than MRI. If the increase is related to a second wave of overproduction of synapses, it may herald a critical stage of development when the environment or activities of the teenager may guide selective synapse elimination during adolescence. The relative prominence of the role of the environment in shaping late synaptogenesis is supported by rat studies[14,15]. That the frontal and parietal gray matter peaks approximately one year earlier in females, corresponding with the earlier age of onset of puberty, suggests a possible influence of gonadal hormones. Studies of healthy monozygotic and dizygotic twins, chromosomal aneuploidies (XXY, XXYY, XYY), congenital adrenal hyperplasia (producing high levels of testosterone *in utero*) and psychiatric illnesses are underway to address the effects of genes, hormones and environment on this process.

RECEIVED 21 MAY; ACCEPTED 9 AUGUST 1999

1. Jernigan, T. L., Trauner, D. A., Hesselink, J. R. & Tallal, P. A. *Brain* **114**, 2037–2049 (1991).
2. Pfefferbaum, A. *et al. Arch. Neurol.* **51**, 874–887 (1994).
3. Caviness, V. S. Jr., Kennedy, D. N., Richelme, C., Rademacher, J. & Filipek, P. A. *Cereb. Cortex.* **6**, 726–736 (1996).
4. Reiss, A. L., Abrams, M. T., Singer, H. S., Ross, J. L. & Denckla, M. B. *Brain* **119**, 1763–1774 (1996).
5. Giedd, J. N. *et al. Cereb. Cortex.* **6**, 551–560 (1996).
6. Lange, N., Giedd, J. N., Castellanos, F. X., Vaituzis, A. C. & Rapoport, J. L. *Psychiatry Res.* (in press).
7. Zijdenbos, A. P., Dawant, B. M. & Margolin, R. A. *Comput. Med. Imaging Graph.* **18**, 11–23 (1994).
8. Giedd, J. N. *et al. Prog. Neurosychopharmacol. Biol. Psychiatry* **23**, 571–588 (1999).
9. Hand, D. J. & Crowder, M. J. *Practical Longitudinal Data Analysis* (Chapman and Hall, London, 1996).
10. Rakic, P., Bourgeois, J. P., Eckenhoff, M. F., Zecevic, N. & Goldman-Rakic, P. S. *Science* **232**, 232–235 (1986).
11. Huttenlocher, P. R. & Dabholkar, A. S. *J. Comp. Neurol.* **387**, 167–178 (1997).
12. Chugani, H. T., Phelps, M. E. & Mazziotta, J. C. *Ann. Neurol.* **22**, 487–497 (1987).
13. Feinberg, I. *J. Psychiatr. Res.* **10**, 283–386 (1974).
14. Kleim, J. A., Lussnig, E., Schwarz, E. R., Comery, T. A. & Greenough, W. T. *J. Neurosci.* **16**, 4529–4535 (1996).
15. Bourgeois, J. P., Jastreboff, P. J. & Rakic, P. *Proc. Natl. Acad. Sci. USA* **86**, 4297–4301 (1989).

A contingent aftereffect in the auditory system

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Pairs of stimulus attributes, such as color and orientation, that are normally uncorrelated in the real world are generally perceived independently; that is, the perception of color is usually uninfluenced by orientation and *vice versa*. Yet this independence can be altered by relatively brief exposure to artificially correlated stimuli, as has been shown for vision[1]. Here we report an analogous contingent aftereffect in the auditory system that can persist for four hours after the initial adaptation.

After a few minutes of alternately viewing an orange-black vertical grating and a blue-black horizontal grating, the white stripes in a vertical black-and-white grating appear blue-green, whereas the white stripes in a horizontal grating appear orange[1]. There are numerous demonstrations of other types of visual contingent aftereffect, such as color-contingent orientation[2] and motion[3,4] aftereffects and spatial frequency[5]- and motion[6,7]-contingent color aftereffects. These visual contingent aftereffects can be extremely persistent. For example, the motion-contingent color aftereffect and the color-contingent motion aftereffect can persist for at least 24 hours[3,6]. The motion-contingent color aftereffect can last as long as six weeks in some cases[7].

