

Figure 3 Trace-element plots for the low-MgO eclogite xenoliths from Koidu, Sierra Leone showing Nb/La versus Nb (**a**) and Ti/Zr versus Ti (**b**) using data from ref. 11 (note log scales). The compositional ratio in chondritic meteorites is shown as a horizontal line across each diagram. Also shown are the compositions of average depleted mantle (DM) and the bulk silicate earth (BSE) from ref. 17, two different average values for the continental crust (crust-M from McDonough¹⁷; crust-R from Rudnick¹⁶) and average Archaean TTG¹⁸ (avg-TTG). The plots show that, given the composition of the bulk silicate Earth, neither average continental crust, nor average Archaean TTG is an exact complement to the depleted mantle and that a 'missing' component, with a composition above the chondritic reference line, is required. The plotted compositions of the Koidu, low-MgO eclogites (grey circles) represent the 'missing' component.

1% rutile in the residue), Ti/Zr = 80–400. These values are very similar to the range of values found in the Koidu eclogites. It should be noted, however, that alteration has disturbed the concentrations of the most incompatible trace elements in these xenoliths, thus it is probable that their major-element chemistry reflects more accurately the *in situ* composition of the eclogites in the mantle.

The results of this study add significant support to the view that Archaean granitoid melts and kimberlitic eclogite xenoliths are respectively the melt and unmelted residue from the partial melting of basaltic source. This does not negate the hypothesis that some kimberlitic eclogites were former ocean floor, but suggests that in at least some cases they have had a silicic melt component extracted⁵. Experimental studies^{7–9} suggest that a melt fraction representing 20–30 vol.% of the original rock has been removed.

An important consequence of the eclogite restite model is that there are large volumes of eclogite, complementary to Archaean TTGs, which are now either stored in the subcontinental lithosphere or at greater depths in the mantle. Recent gravity studies show that the African lithosphere has the greatest effective elastic thickness beneath the oldest cratons²⁰. Two of these regions, the West African and Kaapvaal Archaean cratons are both places from which eclogite xenoliths have been recovered. These old continental roots are compositionally distinctive and differ from their Phanerozoic counterparts^{20,21} and thus match the compositional distinctiveness of Archaean continental crust. □

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Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent

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Ecology has long been troubled by the controversy over how populations are regulated^{1,2}. Some ecologists focus on the role of environmental effects, whereas others argue that density-dependent feedback mechanisms are central^{3–6}. The relative importance of both processes is still hotly debated, but clear examples of both processes acting in the same population are rare^{7,8}. Key-factor analysis (regression of population changes on possible causal factors) and time-series analysis are often used to investigate the presence of density dependence, but such approaches may be biased and provide no information on actual demographic rates^{9,10}. Here we report on both density-dependent and density-independent effects in a murid rodent pest species, the multi-mammate rat *Mastomys natalensis* (Smith, 1834), using statistical capture–recapture models. Both effects occur simultaneously, but

we also demonstrate that they do not affect all demographic rates in the same way. We have incorporated the obtained estimates of demographic rates in a population dynamics model and show that the observed dynamics are affected by stabilizing nonlinear density-dependent components coupled with strong deterministic and stochastic seasonal components.

Multimammate rats are highly suitable for the study of (deterministic) density dependence and (stochastic) density independence, because of their extensive population fluctuations, both within and between years^{11,12}. The timing of reproduction has been demonstrated to be linked to rainfall-induced density-independent factors¹³, but survival and maturation patterns are poorly documented owing to the rarity of capture-recapture studies (but see refs 11, 14, 15). Here we use data from a population of the multimammate rat in Tanzania (Fig. 1a).

Applying a multistate statistical model approach, we investigated time-specific variation in survival, maturation and capture probabilities (Table 1). The most general model allows for full time-specific variation in all parameters. In the reduced models, such variation is restricted, expressing a priori ecological hypotheses with time-specific variation being constrained within categories of sampling periods predefined according to preceding rainfall or population size (thus implying density independence, density dependence, or a combination of both).

