Behavioral/Systems/Cognitive

The Cost and Benefit of Juvenile Training on Adult Perceptual Skill

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Sensory experience during development can modify the CNS and alter adult perceptual skills. While this principle draws support from deprivation or chronic stimulus exposure studies, the effect of training is addressed only in adults. Here, we asked whether a brief period of training during development can exert a unique impact on adult perceptual skills. Juvenile gerbils were trained to detect amplitude modulation (AM), a stimulus feature elemental to animal communication sounds. When the performance of these juvenile-trained animals was subsequently assessed in adulthood, it was superior to a control group that received an identical regimen of training as adults. The juvenile-trained animals displayed significantly better AM detection thresholds. This was not observed in an adult group that received only exposure to AM stimuli as juveniles. To determine whether enhanced adult performance was due solely to learning the conditioned avoidance procedure, juveniles were trained on frequency modulation (FM) detection, and subsequently assessed on AM detection as adults. These animals displayed significantly poorer AM detection thresholds than all other groups. Thus, training on a specific auditory task (AM detection) during development provided a benefit to performance on that task in adulthood, whereas an identical training regimen in adulthood did not bring about this enhancement. In contrast, there was a cost, in adulthood, following developmental training on a different task (FM detection). Together, the results demonstrate a period of heightened sensitivity in the developing CNS such that behavioral training in juveniles has a unique impact on adult behavioral capabilities.

Introduction

A general theory of sensory development holds that early experience can influence CNS function, thereby shaping adult perceptual skills. Support for this idea draws from experiments in which a prolonged alteration of the sensory environment leads to changes in central coding properties and behavior (Feldman and Brecht, 2005; Hooks and Chen, 2007; Sanes and Bao, 2009). The overarching conclusion from these studies is that there is a critical period during which the environment has its greatest impact. Thus, environmental manipulations in adults do not produce the same effects as they do in immature animals. If theories of 'early experience' apply to learning, then we would expect developmental training to have a greater effect on adult performance than if that training occurred in adulthood. Here, we explored the issue by asking whether a brief period of auditory training during development exerts a unique influence on adult performance.

The influence of early sensory experience has been examined with two environmental manipulations: deprivation and chronic exposure. The loss of early auditory experience perturbs normal perceptual maturation in young animals, including children (Gottlieb, 1975; Clements and Kelly, 1978; Kerr et al., 1979; Knudsen et al., 1984; Kelly et al., 1987; Moore et al., 1999; Parsons

et al., 1999; Kidd et al., 2002; Halliday and Bishop, 2005). Similarly, chronic exposure to sound during development can disrupt normal perceptual sensitivity (Gottlieb, 1991; Han et al., 2007; Markham et al., 2008; Zhang et al., 2008). These findings are consistent with an even larger literature showing that neural coding, which often serves as a proxy for behavior, can be impacted by similar manipulations (for review, see Keuroghlian and Knudsen, 2007; Sanes and Bao, 2009).

The development of learning is well characterized (Hyson and Rudy, 1984; Moye and Rudy, 1987; Sullivan and Leon, 1987; Rudy, 1993; Flory et al., 1997), yet few studies have examined the effects of early learning on adult performance (e.g., sensorimotor learning in songbirds) (Doupe et al., 2004). While recent work suggests that short-term training-induced improvements is limited in immature subjects (Hyuck and Wright, 2010; Sarro and Sanes, 2010), it remains possible that there are long-term effects of this training that can only be assessed after maturation.

Training during adulthood demonstrates that perceptual learning (i.e., training-induced improvements in performance) can occur across many acoustic dimensions (Wright et al., 1997; Wright and Fitzgerald, 2001; Kacelnik et al., 2006; Mossbridge et al., 2006; van Wassenhove and Nagarajan, 2007). In contrast to these adult studies, we addressed whether a period of training during development can produce a long-term effect on adult perception that is distinct from the effect of training during adulthood. We trained juvenile gerbils to detect amplitude modulation (AM), a temporal envelope cue that is elemental to animal communication sounds, including speech (Rosen, 1992; Shannon et al., 1995; Singh and Theunissen, 2003). Their AM detection thresholds were subsequently assessed in adulthood, and
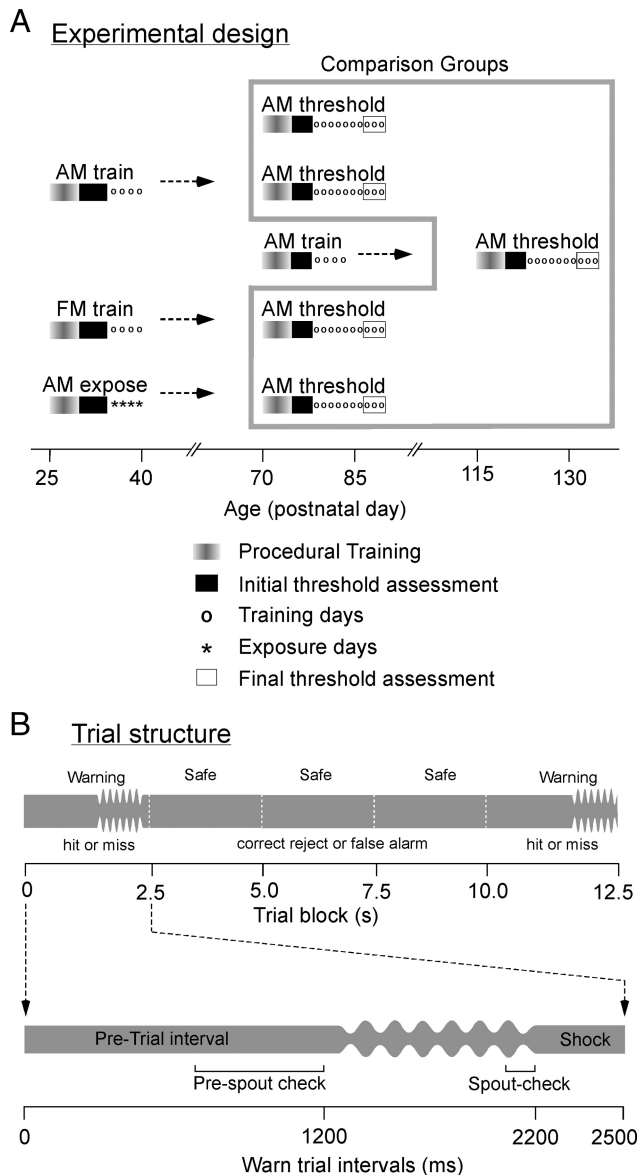
A Experimental design

