depend on the post-partum vigour and survival of the mother rather than of the father. ☐

Methods

Study populations. Olive baboons at Gombe National Park, Tanzania, have been studied since 1967 (ref. 22). These animals have been censused almost daily since 1972, and the demographic data include all birth dates, miscarriages, mortality and reproductive cycle state. Menarche typically occurs during the fourth year, so our analysis includes females that were born as early as 1963. Lions in Serengeti National Park and Ngorongoro Crater, Tanzania, have been monitored since 1966 and 1962, respectively[23]. These animals are censused 2–10 times each month, and relevant demographic data include litter size, birth dates and mortality. Birth dates can be estimated from the body size of animals less than 2 years old, so we include females born as early as 1964 or 1960 in Serengeti and Ngorongoro, respectively. The reproductive state of the lions can be inferred only on the basis of observed births (and not all births are detected), so the lion analysis is restricted to cub productivity and female mortality.

Baboon menstrual cycles. Ovulatory cycle state is assessed from the female's perineum, which undergoes conspicuous phases of tumescence and detumescence and turns scarlet after conception[24]. Analysis of 1,461 menstrual cycles is based on the 29 females of known age who lived for 18 years or more. Cycle length was measured from the last day of maximal tumescence of successive cycles, and analysis is based on medians because of skew and kurtosis; statistical tests are based on the residuals of an analysis of variance (ANOVA) that first removed the variations between individual females. Both the median and mode of 221 fertile cycles was 38 days (as was the median of 1,240 infertile cycles). Irregularity from this 'norm' was calculated for each cycle as $|\ln(\text{observed}/38)|$, which gives the same deviation for a cycle of 19 days as for 76 days.

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Increased auditory cortical representation in musicians

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Acoustic stimuli are processed throughout the auditory projection pathway, including the neocortex, by neurons that are aggregated into 'tonotopic' maps according to their specific frequency tunings[1–3]. Research on animals has shown that tonotopic representations are not statically fixed in the adult organism but can reorganize after damage to the cochlea[4] or after training the intact subject to discriminate between auditory stimuli[5]. Here we used functional magnetic source imaging (single dipole model) to measure cortical representations in highly skilled musicians. Dipole moments for piano tones, but not for pure tones of similar fundamental frequency (matched in loudness), were found to be enlarged by about 25% in musicians compared with control subjects who had never played an instrument. Enlargement was correlated with the age at which musicians began to practise and did not differ between musicians with absolute or relative pitch. These results, when interpreted with evidence for modified somatosensory representations of the fingering digits in skilled violinists[6], suggest that use-dependent functional reorganization extends across the sensory cortices to reflect the pattern of sensory input processed by the subject during development of musical skill.

Three groups, comprising right-handed subjects (Edinburgh handedness questionnaire) with no history of otological or neurological disorders and with normal audiological status, were studied. Subjects were fully informed about the experimental procedures and signed a consent form before participation. The first group ($n = 9$) consisted of musical students with absolute pitch and the second group ($n = 11$) of musical students with relative pitch, who had played their instruments for a mean period of 21 ± 6 and 15 ± 3 years, respectively. Musicians in the first and second groups were recruited from the Conservatory in Münster and reported that they practised for an average of 27 ± 14 and 23 ± 12 hours per week, respectively, during the five years preceding the experiment. Musicians who claimed to have absolute pitch were tested before magnetoencephalographic (MEG) measurements. For this purpose a test was developed according to established methods. A randomized sequence of 35 piano tones between H2 and C7 (concert pitch A 440 Hz, American notation) was presented to the subjects. A musician was accepted to have absolute-pitch ability if >90% of the tones were correctly recognized. Musicians with relative pitch were either self-identified (nine musicians) or did not meet the tested criterion for absolute pitch (two musicians). The third group of subjects (controls; $n = 13$) consisted of students who had never played an instrument. Mean age was 29 ± 6 years for musicians with absolute pitch, 26 ± 5 years for musicians with relative pitch, and 26 ± 4 years for control subjects.

MEG measurements were carried out with a 37-channel BTi Magnes system. From each subject, auditory evoked fields (AEFs) elicited by right-side stimulation were recorded above the left hemisphere. Auditory stimulation (Fig. 1a) consisted of a semirandomized blockwise presentation of the four piano tones C4, C5, C6 and C7 (American notation, having the first harmonics at 262, 523, 1,046 and 2,093 Hz, respectively) and of four pure tones (of 250, 500, 1,000 and 2,000 Hz) that correspond closely with the fundamental frequency of the piano tones. Each tone was presented 128 times while subjects watched cartoon videos intended to fixate their attention. A single equivalent current dipole model was used to explain the field distribution of the auditory evoked field component N1 (occurring ~100 ms after stimulus onset) for each of the eight stimulus conditions. Because the N1 field distributions were dipolar, the applied model was able to explain most of the field variance (goodness of fit calculated over all subjects was within the range of >97%).

