

estimate for each migrant a new F -maximizing remittance of t^w . Using this predictor in the multiple regression described above and in Table 1, and the same methods as above, inclusive fitness accounts for 29 per cent of the observed remittances. The 'wife present' effect remains large (38 per cent of the observed mean remittance ($p < 0.0001$)) in this equation, suggesting that although the wife's contribution to inclusive fitness (as we have modelled it) helps to explain remittances, most of the 'wife present' effect cannot be explained this way.

The measurement of y , w and r^{im} are all subject to error, and this imparts a downward bias to our estimates of β . Moreover, other functional forms would yield different predictions. Finally, in many cases migrants have formed households and fathered children in the locality of their work²⁰, thus raising the marginal fitness costs of remitting in ways that our model does not capture. We experimented by re-estimating t^v assuming plausible (but hypothetical) values for the composition of the typical migrant's secondary family. This reduces the mean predicted transfer, as expected, but it does not increase the fraction of the remittance accounted for by inclusive fitness. We doubt that addressing these limitations would alter the conclusion that inclusive fitness explains part of remittance behaviour, but not all of it. □

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Genetic effects on sperm design in the zebra finch

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Sperm design and function are important determinants of male reproductive success and are expected to be under strong selection^{1,2}. The way that spermatozoa phenotypes evolve is poorly understood, because there have been few studies of the quantitative genetics of sperm^{3–5}. Here we show, in the zebra finch *Taeniopygia guttata*, an extraordinary degree of inter-male variation in sperm design that is independent of sperm swimming velocity. A quantitative genetics study using data from over 900 zebra finches in a complex breeding experiment showed that sperm head, mid-piece and flagellum length are heritable, that negative genetic correlations exist between sperm traits, and that significant indirect (maternal) genetic effects exist. Selection on the zebra finch sperm phenotype may be low because sperm competition is infrequent in this species⁶, and this, in combination with negative genetic correlations and maternal genetic effects, may account for the variation in sperm phenotype between males. These results have important implications for the evolution of sperm in other taxa.

The primary function of the male gamete, the spermatozoon, is to fertilize ova. Sperm are expected to be under strong selection to be efficient fertilizers for two reasons. First, within the female reproductive tract sperm face numerous physical, chemical and immunological barriers that result in only a tiny subset of inseminated sperm reaching the ovum^{7,8}. Second, widespread promiscuity among females results in sperm competition between males, which favours males whose sperm are effective competitors¹. Interspecific differences in these evolutionary forces combined with phylogenetic effects⁹ probably account for the fact that despite their common purpose, sperm vary more dramatically in size and design across species than any other cell type¹⁰. As well as the marked interspecific differences in sperm design, considerable inter-male variation in sperm phenotype exists within species¹¹.

Here, we aimed to investigate the underlying causes of inter-male variation in sperm design in the zebra finch *Taeniopygia guttata* by examining the relationship between sperm phenotype, sperm swimming velocity and the quantitative genetics of sperm traits. Heritabilities and other genetic parameters were estimated using the animal model¹² from a combined full-sibling and half-sibling animal breeding design involving 81 sires producing two sons from each of six dams (972 male offspring; entire pedigree comprising 1,526 individuals) and analysed using the multiple-trait, derivative-free, restricted maximum-likelihood program (MTDFREML)¹³.

Within males the repeatability of sperm traits was substantial, particularly for mid-piece (0.75) and flagellum (0.84) length (repeatability for head length was 0.52, all degrees of freedom (d.f.) = 913, 3,656; $P < 0.001$), and we have shown elsewhere that within-male variation in sperm design is highly consistent across ejaculates and time¹⁴. In contrast, between-male phenotypic variation in sperm design was considerable (Fig. 1 and Table 1). The inter-male coefficients of variation in sperm flagellum length and mid-piece length were two and four times greater, respectively, than for the linear morphological trait of male tarsus length (coefficient of variation = 3.38, $n = 972$ males).