Figure 1. *A*, Experimental design. The age range at which each treatment group was trained on a conditioned avoidance procedure is shown above the time line. This previous experience consisted of procedural training (graded box), an initial threshold assessment (black box), and 4 d of perceptual training (open circles) or exposure only (asterisks). As adults, animals again received procedural training and an initial threshold assessment, but this was followed by 10 d of perceptual training. Final threshold assessment was obtained during the last 3 d of perceptual training (black rectangle surrounding open circles). Naive adults received no previous experience and were assessed from P70 to P90. AM-trained juveniles received previous experience with the AM detection task at P25–P40, and were assessed as adults at P70–P90. The AM-trained adults received previous experience with the AM detection task at P70–P85, and were assessed as older adults from P115 to P135. The FM-trained juveniles received previous experience with the FM detection task at P25–P40 and were assessed on the AM detection task as adults from P70 to P90. Finally, the AM-exposed juveniles received previous experience with the AM stimuli used for training at P25–P40, and were assessed on the AM detection task as adults from P70 to P90. Results were drawn from comparisons between the performances of adult animals only (contained within the gray box labeled Comparison Groups). *B*, Trial structure. A block of warning and safe trials, each lasting 2.5 s, are illustrated (top), along with a single enlarged warning trial (bottom). Each warning trial was separated by a random number of safe trials (containing only unmodulated noise). For warning trials, the pretrial period (1200 ms) contained unmodulated noise (or a 4 kHz tone for the FM detection task). Trials continued only when animals remained in contact with the waterspout for >50% of the 500 ms pretrial spout check period. The warning stimulus (AM noise at a 5 Hz modulation frequency, or FM with a carrier of 4 kHz) was presented for 1000 ms. During the final 100 ms of the warning stimulus, a spout check determined whether the gerbil was in contact with the spout. A 300 ms current was

compared with a control group that received an identical regimen of training as adults. The results revealed a benefit to adult AM sensitivity when animals were trained on the AM detection task during development, but not during adulthood.

Materials and Methods

Animals. All procedures relating to the maintenance and use of animals were in accordance with the "Institutional Animal Care & Use Committee Handbook" and were approved by the University Animal Welfare Committee at New York University. Gerbil (*Meriones unguiculatus*) pups were weaned from commercial breeding pairs (Charles River) at postnatal day 23 (P23)–P30. Males and females were caged separately and maintained in a 12 h light/dark cycle.

Experimental environment. Gerbils were placed in a small wire cage in a room lined with echo-attenuating material, and observed in a separate room via a closed circuit monitor. The test cage contained a stainless steel drinking spout and metal floor plate. When the animal contacted both the plate and spout, a circuit was completed that initiated water delivery via a syringe pump (Yale Apparatus). A personal computer, connected to a digital I/O interface (Tucker-Davis Technologies) controlled the timing of acoustic stimuli, water delivery (0.3 ml/min), and a small current delivered at the end of warning trials. Auditory stimuli were generated by the Tucker-Davis Technologies system and delivered via a calibrated tweeter (KEF Electronics) positioned 1 m in front of the test cage. Sound level at the test cage was measured with a spectrum analyzer (Brüel & Kjaer 3550) via a ¼ inch free-field condenser microphone positioned at the head location when in contact with the spout. The metal waterspout was similar in appearance to that within the home cage.

Procedural training. All training used a conditioned avoidance procedure (Heffner and Heffner, 1995; Kelly et al., 2006). Animals were first placed on controlled water access, and upon introduction to the experimental cage, learned to obtain water from a lick spout. This was done in the presence of an unmodulated noise stimulus [or unmodulated 4 kHz tone for the juvenile animals trained with a frequency modulation (FM) stimulus] while contact with the waterspout was monitored. Animals were then trained to withdraw from the spout when an acoustic cue (modulation of amplitude or frequency) was present. To train the withdrawal response, a low AC current (0.5–1.0 mA, 300 ms; Lafayette Instruments) was delivered through the waterspout immediately after the warning signal. Since animals display large between-subject variability in pain sensitivity (Mogil, 1999; Wasner and Brock, 2008; Nielsen et al., 2009), we adjusted the shock level for each animal to reliably produce withdrawal from the spout, but not so great as to dissuade an animal from approaching the spout on subsequent trials. The animals' behavior was monitored constantly to ensure that the level was set correctly. To train animals on the procedure (i.e., procedural training), warning trials (AM noise: 100% modulation depth; FM 4 kHz tone: 500 Hz modulation depth) were presented until performance reached a criterion of ≥70% correct over 10 consecutive trials. All animals received procedural training to establish criterion performance when they were first introduced to the task as well as when their performance was assessed in adulthood (Fig. 1A, graded boxes).

Perceptual training and the assessment of AM detection thresholds. Once animals in each experimental group reached criterion on the conditioned avoidance procedure, we obtained an initial assessment (Fig. 1A, black box) of AM detection threshold by testing animals on a broad range of AM depths (10–100% AM depth, 10% steps) presented in a randomized order, with the same order being delivered to each animal. For those juvenile animals trained to detect FM stimuli, an initial assessment (Fig. 1A, black box) of FM detection threshold was obtained by presenting each animal with a broad range of FM depths (50–500 Hz) presented in randomized order. Each depth was presented a total of 10 times, and a

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delivered through the waterspout immediately after the warning stimulus as the aversive unconditioned stimulus. Safe trials were identical in timing, although there was no AM or FM stimulus or shock. Spout contact was monitored at an identically positioned spout check interval during the safe trials.

single psychometric function was constructed from performance on these randomized trials.

After the initial assessment of detection threshold was obtained, all animals received a period of perceptual training (Fig. 1*A*, open circles). Our goal was to examine the effect of a prior experience with auditory training on the performance of adult animals when assessed at a later time. Therefore, several of the experimental animal groups received procedural and perceptual training at two different time points (Fig. 1*A*), and their performance on the second period of training was compared with those animals that did not have a previous experience. Perceptual training consisted of the presentation of 5 AM (or FM) depths a minimum of five times in descending order, bracketing each animal's detection threshold from their initial assessment. On each subsequent day of perceptual training, an animal's performance on the previous day determined the range of depths that were presented (i.e., always bracketing the previous detection threshold). From these data, we tracked AM detection thresholds from the initial to the final assessment. This protocol was used for all adult animals in each experimental condition.