The goodness-of-fit *G*-statistic provided no evidence of lack of fit

($P > 0.9$) for the full time-specific model. The Akaike's information criterion (AIC; see Table 1) for the general model was the smallest of all the models considered, suggesting strong time-specific variation of survival and maturation (Table 1). Among the reduced models, the ecologically plausible model combining density-dependent and density-independent effects (DD/DID) was the most parsimonious; it was significantly better than the models implying density (DD; likelihood ratio $\chi^2 = 220.0$, d.f. = 12, $P < 0.001$) or rainfall (DID; $\chi^2 = 34.2$, d.f. = 9, $P < 0.001$) alone; but it was still different from the full time-specific model ($\chi^2 = 107.8$, d.f. = 49, $P < 0.001$). The full time-specific model is not useful here from the perspective of ecological explanation. Among the models incorporating ecological hypotheses, the DD/DID model was the most appropriate and explained much of the variation. Further empirical work is needed to disentangle the additional sources of month-to-month variation and provide an ecological explanation for this variation.

For the DD/DID model (Fig. 1c), sub-adult survival shows no clear effects of either previous rainfall or density (although there is a certain degree of inverse density-dependence). The estimated maturation rate of the sub-adults increases with an increasing amount of preceding rainfall; for the higher-rainfall category, there is also evidence of a strong negative density dependence. For adult survival there seems to be no effect of previous rainfall, whereas there is a clear tendency for decreased survival at higher densities, particularly after wet periods. The deduced rainfall effect