In contrast to the rich variety of reported visual contingent aftereffects, there are no reports of contingent aftereffects for

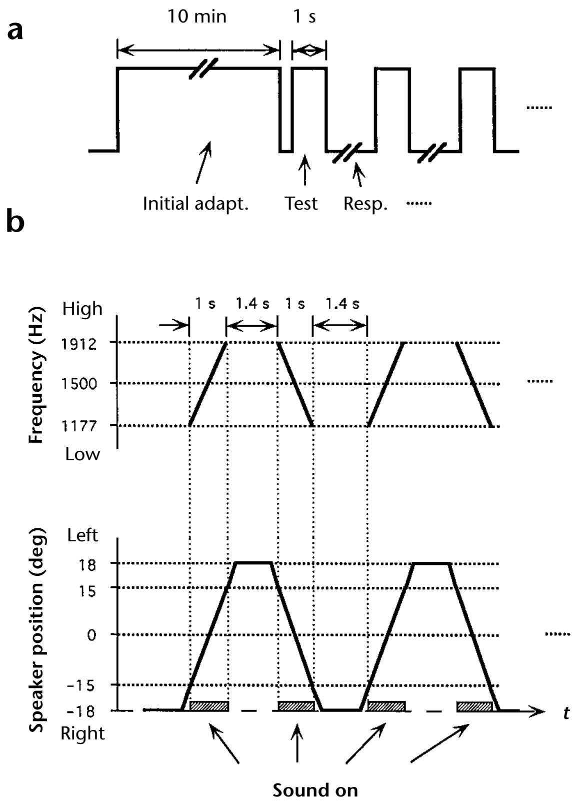

Fig. 1. Stimulus protocols. (**a**) Time sequence of stimuli. Each run began with 10 minutes of adaptation, followed by a series of brief test sounds (1 s), with either a rising (0.7 octaves per s) or a falling (–0.7 octaves per s) pitch presented by a loudspeaker moving at one of six different velocities (2°, 6° or 10° per s, either to the left or the right). For each test presentation, the subject was asked to press one of two buttons to indicate the direction (leftward or rightward) of spatial movement. (**b**) Detailed time sequence of adapting stimuli. While the central frequency of an adapting sound (1-octave band-pass noise) was moving upward (0.7 octave per s), the loudspeaker moved to the left (30° per s) for 1 second (from –15° to 15° in azimuth). Following a silent interval of 1.4 seconds, the loudspeaker moved to the right (–30° per s) for 1 second, while the central frequency of the sound moved downward (–0.7 octave per s). During adaptation, this sequence was repeated continuously. In the control condition, the loudspeaker moved over the same trajectory with the same time course, but the center frequency of the adapting sound was kept constant at 1.5 kHz. Note that the vertical axis in the top panel has a logarithmic scale.