Experimental groups. AM detection thresholds were obtained from an initial assessment (Fig. 1*A*, black boxes), followed by a period of perceptual training (Fig. 1*A*, open circles) for adult gerbils in 5 treatment groups, as described above. Naive adults ($n = 10$) received procedural and 10 d of perceptual training from P70 to P90, the age at which gerbils reach sexual maturity (Field and Sibold, 1999). These animals did not have any prior experience with the task. AM-trained juveniles ($n = 14$) received a prior experience at the AM detection task that consisted of procedural training and 4 d of perceptual training at P25–P40, the earliest age at which animals could be weaned and placed on controlled water access. As adults, these animals received procedural and 10 d of perceptual training from P70 to P90, identical to the naive adults. AM-trained adults ($n = 13$) also received a prior experience with the AM detection task that consisted of procedural training and 4 d of perceptual training from P70 to P90. As older adults, at P115–P135, these animals received procedural and 10 d of perceptual training, in an identical manner to the naive adults. The FM-trained juveniles ($n = 12$) received a prior experience with the behavioral task that consisted of procedural training and 4 d of perceptual training on an FM detection task at P25–P40. As adults, at P70–P90, these animals received procedural and 10 d of perceptual training on the AM detection task in an identical manner as the naive adults. Finally, the AM-exposed juveniles ($n = 7$) received a prior experience with the auditory stimuli that consisted of drinking from the waterspout in the presence of AM stimuli at P25–P40. As adults, at P70–P90, these animals received procedural and 10 d of perceptual training on the AM detection task, identical to the naive adults. The AM stimuli presented to these juveniles were identical to those used for training the AM-trained juveniles. We have reported modest improvement of AM detection between the ages of P30 and P40 (Sarro and Sanes, 2010). Since we sought to avoid as much developmental improvement as possible during the juvenile training period, we completed all training by P40. Thus, the juveniles received only 4 d of perceptual training after the initial detection threshold was obtained. For the adults, we sought to measure performance during an identical, finite assessment period (10 d). All animals that entered the protocol were included in the analyses. No selection criteria were imposed and poor performers were not eliminated during any phase of the procedure. This permitted us to compare both mean performance and between-animal variability within and across all experimental groups.

Schematics of a series of warning and safe trials, and the structure of a single warning trial is shown in Figure 1*B*. Each warning or safe trial was 2500 ms long. The sound pressure level remained constant (45 dB eqSPL) during the pretrial and warning intervals to exclude the use of an energy cue. The noise stimulus was broadband (measured as an RMS), with a 25 dB roll off at 3.5 kHz and a 25 dB roll off at 20 kHz. Each warning trial contained 1200 ms of unmodulated noise (or 4 kHz tone for FM) during the pretrial interval, and the spout was monitored for contact during the final 500 ms interval. The trial proceeded only if the animal remained in contact with the spout for >250 ms during this interval. The warning stimulus was 1000 ms of sinusoidally amplitude modulated noise at a modulation frequency of 5 Hz and at varying depths. For FM stimuli, the

warning stimulus was 1000 ms of sinusoidal modulation about a 4 kHz center frequency at a modulation frequency of 5 Hz and at varying frequency depths. Warning stimuli were followed immediately by an aversive unconditioned stimulus (300 ms electrical current delivered via the lick spout). To determine whether the animal detected the warning stimulus, contact with the spout was monitored during the final 100 ms of the warning stimulus. A contact time of <50 ms was scored as a hit and a contact time of >50 ms was scored as a miss. For safe trials, a contact time of <50 ms was scored as a false alarm and a contact time of >50 ms was scored as a correct rejection. Warning trials always occurred at the end of a block of 2–4 safe trials, randomized to avoid temporal conditioning.

Data analysis. A performance value, $d' = z_{\text{false alarm}} - z_{\text{hit}}$, was obtained for z scores that corresponded to the right-tail p values (Swets, 1973; Yanz, 1984), and was calculated for each AM depth. Thresholds were defined as the AM (or FM) depth at which performance reached a $d' = 1$ and only sessions in which animal performed a minimum of 25 trials were included in the analysis. The results presented here are from the adult performance of each treatment group. Psychometric functions were constructed from the initial assessment with random stimuli and throughout each day of perceptual training. The best or average performance during the final 3 d of perceptual training served as the final assessment of AM detection thresholds (Fig. 1*A*, black rectangle surrounding open circles). To measure the perceptual learning, the change in detection threshold from the initial assessment was compared with this final assessment. Procedural learning was measured by quantifying the amount of procedural training trials presented to each animal before performing at criterion ($\geq 70\%$ correct). We also compared the within-animal performance variability across testing sessions.

Results

The effect of training juveniles on their performance as adults

To address whether training during juvenile development on an AM detection task would influence adult performance, we obtained the AM detection thresholds from adult animals that were trained on AM detection as juveniles, and compared them with those obtained from naive adult animals. We confirmed that juveniles could perform the AM detection task, and did display learning during the course of training. The juveniles improved from an average initial AM detection threshold of 41.2 ± 2% AM depth to an average final threshold of 36.0 ± 2% AM depth (consistent with Sarro and Sanes, 2010). All values are reported as mean ± SEM.

The AM-trained juveniles displayed significantly lower AM detection thresholds as adults (naive adults: 17.9 ± 1.2%; AM-trained juveniles: 11.9 ± 0.7%; t test: $p < 0.001$, df = 21, $t = 4.35$). Figure 2*A* shows psychometric functions for each animal's best performance during the final assessment of adult performance over the final 3 d of perceptual training. The detection thresholds at $d' = 1$ are shown below the curves. A similar result was obtained when performance was averaged over the final 3 d of training (naive adults: 23.0 ± 1.3; AM-trained juveniles: 15.4 ± 0.7; t test: $p < 0.001$, df = 22, $t = 5.08$) (Fig. 2*B*). Thus, training on AM detection during juvenile development leads to better AM detection thresholds in adulthood, compared with adults with no developmental experience.