Sperm motility is determined largely by the flagellum and the

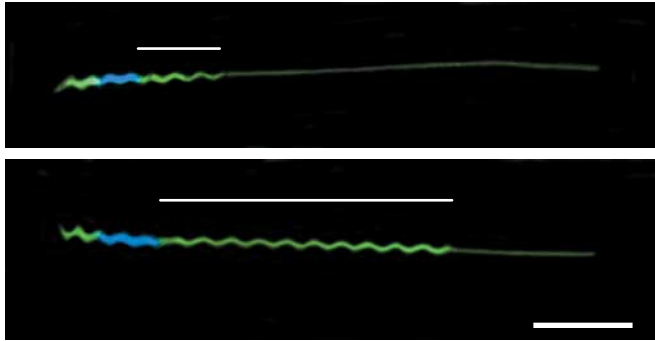


Figure 1 Examples of sperm of approximately the same total length from two zebra finch males showing the marked difference in size of the mid-piece (that is, the mitochondrial helix (bright green and indicated by a horizontal line)). The nucleus is stained blue and the acrosome at the tip is stained green. Scale bar, 10 μm .

mid-piece—flagellar forces are fuelled by ATP supplied by mitochondria in the mid-piece via the oxidative phosphorylation system¹⁵. As a result, because in some species sperm velocity predicts fertilization success^{16,17}, it is often assumed that sperm morphology influences sperm swimming velocity and thus fertilization success¹⁸. However, as far as we are aware there is no direct evidence for a relationship between sperm phenotype and sperm swimming velocity, either within or between species.

To determine whether the considerable inter-male variation we observed in zebra finch sperm had any effect on sperm motility, we measured the average path velocity (in $\mu\text{m s}^{-1}$) of sperm for a subset of 105 random males using a Hobson Sperm Tracker¹⁹ but found no relationships between velocity and any sperm morphology trait either individually or in combination (Fig. 2). In the present study it

was not possible to check the repeatability of sperm velocity for the same male; however, in an earlier investigation we found no significant within-male repeatability of sperm velocity across successive ejaculates for the zebra finch¹⁴. This confirms the findings of the present study (using a much larger sample of males) that despite a very high degree of within-male repeatability of flagellum and mid-piece size, there was no association between sperm design and sperm velocity. Sperm motility is complex, and although *in vitro* assays of sperm performance can in some cases predict fertilization success^{16,17}, in general the motility and velocity of sperm will depend very much on the environmental conditions they experience, which for internally fertilizing species is the female reproductive tract⁸.

The degree of inter-male variation in zebra finch sperm design that we observed was extremely high (Fig. 1), and the pattern of variation was surprising. In terms of sperm design we expected a positive, isometric or allometric relationship between flagellum and mid-piece length. Indeed, a positive relationship between these variables exists across passerine species (Fig. 3a), but within the zebra finch the phenotypic correlation between these traits was negative ($r = -0.165$, d.f. = 911, $P < 0.05$), although visual inspection of the data suggests the existence of a positive allometric relationship, albeit with considerable noise (Fig. 3b). Comparison with a small number of samples from wild zebra finches suggests that the observed pattern of variation is not an artefact of captivity or domestication (Fig. 3b).

To elucidate the basis for this inter-male sperm variation we examined the quantitative genetics of flagellum and mid-piece length. Some earlier studies of sperm traits in mice provided inflated heritability estimates³ because they were unable to separate direct genetic and ‘maternal effects’ in their analyses. However, the model that we used here distinguishes between direct and maternal effects and therefore avoids this problem (see Methods). It is important to clarify what is meant by maternal effects because the term has been

