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Reproductive cessation in female mammals

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In female mammals, fertility declines abruptly at an advanced age. The human menopause is one example, but reproductive cessation has also been documented in non-human primates, rodents, whales, dogs, rabbits, elephants and domestic livestock[1–3]. The human menopause has been considered an evolutionary adaptation[4–7], assuming that elderly women avoid the increasing complications of continued childbirth to better nurture their current children and grandchildren. But an abrupt reproductive decline might be only a non-adaptive by-product of life-history patterns. Because so many individuals die from starvation, disease and predation, detrimental genetic traits can persist (or even be favoured) as long as their deleterious effects are delayed until an advanced age is reached, and, for a given pattern of mortality, there should be an age by which selection would be too weak to prevent the onset of reproductive senescence[4,5,8]. We provide a systematic test of these alternatives using field data from two species in which grandmothers frequently engage in kin-directed behaviour. Both species show abrupt age-specific changes in reproductive performance that are characteristic of menopause. But elderly females do not suffer increased mortality costs of reproduction, nor do post-reproductive females enhance the fitness of grandchildren or older children. Instead, reproductive cessation appears to result from senescence.

Age-specific rates of mortality and maternity are broadly similar in olive baboons and African lions (Fig. 1). In baboons, female mortality reaches a minimum between 4 and 5 years of age and then accelerates; no female has survived beyond 27 years of age (Fig. 1a). But the maternity rate remains constant until 21 years of age, when it decreases (Fig. 1c). In female lions, mortality reaches a minimum between 3 and 4 years and then rapidly accelerates; no lioness has survived beyond 17 years of age (Fig. 1b). Lion maternity rates remain relatively constant before decreasing at 14 years of age (Fig. 1d).

Infant survival declines rapidly when female baboons reach 21 years (Fig. 2a), which is the age at which pregnancies are more likely to end in miscarriage (Fig. 2b). Baboons also show striking changes in menstrual cycles with advancing age. The length of the cycle remains constant until about 23 years of age (Fig. 3a), when cycles also become more irregular (Fig. 3b). Fertility decreases at 23 years of age and essentially ceases at 24 (Fig. 3c). Because of low fertility, elderly females experience a peak number of cycles during their 24th year (comparable to the period of 'adolescent sterility'), but cycling diminishes thereafter until ceasing altogether (Fig. 3d). Constant cycling is known to lower the age of menopause in women[9], and one female baboon stopped cycling at 20 years and remained acyclic until her death aged 26. She had shown unusually low fertility throughout life and experienced 127 menstrual cycles by her 20th birthday, whereas all other 20-year-old females averaged only 50 cycles (range 35–98, $n = 23$).

Less detailed data are available on the precise reproductive performance of ageing female lions (see Methods). The survival of lion cubs remains constant with maternal age (Fig. 2c), but litter size declines markedly at 14 years (Fig. 2d). Falling litter size cannot account for the overall decline in maternity rates between prime- and old-aged females (Fig. 1d), so elderly lions must also experience a reduction in cycling and/or fertility.

Are these declines adaptive? Baboons and lions are good candidates for an 'adaptive menopause' because both species engage in a high degree of kin-directed cooperative behaviour. Typical of cercopithecine monkeys, baboon mothers help to determine their daughters' dominance rank, and they also groom and intervene on behalf of their descendent kin[10]. Female lions participate in joint territorial defence[11–13] and, when raising cubs communally, nurse their daughters' cubs as often as their own[14].

The adaptive menopause hypotheses assume that post-reproductive females actively enhance the fitness of their prior offspring[4–6]. This benefit would be lost by her death in the 'risky childbirth' hypothesis[4] or by the intensive demands of infant care in the 'opportunity costs' hypothesis[7]. However, neither the survival of grandchildren nor the reproductive performance of adult daughters is improved in the predicted manner (Fig. 4). Lion cubs only show higher survival when their grandmothers are reproductively active: elderly female lions only engage in allomothering while tending their own cubs[14]. The typical interbirth interval is two years in both species and, whereas infant survival is highly dependent on maternal survival (Fig. 5), juvenile survival is unaffected by either the mother's survival or her subsequent reproduction (Fig. 5). Thus mothers do not invest in subsequent offspring until their prior brood has been successfully 'fledged' and continued reproduction inflicts no opportunity costs.