The unique long-term effect of training juvenile animals

To examine whether training during development exerts a unique influence on adult performance, we examined whether adult animals subjected to an identical training protocol would display a similar long-term enhancement when reassessed at an identical interval. Adults were trained on the AM detection task beginning at P70, and reassessed as older adults at P115–P130 (Fig. 1*A*). Their performance was then compared with the performance of adults trained as juveniles. The AM-trained juveniles
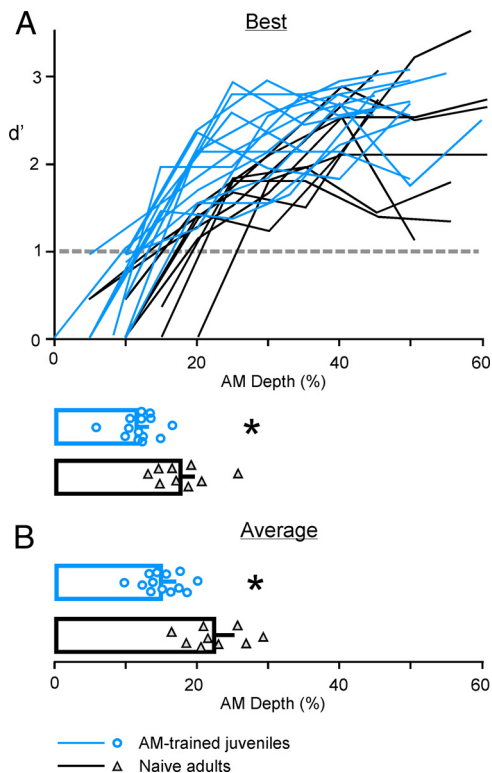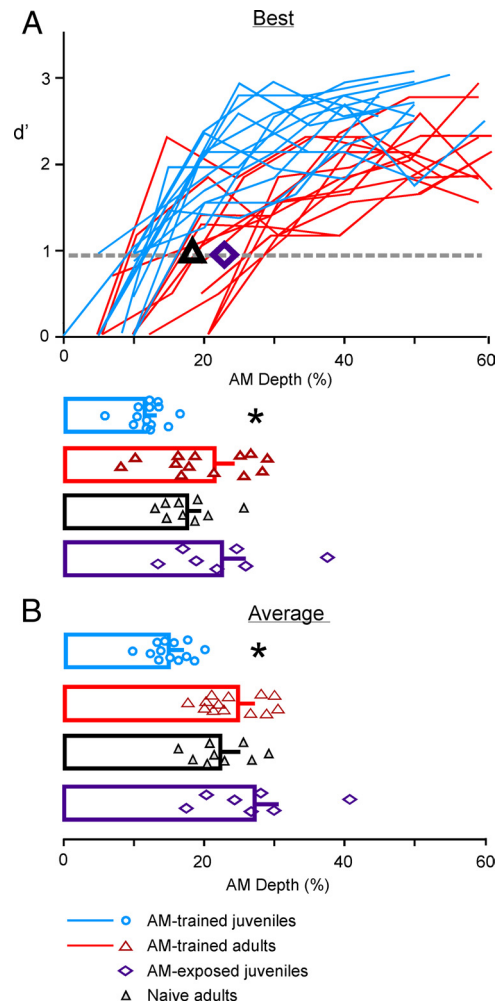
Figure 2. Juvenile training improved adult performance. ***A***, Individual psychometric functions (top) and detection thresholds (bottom) are shown for the AM-trained juveniles (blue lines, circles) and naive adults (black lines, triangles). These represent each animal's best day of performance during the final 3 d of training in adulthood (see Materials and Methods). Detection thresholds were obtained at $d' = 1$ (dashed gray line on plot) from the psychometric functions. Note that the AM-trained juveniles performed significantly better than the adults that had no previous training. Bars display mean AM detection (+SEM). ***B***, The average performance over the final 3 d of training is depicted by the data points and bars (*$p < 0.001$).

Figure 3. Adult training did not improve adult performance. ***A***, Individual psychometric functions (top) and detection thresholds (bottom) are shown for the AM-trained juveniles (blue lines, circles) and the AM-trained adults (red lines, triangles). These represent each animal's best day of performance during the final 3 d of training (see Materials and Methods). Detection thresholds were obtained at $d' = 1$ (dashed gray line on plot) from the psychometric functions. For the purpose of comparison, individual psychometric functions and data points from the AM-trained juveniles, and data points from the naive adults are replotted from Figure 2. Those animals with training during juvenile development performed significantly better than adults trained initially as adults and reassessed later in adulthood. These animals did not display a significant difference from the performance of the naive adults. For comparison, the black triangle and purple diamond on the plot represents the average performance of the naive adults and AM-exposed juveniles, respectively. Bars display mean AM detection (SEM). ***B***, The average performance over the final 3 d of training is depicted by the data points and bars (*$p < 0.001$).

animals displayed significantly better detection thresholds than the AM-trained adults (AM-trained adults: 21.6 ± 2.1; AM-trained juveniles: 11.9 ± 0.7; *t* test: $p < 0.001$, df = 25, $t = 4.41$). Figure 3*A* displays individual psychometric functions for each animal's best performance during the final 3 d of testing. The detection thresholds at $d' = 1$ are shown below the curves. In comparison, the best performance of the naive adults was not significantly different from that of the trained adults (naive adults: 17.9 ± 1.2%, *t* test: $p = 0.15$, df = 20, $t = 1.51$; shown graphically as a black triangle on the plot of psychometric functions). A similar result was obtained when performance was averaged over the final 3 d of training (AM-trained adults: 24.3 ± 1.2; AM-trained juveniles: 15.4 ± 0.7; *t* test: $p < 0.001$, df = 25, $t = 6.42$) (Fig. 3*B*). Again, the average performance of the naive adults was not significantly different from that of the trained adults (naive adults: 23.0 ± 1.3, *t* test: $p = 0.45$, df = 20, $t = 0.78$). Thus, auditory training during juvenile development results in a long-term benefit to performance, whereas adult animals do not display this effect.

**Learning a FM detection task during development disrupts adult AM detection**

It was possible that training during development improved the subsequent performance of animals in adulthood due to procedural learning alone. To test this possibility, juveniles were trained on a different auditory task, FM detection, and then assessed on AM detection as adults. The identical conditioned

avoidance procedure was used for both tasks. We confirmed that juveniles could perform the FM detection task, and that they did display learning during the course of training. The average initial FM detection threshold was 113.1 ± 9 Hz, and this improved to a final threshold of 73.5 ± 5 Hz.