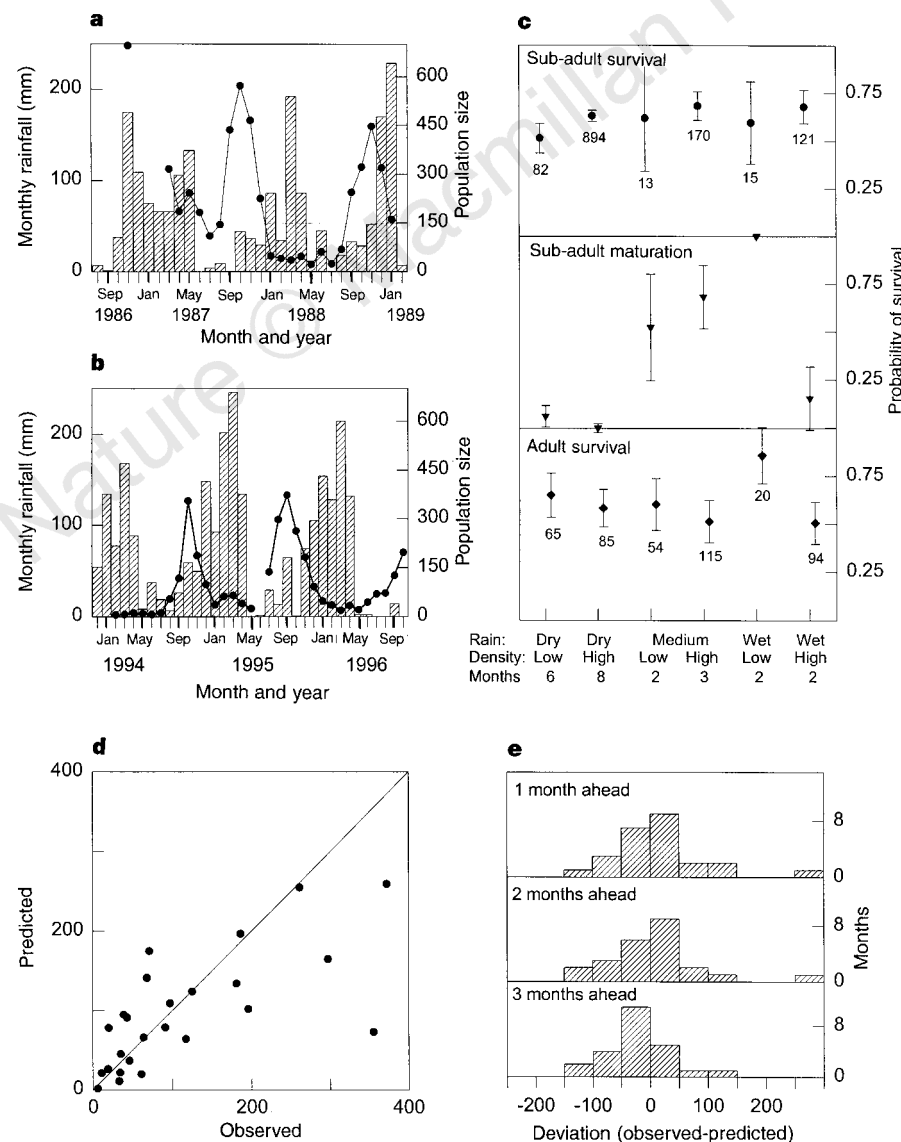


Figure 1 Actual data (a, b), statistical model estimates (c) and mathematical model predictions (d, e). a, b, Rainfall (columns) and population size estimates (lines). a, Data used for statistical analysis; the horizontal line indicates the cutoff between 'high' and 'low' densities. b, Data used for testing the population dynamics model. c, Estimated survival/maturation probabilities \pm variance inflated s.e. from model DD/DID (Table 1); the number of animals released in each category is shown. d, One-month-ahead predicted versus observed (Schnabel estimated) population sizes, for 1994-1996 (correlation $r^2 = 0.489$, $n = 25$, $P = 0.0001$); the diagonal line represents the 1:1 ratio. e, Frequency distribution of deviations (Schnabel estimates-model predicted population sizes) for one-, two- or three-month-ahead predictions, as in d.

Table 1 Statistical models

Model	Model specification (time dependence)	No. of parameters estimated	Log-likelihood	AIC*
$(S_i, \psi_{12,i}, P_{r,i})$	Full model	113	-283.3	792.7
(S, ψ_{12}, P_r)	None	5	-661.7	1333.4
$(S_r, \psi_{12}, P_{r,i})$	Capture probability only	49	-451.0	1000.1
$(S_{r,DD}, \psi_{12,DD}, P_{r,i})$	According to density†	52	-447.2	998.5
$(S_{r,DID}, \psi_{12,DID}, P_{r,i})$	According to rainfall†	55	-354.3	818.6
$(S_{r,DD/DID}, \psi_{12,DD/DID}, P_{r,i})$	According to rainfall and density†	64	-337.2	802.4

The statistical models tested are denoted according to each model's time-specific variation in survival for each state (S_i), sub-adult-to-adult transition (ψ_{12}) and capture probability (P_r) in each state. Subscripts denote time-specific variation of the parameters: i denotes full time-specific variation (one value for each sampling month); DD denotes time-specific variation according to high or low density characterization of the sampling month (see Fig. 1); DID denotes time-specific variation according to rainfall characterization of the sampling month; DD/DID denotes a combined density-rainfall characterization; no subscript denotes no time-specific variation (one single value for all sampling months).

* Akaike's information criterion; lower values indicate a more parsimonious model²².

† Capture probability is fully time specific.

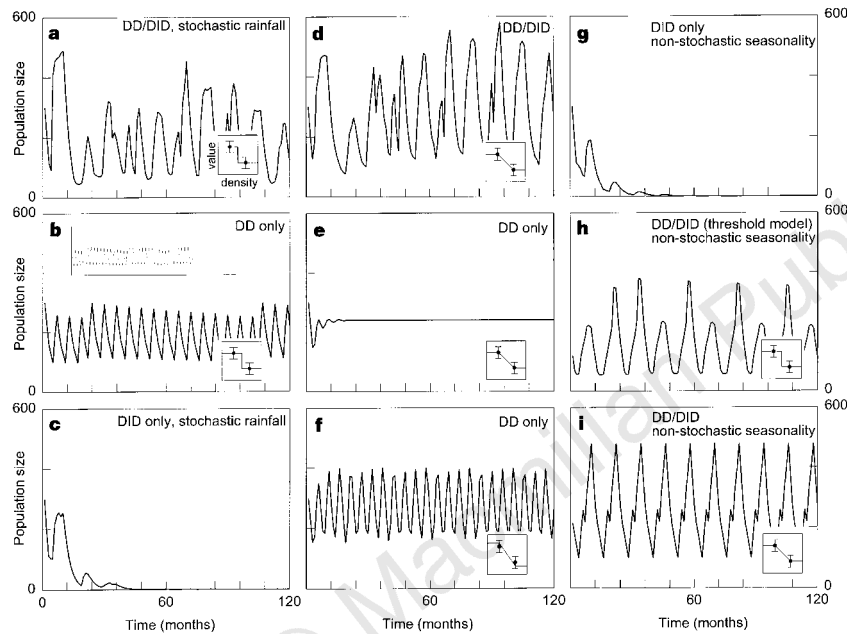


Figure 2 a-c, Simulation runs with parameter estimates from models DD/DID, DD and DID. Inset in **b**, 300 months run; inset in **c**, assumed threshold nature of the density dependence. **d-f**, Simulation runs with a piecewise nonlinear density dependence in the DD/DID and DD models. Insets show whether the estimated means or means \pm s.e. were used as parameter values. **g-i**, Simulation runs with non-stochastic seasonal rainfall (mean monthly rainfall values for 1981–1995; no variation among years), in the DID and DD/DID models with threshold or piecewise nonlinear density dependence (see insets).

is consistent with earlier analyses¹³, whereas the density dependence has not previously been reported for this species. Further studies are certainly needed before we understand the underlying mechanisms causing the density dependence in the demographic rates. Detailed studies of the social organization, possibly supplemented with a genetic approach, could indeed be very rewarding.