In both species, breeding females showed similar survival to non-

breeders (Fig. 6a, b), and a proportional hazards analysis using parity as the time-dependent covariate found mortality among reproductive females to be only 84% of that of non-reproductives in baboons ($c_2 = 24.06$, $\exp(b) = 0.843$) and 72% in lions ($c_2 = 70.65$, $\exp(b) = 0.719$). Without controlled experiments, we cannot distinguish these results from sample heterogeneity, as good

health may promote survival as well as reproduction (see ref. 15). Despite the possibility of heterogeneity, our data can still show whether reproductive costs increase with age. However, the relative risk of reproduction in both species remains constant with age (although it is possible that sample heterogeneity also changes with age[16]). Further, baboons showed no significant change in mortality
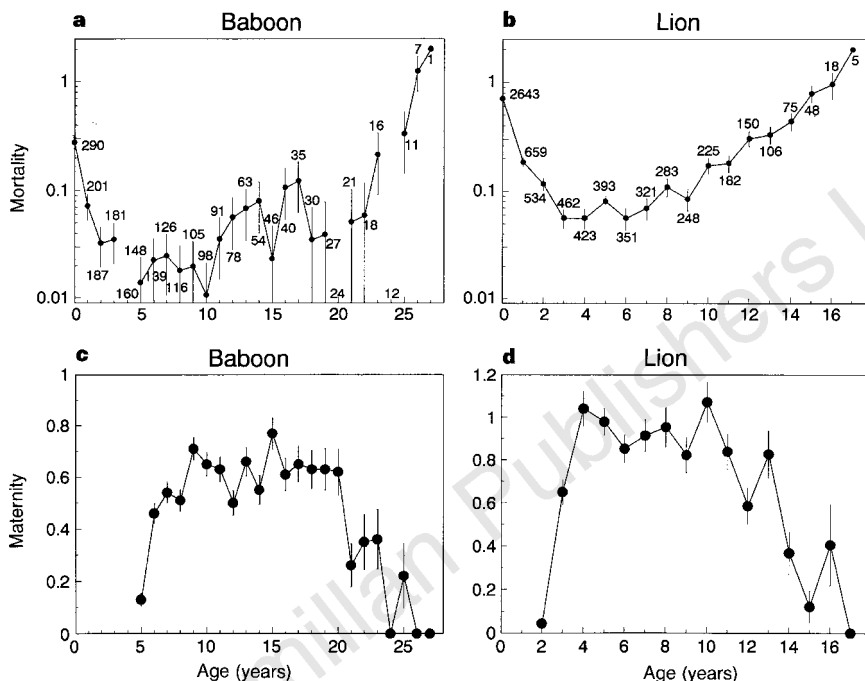

Figure 1 Age-specific mortality and maternity in female baboons and lions. Bars represent standard errors; numbers are sample size. **a**, **b**, Annual mortality is estimated from weekly intervals for baboons (**a**; 201 yearlings, 60.7% censored) and from monthly intervals for lions (**b**; 652 yearlings, 18.4% censored). Mortality rate $= d_i / b_i(n_i - 0.5d_i)$, where d_i is the number dying in the ith interval, b_i is the width of the ith interval, and n_i is the number at risk during the ith interval[25]. No