The AM-trained juveniles displayed significantly better detection thresholds than the FM-trained juveniles (FM-trained juveniles: 35.1 ± 3.5; AM-trained juveniles: 11.9 ± 0.7; *t* test: $p < 0.001$, df = 24, $t = 6.56$). Figure 4*A* shows psychometric functions for each animal's best performance during the final 3 d of testing. The detection thresholds at $d' = 1$ are shown below the curves. In comparison, the best performance of the naive adults was also significantly better than that of the FM-trained juveniles (naive adults: 17.9 ± 1.2%, *t* test: $p < 0.001$, df = 20, $t = 4.66$, shown graphically as a black triangle on the plot of psychometric
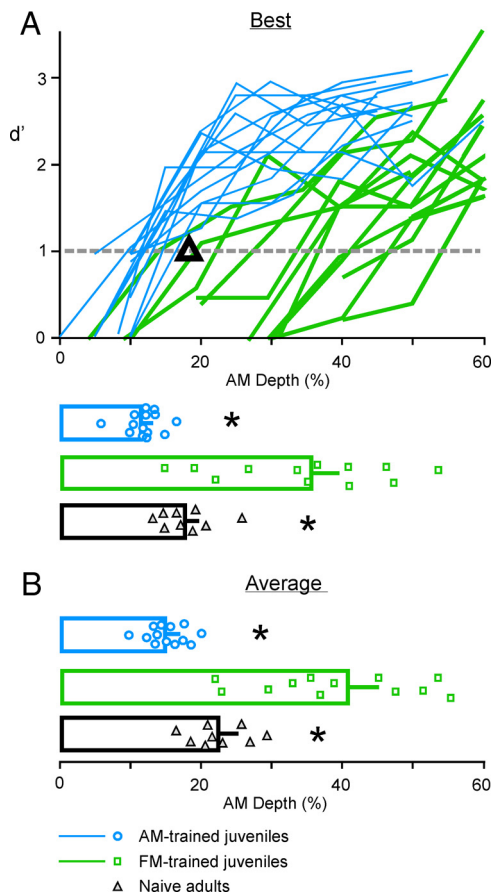
Figure 4. Juveniles trained on FM detection did not display improved AM detection as adults. ***A***, Individual psychometric functions (top) and detection thresholds (bottom) are shown for the AM-trained juveniles (blue lines, circles) and the FM-trained juveniles (green lines, squares). Detection thresholds are also displayed for naive adults (black triangles). These represent each animal's best day of performance during the final 3 d of training (see Materials and Methods). Detection thresholds were obtained at $d' = 1$ (dashed gray line on plot) from the psychometric functions. For the purpose of comparison, individual psychometric functions and data points from the AM-trained juveniles, and data points from the naive adults are replotted from Figure 2. Those adults with AM-training during juvenile development performed significantly better than those adults with FM-training during juvenile development. These animals also displayed poorer performance than that of the naive adults. Bars display mean AM detection (SEM). For comparison, the black triangle on the plot represents the average performance of the naive adults. ***B***, The average performance over the final 3 d of training is depicted by the data points and bars (*$p < 0.001$).

functions). A similar result was obtained when performance was averaged over the final 3 d of training (FM-trained juveniles: 40.0 ± 3.2; AM-trained juveniles: 15.4 ± 0.7; t test: $p < 0.001$, df = 24, $t = 7.43$) (Fig. 4B). Again, the average performance of the naive adults was significantly better than that of the FM-trained juveniles (naive adults: 23.0 ± 1.3, t test: $p < 0.001$, df = 20, $t = 4.57$). Thus, enhanced AM detection in adulthood did not occur when animals were trained on a different auditory detection task during development. In fact, training on FM detection during development led to poorer performance on the AM detection task in adulthood, compared with what would have been expected from a normal adult animal.

### AM exposure during development was not sufficient to effect adult performance

Since many developmental plasticity studies have demonstrated an effect of stimulus exposure on CNS physiology and behavior, we asked whether exposing juveniles to AM stimuli would be

sufficient to influence their performance in adulthood. Animals were exposed to AM stimuli as juveniles, but were not trained to perform the AM detection task until they reached adulthood (Fig. 1A). The AM depths and number of AM stimuli were identical to the group trained on AM detection as juveniles. The AM-trained juveniles displayed significantly better detection thresholds during the final 3 d of training, compared with adults that were merely exposed to AM stimuli as juveniles (Fig. 3A; AM-exposed juveniles: 22.7 ± 3.0; AM-trained juveniles: 11.9 ± 0.7; t test: $p < 0.01$, df = 19, $t = 3.51$). In comparison, the best performance of the naive adults was not significantly different from that of the AM-exposed juveniles (naive adults: $17.9 \pm 1.2\%$, t test: $p = 0.18$, df = 15, $t = 1.47$). A similar result was obtained when performance was averaged over the final 3 d of training (Fig. 3A; AM-exposed juveniles: 27.3 ± 2.7; AM-trained juveniles: 15.4 ± 0.7; t test: $p < 0.005$, df = 19, $t = 4.32$). Again, the average performance of the naive adults was not significantly different from that of the AM-exposed juveniles (naive adults: 23.0 ± 1.3, t test: $p = 0.18$, df = 15, $t = 1.48$). Thus, to improve adult performance, it is not sufficient to merely expose juveniles to the same stimuli used for training.

The effect of training during development on perceptual learning in adulthood

Figure 5A shows the average daily detection thresholds for each animal group across all sessions. Even the initial thresholds of the AM-trained juveniles were superior to the other groups with previous experience (i.e., AM-trained adult, and FM-trained juveniles) (ANOVA: $p < 0.01$, df = 3, $F = 6.33$). The AM-trained juveniles had lower initial AM thresholds ($30.6 \pm 1.9\%$) than the AM-trained adults (37.5 ± 2.3; t test: $p < 0.05$, df = 25, $t = 2.3$). In contrast, the FM-trained juveniles displayed significantly poorer initial detection thresholds ($43.7 \pm 3.1\%$) than the AM-trained adults (t test: $p < 0.01$, df = 22, $t = 3.25$).