In the human auditory cortex, tonotopic representation of the cortical sources corresponding to tones with different spectral content distributes along the medial–lateral axis of the supratemporal plane when measured by the N1 component, with the medial–lateral centre of cortical activation shifting toward the sagittal midline as the frequency of the tone increases[7]. The averaged values of the medial–lateral coordinates of areas of the brain that respond to pure and piano tones, and linear regressions fitted to these data, are shown for the three study groups in Fig. 1b. The dependence of the medial–lateral coordinate on the stimulus frequency was less pronounced for the piano tones; this can be explained by the spectral content of these tones. The spatial location of the cortical sources activated by the piano tones is determined by the fundamental frequency of the tones. However, the relative contribution of higher harmonics of the fundamental frequency to the spectral energy is highest for the lowest piano tones and decreases as the fundamental frequency increases (Fig. 1a). No significant differences between the three groups of subjects were seen (Fig. 1b).

A significant difference between the two groups of musicians and the control group was found, however, in the strength of activation of the cortical sources by the piano tones compared with the strength of activation by the pure tones (Fig. 2a). For both groups of musicians with absolute or relative pitch, the equivalent dipole moment was 21–28% larger for piano tones compared with pure tones ($P < 0.0001$, paired t-test). This effect was found even though the two types of tone were matched in loudness. For the control group, no significant difference was found in dipole moment in response to piano and pure tones ($P = 0.72$). Given a constant direction of the single-current dipole, the equivalent dipole moment indicates the total strength of cortical activation (the number of neurons simultaneously active at the time of the auditory evoked field N1). Cortical activation may have increased at the time of the N1 event because more neurons were engaged in the processing of these tones in skilled musicians or because the synchrony of neural activity was greater as a consequence of their

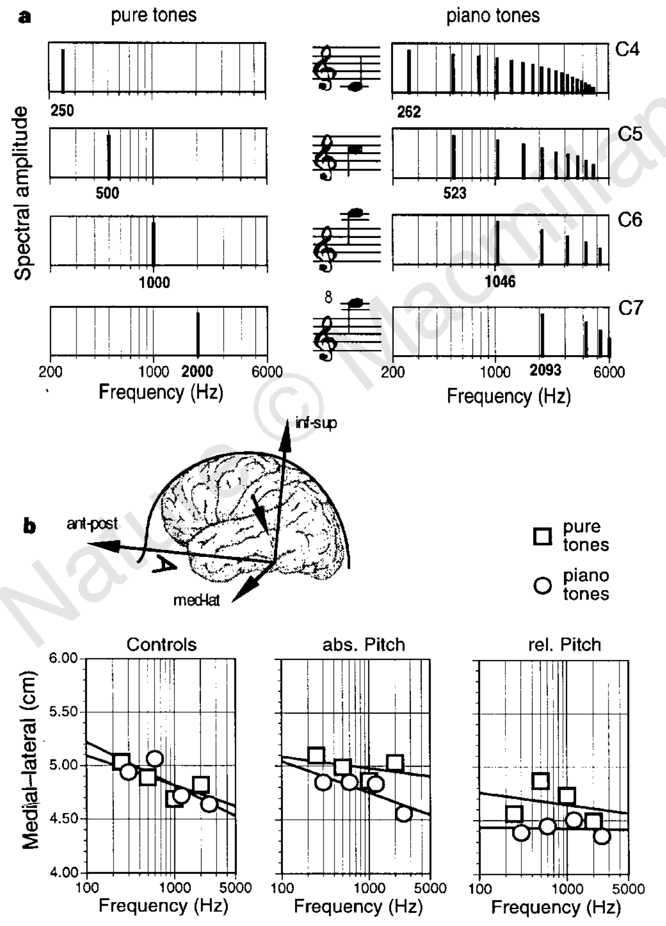

Figure 1 Cortical stimulation by pure and piano tones in musicians and non-musicians. **a**, Spectra of pure tones and piano tones. **b**, Medial-lateral coordinates are shown for single equivalent current dipoles fitted to the field patterns evoked by pure tones and piano tones in control subjects and subjects with absolute or relative pitch. The inset defines the coordinate system of the head. Equivalent current dipoles shift toward the sagittal midline along the medial-lateral coordinate as a function of the frequency of the tone. Ant-post, anterior-posterior; med-lat, medial-lateral; inf-sup, inferior-superior.