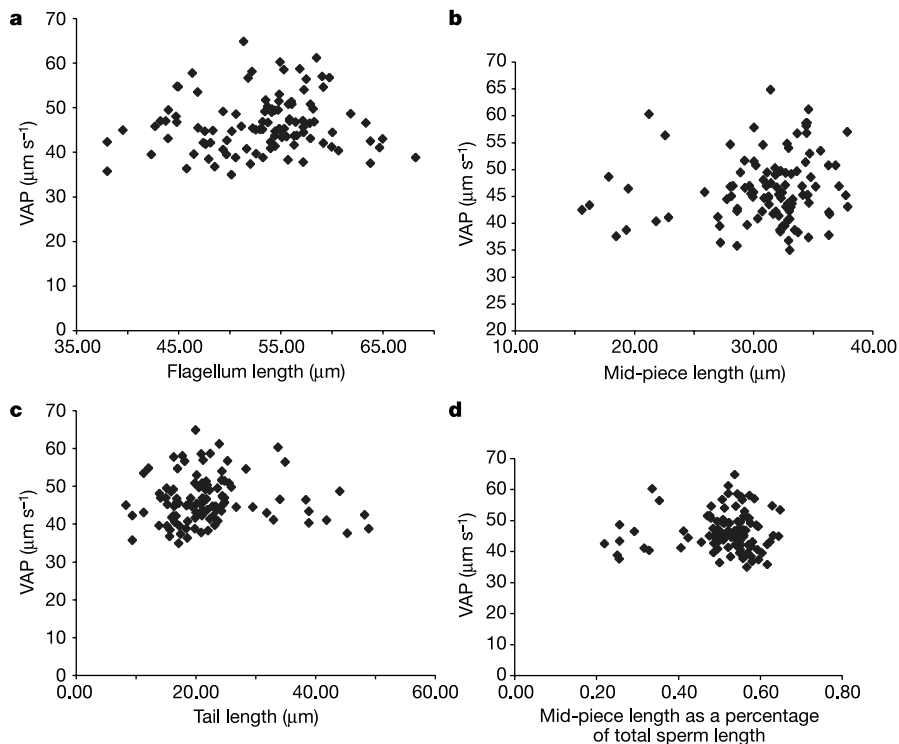


Figure 2 Relationships between zebra finch sperm velocity (VAP) and sperm traits. **a–d**, Relationship between VAP and flagellum length ($r = 0.094$, $P = 0.341$) **(a)**, mid-piece length ($r = 0.139$, $P = 0.157$) **(b)**, tail length (the portion of the flagellum beyond the mid-piece; see Fig. 1) ($r = -0.007$, $P = 0.945$) **(c)** and mid-piece as a percentage

of flagellum length ($r = 0.032$, $P = 0.746$) **(d)**. Degrees of freedom = 103 in all cases. There were no significant correlations between combinations of traits using multiple regression analyses.

Table 1 Data for zebra finch sperm traits

Trait	Mean (\pm s.d.)	CVP	CVA (total)	CVA (direct)	CVA (indirect)	CVR	Heritability (direct genetic effect)	Indirect genetic effect
Head length (μ m)	11.02 \pm 0.61	5.56	3.84	3.84	–	4.02	0.48	–
Mid-piece (μ m)	32.94 \pm 4.36	13.23	9.71	8.84	4.03	8.74	0.45	0.09
Flagellum (μ m)	53.59 \pm 5.11	9.53	8.24	7.49	3.44	4.52	0.62	0.13

CVP, phenotypic coefficient of variation; CVA (total), total additive genetic coefficient of variation; CVA (direct), direct additive genetic coefficient of variation; CVA (indirect), maternal additive genetic coefficient of variation (note that no indirect genetic effect on sperm head length was detected); CVR, environment coefficient of variation. Estimates are based on MTFREML variance component estimates and using an animal model.

Table 2 Genetic correlation matrix for direct and indirect effects on zebra finch sperm traits

	Head	Flagellum (direct)	Flagellum (indirect)	Mid-piece (direct)	Mid-piece (indirect)
Head	0.485 (0.03)	0.127 (0.08)	0.447 (0.23)	–0.185 (0.12)	0.054 (0.05)
Flagellum (direct)	–	0.599 (0.12)	0.258 (0.15)	– 0.505 (0.16)	– 0.284 (0.12)
Flagellum (indirect)	–	–	0.098 (0.05)	0.036 (0.04)	– 0.965 (0.11)
Mid-piece (direct)	–	–	–	0.463 (0.09)	0.195 (0.12)
Mid-piece (indirect)	–	–	–	–	0.092 (0.04)

Diagonal values are heritabilities; non-diagonal values are genetic correlations. Values in parentheses are standard errors; values in bold are statistically significant ($P < 0.05$).

used in several different ways. Maternal effects can be entirely environmental, entirely genetic, or a combination of both environmental and genetic factors. To avoid ambiguity we follow ref. 20 and refer to entirely genetic maternal effects as ‘indirect genetic effects’ and additive genetic effects as ‘direct genetic effects’. Our model (see Methods) estimates only the direct genetic effects and the indirect genetic effects, and specifically excludes maternal environmental effects.