Thus, performance was enhanced for the AM-trained juveniles (blue line) over the entire period that animals were trained in adulthood. In contrast, the FM-trained juveniles (green line) displayed poorer initial thresholds and less improvement over the course of perceptual training in adulthood. This implies that early training on a FM detection task impaired the animals' ability to improve with training on an AM detection task or profoundly delayed improvement. When all groups were compared, there was a main effect of previous training on the final detection thresholds obtained during the final 3 d of training (Fig. 5B; ANOVA: $p < 0.001$; df = 3; $F = 32.9$). Pairwise comparisons indicated that the AM-trained juveniles (blue box) displayed significantly better performance than the AM-trained adults (red box; AM-trained adults: 24.3 ± 1.2; t test: $p < 0.001$, df = 25, $t = 6.42$), FM-trained adults (green box; FM-trained juveniles: 40.0 ± 3.2; t test: $p < 0.001$, df = 24, $t = 7.43$), and naive adults (gray filled box; naive adults: 23.0 ± 1.3; t test: $p < 0.001$, df = 22, $t = 5.08$). There was also a main effect of experience on the amount of improvement from the initial to the final assessment of AM detection in adulthood (Fig. 5C; ANOVA: $p < 0.01$, df = 3, $F = 4.39$). Improvement was similar between adults trained on AM as juveniles to adults trained on AM as adults (AM-trained juveniles: $\Delta15.3 \pm 2\%$; AM-trained adults: $\Delta13.3 \pm 2\%$; t test: $p = 0.5$, df = 24, $t = 0.71$), as well as to naive adults ($\Delta10.1 \pm 2\%$; t test: $p = 0.09$, df = 22, $t = 1.76$). However, the adults trained on FM as juveniles displayed significantly less improvement ($\Delta4.5 \pm 3\%$; t test: $p < 0.05$, df = 19, $t = 2.82$).

A Performance of Adults with previous experience
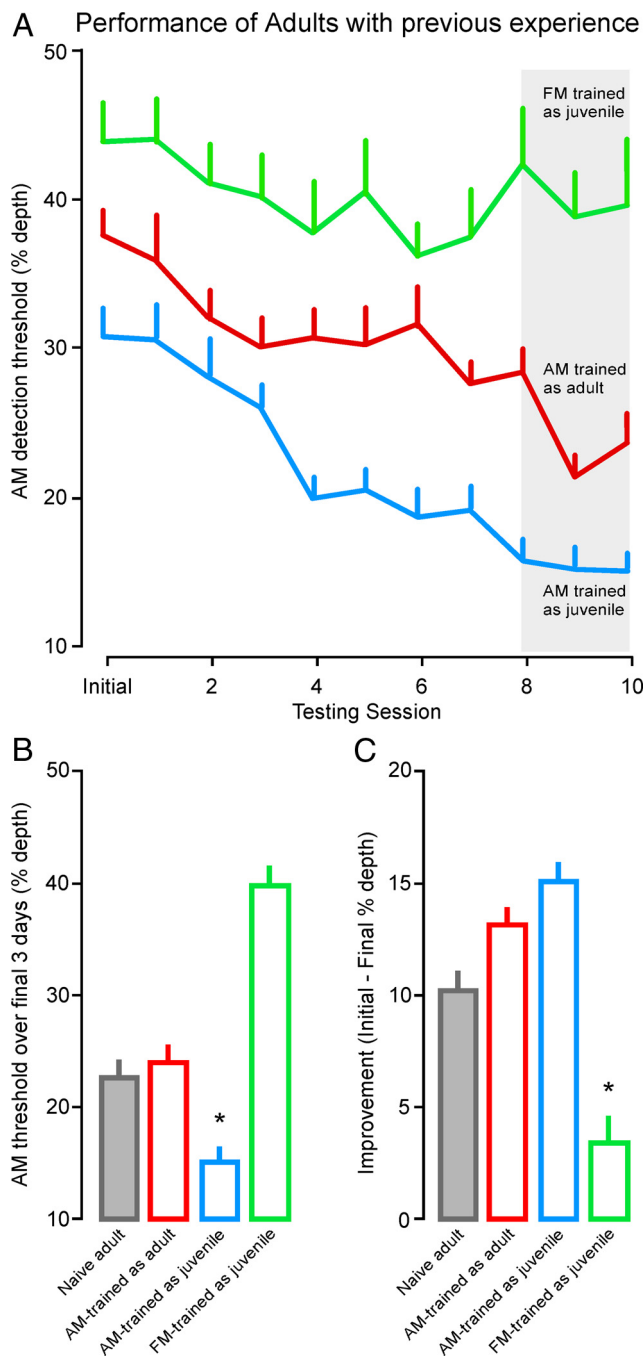
Figure 5. The cost and benefit of development training on adult performance. **A**, The average daily AM detection thresholds in adulthood are shown for animals that had two experiences with auditory training: the AM-trained juveniles (blue), AM-trained adults (red), and FM-trained juveniles (green). Those animals, with previous training on the AM detection task as juveniles, displayed the lowest initial and final thresholds. In contrast, those animals with training on FM detection as juveniles, displayed the poorest initial and final AM detection thresholds. **B**, Bar graph shows the average daily AM detection threshold over the final 3 d of perceptual training. The AM-trained juveniles (blue) display the best average performance for the final 3 d. Similar performance is shown for the AM-trained adults (red) and the naive adults (gray) while the FM-trained juveniles (green) display the worst average performance. **C**, Bar graph shows the average improvement displayed by each of these groups determined as the difference between the initial assessment of detection thresholds and the average during their final 3 d of training. The improvement displayed by the naive adults was similar to the AM-trained adults as well as AM-trained juveniles (*p < 0.05).
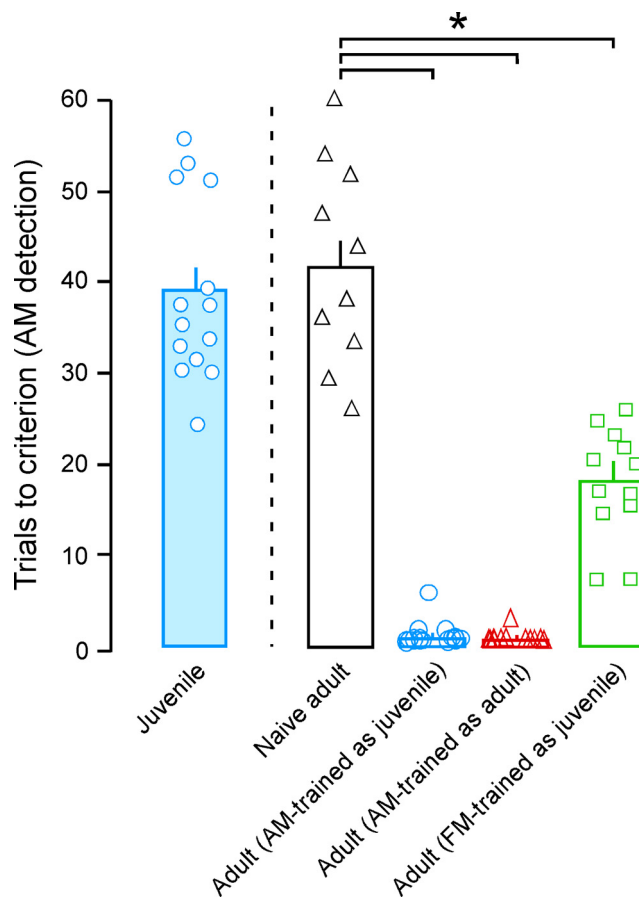
Figure 6. Effect of auditory training on procedural learning. Bar graph depicts the number of training trials each animal received before performing at criterion on the AM detection task. Vertical dashed line separates the juvenile animals (blue bar, light blue fill, circles) from the adults. On the right of the vertical dashed line are the naive adults (black bar, triangles), the AM-trained juveniles (blue bar, circles), the AM-trained adults (red bar, triangles) and the FM-trained juveniles (green bar, squares). Animals with previous AM detection training were able to retain the procedure regardless of when they were first trained. Animals with previous FM detection training carried forward a benefit of learning the detection task, and needed fewer trials during procedural training to reach criterion. (*p < 0.001).