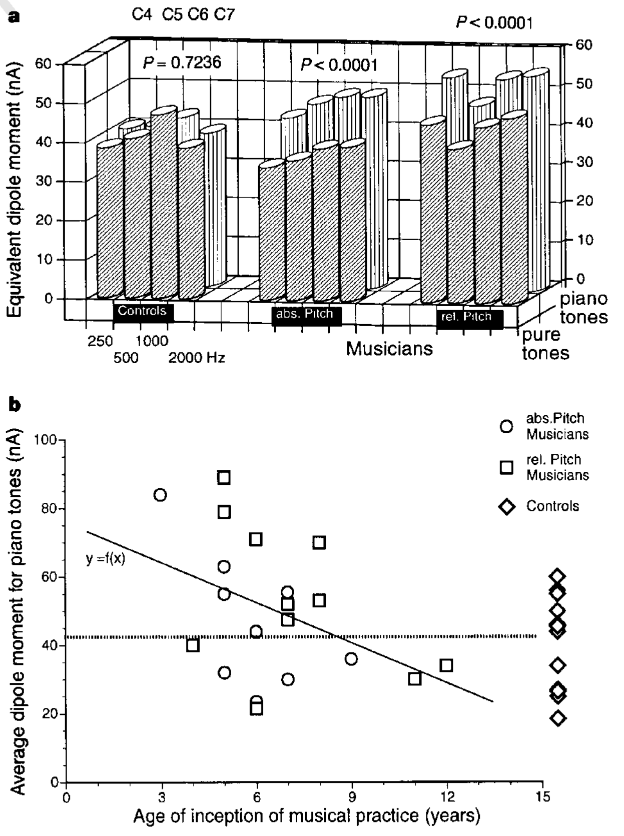

Figure 2 Strength of cortical activation is higher in response to piano, rather than pure, tones and in musicians who began practising before age 9. **a**, Equivalent dipole moment (strength of neuronal activation during the auditorily evoked field N1) is shown for pure tones (diagonally striped columns) and piano tones (vertically striped columns) in control subjects and subjects with absolute or relative pitch. **b**, Mean dipole moment as a function of the age at which musical training began in musicians with absolute pitch or relative pitch. The solid line is the linear correlation fitted to the data of the combined groups ($r = -0.426$, $P = 0.031$). The broken line denotes mean dipole moment in control subjects who never played a musical instrument.

musical training.

Before the experiments, our musicians were interviewed to determine the age at which their musical training had begun. There was a significant linear correlation between mean dipole moment for the piano tones and the age of inception of musical training when the two groups of musicians were combined (coefficient of correlation (r) $= -0.426$, $P = 0.037$) (Fig. 2b), and in the absolute-pitch group separately ($r = -0.621$, $P = 0.031$). A similar trend was seen in the relative-pitch group ($r = -0.452$, $P = 0.082$; one-tailed tests). These data indicate that the younger the subjects started playing their instrument, the larger their cortical reorganization in recognition of piano tones was. Enhanced cortical representations was seen in subjects who began to practise before the age of 9 years. This correlation is similar to that reported in a previous study, which examined somatosensory representations of fingering digits in highly skilled string players[6]. In that study, enhancement of the somatosensory representation was most evident in musicians who had begun to practise before the age of 10 years. The similar dependence of auditory and somatosensory representations on practice beginning before the age of about 10 years indicates that cortical reorganization induced by training to learn a musical skill conforms with the pattern of sensory input experienced during practice. Although we cannot separate effects due to duration of training from effects dependent on the age at which training commenced, it seems unlikely that duration of training alone is the critical variable, because our musicians had practised their skill for an average of 18 ± 5 years when our measurements were taken.

The dipole moments evoked by the piano tones did not differ significantly between musicians reporting the piano ($n = 9$) or woodwinds or strings ($n = 11$) as their principal instrument. However, eight of the eleven subjects who reported woodwinds or strings as their principal instrument reported the piano to be a secondary instrument. Therefore, we cannot determine whether cortical reorganization is a specific response to piano tones that were experienced during musical training, or whether it is specialized more broadly for processing of musical or non-musical stimuli with complex harmonic spectra. Enhancement of the cortical representation of piano tones might have been caused by greater attention having been paid to these tones during the experiments by musicians than by non-musicians, despite our video-viewing requirement which was intended to fixate attention, but this seems unlikely. Attentional modulation during testing cannot explain why the degree of cortical activation seen among our skilled musicians depended on the extent of their musical experience gained several years before testing (Fig. 2b), unless the ability to command attention is itself a consequence of cortical reorganization.