deaths were observed in three baboon age classes, and ln(mortality rate) is undefined. Infant mortality in lions includes all known females as well as unsexed cubs whereas later ages only include known females. Gross maternity for baboons (**c**) and lions (**d**) is the number of live offspring produced at each age and is estimated by the total number of live offspring born to age class i divided by the midpoint number of females in age class i.
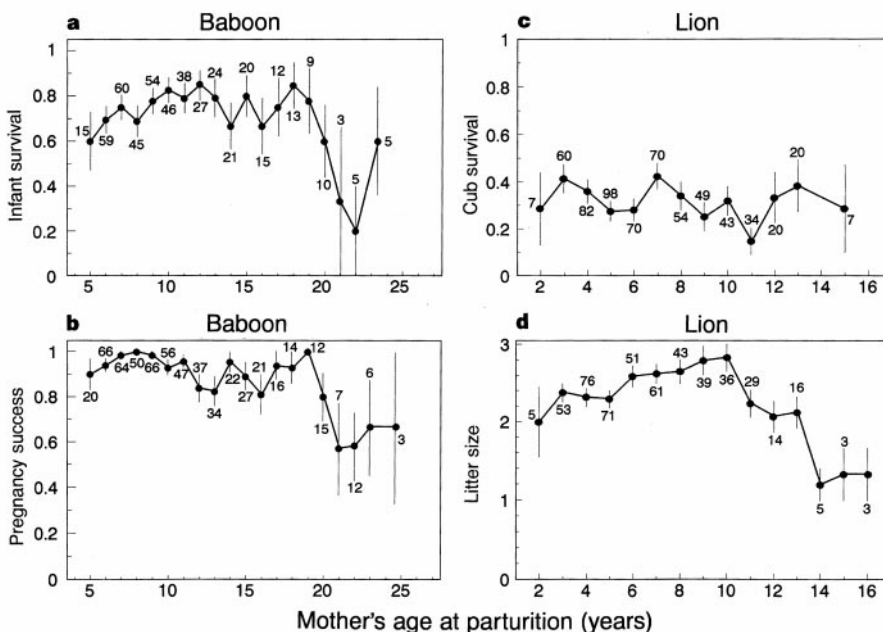

Figure 2 Age-specific aspects of female reproduction. **a**, First-year infant survival in baboons. **b**, Proportion of baboon pregnancies that ended in live birth. **c**, Average first-year survival for lion litters. **d**, Average lion litter size. Bars represent standard errors, and numbers indicate number of infants, pregnancies or litters.