All sperm components were heritable (Table 1) and apart from sperm head length also showed significant indirect genetic effects

(Table 2). Indirect genetic effects on sperm have been suggested by other studies, especially for the mitochondria in the mid-piece, as these are inherited maternally^{21,22}. However, the existence of significant indirect genetic effects for the flagellum (Table 2) was unexpected. If sperm development is influenced by both nuclear and mitochondrial genomes the inevitable antagonistic coevolution may constrain optimal sperm design. Because males are unable to pass maternally inherited traits on to their sons, traits with a maternally inherited component can respond to selection only through the female line and in many instances may be an evolutionary dead end^{20–23}.

Although our analysis suggests that the indirect effects we detected are entirely genetic, quantitative genetics techniques do not allow us to completely rule out the existence of non-genetic maternal effects, mediated, for example, by differential investment in eggs. Because differential endocrine and antioxidant investment in eggs with laying order has been found in the zebra finch²⁴, we tested whether laying order had any effect on sperm flagellum or mid-piece length, but found no such effects despite our extensive data set ($n > 900$ clutches). Although this suggests that little if any of the variance in flagellum or mid-piece length is mediated via non-genetic maternal effects, we cannot completely exclude other possible egg effects.

The genetic correlations between flagellum length and mid-piece length in the zebra finch were negative and pronounced (Table 2), indicating that the alleles for these traits are either antagonistically pleiotropic or in linkage disequilibrium. Another possibility is that if maternal environmental effects on sperm phenotype are small, as we suggest, sperm construction may involve an interaction between the mitochondrial and nuclear genomes. Negative genetic correlations between direct and indirect effects are common, variable across traits and species, and unexplained²⁵, but they are biologically important in the present context because like indirect effects, they can constrain the evolution of optimal sperm design²⁰. For example, the negative genetic correlation between flagellum (direct) and mid-piece (indirect) length (Table 2) indicates that if a male obtains genes from both parents that make his sperm flagellum longer, he will also get genes from his mother that make his sperm mid-piece shorter (and vice versa). Similarly, the pronounced negative genetic correlation between flagellum (indirect) and mid-piece (indirect) length (Table 2) indicates that genes a male obtains from his mother that make his sperm flagellum longer will make his sperm mid-piece shorter (and vice versa). Indeed, this particular negative genetic correlation is so close to 1 it suggests a powerful genetic constraint on sperm design. However, the way that these kinds of genetic processes influence the developmental pathways of sperm is not clear.

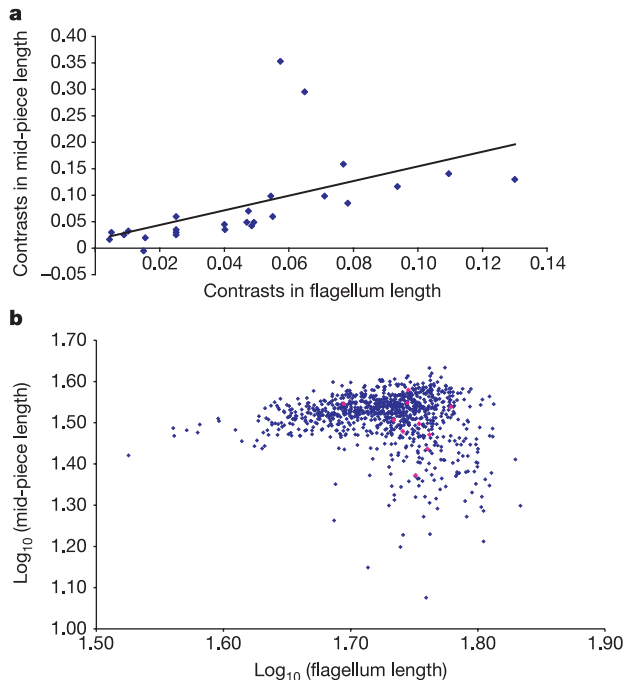


Figure 3 Relationship between sperm flagellum and mid-piece length. **a**, Relationship between contrasts in flagellum and mid-piece length for 29 passerine species controlling for phylogeny using CAIC³⁰: the relationship is significant ($F_{1, 26} = 43.95$, $P < 0.0001$; regression equation: $\log(\text{mid-piece}) = 1.61 \times \log(\text{flagellum})$; ($r^2 = 0.64$)). **b**, Log-log plot of sperm flagellum length versus mid-piece length for 913 zebra finches. The phenotypic correlation is negative ($r = -0.165$, 911 d.f., $P < 0.05$) and the slope is significantly less than 1: 0.876 ± 0.0015 (standard error) ($t = 592.0$, $P < 0.0001$). Coloured points ($n = 10$) are data from wild zebra finches and are not included in the analysis.