The enhanced cortical representation for tones of the musical scale that we observed in musicians corresponds to the results of an earlier magnetic resonance imaging study[8]: a structural enlargement of the planum temporale of the left hemisphere in musicians compared with non-musicians was found. Our data thus associate a use-correlated functional property with cortical architectonics and also raise the possibility that musical experience during childhood may influence structural development of the auditory cortex. A special role for early experience is compatible with evidence for maturation of fibre tracts and the presence of an intracortical neuropil persisting to the age of 7 years (ref. 9). Left-hemispheric enlargement of the planum temporale has been reported to be more pronounced for musicians with absolute pitch than for musicians with relative pitch. The functional reorganization shown here did not relate to this perceptual skill, perhaps because absolute pitch is supported by cortical mechanisms not seen in the auditory N1 response occurring up to 100 ms after tone onset, or is based on temporal rather than structural coding of auditory information. ☐

Methods

Subjects. Before the experiment we interviewed our musicians to collect information about hours of practice, knowledge of music theory, sight-reading ability, absolute- or relative-pitch ability (people have absolute pitch if they are able to perfectly map specific tone frequencies onto response choices), principal instrument, other instruments played, musicians in the family, and the age at which musical training began. The principal instruments of our musicians were piano (nine subjects), woodwind instruments (seven subjects), and strings (four subjects). Control subjects were asked as part of a standardized pre-experimental interview whether they had any special ability with respect to pitch perception or whether they currently played or had previously played a musical instrument and that to their knowledge they had no special pitch-perception ability. Although the pitch-perception abilities of control subjects were not explicitly tested, the incidence of absolute pitch in the general population is estimated to be $<0.01\%$ (ref. 10). Relative pitch is typically an ability of professional musicians only[11,12]. All subjects had air-conduction and bone-conduction hearing-level thresholds of no more than 10 dB, in the range from 250 Hz to 8000 Hz. The thresholds for pure and piano tones were measured to within 2 dB for each subject. The intensity of each tone was set at 60 dB above each subject's measured threshold.

Source analysis. Magnetic fields evoked by acoustic stimuli were averaged and filtered within the band 0.1–20 Hz. For each evoked magnetic field a single equivalent current dipole (ECD) was fitted. The means of the dipole moments were computed to within a 40-ms time interval around the maximum of the dipole moment. The coordinates of the dipole location were calculated as a mean of the data points within the time interval between the maximum and the minimum of the evoked field, and satisfied the following requirements: first, a goodness of fit of $>95\%$ of the ECD model to the measured field; second, variation of the source coordinates, around the maximal root mean square field value, of <15 mm within an interval of 40 ms; and third, anatomical distance of the ECD to the midsagittal plane of >2 cm and inferior–superior value of >2 cm. Given a constant direction of the equivalent current dipole, the dipole moment indicates the total strength of cortical activation, that is the number of neurons involved during a cortical response. If this number increases, the dipole moment also increases. Any active focal area can be modelled by an equivalent current dipole. Each dendritic current flow has been estimated[13] to contribute to the dipole moment according to the formula dipole moment = (conductivity) × (cross-section of the dendrite) × (potential difference along the dendrite). If the diameter of an apical dendrite is assumed to be 4 μm with an intracellular conductivity of about 0.25/Ωm and a potential difference of 10 mV, about 30,000 dendrites would be necessary to produce a dipole moment of 10 nA (ref. 13). Only currents flowing tangentially with respect to the surface of the volume conductor (head) are detected. Magnetic fields generated by axonal currents are assumed to be quadrupolar and are neglected in the calculation.

Statistical analysis. We expected on the basis of previous results from studies of skilled string players[6] and animals[14] that changes in cortical representation are more readily induced by sensory experience in the young brain than in the adult brain. One-tailed tests were therefore accepted for evaluation of age-related effects (negative correlations were predicted). Although it made no difference to the outcome, two-tailed probabilities are reported for group comparisons.

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Dynamic cortical activity in the human brain reveals motor equivalence

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That animals and humans can accomplish the same goal using different effectors and different goals using the same effectors attests to the remarkable flexibility of the central nervous system. This phenomenon has been termed 'motor equivalence'[1,2], an example being the writing of a name with a pencil held between the toes or teeth. The idea of motor equivalence has reappeared because single-cell studies in monkeys have shown that parameters of voluntary movement (such as direction) may be specified in the brain, relegating muscle activation to spinal interneuronal systems[3,4]. Using a novel experimental paradigm[5] and a full-head SQUID (for superconducting quantum interference device) array to record magnetic fields corresponding to ongoing brain activity, we demonstrate: (1), a robust relationship between time-dependent activity in sensorimotor cortex and movement velocity, independent of explicit task requirements; and (2) neural activations that are specific to task demands alone. It appears, therefore, that signatures of motor equivalence in humans may be found in dynamic patterns of cortical activity.