All measures except lion-cub survival show significant heterogeneity with maternal age (ANOVA, $P < 0.01$) and a significant ($P < 0.01$) decline at advanced ages. Because maternal survival influences infant survival (see Fig. 5), data in **a** and **c** are restricted to mothers who survived at least one year post partum.
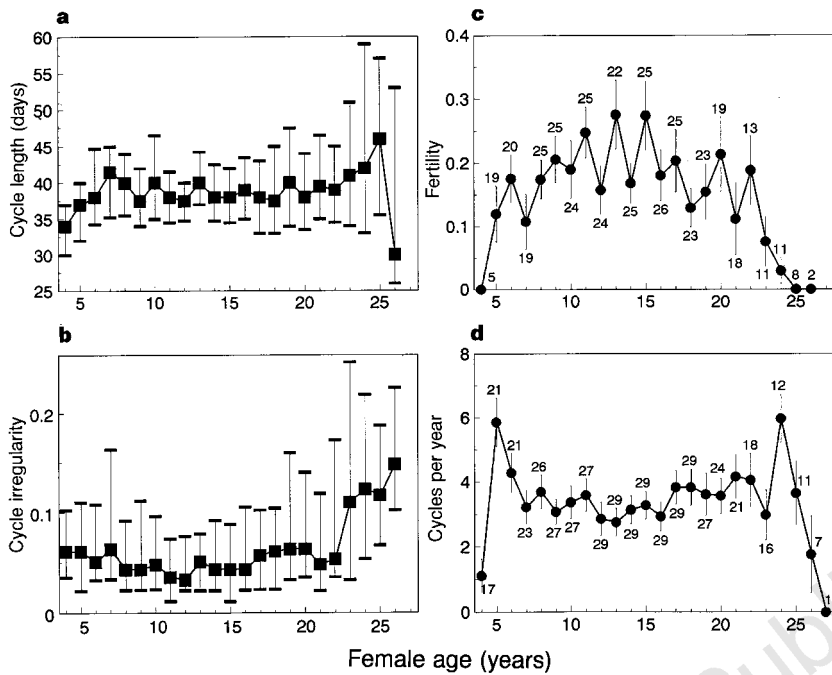
Figure 3 Age-specific aspects of baboon menstrual cycles. **a**, Median (squares) and quartile (bars) cycle lengths at each age. **b**, Median and quartile 'irregularity' of menstrual cycles (see text). **c**, Mean proportion of cycles resulting in pregnancy (plotted with standard errors and the number of cycling females at each age). **d**, Annual cycling rates (with standard errors and the total number of females of each age). All four measures show significant heterogeneity with age (Kruskal–Wallis or ANOVA, $P < 0.01$). Cycles become significantly more irregular while fertility declines at advanced ages (both with $P < 0.001$).
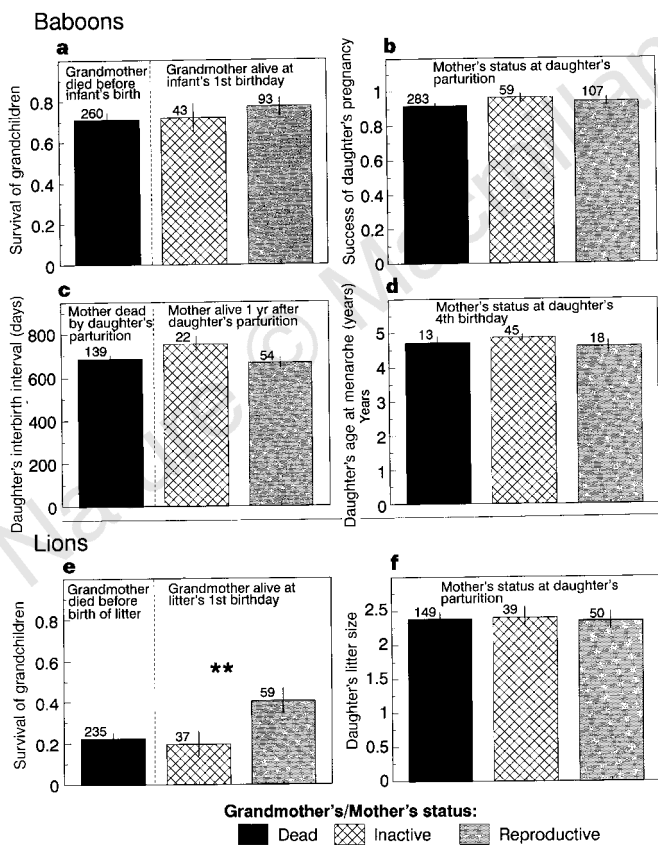