A possible explanation for our findings is as follows. The marked inter-male variation in sperm design in the zebra finch indicates that there has been little or insufficient selection to break the various negative genetic correlations between sperm traits. Post-copulatory sexual selection is likely to be an important selective force influencing sperm design^{1,2}, but because sperm competition in the zebra finch is not particularly intense⁶ this may account for the observed variation. Sperm design in passerine birds (see Fig. 1) seems to be highly conserved²⁶, and it will be interesting to establish whether in more promiscuous species the negative genetic correlations between flagellum and mid-piece length that we observed are conserved or broken²⁷, and whether the phenotypic variation in sperm design is less than in the zebra finch. □

Methods

Study animals

We used domesticated, wild-type zebra finches (part of an outbred study population based at the University of Sheffield since 1985). Birds were maintained on a 14/10 h light/dark regime at ~20 °C on a standard *ad libitum* zebra finch seed diet and water, which was supplemented with hard-boiled egg and soaked seed during breeding. We used a combined full-sibling and half-sibling breeding design^{12,13}; 81 sires produced two sons from each of six dams, a total of 972 male offspring (entire pedigree comprising 1,526 individuals). Sires were unrelated to each other as far back as grandparents, dams were unrelated to their male partner (back as far as grandparents) and all the females paired to a particular breeding male were unrelated to each other (as far back as grandparents). However, sisters were used (no more than two full sisters) but paired to different males. Each female was paired twice, once each with a different male to increase our ability to detect maternal effects. Pairs in individual cages (50 × 45 × 46 cm high) were established in batches of ~30 over 35 months, producing 15 cohorts each of 100–120 individuals. Eggs were numbered and randomly assigned to foster parents on an individual basis to help separate maternal genetic from maternal environmental effects. Chicks were individually marked soon after hatching and removed from foster parents aged 37 days; their sex (from plumage characteristics) and body mass (referred to as fledging mass) were recorded (between 14:00–16:00 local time). The study focused on male offspring. At sexual maturity (100 d (ref. 28)) various traits were measured relative to a period of exercise in which birds flew ~4 km day⁻¹ for 42 days aged 168–203 days to minimize any effects of a lack of exercise or overeating. After the period of exercise, sperm were obtained from the ejaculatory duct region of the seminal glomerus by dissection, fixed in 5% formalin and viewed using a Spot Diagnostics (version 3) image analysis system at a magnification of × 400. We obtained data for five sperm from each of 913 out of 972 males. Because the degree of coiling of the mid-piece varied between males we estimated the straight mid-piece length (*T*), thus $T = (L/d)l$, where $l = \sqrt{l^2 + (2\pi r)^2}$, $d = L/N$, L = the length of the mid-piece and N = the number of complete helix gyres, and where r = the radius from the centre of the sperm flagellum to the centre of the mid-piece helix, measured from electron micrographs and assumed to be the same for all males (3 μm).

Genetic analyses

The model used to estimate (co)variance components was a bivariate linear mixed maternal animal model, considering two traits affected by both direct and maternal genetic effects. In matrix notation:

$$\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} B_1 \\ B_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} M_1 & 0 \\ 0 & M_2 \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where Y_i is the vector of observations for the *i*th trait; B_i is the unknown vector of fixed effects for the *i*th trait; u_i is the unknown vector of random animal effects for the *i*th trait; w_i is the unknown vector of random maternal genetic effects for the *i*th trait; e_i is the vector of residual environmental random effects for the *i*th trait; and X_i , Z_i and M_i are known incidence matrices relating observations of the *i*th trait to fixed effects (cohort, clutch size and dam age, when declared significant, or the general mean otherwise), animal genetic effects and maternal genetic effects, respectively.