The first experiment required human volunteers to flex or extend the preferred index finger either on the beat of a metronome or between metronome beats, the frequency of which was fixed at 1 Hz (see Methods). Notice that these experimental conditions may be grouped either according to the kinematics of motion (flexion versus extension movements and their derivatives) or according to the coordination task (synchronization or syncopation). Figure 1 shows the relative phase between stimuli and movement peaks across cycles for all four conditions. As requested, the peak of the movement is synchronized closely to the stimulus in the flexion-on-the-beat and extension-on-the-beat conditions. Likewise, subjects are able to place a movement between stimuli in the flexion-off-the-beat and extension-off-the-beat, syncopation conditions. Also shown are histograms that measure task success. In general, the distributions for the syncopation conditions are broader than those for synchronization, indicating performance is more variable. Subjects had more difficulty syncopating than synchronizing, which conforms to everyday experience and behavioural evidence[5].

Brain activity was recorded continuously during these tasks, using a 64-channel magnetometer sampled at 250 Hz. All the magnetic fields generated by the brain arise from the flow of electrical current, which is mainly ionic and originates in the dendrites and cell bodies of cortical neurons[6]. Figure 2 gives an example of the field pattern shown on a model head (Fig. 2a) and the same pattern shown in polar projection on the plane (Fig. 2b). The dominant field over the sensorimotor area of the left hemisphere is expected for right-handed movements. How is this evolving brain activity related to the behaviour produced? Figure 3a shows cortical activity patterns averaged across subjects for each task sampled at various time points (red line) throughout the movement. The average amplitude profile of the movement is also shown (green line). To ease viewing across conditions, the movement profiles are all plotted in the same positive-going direction. Notice the strong dipolar field in the sensorimotor area of the left hemisphere during the first part of the movement, regardless of whether it involves flexion or extension. Notice also that the field reverses just after the peak movement (column 5) and then becomes much weaker and more distributed. Figure 3b plots the time series of the average brain activity obtained from single sensors for the flexion-on (the beat) condition. On the lower left is plotted the movement profile and its derivative, velocity: particularly on the left side of the array, brain activity and movement velocity are nearly superimposed, as confirmed by correlation analysis. The cross-correlation between movement velocity and time-varying brain signal is almost 1 (or −1) in the yellow area of Fig. 3b, corresponding precisely to maxima and minima of the field.

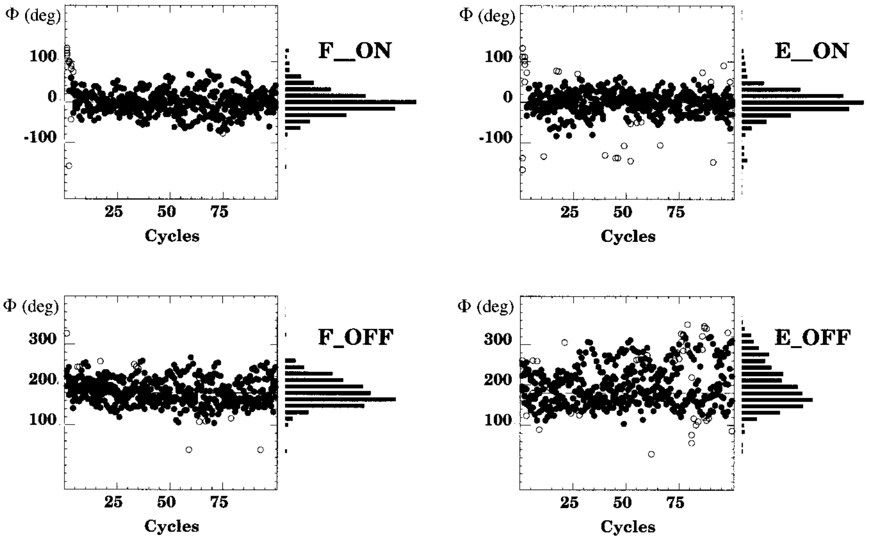

Figure 1 Relative phase across cycles for all conditions (top row, synchronization; bottom row, syncopation) and all subjects, a total of ~500 observations per condition. Solid circles indicate cycles within a ±60 degree range of the average phase for single subjects. Open circles are outside this range and were rejected from further analysis.