Figure 4 Effects of female survival and reproduction on descendants' productivity. Females were 'inactive' if they had not reproduced during the previous 12 months and for 6 months thereafter; otherwise they were 'reproductive'. **a**–**d**, Baboons. **a**, Proportion of infant grandchildren that survived their first year. **b**, Proportion of daughters' pregnancies that reached full term. **c**, Interval from birth of surviving grandchild until the next live birth. **d**, Age at which daughters experienced their first sexual swelling. **e**, **f**, Lions. **e**, Proportion of grandchildren in each litter that survived their first year. **f**, Daughters' average litter size. The only significant effect was in lions, where grandchildren of reproductively active grandmothers enjoyed higher survival (ANOVA, $F = 6.14$, d.f. = 2,328, $P = 0.0026$). Double asterisks indicate $P < 0.01$.
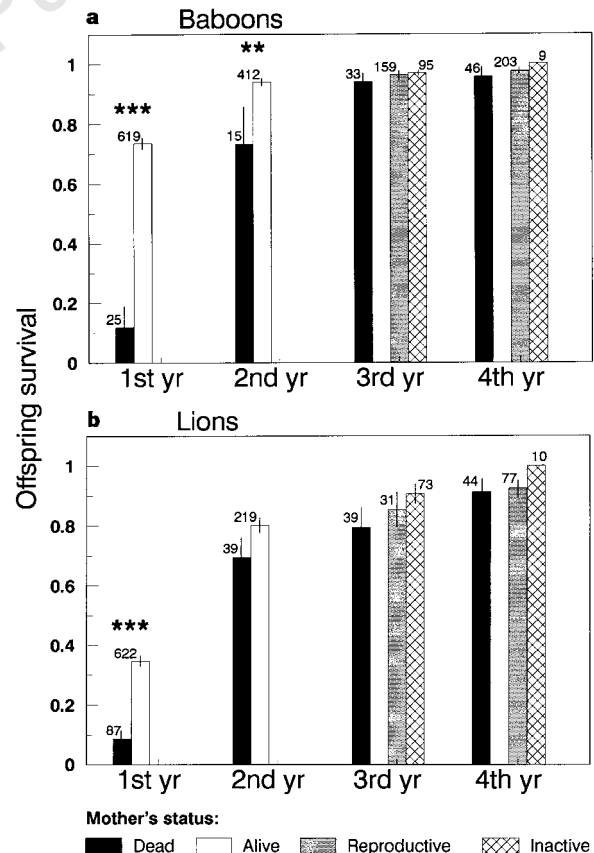

Figure 5 Effects of female survival and subsequent reproduction on offspring survival. **a**, Baboons and **b**, lions. Survival was significantly lower for animals orphaned during either their first year (baboons: $\chi^2 = 17.79$, $P = 0.0000$; lions: $z = 4.467$, $P = 0.0000$) or their second year (baboons: $\chi^2 = 6.72$, $P = 0.0095$). The typical interbirth interval for both species is two years, so effects of subsequent reproduction could be measured only in older juveniles. Mothers who gave birth before their prior offspring's second birthday were 'reproductive' for the juvenile's third year, otherwise they were 'inactive'. Juvenile survival was not influenced by the mothers' reproduction. Because of male dispersal in lions, 'juveniles' include only females. Double asterisks indicate $P < 0.001$; triple asterisks indicate $P < 0.0001$.

during pregnancy, parturition and the first year post partum (Fig. 6c), nor is there any evidence that such mortality increases with age. However, even if reproductive costs are higher than our measurements imply, both species fledge each brood before breeding again, so the effects of maternal mortality would be restricted to her youngest brood.

The rapid decline in reproductive performance of elderly females may result from low selection pressure on later ages[5]. If the force of natural selection is sufficiently weak at 21 and 14 years in baboons and lions, respectively, the observed reproductive declines could evolve through alleles with late-age-limited effects[17]. In this case, the difference in fitness between the observed cohort and a hypothetical non-menopausal cohort should be very small. We estimated this difference by calculating the population growth λ (the dominant eigen-value of the population projection matrix[18]) for each species using first the observed vital rates, and second the rates of a hypothetical cohort where fertility at advanced ages was the same as for younger females. Among baboons, the observed λ was 1.1329 compared with 1.1355 for a non-menopausal population. Among lions, the observed λ was 1.1970 compared with 1.1985 for the hypothetical population. Thus maintaining reproduction at advanced ages would make only a negligible contribution to fitness in either species. Natural selection therefore has little opportunity to oppose the evolution of reproductive senescence resulting from either pleiotropic alleles that confer benefits in early life or the accumulation of deleterious mutations with late-age-limited effects.

The age-specific reproductive performance of female mammals shows a pattern of constancy followed by sudden decline. Physiologically, declining fertility is caused by a deteriorating ovarian environment, and menopause results from the breakdown of neural pacemakers which depletes the finite store of oocytes[1,19]. Senescence is predicted (and mortality senescence is generally observed; Fig. 1a, b) to begin at the age of first reproduction, and reproductive performance declines monotonically in many reptiles, birds and invertebrates[2]. But gradual reproductive senescence in mammals may be masked by extensive maternal care and small litter size. Young females may be physiologically capable of producing larger litters than they could successfully rear, but this capacity eventually declines until they can no longer produce typical numbers of offspring (Fig. 2b, d) before ceasing altogether (Fig. 3).