An evaluation of acquisition and proficiency on the conditioned avoidance procedure

To determine how rapidly the conditioned avoidance procedure was acquired, and how well it was retained, we measured the amount of training each animal required to reach a performance criterion on the AM detection task (see Materials and Methods). As shown in Figure 6, animals being trained on the AM detection task for the first time required ~40 trials to reach criterion performance, whether they were juveniles (blue bar with light blue fill) or adults (naive adults, black bar) (juveniles: 39.1 ± 3.2; naive adults: 42.5 ± 3; t test: $p = 0.39$, df = 18, $t = 0.9$). This suggests that there was no difference in the ability of juveniles and adults to learn the AM detection task (consistent with Sarro and Sanes, 2010). However, there was a main effect of experience on acquisition of the AM detection task (ANOVA: $p < 0.001$, df = 3, $F = 142.5$; t tests below are compared with the naive adults). Animals that had received previous training on the AM detection task, as juveniles or adults, missed only 1–2 trials before they performed at criterion when they were reassessed on the AM detection task, significantly less than naive adults (AM-trained juveniles, blue bar: 1.42 ± 0.4, t test: $p < 0.001$, df = 23, $t = 13.15$; AM-trained adults, red bar: 1.17 ± 0.2; t test: $p < 0.001$, df = 21, $t = 13.3$).

This suggests that animals retained the procedure regardless of when they were trained initially. The number of training trials presented to the FM-trained juveniles (18.3 ± 1.7) was also significantly less than the naive adults (t test: $p < 0.001$, df = 21, t = 6.8). This suggests that animals carried forward a benefit from performing the conditioned avoidance procedure with FM stimuli as juveniles.

To determine whether the difference in detection thresholds between groups was due to unequal proficiency at the AM detection task, we compared the sensitivity (d') of animals at AM depths of 80–100% during initial testing with random stimuli (see Materials and Methods). The average performance of each animal group at 80–100% depth did not differ significantly from one another (ANOVA: $p = 0.3$, df = 3, $F = 1.4$).

To examine whether the ability of juveniles to perform this task was associated with their ability in adulthood, we compared several performance measures for juveniles and asked whether they correlated with performance in adulthood. Several trends emerged, but none were significant. First, a comparison of the initial juvenile threshold displayed by the AM-trained juveniles on the AM detection task was not significantly correlated with their best performance during adulthood ($R^2 = 0.17$, $p = 0.1$). In addition, we found no significant relationship between the improvement that juveniles displayed from their initial to final performance and the best performance of these animals as adults ($R^2 = 0.23$; $p = 0.08$). Finally, the improvement that the FM-trained juveniles displayed during their initial FM training was not significantly correlated to their adult AM performance ($R^2 = 0.41$, $p = 0.09$). These data suggest that juvenile abilities may not be predictive of adult performance.

Discussion

The premise of this study, that developmental experience influences adult behavior, draws largely from paradigms in which the sensory environment is altered. Here, we demonstrated that developmental training resulted in better performance when reassessed as adults. Specifically, adult gerbils that received AM training during juvenile development displayed better AM detection thresholds than age-matched controls (Fig. 2). Furthermore, training was more effective at an age when AM detection thresholds are immature (Sarro and Sanes, 2010). Thus, a control group that received an identical regimen of initial training as adults did not display enhanced thresholds when reassessed (Fig. 3).

Mere exposure to the AM stimuli used for training was not sufficient to improve adult detection thresholds. This suggests that juveniles must participate in a stimulus-associated task for the long-term effects to occur. Furthermore, the effect of training during juvenile development displays stimulus specificity. When juveniles were trained on a FM detection task, their performance on an AM detection task was not enhanced in adulthood; in fact, it led to a deficit (Fig. 4). Together, these results demonstrate a unique effect of developmental training. Furthermore, the cost or benefit of this developmental experience depends on the specific stimuli used in training, as discussed below.

A benefit of training during development

Although learning is studied broadly in adults, the effect of developmental training on adult perception has rarely been examined systematically. Those studies that are consistent with a unique developmental effect of training generally lack a key control group: subjects trained initially as adults and reassessed later in adulthood. Thus, speech and language acquisition is better when children with hearing loss receive cochlear implants earlier in development (Svirsky et al., 2004; Nicholas and Geers, 2006). However, we do not know how similarly deprived adults would respond to an identical treatment. Developmental experience with a reflexive auditory behavior also enhances adult sensitivity for rats but, again, it is not known whether an identical regimen in adulthood would similarly improve sensitivity (Threlkeld et al., 2009). Here, a unique influence of early training on adults is apparent since an identical regimen of training in adulthood did not produce the effect (Fig. 3). This is consistent with a developmental window (i.e., critical period) during which the CNS is most malleable to auditory training.

The neural basis for our finding remains unknown but developmental experience is know to exert a profound influence on single neuron response properties and topographic maps (for review, see Keuroghlian and Knudsen, 2007; Sanes and Bao, 2009). The simplest explanation for the enhanced adult performance is that developmental training has enhanced the primary sensory representation of AM stimuli. This would be broadly consistent with studies from adult animals (for review, see Weinberger, 2004; Polley et al., 2006). Thus, it is plausible that the neurophysiological consequences of developmental training can be measured in the juvenile CNS, even before assessment of adult behavior.