It is assumed that

$$\text{var} \begin{bmatrix} u_1 \\ u_2 \\ w_1 \\ w_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & g_{13}A & g_{14}A & 0 & 0 \\ g_{21}A & g_{22}A & g_{23}A & g_{24}A & 0 & 0 \\ g_{31}A & g_{32}A & g_{33}A & g_{34}A & 0 & 0 \\ g_{41}A & g_{42}A & g_{43}A & g_{44}A & 0 & 0 \\ 0 & 0 & 0 & 0 & r_{11} & r_{12} \\ 0 & 0 & 0 & 0 & r_{21} & r_{22} \end{bmatrix}$$

where g_{ij} are elements of *G* and represent the additive genetic covariance between variables *i* and *j*, where *i* = 1, 2 refers to animal direct effects for traits 1 and 2 and *i* = 3, 4 refers to maternal genetic effects for traits 1, 2. Similarly r_{ij} are elements of *R*, the variance and covariance matrix for residual effects.

Genetic parameters were obtained through an iterative process that estimates *G*, the genetic (co)variance matrix, which is based on calculating the variance of the animal genetic effects, the variance of the maternal genetic effects and the additive relationship matrix among all the animals in the pedigree file (matrix *A*). Calculations using this model

are based on the additive genetic effects. No other genetic effects (dominance, epistasis) or permanent environmental effects are considered in this model. In separate analyses we found no significant paternal environmental effects.

Subsets of two traits at a time were analysed. Traits studied were mid-piece length and flagellum length. There were 972 birds present in the data but the number of animal effects (the size of *A*, the numerator relationship matrix) included in this pedigree file was 1,526. We obtained sperm samples from 913 of the 972 male offspring. The animal model was used for estimating genetic and environmental variance components to estimate heritabilities and genetic correlations. The strategy involved obtaining univariate estimates for genetic and environmental (co)variances using the multiple-trait, derivative-free REML algorithm implemented in MTDREML software and using them as starting values in the bivariate analysis¹³. Convergence criteria were attained when the variance of the simplex values was ≤ 10⁻¹². It was assumed that the global maximum was obtained when two restarts, using previously converged values as starting values, produced convergence with no changes in the first three decimal places of the *F*-value¹³. Linear models were used to identify important sources of fixed effect variation for each trait. Terms fitted as fixed effects were dam age (quantitative continuous), clutch size (categories 2–11), number of fertile eggs (categories 1–10) and cohort (categories 1–15). Linear associations among all traits were estimated. No linear associations between sperm traits and environmental traits were found. As a first approach single-trait animal models (using MTDREML) that included identified significant fixed effects, animal effect and residual were used to estimate heritabilities for each trait. We used likelihood ratios to test whether the estimates of heritability and genetic correlation were significantly different from zero²⁹. For single-trait animal models, a test statistic for the additive genetic variance was obtained by computing twice the difference in log likelihoods between a complete model where the additive genetic variance is freely estimated and a reduced model where it is constrained to be zero: likelihood ratio statistic = 2(log(*l_c*) - log(*l_r*)), where *l_c* is the likelihood for the complete model and *l_r* is the likelihood for the reduced model. This likelihood ratio statistic is compared with a χ² distribution with one degree of freedom using a one-tailed region of rejection. As a second approach, single-trait animal models that additionally included the maternal effect were used to estimate direct (narrow sense) heritability and maternal heritabilities (additive maternal genetic/total phenotypic variance) and the genetic correlation between these two genetic components for each sperm trait. As for multiple-trait animal models, a test statistic for the genetic covariance was obtained by computing twice the difference in log likelihoods between a complete model where genetic correlation is freely estimated and a reduced model where the genetic covariance is set to zero. This test statistic is compared with a χ² distribution with one degree of freedom. The coefficients of variation for the direct and maternal additive genetic effects, for the environmental effect as well as for the phenotypic values were calculated as the square root of the respective variance component divided by the mean for the trait and multiplied by 100.

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Optimal eye movement strategies in visual search

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To perform visual search, humans, like many mammals, encode a large field of view with retinas having variable spatial resolution, and then use high-speed eye movements to direct the highest-resolution region, the fovea, towards potential target locations^{1,2}. Good search performance is essential for survival, and hence mammals may have evolved efficient strategies for selecting fixation locations. Here we address two questions: what are the optimal eye movement strategies for a foveated visual system faced with the problem of finding a target in a cluttered environment, and do humans employ optimal eye movement strategies during a search? We derive the ideal bayesian observer^{3–6} for search tasks in which a target is embedded at an unknown location within a random background that has the spectral characteristics of natural scenes⁷. Our ideal searcher uses precise knowledge about the statistics of the scenes in which the target is embedded, and about its own visual system, to make eye movements that gain the most information about target location. We find that humans achieve nearly optimal search performance, even though humans integrate information poorly across fixations^{8–10}. Analysis of the ideal searcher reveals that there is little benefit from perfect integration across fixations—much more important is efficient processing of information on each fixation. Apparently, evolution has exploited this fact to achieve efficient eye movement strategies with minimal neural resources devoted to memory.