The estimated demographic rates were combined into a stage-structured population model^{16,17}, using parameter estimates from the DD/DID model for months characterized by different levels of density and rainfall (see Methods). There is a close relation between 'observed' (estimates based on capture-mark-recapture (CMR) data) and 'predicted' (one month ahead) population sizes when the model is run with actual rainfall data for March 1994 to October 1996 (Fig. 1b, d); predictions two and three months ahead yield similar results. Note that the data set used for these predictions was not used for developing the model. Deviations between predictions and observed values are symmetric for predictions one, two or three months ahead (Fig. 1e). There seems to be some bias for predictions that are too low at high densities (Fig. 1d), perhaps because of an underestimation of the proportion of juveniles in the population that could be trapped at the end of the breeding season. Simulations with seasonal and stochastic seasonal rainfall data result in dynamics (Fig. 2a) that compare favourably with observed patterns (Fig. 1a, b).

We may understand the relative importance of density dependence and density independence by using the different components in the demographic rates separately, as estimated from the DD and DID models (Table 1). Including only the density-dependent effects (Fig. 2b) shows that the dynamics of the DD/DID model (Fig. 2a)

result partly from a strong intrinsic nonlinear deterministic component in the demographic rates. Comparing the dynamics incorporating only density-independent effects in demography (Fig. 2c) with the DD/DID model furthermore suggests that the density-dependent component prevents population density from becoming too low (and too high).

The models summarized in Fig. 2a, b assume a threshold level for the density dependence. Because such a threshold may overemphasize both the degree of nonlinearity in and strength of density dependence, we also investigated a piecewise linear model (Fig. 2d): below a lower density cutoff and above an upper one, the demographic rates are fixed at the estimated levels; within this density interval, a linear approximation is assumed. This is a conservative model in the sense that we make a minimal number of assumptions over and beyond what we have estimated.

Incorporating density dependence only in the piecewise nonlinear model, the resulting dynamics are highly stable (Fig. 2e). Intermediate slopes of the linear density dependence in the model are obtained either by varying the size of the interval over which the linear density dependence was assumed (Fig. 3a) or by increasing the difference between the higher and lower parameter estimates (Figs 3b, 2f). The different dynamics seen in this exercise show an area of highly stabilizing density dependence at shallow slopes and several areas of regular fluctuations at steeper slopes. We therefore conclude that the deduced strong effect of nonlinearity seen in Fig. 2 is not only due to the threshold formulation.

The overall negative population growth under the density-independent regime observed in Fig. 2c persists under conditions of deterministic seasonality (seasonal variation in rainfall, but no

