

batholithic equivalents. The similarity of these volcanic and batholithic rocks extends beyond bulk composition to many of the petrological features discussed here¹⁶.

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Test of optimal sampling by foraging great tits

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When great tits forage in an unknown environment containing two feeding places of different profitability, they first sample the two places and then exploit the more profitable one. The balance between sampling and exploitation shown by the birds is close to an optimal solution for maximising the number of food-items obtained during a feeding period.

OPTIMAL foraging models, based on the premise that animals collect food in a way which maximises their net rate of food intake, have been quite successful in predicting the decision rules used by predators in laboratory experiments¹⁻⁹, but so far, little work has been done on the problem of how a predator samples the environment. Sampling is an implicit necessity of optimal foraging models, which assume that the predator behaves as if it knows the availability of different prey types or patches of food. We describe here an experiment designed to test whether or not the great tit, *Parus major*, uses a maximally efficient set of rules when sampling a patchy environment.

Two possible methods of obtaining maximal food intake with a choice of foraging area

Our experimental set up is extremely simple. The naïve bird is faced with a choice of two foraging places (patches) which differ

in availability of food. The availabilities remain constant throughout a particular experiment, and the bird can only discover by exploration which of the two patches is better. Once the bird has distinguished between the quality of the two patches, it should concentrate on exploiting the better one; however, in our experiment we are concerned with how the bird makes the decision about which patch to exploit. We suggest that there are two simple types of maximising rules. On the one hand, the predator might attempt to maximise its rate of food intake at every instant in time by always foraging in the patch with the higher expected reward rate. We refer to this strategy as 'immediate maximising'. Alternatively, the predator might attempt to maximise its intake over the total foraging time and sacrifice short-term gain in order to acquire more information about the relative quality of the two patches. In this second strategy, an efficient predator has to choose the appropriate balance between exploration and exploitation. Our main aim was to test whether or not great tits follow this strategy and if so, whether they approximate an optimal balance between exploring and exploiting. The advantage of the sample-then-exploit strategy is that, in contrast to the strategy of immediate maximising, there is no risk of choosing to exploit the less profitable patch.

Simulation of the 'two-armed bandit' problem

The predator's problem of choosing the optimal balance between exploration and exploitation is similar to the classical 'two-armed bandit' problem, in which the player is faced by two

