male genetic quality, at least as it relates to these measures of fitness.

The quantitative genetic techniques used here are applicable to any organisms in which the attractiveness of males is measurable in the field, if those males can be brought into the laboratory to breed with randomly chosen females, subject to certain constraints. First, a knowledge of the variance in attractiveness of individual males is essential for interpreting the genetic results appropriately; a knowledge of the variance in female response to males would also be useful. In other words, a single test of each male's attractiveness is insufficient. Second, large numbers of families are necessary for the reliable estimation of heritability of components of fitness (*9, 11*).

In most organisms components of male mating displays are likely to be under polygenic control, as is fitness. Thus, "good genes" arguments can be seen as falsifiable hypotheses, subject to the type of tests that I have described.

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7. Two males died before they could be tested more than twice.
8. Differences between males accounted for 45 percent of the variance in the results. Duncan's multiple range test [R. J. Freund and R. C. Littell, *SAS for Linear Models* (SAS Institute, Cary, N.C., 1981), chapter 3] revealed three groups of males that were indistinguishable within each group; in Fig. 1, these are A through I, B through O, and P.
9. D. S. Falconer, *Introduction to Quantitative Genetics* (Longman, New York, ed. 2, 1981), chapter 10.
10. Animals were kept in flour-yeast medium (95 percent flour by weight) in an incubator held at 29° to 30°C and 70 percent relative humidity.
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12. Significant heritability of components of fitness is probably common, even though total fitness may not be heritable [R. Landon, *Ecology* **63**, 607 (1982)].
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Visual Flow and Direction of Locomotion

Regan and Beverley (*1*) simulated the optic array of a moving observer looking to one side while approaching a line of static objects, such as fence posts. From their data they concluded that, in judging the direction of locomotion, the point of maximum rate of magnification may be sufficient, but the optical focus of expansion is not. The latter conclusion may be warranted (*2, 3*), but the former seems not.

First, within 10° of the direction of the point of impact, the normal optic flow of objects is well approximated by a power function with exponent $n = 1.0$ (Fig. 1A). Beyond 10° or with other exponents, however, it becomes seriously discrepant, simulating either the view through a zooming photographic lens, or an unstable, nonrigid world that continuously bends. Neither situation is natural for any organism.

Second, in the real world, the point of maximum rate of magnification is surrounded by other points with rates nearly as great. The function is not highly articulated until the observer is near the point of impact on a flat plane (Fig. 1B).

Third, their display presented a visual array of 20° by 16°, vastly reduced from the roughly 180° by 100° available in normal vision. Visual flow is greatest, and perhaps most useful, outside the parafoveal region. Since their display excluded more than 97 percent of the solid visual angle of the optic array, it is not clear that information in optic flow was given a fair test.

As an example, consider a situation in which one cannot look in the direction of motion and yet it is essential to be able to judge its direction—the landing of a single-engine, propeller-driven aircraft, particularly one with a radial engine. On final approach to landing, in nose-up attitude, the pilot is obliged to look out to one side because the direction of motion is completely obscured by the engine and its housing. The point of maximum rate of change of magnification lies halfway between the point of impact and that point on the ground nearest the pilot [note 6 in (*1*)] and is simply unavailable. The pilot must know and maintain direction without ever seeing that point, and the cost of error is high. Yet pilots routinely make such judgments with accuracy, despite the implications of Regan and Beverley (*1*).

Finally, their analysis assumes no vi-

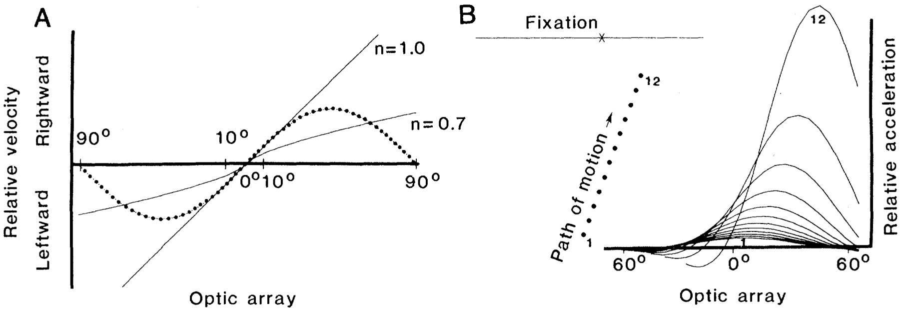

Fig. 1. (A) Relative velocities for two exponential flows used by Regan and Beverley (*1*) in their simulations, and the flow (dotted line) for actual orthogonal approach to a plane [$d\theta/dD = -x \sin\alpha(D^2 - 2Dx\cos\alpha + x^2)$, where θ is the angle of gaze with respect to motion, α the angle of approach to the plane, D the distance of the observer from the plane along the path of motion, and x the distance along the plane to the observed texture element from the point of impact]. Within ±10°, true flow is well approximated by $n = 1.0$; it is not for $n = 0.7$. (B) Nonorthogonal approach to a plane, with a maintained fixation point off to the left. Relative accelerations of textures are measured, with 0° the fixation point. Peaks in the functions correspond to the points of maximum rate of change of magnification. When an observer is relatively distant from the plane, functions are flat and this point is surrounded by neighbors of similar expansion rates. The function generated is $d^2\theta/dDdx = -\sin\alpha(x^2 - D^2)/(D^2 - 2Dx\cos\alpha + x^2)^2$.