The influence of developmental deprivation or chronic exposure on adult behavior

There is general agreement that developmental deprivation, including childhood hearing loss, produces deficits in auditory perception (Clements and Kelly, 1978; Knudsen et al., 1984; Hall and Grose, 1994; Wilmington et al., 1994; Hall et al., 1995; Moore et al., 1999; Parsons et al., 1999; Halliday and Bishop, 2005, 2006). Chronic exposure studies support a similar conclusion. Thus, auditory experience plays a fundamental role in vocal imprinting and song learning (Marler, 1970; Gottlieb, 1980; White, 2001). However, the acoustic environment may have less of an influence in adult animals. Adult birds can maintain normal song patterns longer than juvenile birds following deafening (Lombardino and Nottebohm, 2000), and following a period of deprivation, reacquisition of their pretreatment song exhibited by adult zebra finches is limited (Zevin et al., 2004). Although these results suggest that there is a critical period where the capacity for sensorimotor learning is at its greatest, they do not address whether early learning improves adult performance (Figs. 2, 3).

Since our chronic exposure manipulation did not affect adult performance, it is important to recognize that duration and context are key variables (Gottlieb, 1991; Saffran et al., 1996; Sleigh et al., 1996; Maye et al., 2002, 2008; Sakai and Kudoh, 2005; Toro et al., 2005; Markham et al., 2006; Kuhl, 2007; Wright et al., 2010). Thus, most chronic exposure studies provide continuous exposure for days to weeks (Gibson and Walk, 1956; Han et al., 2007; Zhang et al., 2008). In contrast, the present study showed that exposure to the identical AM stimuli used for training was insufficient to induce a long-term effect in adulthood. This indicates that active participation in the procedure was necessary. Thus, the effects of chronic exposure studies may differ qualitatively from those in which animals learn a stimulus-related task.

Procedural learning during development

Animals trained on AM detection as juveniles could have performed better as adults for several reasons, one being the beneficial effect of procedural learning (e.g., learning to withdraw from the lick spout when a change in the stimulus was detected) (for review, see Ortiz and Wright, 2009). We examined the contribu-

tion of procedural learning by training a group of animals on a different task as juveniles. FM training during juvenile development did reveal an effect of procedural learning. As adults, these animals reached criterion on the AM detection procedure in fewer trials, compared with naive adults (Fig. 6). This suggests that animals trained as juveniles on FM detection carried forward some benefit of procedural learning. However, they did not reach criterion as fast as animals trained initially on AM detection, either as juveniles or adults. Thus, these FM-trained juveniles apparently lacked a benefit that can be attributed to developmental experience with AM detection itself.

A cost of training during development
Animals trained on FM detection as juveniles subsequently displayed poorer AM detection thresholds in adulthood, both during the initial assessment (i.e., after reaching criterion on the AM task), and after 10 d of perceptual training (Figs. 4, 5). This suggests that adult animals were penalized due to the training they received on a task other than AM detection as juveniles. Although this result was not predicted by our theoretical framework, there is a precedent for observing diminished performance on an untrained task. When human subjects are trained to discriminate AM rate (using 100% modulated signals), they improve on this task. However, these same subjects display a decline in performance on an AM detection task, even 1 month after the training (Fitzgerald and Wright, 2005). In explaining these results, the authors note that the subjects probably listened to the pitch at the modulation frequency to perform the trained AM discrimination task. Furthermore, a larger modulation depth is required to discern pitch, than is needed to detect the presence of modulation. Therefore, the authors posit that the subjects became worse at detecting AM after learning to discriminate AM rate because they continued to listen for pitch. Put another way, subjects learned to use a cue that helped them with the trained task (i.e., a benefit), but use of this cue was suboptimal for a second, untrained task and led to diminished performance (i.e., a cost). There is a second example of this phenomenon in which human subjects are trained to discriminate spectrotemporal modulation. The subjects, again, improve on the discrimination task, but their performance on an untrained modulation detection task worsens. Furthermore, there is a strong correlation between improvement on the trained task and worsening on the untrained task (Sabin et al., 2010). A similar phenomenon could explain the deleterious effect of FM-training during juvenile development. For example, the FM-trained juveniles may have learned to perform this task by listening for the energy at a frequency near the edge of the frequency modulation; in effect, listening for a large modulation in amplitude at a single critical band. As adults, these animals may continue to be listening for a large modulation depth in accordance with their original strategy. This would explain both the poorer detection thresholds, as well as the ability of the animals to reach criterion quickly (Fig. 6). It is not clear whether animals would eventually have reached AM detection thresholds of normal adults, or whether this was permanent. In any event, their response to the training regimen was entirely different from that displayed by adults with previous AM detection experience (Fig. 5).

Perhaps the most impressive feature of this phenomenon was that these animals did not recover from the deficit during perceptual training in adulthood. While the mechanistic basis for this finding is unclear, perceptual learning is known to be associated with changes in auditory cortex that specifically reflect the behaviorally relevant stimulus dimension (Polley et al., 2006). Furthermore, activity-dependent perturbations in the cortical

representation of frequency are associated with improvements and deficits in frequency discrimination performance (Han et al., 2007). Thus, it is possible that developmental training on FM detection biased the cortical representation toward FM sensitivity, thereby diminishing the animal's performance on AM detection.

Summary
The present results illustrate both the cost and benefit of developmental training. Juvenile training led to either enhanced or deficient performance in adulthood, depending on the stimuli used for initial training (Figs. 2–4) when compared with adults that had no previous training. An identical training regimen initiated in adulthood did not produce this effect when tested at a later time. While not directly tested in this study, the results suggest that a critical period may exist for training-induced modifications of the CNS, similar to the sorts of critical periods demonstrated by deprivation and chronic exposure manipulations. This is not to deny the significant plasticity displayed by adult animals, but rather to point out differences in their form. Indeed, adults improved over the course of training, but those animals with a previous training experience that occurred before sexual maturation displayed greater overall performance in adulthood (Fig. 5).

Our findings beg the question of whether alternative manipulations in adulthood could induce the kind of plasticity found during development. The sensitivity of adult brains may be different (Linkenhoker and Knudsen, 2002; Bergan et al., 2005), and may have the capacity to reacquire a measure of plasticity (Woolley and Rubel, 2002; Kacelnik et al., 2006; He et al., 2007). Thus, we might expect that auditory training will have a greater effect in adult animals immediately after they undergo a period of deprivation.

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