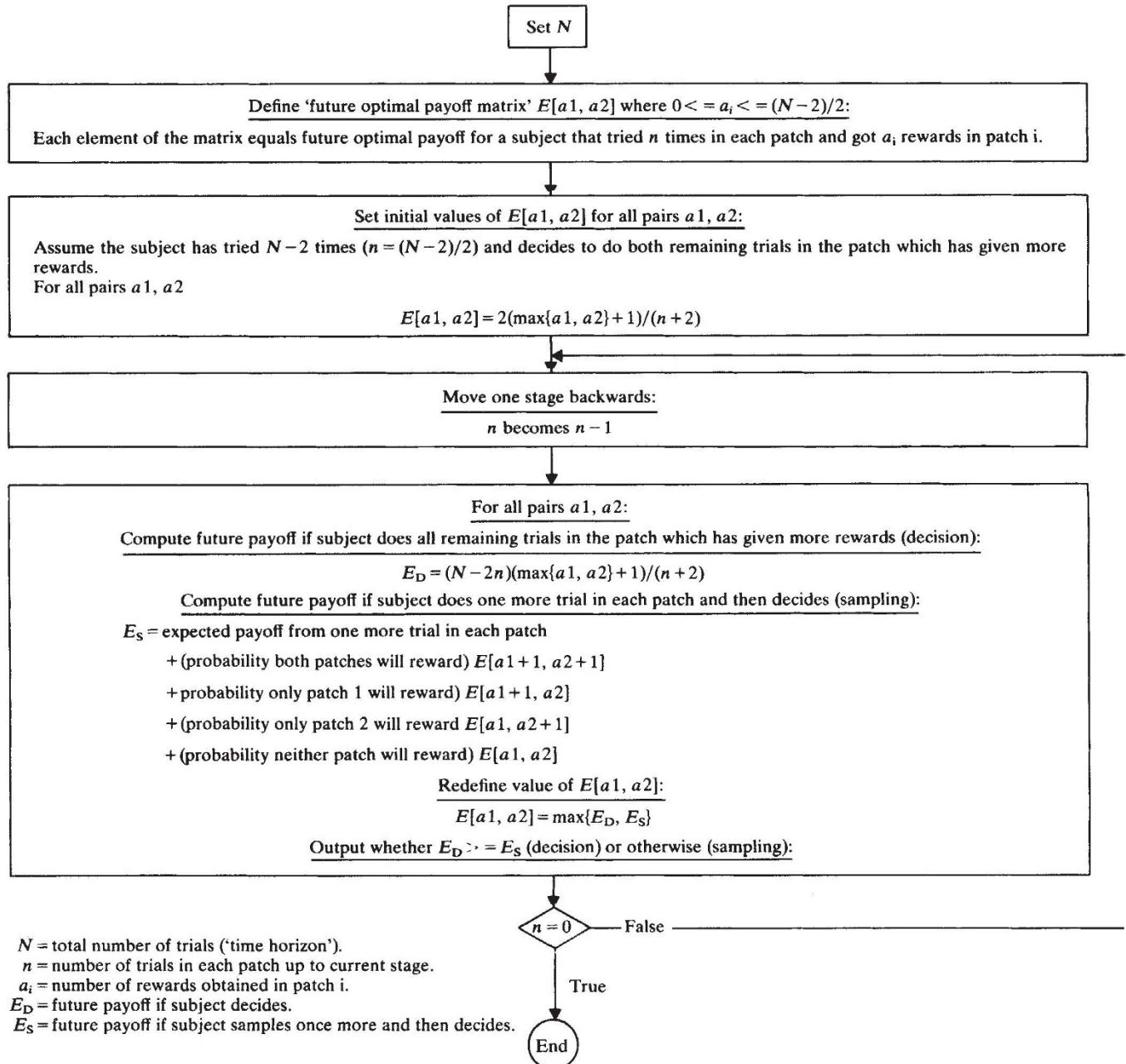


Fig. 1 'Two-armed bandit' simulation.

machines, each with a characteristic, unknown reward rate on a random schedule, and the goal is to maximise the expected number of rewards in *N* trials^{10,11}. This problem can be solved with a dynamic programming algorithm which works backwards from the *N*th trial, at which point the machine with the higher percentage rewards is chosen. The algorithm involves analysing at each stage, *n*, the payoff for two possibilities (exploring or exploiting) in terms of the known optimal behaviour at stage *n* + 1.

Our model is a modification of the optimal solution of the two-armed bandit problem¹². We consider that the bird has a total of *N* trials (the meaning of which will become apparent), and at the beginning of an experimental session it samples each patch alternately. After *M* trials in each patch the bird commits itself to one patch or the other, so that all strategies have the form: *M* trials in each patch (exploration) followed by *N* - 2*M* trials on one patch (exploitation). In our model we introduced the constraint of equal sampling effort in the two patches during exploration, because this simplifies the model without significantly altering its predictions. The model predicts how the

value of *M*, the point at which the predator decides to exploit, changes with p_1 and p_2 , the reward probabilities in the two patches. Intuitively, one would expect *M* to decrease as $|p_1 - p_2|$ becomes larger, and our model predicts the exact shape of the curve.

The details of our algorithm, which uses a Bayesian approach to describe the information possessed by the bird at each stage, are as follows. At the start of the experiment, the birds' prior estimate of *p* (the parameter of the Bernoulli process which is the reward rate in a patch) is considered to be β -distributed with parameters (α, β) , and therefore, with mean $(\alpha + 1)/(\alpha + \beta + 2)$ and variance $(\alpha + 1)(\beta + 1)/(\alpha + \beta + 2)^2(\alpha + \beta + 3)$. The distribution has the property that after *n* trials with *r* successes, the posterior estimate of *p* is also β -distributed with new parameters $(\alpha + r, \beta + n - r)$. Thus, it is easy to follow the state of the bird's information about the two patches by updating α and β after each trial. In simulating the model, we used starting values of $\alpha = 0, \beta = 0$ for both patches. This means that the bird's initial estimate of the mean reward probability in the two patches is 0.50 with a uniform distribution between 0 and 1.0. Thus, after *n*

trials with a_i successes, the bird's revised estimate of the reward rate p in patch i is $(a_i + 1)/(n + 2)$. We investigated the effect of varying the prior, by calculating our predictions for the following values of α and β : $\alpha = 0, \beta = 2$; $\alpha = 0, \beta = 0$; and $\alpha = 2, \beta = 0$. The model was rather insensitive to changes in the prior, most of the changes in prediction being between 10% and 20%.