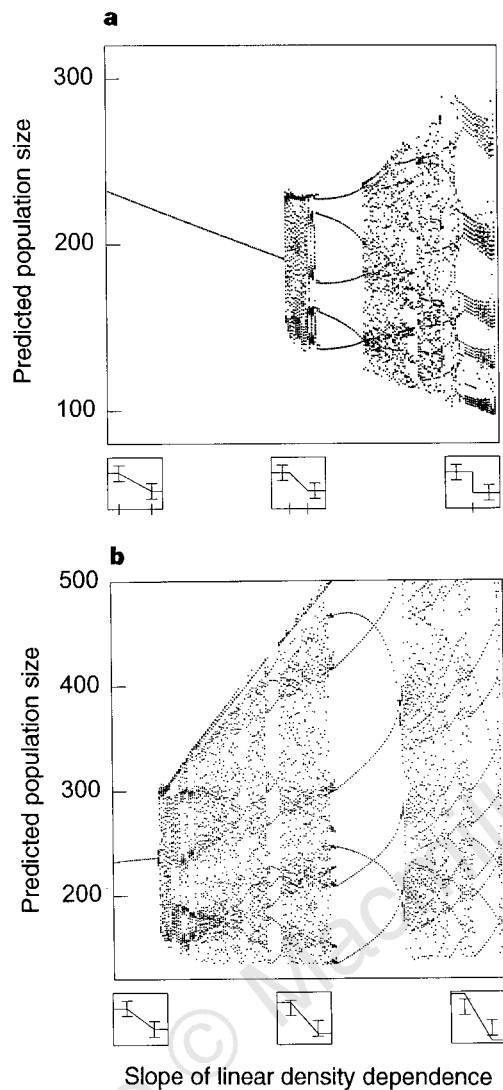


Figure 3 Bifurcation diagrams showing the dynamics of the mathematical model at different slopes of the linearly decreasing segment of the density-dependent function. **a**, Slope changed by decreasing the interval between the lower- and higher-density cutoffs between which density-dependence is linear. **b**, Slope changed by increasing the higher, respectively decreasing the lower, demographic parameter estimates.

variation among years), and is thus not necessarily dependent on random variation in rainfall (Fig. 2g). The periodicity of the fluctuations generated by density-dependent components is adjusted by seasonality (Fig. 2h, i), whereas stochasticity of the rainfall destabilizes the amplitude of the fluctuations (Fig. 2a, d). Abnormal unseasonal rainfall is indeed known to be correlated with population outbreaks¹².

Taken together, this suggests that the interaction between density-dependent and density-independent factors that we observe at the demographic level is also important at the population dynamics level. Such combined effects at both levels have not, to our knowledge, previously been reported. The apparent strong density-dependent component in the demography of *Mastomys* furthermore raises optimism for the development of outbreak-forecasting strategies.

Many of the controversies in population ecology in the last half-century result from an inadequate integration of the relative importance of density-dependent (deterministic) and density-

independent (both deterministic and stochastic) processes. A recent example is the current debate over coloured spectra in ecological time series data^{18–20}. We have demonstrated that an understanding of the interaction of both deterministic and stochastic processes is crucial to an understanding of the dynamics of an ecological system. Even though it is generally assumed that populations exposed to a purely density-independent process will eventually become extinct, this is not a certainty within an ecological time frame¹⁷. Furthermore, it is also often forgotten that much of the current debate on the relative importance of deterministic and stochastic processes really centres around the very same issue that historically was initiated by Nicholson² and Andrewartha and Birch¹, namely the relative importance of density-dependent and density-independent processes, the assessment of which only can be made through a combined empirical and theoretical approach. □

Methods

The capture-mark-recapture study. Data for the statistical analysis originated from a capture-mark-recapture (CMR) study on fallow land in Morogoro, Tanzania (06° 51' S 37° 38' E) between October 1986 and February 1989. A 1-Ha grid was used with 100 trapping stations 10 m apart with, depending on density, one to four Sherman traps per station to avoid trap saturation. The study followed a robust design²¹ with three consecutive nights of live-trapping each month. In total we made 6,728 captures of 2,481 individual *M. natalensis* (Fig. 1a). We obtained rainfall data from the Meteorological Station, Morogoro. CMR data were analysed using multistate models of the type presented in ref. 22. In standard age-specific models^{23,24}, the time between sampling periods corresponds to the time required for transition from one age class to the next. However, maturation from sub-adult to adult is not deterministic in *M. natalensis*, but occurs with unknown probabilities. Our multistate statistical models therefore incorporate three kinds of parameters: survival parameters ($s_{r,i}$, the probability that an animal in state r ($r = 1$ denoting sub-adult, $r = 2$ denoting adult) in month i survives (locally) until month $i + 1$); maturation probability ($\psi_{12,i}$, the probability that a sub-adult in month i is an adult in month $i + 1$, given that it is alive in month $i + 1$); and capture probability ($p_{r,i}$, the probability that an animal in state r in month i is captured in month i). We tested statistical models using the program MSSURVIV²⁵ with and without constraints on temporal variation of survival in periods with high or low densities (see cutoff value in Fig. 2a) and periods based on rainfall during the previous three months (dry, less than 200 mm; medium, 200–300 mm; wet, more than 300 mm). Only sub-adult (>1 month old but not yet sexually mature) and adult (sexually mature) females were used; they were considered sexually mature once they had displayed perforated vagina, lactating nipples or palpable pregnancy. Closed model estimates of the population size (Schnabel's method²⁶) were used as they generally exhibit negligible sampling correlations with open-model estimates of survival rate, supporting the recommendation to use a robust design in studies of density dependence^{27,28}. Such an approach is superior to the key-factor approach, in which the abundance estimates appear in both the 'dependent' and 'independent' variables of the regression analysis. Sampling variation associated with estimation of abundance will therefore produce a positive sampling covariance between abundance and mortality, and may result in the inference of density-dependent mortality, even in cases where there is no such relationship^{9,29,30}. We dealt with the residual variation of the selected most appropriate model by using a quasi-likelihood approach, characterizing the lack of fit of the model by the likelihood ratio test between it and the full time-specific model, and computing a variance inflation factor (likelihood ratio $\chi^2/\text{d.f.}$) for the parameter estimates²³.

