	*
75×0	*	*	*	*	*
50×0	–	*	*	*	*
40×0	–	*	*	*	*
30×0	–	*	*	*	*
20×0	–	–	*	*	*
10×0	–	–	–	–	–
5×0	–	–	–	–	–
2×0	–	–	–	*	–
<i>(c) P64</i>					
100×0	*	*	*	*	*
75×0	*	*	*	*	*
50×0	*	*	*	*	*
40×0	*	*	*	*	*
30×0	–	*	*	*	*
20×0	–	*	*	*	*
10×0	–	–	*	*	*
5×0	–	–	–	–	–
2×0	–	–	–	–	*

Absolute startle amplitude to a single gap duration (2–100 ms) is compared to the 0-ms gap (uncued/baseline condition) on each day using pairwise *t*-tests at each age: (a) P15 group, (b) P35 group and (c) P64 group. A dash (–) denotes a non-significant *t*-value and a star (*) denotes a significant *t*-value at the $p < 0.05$ level. Unexpected significant findings at the $p < 0.05$ level were observed for the 2-ms gap duration on day 4 for the P35 group and on day 5 for the P64 group. The gap duration of 2 ms is the lowest reported threshold in the literature for adult animals. It is surprising to find a significant difference between the 0- and 2-ms gaps in the present studies on isolated days and in the absence of significant findings for the 0- vs. 5-ms gap duration on any day. This finding will be further explored in future research.

present data, we will not speculate further because this pattern of results was not experimentally addressed. However, further research will do so.

In sum, in the present experiment, we failed to find differences between subjects with focal freezing lesions and sham subjects and did not observe any effects of litter. Therefore the data were pooled for further analyses. The interesting thing we did find was a developmental shift in gap detection thresholds, as well as an effect of repeated daily testing indicating experience-based improvements in all age groups, including the youngest. Specifically, a developmental decrease in gap detection threshold was observed, with the P15 and P35 groups having thresholds between 10 and 20 ms, and the P64

group achieving a threshold between 5 and 10 ms. These thresholds are the same whether responses are averaged over all days of testing or are determined using data from day 5 only. Thus, the age at which the animals were tested appears to influence the overall detection of gaps as measured by the amount of pre-pulse inhibition. In addition, repeated daily testing improves gap detection thresholds within each age group, especially the P35 and P64 groups.

4. Discussion

The purpose of this study was to investigate changes in gap detection thresholds in rats over the course of development, as well as examine the effects of repeated daily testing for 5 consecutive days. Consistent with previous research [6,30], no differences were found between animals with microgyric lesions and shams in the gap detection task used here, and thus the data was pooled (but see Ref. [30], which explores sham/lesion differences in juvenile rats using a more fine-grained gap detection task). Our results demonstrate that developmental shifts in gap detection abilities are observable in the maturing rat, and that improvements in auditory acuity due to repeated testing were observed in all age groups, including the youngest age group reported to date (P15). Across species, gap detection thresholds are typically reported in the range of 2–6 ms for adults (rats [15,22] and humans [16]). Results from the adult rat subjects in the present study are consistent with these values and with other results obtained in our lab (P64 rats have a threshold between 5 and 10 ms [30]). The developmental trajectory observed in the present study is also consistent with previous reports of maturational changes in gap detection thresholds in the rat [8], and parallels developmental changes seen in human infants (i.e., acuity improves with age [36,37]). Werner and colleagues (1992) found that 3–6-month-old human infants have gap detection thresholds considerably higher than adults (means of 36 and 16 ms, respectively). Trehub et al. (1995) also determined that 6.5–12-month-old infants have higher gap detection thresholds than adults, but by using modified stimulus parameters they were able to show that infants' auditory processing thresholds are significantly lower (i.e., better) than previously indicated by Werner and colleagues (11 ms). This suggests that stimulus parameters and the demands of a task may influence sensory processing thresholds, at least as measured.

Similarly, in studies of rapid auditory processing with rats, tone pair identification thresholds in a go/no-go operant paradigm [11,12] were much higher than thresholds obtained using a reflex modification paradigm with identical stimuli [6]. This cross-task comparison indicates that experimental parameters, including task demands (e.g., active vs. passive response) may influence apparent

perceptual thresholds. Similar results have been found in human studies as well [3].

In addition to cognitive load, repeated testing also affects performance on tasks measuring the limits of auditory resolution. While it has been shown that amplitude, latency, and incidence of the acoustic startle response are not altered by experience [32], reflex inhibition to gap stimuli does increase with repeated testing (reaching asymptotic levels after five to six daily sessions in adult rats [7]). In a study investigating the effects of both age and experience on inhibition of the acoustic startle response by gaps, Dean and colleagues found that both the magnitude of inhibition by gaps (less than 16 ms) and acuity (in rats P35 and older) were dependent on both maturation and repeated daily testing [8]. Repeated testing affects the amount of pre-pulse inhibition, with more experience leading to a more attenuated startle response.