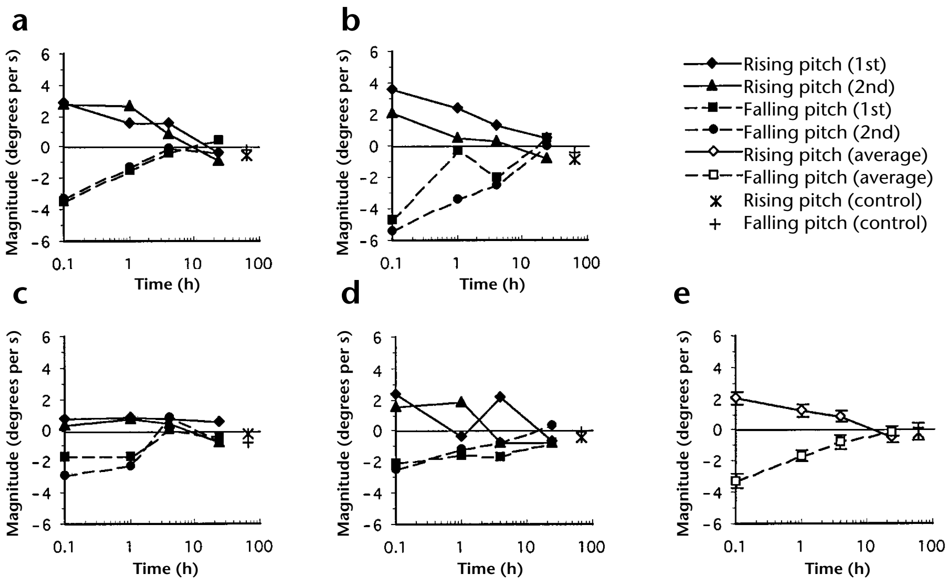

Fig. 2. The magnitude of the auditory contingent aftereffect, in degrees per second, as a function of time after exposure. Four subjects who had participated in a previous study of simple auditory motion aftereffect were tested. The spatial velocity that sounded stationary to the subject was determined by probit analysis of the psychometric functions representing the subject's responses (see refs. 10, 11 for details). (**a–d**) Results for different subjects. For each subject, two sets of measurements of the aftereffect were taken immediately and then 1, 4 and 24 hours after adaptation. (**e**) The averages of the aftereffects for both a rising and a falling pitch across all four subjects. Error bars indicate s.e. The time axis is shown on a logarithmic scale.

other sensory modalities. We therefore designed experiments to determine whether a contingent aftereffect could be demonstrated in the auditory system.

In vision, stimulus attributes that produce contingent aftereffects when paired generally give simple aftereffects when presented singly. In audition, we have previously demonstrated aftereffects to sounds that move in space or in frequency[8–10]. For example, after a few minutes of listening to a sound moving in one direction in frequency space or along an azimuthal trajectory, a spectrally or spatially stationary sound seems to move in the opposite direction in frequency or in azimuth, respectively. The magnitude of the auditory spatial motion aftereffect tends to increase with adapting velocities up to at least 30° per second[10]. Spectral motion aftereffects are strongest at adapting velocities between 0.5 and 1 octaves per second across a 1–2 kHz frequency range[8]. Based on these observations, we paired the directions of sound movement in frequency and in azimuth, and used a sound with a rising or falling pitch (0.7 octaves per s) that was generated by a loudspeaker moving at a velocity of 30° per second in azimuth as the adapting stimulus (**Fig. 1**).

After about ten minutes of adaptation, during which the subject listened to a spatially rightward-moving sound with falling pitch alternated with a spatially leftward-moving sound with rising pitch, the perception of the direction of spatial movement of a sound was strongly influenced by the direction of spectral movement of the sound. When a sound had a rising pitch, leftward motion was judged as stationary and, correspondingly, a spatially stationary velocity was heard as moving to the right. Similarly, when a spatially stationary sound had a falling pitch, it was perceived as moving leftward. Figure 2 displays the magnitude of the auditory contingent aftereffect as a function of time for all four subjects tested. These effects declined over time, but could still be observed after one hour in all subjects and after four hours in two subjects following the initial adaptation (**Fig. 2b** and **d**). The aftereffect was averaged across all four subjects for both directions in frequency (**Fig. 2e**). Analysis of variance (ANOVA) indicated a significant difference ($p < 0.01$) among the sizes of the aftereffects measured at different times for both directions. *Post-hoc* Newman-Keuls tests showed that the aftereffect measured immediately after adaptation was significantly stronger ($p < 0.05$) than at other times (1, 4 or 24 hours following adaptation) for either direction in frequency, except for that measured 1 hour after adaptation for the sound with a rising pitch. The aftereffect measured 24 hours after adaptation was weaker ($p < 0.01$) than those measured immediately or 1 or 4 hours after adaptation. The difference between the aftereffects measured one hour and four hours after adaptation was not statistically significant ($p > 0.05$).