If, after n trials in each patch, the bird decides to sample once more, its expected payoff for the remainder of the foraging time is E_S , whereas if it decides to exploit, its payoff is E_D . The optimal strategy is to choose the larger (E) of these two values. E_S can be calculated in terms of the values of E at stage $n + 1$ as follows:

Let

$$\pi_i = (a_i + 1)/(n + 2)$$

Then

$$\begin{aligned} E_S(a_1, a_2, n) = & \pi_1 + \pi_2 + \pi_2 \pi_1 E(a_1 + 1, a_2 + 1, n + 1) \\ & + \pi_1(1 - \pi_2)E(a_1 + 1, a_2, n + 1) \\ & + (1 - \pi_1)\pi_2 E(a_1, a_2 + 1, n + 1) \\ & + (1 - \pi_1)(1 - \pi_2)E(a_1, a_2, n + 1) \end{aligned}$$

and

$$E_D(a_1, a_2, n) = (N - 2n) \max \{\pi_1, \pi_2\}$$

Figure 1 gives further details.

The model is simulated by starting with $2n = N$ and working backwards, generating E_S , E_D and E recursively. At each stage, the model produces an $n \times n$ matrix giving the value of $(E_D - E_S)$ for each combination of values of a_1 and a_2 . When the bird is at the last pair of trials, E_D is clearly higher than E_S , assuming there is a difference in the two reward probabilities. As the simulation works backwards, it becomes more likely that, for any particular combination of a_1 and a_2 , the payoff for sampling once more in each patch (and hence acquiring more information about the profitability of the two patches) is higher than the payoff for deciding to exploit. The exact point at which this change from sampling to decision occurs depends on the value of the total number of trials N , which in effect represents the bird's time horizon. For given values of a_1 and a_2 , the larger the value of N , the longer the bird should sample before deciding. We ran the model with a range of values of N .

The experiment

In our experiments, the two patches consisted of two identical operant feeding places at opposite ends of an indoor aviary (measuring 4.3×3.7 m). The feeding places consisted of a perspex disk 35.5 cm in diameter enclosed in a shallow metal box measuring $38.5 \times 38.5 \times 9$ cm. The disk was drilled with 72 holes (diameter 0.7 cm, depth 0.4 cm) around the perimeter of its upper surface. Each of these holes contained a piece of mealworm (weight 0.07 g), and the bird had access to one hole at a time through a small horizontal window in the top of the box which enclosed the disk. To get at the next piece of food, the bird hopped on a perch next to the disk, which operated a solenoid-driven stepping cog to turn the disk through a small angle, bringing the next hole into line with the window. The reward rate was set on a pseudo-random variable ratio schedule using BRD modular logic units. This experimental set up is exactly analogous to that used in probability learning experiments¹³.

The experiments were carried out between June 1976 and February 1977 and involved testing nine wild-caught, adult great tits. Each bird was first trained to perform the operant task and then given a series of tests of different treatments consisting of various percentage reward rates in the two disks. The values we used were 50:0; 40:10; 35:15; 30:20. It is important that although these ratios always summed to 50%, we think the birds did not learn this, as between each treatment they were subjected to a series of one to four 'neutralisation' tests in which both disks offered a 7.5% reward rate. These tests were always continued until the bird showed no marked preference for one

disk over the other; we used a low reward rate during neutralisation sessions because we found this to be effective. If there was a slight preference, the less preferred disk was used as the more profitable place in the next treatment. A 'treatment' (for example, 20:30) consisted of a series of between 1 and 5 10-min tests. We had to run a series of short tests because the birds sometimes emptied one of the disks of rewards before a treatment was completed. When this happened, we interrupted the treatment for a short time while the disk was refilled. During these interruptions the bird was locked outside the test aviary without food, and in our analysis we always discounted the first 20 hops after an interruption. Any particular treatment was continued until the bird had 'decided' to exploit one disk or the other (nearly always the more profitable place).

The decision criterion was that the bird should perform more than 90% of a sequence of 100 hops on the preferred perch. This decision criterion was chosen after calculating the probability of the bird going back to the less profitable perch for a bout of 20 or more hops after different lengths of hopping bouts on the profitable perch. With the 100-hop criterion the probability of this type of reversal is nearly asymptotic and is less than 5%. Each bird was tested twice with all five treatments, the sequence of testing being randomly chosen. At the beginning of each treatment, the test bird was deprived of its normal food and excluded from the indoor aviary while the disks were being loaded with prey. Preliminary trials showed that the birds worked at a constant rate (15 hops per min) throughout a series of tests after an initial 60-min deprivation, which was the minimum period we used. The data were recorded on a computer-compatible event recorder which stored the information on magnetic tape.