Though we are in agreement with Dean and colleagues regarding the general conclusions that experience and age alter acuity for gaps in the rat, there are several notable differences between the study by Dean et al. (1990) and the present experiment. First, Dean and colleagues presented the SES at fixed intervals, while here the interval between the SES was variable to reduce the possibility of anticipation. This is paramount, as anticipatory responses (e.g., lower startle amplitudes) would confound the inference that attenuation of the ASR reflects the detection of a gap. Second, we used littermate pairs across each age group (also a within litter design variable) to largely eliminate inter-litter variability, and thus we were able to compare performance continuously across age groups. Genetic variability makes it difficult to compare absolute ASR responses across litters; thus, we removed this potential confound with careful experimental design.

Third, Dean and colleagues tested each age group for 3 consecutive days. We tested for five consecutive daily sessions based on the work of Crofton et al. (1990), who found that inhibition of the ASR due to gaps asymptotes after 5–6 days of testing. In the present study, the attenuated responses over all 5 days of gap detection testing were averaged to determine the overall threshold. In this way, daily increases in inhibition were taken into account. We also examined gap thresholds on each day of testing in each age group and found that thresholds on days 3 through 5 were the same as the thresholds obtained when averaging over the entire 5-day testing battery. Because of these measures, we do not feel that effects of repeated testing impinge upon the interpretation of the overall gap detection threshold results presented here.

Finally, unlike Dean et al. (1990), we found that repeated testing did alter acuity in very young animals. Consistent with the findings of Dean and colleagues, we found experience-related changes in gap detection thresholds in the P64 and P35 age groups. The adult (P64) rats were able

to detect gaps of 40, 20 and 10 ms on days 1, 2 and 3, respectively. A similar decrease was observed in the P35 group, with thresholds decreasing from 75 ms on day 1 to 30 and 20 ms on days 2 and 3, respectively. Consistent thresholds were maintained across days 4 and 5 in both the P64 and P35 groups. However, in the present study, we observed experience-based changes in animals as young as P15, whereas Dean and colleagues (1990) report effects of experience only in animals P35 and older (no effects of repeated testing in animals P14–30). Here, the P15 group showed no evidence of gap detection (at any duration) on days 1 and 2, but by day 3 (through day 5) these animals were significantly attenuating ASRs to gaps of 20 ms and greater. This is an extremely pertinent finding as it demonstrates that experience-enhancing behavioral effects are observable quite early in development.

The experience-related changes in gap detection thresholds found in all three age groups suggest that an improvement in auditory acuity or perceptual learning, or both, occurred over the course of experimental testing. The enhancing effects of practice on sensory thresholds (indicative of brain plasticity) are well documented (for review, see Ref. [17]). Practice or experience-induced changes in threshold may be evident in various sensory modalities, including low level processing tasks. For example, Karni and Sagi [18,19] assessed preattentive (automatic) processing of simple visual texture, a property that is processed very early in the visual stream and is independent of attention or conscious recognition. The authors found that discriminations improved with practice, indicating experience-dependent perceptual learning for basic visual processing. Further, there appeared to be permanent neural changes related to this experience-dependent improvement in the early stages of processing in the adult visual system. Additionally, Crofton et al. (1990) report changes in the amplitude of the ASR in rats with repeated daily testing, suggesting an unexpected associative learning component in this passive, reflex-modification paradigm. In light of these reports, the present findings of experience-induced changes of low-level auditory processing in the rat suggest perceptual learning in mature (P64), adolescent (P35) and very young (P15) animals. This observation is relevant to studies of experience-dependent plasticity, and may be germane to studies of remediation of auditory processing deficits at different stages of development (see Refs. [27,33]).

As the significance of experience in auditory processing tasks, including gap detection, are further explored, the stability of threshold may be questioned. Reflex modification paradigms may thus be useful in the assessment of experience-related changes in sensory processing. There is much room for future investigation of the effects of experience on discrimination of gaps and other types of auditory stimuli in cross-sectional and longitudinal study designs. In sum, the results of the present study support and extend previous research in the rat that demonstrates

observable shifts in gap detection thresholds over the course of development, and with experience. The maturational changes in gap detection in the rat parallel developmental trajectories reported across species [8,16,36], and the effects of experience, suggestive of perceptual learning and/or improvements in auditory acuity, are also in agreement with previous research [8]. However, we find that effects of repeated testing are observable in rats as young as P15, the youngest age group reported to date. This suggests that experience-dependent plasticity is operational very early on in development, even in a reflex modification paradigm. These results support the use of animal models in further behavioral investigations of the mechanisms underlying finely tuned auditory resolution, specifically the study of developmental changes in the auditory system.

Acknowledgements

This research was supported by a grant from NICHD (RO1 HD29419) to AAB, with additional support from the Elizabeth H. Solomon Center for Neurocognitive Research and HD20806 to RHF.

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