The population dynamics model. The parameter estimates from the DD/DID model (Fig. 1c) were used to define parameters for a population dynamics model defined by the transition matrix:

$$M = \begin{bmatrix} 0 & 0 & B(P, N) \\ s_0 & s_1(P, N)(1 - \psi_{12}(P, N)) & 0 \\ 0 & s_1(P, N)(\psi_{12}(P, N)) & s_2(P, N) \end{bmatrix}$$

where $B(P, N)$ is the monthly net reproductive rate per adult female (calculated from data used in ref. 11; pregnancy rates and litter size were determined from

5,196 females in snap trapping studies about 2 km from the CMR grid); s_0 is the survival rate from newly born to sub-adults, assumed to take place in one month and assumed to be 0.5; $s_1(P, N)$ is the monthly survival rate of sub-adults; $\psi_{12}(P, N)$ is the maturation rate from sub-adult to adult; and $s_2(P, N)$ is the monthly survival rate of adults; P and N refer to the precipitation and density categories, respectively. We implemented the model in Stella II (High Performance Systems; Hanover, NH) using one-month time steps. Predictions (adults, sub-adults and half of the juveniles) from the population dynamics model were compared with estimates obtained in another CMR study, at the same site, between March 1994 and November 1996 (8,796 captures of 3,331 individuals), using the actual rainfall data for this period (Fig. 1b). Other simulation runs used either stochastic monthly rainfall values (bootstrapped for each particular month among the observed values for that month in 1981–1995) or non-stochastic seasonal rainfall (mean monthly rainfall values for 1981–1995; no variation among years). We investigated the form of the density-dependent function in the mathematical model by changing the slope, in 200 steps, of the linearly decreasing segment of the density-dependent function. We changed the slope by 1° decreasing the interval between the lower- and higher-density cutoffs between which density dependence is linear, or 2° by increasing the higher, respectively decreasing the lower, demographic parameter estimates by adding or subtracting from 0 to 3 standard errors. In the latter case, we constrained variation so that parameter values never became negative and survival and maturation rates never became larger than 1. The model was run for 1,000 cycles at each slope and the values obtained during the last 50 cycles were plotted, resulting in numerical analogues of bifurcation diagrams.

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Functional relevance of cross-modal plasticity in blind humans

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Functional imaging studies of people who were blind from an early age have revealed that their primary visual cortex can be activated by Braille reading and other tactile discrimination tasks¹. Other studies have also shown that visual cortical areas can be activated by somatosensory input in blind subjects but not those with sight^{2–7}. The significance of this cross-modal plasticity is unclear, however, as it is not known whether the visual cortex can process somatosensory information in a functionally relevant way. To address this issue, we used transcranial magnetic stimulation to disrupt the function of different cortical areas in people who were blind from an early age as they identified Braille or embossed Roman letters. Transient stimulation of the occipital (visual) cortex induced errors in both tasks and distorted the tactile perceptions of blind subjects. In contrast, occipital stimulation had no effect on tactile performance in normal-sighted subjects, whereas similar stimulation is known to disrupt their visual performance. We conclude that blindness from an early age can cause the visual cortex to be recruited to a role in somatosensory processing. We propose that this cross-modal plasticity may account in part for the superior tactile perceptual abilities of blind subjects.

Invasive^{8,9} and non-invasive^{10–12} cortical stimulation can transiently disrupt specific cognitive functions, such as naming objects. Trains of stimuli are more effective than single stimuli in inducing these effects^{13–15}. Task disruption by focal stimulation has been interpreted as a sign that the stimulated region is functionally important for performance⁹. When applied to occipital regions in subjects with normal sight, transcranial magnetic stimulation (TMS)¹⁶ can transiently suppress visual perception of letters¹⁷ and extrafoveal targets¹⁸, an effect thought to occur by interference with visual calcarine¹⁷ and association cortical areas at depths of 1.5–2.25 cm below the scalp surface¹⁹. We have applied TMS to different scalp locations (Fig. 1a) to interfere with the function of different cortical areas during tactile identification of Braille letters and