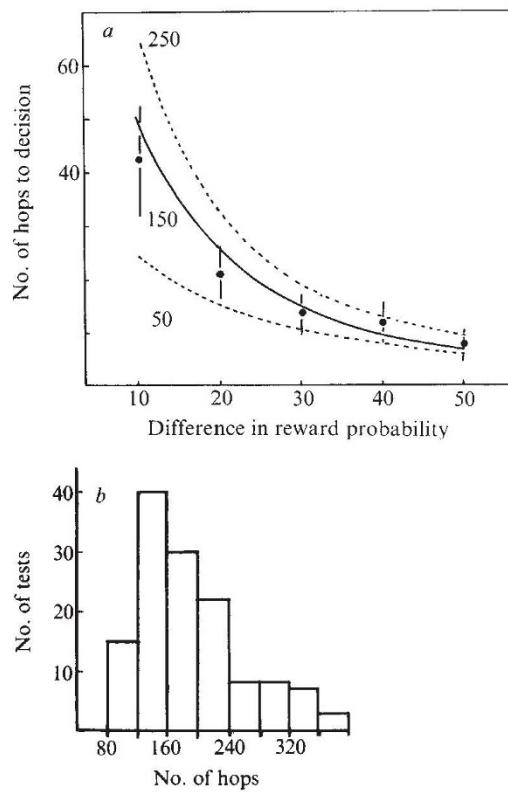


Fig. 2 *a*, The predicted (—, ---) and observed (●) number of hops before making a decision (nine birds). Three predicted curves based on the 'sample-then-exploit' model are shown, for $N = 50$, 150 and 250. The observed means are close to 150 (continuous line) curve. Also shown are the 95% confidence intervals of the observed geometric means (we used geometric means to normalise the distribution). The x axis is the difference in reward probability between the two perches for the five experiments (for example, 50:0, difference = 50; 35:15, difference = 20). *b*, A frequency distribution of lengths of tests. The modal value is close to $N = 150$, which gave the best fit in Fig. 3a. $\bar{x} = 199$.

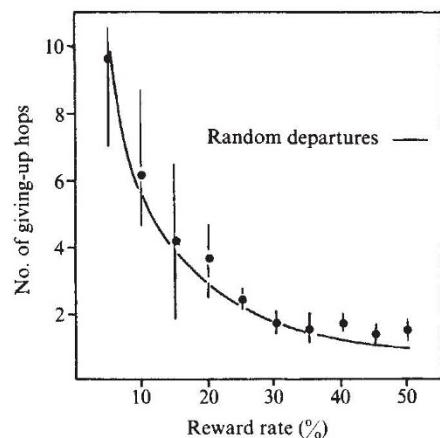


Fig. 3 The observed number of 'giving-up hops' (unsuccessful hops before a departure) plotted against reward probability. The random curve is calculated taking into account the fact that the birds tend to hop in short bouts. If p is the probability of getting a reward on a single hop and $q = (1 - p)$, then the expected number of giving up hops for bouts of $5 = qp + 2q^2p + 3q^3p + 4q^4p + 5q^5p$. The observed points lie very slightly, but consistently above the random departure line, indicating that the birds tend to leave a perch after a run of bad luck. The observed points are \pm standard error.

Treatment of results

The results of these experiments showed that the birds followed the general pattern of behaviour assumed by our version of the two-armed bandit model. There was an initial sampling period during which the birds performed on average 42% of hops on the more profitable and 58% on the less profitable perch. This proportion does not differ significantly from 50:50, and is consistent with the constraint of equal sampling in our model. The slight bias towards the less profitable perch resulted from our experimental procedure of always starting with the higher reward rate in whichever perch was used less in the preceding neutralisation test. After the decision point, the birds spent virtually all their time on the more profitable perch; on average, 95% of hops were on this perch, and the range for individual treatment means was 88–99%. Similar results, referred to as 'maximising' on concurrent variable ratio schedules, have been obtained with pigeons¹³.