Recent decades have seen considerable progress in understanding visual search^{11,12}, eye movements^{1,2,13} and active robotic vision¹⁴; however, there is no formal theory of optimal eye movement strategies in conducting visual search. Such a theory would provide insight into the design requirements for effective control of eye movements and attention, and hence could serve as a powerful framework for analysing the behaviour and neurophysiology of eye movements and attention, and for developing robotic applications.

We consider the task of finding a known target that is embedded (added) at a random location in backgrounds of spatial $1/f$ noise, which have the same spatial power spectra as images of natural scenes⁷. Figure 1a shows the target (a spatial sine wave) and a sample of $1/f$ noise.

Not surprisingly, the optimal eye movement strategy depends critically on how the visibility (detectability) of the target varies across the retina. Thus, to specify the ideal searcher, it is necessary first to characterize the visibility maps of the visual system under consideration, for the targets and backgrounds of interest.

To characterize the visibility map for each of the conditions in the search experiment described below, detection accuracy was measured for the sine-wave target as a function of target contrast and background noise contrast, at the 25 spatial locations indicated by the small circles in Fig. 1a. The observer fixated on the centre of the display, which was monitored with an eye tracker, and for each block of trials the target was presented at only a single known location. Figure 1b shows the measurements of detection accuracy (psychometric functions) in the fovea, as a function of target contrast. Each curve is for a different root-mean-squared (r.m.s.) contrast of the noise background, where the r.m.s. contrast is defined as the standard deviation of the pixel luminance divided by the mean luminance. Each of these psychometric functions can

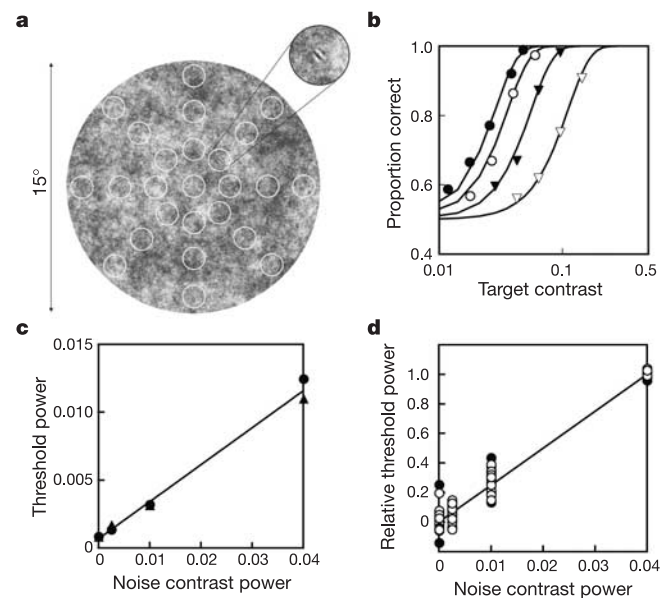


Figure 1 Measurement of the visibility maps. **a**, The target was a windowed sine-wave grating (see inset). Target visibility was measured at each of the locations indicated by the circles (which were not in the stimulus), in a two-interval forced-choice detection task. Each interval was 250 ms, the approximate duration of single fixations in our visual search experiments (280 ms). **b**, Proportion of correct responses in the fovea, as a function of target contrast, for four levels of background noise contrast: filled circles, 0; open circles, 0.05; filled triangles, 0.10; open triangles, 0.20. **c**, Detection threshold power in the fovea for two observers, J.N. (circles) and W.G. (triangles). **d**, Relative threshold power for all measured locations in **a**. These plots were obtained by normalizing the data so that the best-fitting line in each condition had an intercept of 0 and a value of 1.0 at a contrast power of 0.04. Observers: filled circles, J.N.; open circles, W.G.