The timing of reproductive senescence will be set by both the female's age-specific life expectancy and the duration of infant dependency. Even in species in which reproduction inflicts no mortality, females will eventually reach an age where they would either die (Fig. 1a, b) or lose their vigour (Fig. 2a) before they could fledge additional offspring. At this point, any degeneration of reproductive performance will be unopposed by selection because no further fitness can be gained from continued parturition. However, selection will maintain somatic function long enough to rear any offspring that are dependent on the mother when she reaches menopause. Consequently, the time lag between reproductive and somatic senescence should be greatest in species in which infant dependency is most prolonged. Infant baboons suffer significant mortality when orphaned at 2 years of age (Fig. 5), and the females' life expectancy at 21 years is an additional 5.0 years; lion cubs are only vulnerable during their first year, and life expectancy at 14 years is only 1.8 years. Assuming a childhood dependency of 10 years and extrapolating from the observed relationship between mortality and maternity in baboons and lions, the expected lifespan of women who have reached 40 years (when reproduction starts to decline[9,19,20]) would be 58–65 years. There is no consensus on mortality in pre-technological societies[21], but prolonged infant dependency seems sufficient to account for a midlife menopause in human females (although increased reproductive costs would lead to an even younger menopause in any species in which interbirth intervals are shorter than the period of infant dependency). Infant dependency also explains why reproductive cessation is more striking in females than males: most mammalian infants
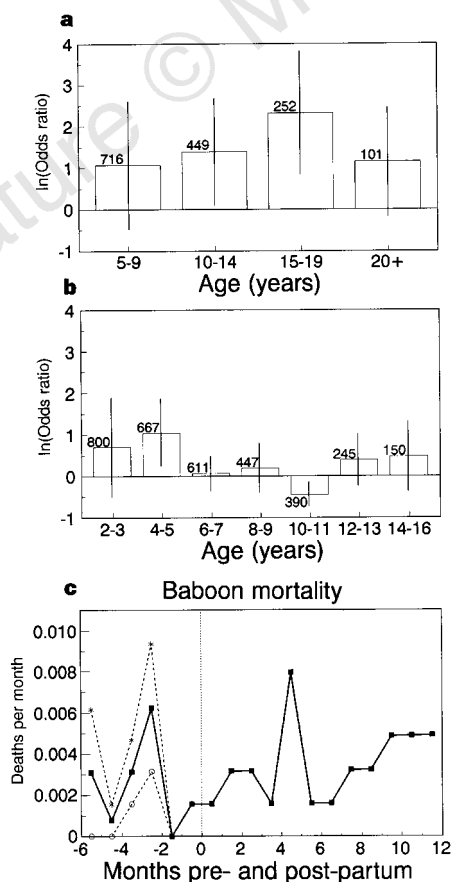
Figure 6 Costs of active reproduction. Logarithm of odds ratio (95% confidence interval) for survival at each age for reproductive females compared to non-reproductive females in baboons (**a**) and lions (**b**). Values are summed into multi-year classes to ensure non-zero frequencies; numbers refer to female years. Baboons aged 15–19 years were the only age class to show a significant deviation from zero ($\chi^2 = 7.08$, $P < 0.01$). **c**, Monthly mortality rates for female baboons throughout pregnancy and lactation. Post-partum mortality is based on the 635 live births of 160 females. 'Known pregnancy' (open circles) includes four females who were clearly pregnant at their death; 'possible pregnancy' (asterisks) includes these four plus 11 additional females who died within 6 months of their final cycle; filled squares indicate the midpoint between alternatives. Mortality did not vary across months in these data, nor during 12 months following miscarriage.

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,