In terms of our optimal decision model, we can consider a hop as being equivalent to a single trial, so that we can predict, for each combination of reward rates, how many hops on each perch the bird should do before making the decision to exploit. Figure 2a shows the observed mean decision point in each experimental treatment and the predictions of the model for three values of N (total number of hops in the experiment), 250, 150 and 50. The fit to the model with $N = 150$ is good; not only is the observed curve the same shape as predicted, but the predicted values are all fairly close to the observed means. The other values of N give curves of the same general shape, but with predicted values too high or too low. The value of N which fits the data (150) is the modal value for the number of hops performed in a test (Fig. 1b). This suggests that birds are optimising over the 'time horizon' which they experienced most often during our experiments, but we do not know if the birds would optimise with a bigger value of N if they were accustomed to longer tests. We plan to test this possibility. There is a slight difference in the modal value of test lengths for different treatments, but as the treatments were presented in a random order there is no reason to suspect that the birds could modify their behaviour according to treatment.

One way in which the birds' behaviour differed from that implied in our model is that they did not sample by doing one hop on each perch at a time, but instead they hopped in bouts of about five. (The overall mean bout length before decision was

5.00, the range 3.00–16.5.) This makes no difference in predicting the average decision point, but if the birds had hopped in rigidly determined bouts, the predicted decision point for a particular experiment would have to be a multiple of 5, which would involve reading every fifth matrix of the model's output. This tendency to hop in bouts probably explains why the observed points are above those predicted at the right-hand end of the graph where the bird should make a decision after about 10 hops.

The alternative goal we considered above was the strategy of immediate maximising, in which the bird always switches to the perch with the higher current expected reward rate. We used the β -distribution and the same starting values of α and β as above to predict, for any given experiment, at which point the birds should no longer switch back and forth if they were following this strategy. This predicted point is reached when expected payoff in the current patch never drops below that expected in the other one. The observed point was based on the decision criterion discussed above. The expected number of switches depends on the actual sequence of obtaining rewards in the first few moments of the experiment. In calculating the expected values we made the conservative assumption that the birds would continue to switch until the difference between patches in expected reward rate was greater than 5%. The observed mean values for the five treatments (50:5, 45:5, 40:10, 35:15, 30:20) were 3.3, 3.6, 3.8, 6.4 and 9.6, whereas the corresponding expected values were 0.93, 1.3, 1.36, 1.3 and 3.25. If we relax the assumption that the birds cannot discriminate differences of less than 5% in our experiments, the difference between observed and predicted values becomes even greater. Clearly, the birds switch more than expected. In other words, they are not maximising in the very short term, but instead they behave as if they acquire information to achieve a longer-term optimum.

Although the birds do not seem to switch according to the rule of immediate maximising, there is some evidence that switches between perches are related to short-term changes in reward rate. In Fig. 3 we plot the number of unsuccessful hops before a switch during the sampling period as a function of reward rate. The points lie very close to, but slightly above, the random departure curve. This random curve takes into account the fact that the birds work in bouts rather than single hops. Eight out of 10 means lie just above the random curve ($P = 0.05$). This shows that birds have a slight tendency to switch after a run of bad luck. In other words, they have a weak component of immediate maximising in their sampling strategy.

Discussion

The bird's behaviour approximates the prediction of a simple model based on a constrained optimal balance between exploration and exploitation, and does not fit the model of pure exploitation. The fit to the former model is close in spite of the fact that we have not yet directly incorporated a cost of switching between patches. In effect, we incorporated a small cost by using the rule that if the payoffs for sampling and exploiting were exactly equal, then the bird should exploit. In our experiment, this cost was small both in energetic terms and in time. However, in further developments of the model the cost of switching might be an important consideration.

Our comparison of the two maximising models has been in terms of predicting the details of the bird's behaviour, but an alternative approach is to compare the payoff, measured as number of rewards per test. On average, the two-armed bandit model achieves a slightly higher payoff than immediate maximising, except in very short experiments with less than five trials¹⁴, but when the reward rates are very different in the two patches (for example, 50:0) and the risk of a wrong decision is negligible, immediate maximising is just as effective. The difference between the birds' behaviour and that predicted by the two-armed bandit model, although small, is sufficient for the birds to do slightly worse than either of the two models in terms of payoff. However, the difference is less than 5% of the

predicted optimum of the two-armed bandit model (A.K. and J.K., in preparation). Thus, an analysis of payoffs enables us to say that the birds are close to the optimum but does not discriminate between the two models, unlike the analysis of the birds' behaviour.