Simple auditory motion aftereffects are rather transient, lasting for about one to two seconds following two minutes of adaptation[12]. But this seemingly much shorter persistence of simple aftereffects compared with that of contingent aftereffects might be attributed to the shorter adapting duration. To determine whether or not the contingent and simple auditory aftereffects had similar time courses, we used the same procedures for inducing and measuring contingent aftereffects to study the persistence of simple motion aftereffects. We found that with the same adapting

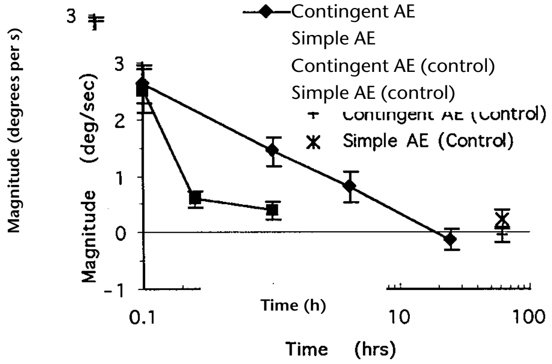

Fig. 3. Comparison of decays of contingent and simple auditory motion aftereffects as a function of time after adaptation. The points representing the grand average of the contingent aftereffects were obtained by pooling the data collected with a falling pitch and with a rising pitch, after the sign of the aftereffect measured with the falling pitch was reversed (negative sign was changed to positive and *vice versa*). Error bars indicate s.e. The time axis is logarithmic.

duration, simple auditory aftereffects decayed much faster than did contingent aftereffects (**Fig. 3**). Although their sizes were comparable to those of contingent aftereffects when measured immediately after adaptation, simple aftereffects were absent ten minutes after adaptation.

The present findings imply that the neural mechanisms underlying contingent aftereffects are not specific to vision, but reflect general properties of sensory neural processing, and possibly, higher associative centers as well. In principle, there are two types of neural mechanism that might be proposed to account for these effects. In one, the sensory systems contain 'built-in' double-duty units that are sensitive to paired-stimulus attributes and that become less responsive following repeated stimulation[1,3,6]. It seems unlikely, however, that simple neuronal adaptation or fatigue could account for aftereffects that can persist for hours or days. Another explanation is that new, or additional, units representing the paired attributes are formed during adaptation by some kind of cortex-based learning[4]. The long time course of the auditory contingent aftereffect observed in the present study suggests that this latter explanation is more likely. Functionally, contingent aftereffects might help to optimize neural coding[13], or be involved in shifting the subject's reference frame according to recent experience to keep the external world and its internal sensory representations in correspondence[14].

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1. McCollough, C. *Science* **149**, 115–116 (1965).
2. Held, R. & Shattuck, S. R. *Science* **174**, 314–316 (1971).
3. Favreau, O. E., Emerson, V. F. & Corballis, M. C. *Science* **176**, 78–79 (1972).
4. Mayhew, J. W. & Anstis, S. M. *Percept. Psychophys.* **12**, 77–85 (1972).
5. Lovegrove, W. J. & Over, R. *Science* **176**, 541–543 (1972).
6. Hepler, N. *Science* **162**, 376–377 (1968).
7. Stomeyer, C. F. & Mansfield, R. W. *Percept. Psychophys.* **7**, 108–114 (1970).
8. Shu, Z. J., Swindale, N. V. & Cynader, M. S. *Nature* **364**, 721–723 (1993).
9. Grantham, D. W. *Acustica/Acta Acustica* **84**, 337–347 (1998).
10. Dong, C. J., Swindale, N. V., Zakarauskas, P., Hayward, V. & Cynader, M. S. *Percept. Psychophys.* (in press).
11. Finney, D.J., *Probit Analysis* (Cambridge Univ. Press, Cambridge, 1971).
12. Grantham, D. W. & Wightman, F. L. *Percept. Psychophys.* 26, 403–408 (1979).
13. Barlow, H. B. in *Vision: Coding and Efficiency* (ed. Blakemore, C.) 363–375 (Cambridge Univ. Press, Cambridge, 1990).
14. Dodwell, P. C. & Humphrey, G. K. *Psychol. Rev.* **97**, 78–89 (1990).