We have presented averaged data for the nine birds we tested, but individual variation was very marked. We considered the possibility that some individuals are more cautious (do more exploring) but are less likely to make mistakes. Five of the nine individuals tested made one or more mistakes (that is, chose the poorer patch) in the 30:20 or 35:15 tests. These individuals did not make decisions after fewer hops than the other four birds. The average number of hops before a decision for all treatments was 23.9 ± 9.6 and 18.4 ± 9.8 for the fallible and infallible individuals, respectively. If, however, we examine individual treatments in which a bird made an incorrect decision, it is apparent that these tend to be cases in which the bird did little or no sampling. Examining the 18 '20:30' treatments (nine birds, two treatments each), only three out of the 13 in which a correct decision was made involved no sampling, whereas two out of the five in which the bird made a mistake were tests in which there was no sampling period at the beginning.

Although the birds in our experiments behaved on average as if they were calculating an optimal balance between exploration and exploitation, we suggest that they use some simple rule to

approximate the optimum. We have simulated various potential rules including 'matching' future responses to rewards obtained so far, an empirically derived rule applying concurrent choice experiments¹⁵. The extent to which these proximate rules mimic the behaviour of the birds and match the total payoff achieved will be discussed elsewhere (A.K. and J.K., in preparation).

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Electrophoretic movement and localisation of acetylcholine receptors in the embryonic muscle cell membrane

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A steady electric field of 30 mV across a single embryonic muscle cell produces accumulation of acetylcholine receptors toward one pole of the cell within 1 h. The movement is electrophoretic in nature and the accumulation results in the formation of stable, metabolically independent receptor aggregates.

MANY cell membranes are fluid in structure¹, and proteins and lipids are free to undergo long-range movement in the plane of the membrane²⁻⁵. Under many circumstances, however, mobile membrane components may be localised and concentrated at specific regions of the cell membrane. The mechanism that modifies and stabilises their topographic distribution in the fluid matrix is poorly understood. One notable example is the acetylcholine (ACh) receptors at the neuromuscular junction. Embryonic muscle membrane before innervation is sensitive to ACh over the entire surface of the muscle^{6,7}. After synaptogenesis, the ACh sensitive site is essentially confined to the junctional region of the muscle membrane^{6,8,9}. Embryonic muscle cell membranes are fluid^{10,11}, and redistribution of ACh receptors during the course of innervation has been demonstrated^{12,13}. We present here our study on electric field induced movement and localisation of the ACh receptor in muscle cell membranes. We found that when a steady electric field of 10 V cm^{-1} (corresponding to a potential difference of 30 mV across a cell 30 μm in diameter) was applied along the surface of spherical *Xenopus* muscle cells, the ACh receptors

rapidly accumulated towards one pole of the cell. This accumulation of receptors is consistent with the electrophoretic redistribution of mobile, charged receptors in the plane of the cell membrane. The redistribution is independent of metabolic energy, blocked by the preincubation of the cells with concanavalin A (Con A) and reversed in direction after surface charge modification with neuraminidase. Moreover, the accumulation of the ACh receptors leads to the immediate formation of stable receptor aggregates which persist against back diffusion, resist treatment with cytoskeletal disrupting agents, and require no metabolic energy supply for their stability.

Iontophoretic mapping of ACh receptors

Single embryonic muscle cells, obtained by dissociating the neural tubes of *Xenopus laevis* embryos (stage 18-19, ref. 14), were plated as a monolayer on clean glass culture chambers and were used for experiments after 2.5-3.5 d in culture. Culture medium contained 85% Steinberg's saline¹⁵ (58 mM NaCl, 0.7 mM KCl, 0.4 mM $\text{Ca}(\text{NO}_3)_2$, 0.1 mM MgSO_4 and 4.6 mM Tris), 10% Leibovitz medium (L-15, Gibco), and 5% fetal calf serum (Gibco). Within 2.5 d of culture, embryonic muscle cells of two distinct morphologies were observed, extended spindles and spheres. All experiments were carried out on the isolated, spherical mononuclear cells (diameter $35 \pm 5 \mu\text{m}$) that adhered tightly to the culture substratum (Fig. 1a). Details of electrophoresis methods and apparatus have been reported elsewhere¹¹. Briefly, an electric current was applied to the thin, rectangular culture chamber of defined geometry ($6.0 \times 1.0 \times 0.02 \text{ cm}$) containing culture medium. A current of 1.5 mA