sual flow across the line of sight. With orthogonal approach to a single plane this assumption is true. However, with objects arrayed in three dimensions it is not. Flow will always occur across the line of sight if one is not looking where one is going (or has come from). Shearing motion, known as motion parallax, is created. The retinal images of objects farther away than a fixated object will shift in the direction of motion, whereas those representing nearer objects will shift the other way. Thus, in order to look where one is going, one need only neutralize all flow across the line of sight. In an experiment that replicated many of the conditions of Regan and Beverley (1), but in which objects were laid out on three parallel planes in depth, rather than just a single plane, observers could determine their direction of gaze with respect to locomotion within 36′ of arc using motion parallax information alone (3).

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Regan and Beverley represented James Gibson's theory as holding that "the center of the expanding flow pattern in the retinal image [provides] a generally useful aid to accurately judging the direction of self motion" (1, p. 195). This idea cannot be generally correct, they maintained, since retinal displacement of image elements will be affected not only by the direction of locomotion, but by concurrent changes in direction of gaze. They showed that for some visual environments the position of maximum rate of change in magnification within an image is specific to, and thus potentially informative about, direction of movement. Their subjects detected such a maximum in the image poorly, a finding they interpreted as contrary to Gibson's theory.

In his 1958 paper, however, Gibson (2) made it clear that it is not flow in the retinal image that is of primary interest, but flow in the ambient optic array defined as the projection of an illuminated environment to a point of observation, without reference to an observer. Elements in this array are "anchored" to corresponding elements of the environment. Even when the point of observation moves, flow in the array will depend only on the layout of environmental surfaces and the path of movement. "The part of the structure of the array from which the flow radiates corresponds to that part of the solid environment toward which [the observer] is moving" (2, p. 187).

Gibson recognized that when a moving observer fixates some object not directly ahead, gaze direction must change smoothly to maintain coincidence between the fovea and the sector of the array being attended. During such episodes, flow in the image does not copy flow in the array, and the focus of image flow cannot specify the direction of movement. Neither, however, can Regan and Beverley's proposed rate maximum, except in the special cases of approach along the normal to a plane or convex surface (the only visual environments they studied).

Because Regan and Beverley's experiment rested on identification of the optic array with the retinal image, the relevance of its outcome to Gibson's theory must be questioned. Nevertheless, various hypotheses regarding their subjects' poor performance might be advanced. Foremost among these must be that the exclusion of real eye movements made it impossible to separate the significant features of flow in the array from the irrelevant "noise" added by the attempt to externally simulate the retinal consequences of eye movements (3). Invariants become evident against a background of change: the invariant focus of flow in the array may emerge most clearly from the varying foci of image flow when the observer engages in active exploration of the array.

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3. The normal retinal consequences of eye movements were not accurately simulated in the experiment: the edges of the display screen projected to a fixed locus on the subject's motionless retina, and hence provided optical information specific to the nonoccurrence of eye movements, regardless of what information was present in the display itself.

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If an automobile or aircraft is going the way it is pointing, the problem of visual guidance can be solved trivially by aiming at the desired destination, using the front of the vehicle like a rifle's sights (1). Visually estimating the destination is more difficult when the vehicle is rotating as well as translating. It has been shown mathematically that motion parallax information allows the destination to be correctly estimated (2), although parallax information is available in only a subset of visual environments. Priest and Cutting's (3) estimate agrees closely with ours (4) that, when parallax is available, observers can achieve a directional accuracy of about 30 minutes of arc. A further visual cue is available when the observer's gaze is maintained at a fixed angle relative to the direction of motion, for the focus (5) of the optic flow pattern in the retinal image then coincides with the observer's destination.

All this has more to do with geometry than with visual physiology. Of more physiological interest is the general case in which the direction of gaze is not maintained at a fixed angle relative to the direction of locomotion, so that the eye rotates as the observer moves. Consequently, a translational velocity is impressed on the entire retinal image [figure 1 in (1) (2, 6)]. Gibson (7, 8) pointed out that, in general, the necessary information for guidance is available in the optic flow pattern. Given this, specific and quite different ways of extracting guidance information can be suggested, and their predictions tested by experiment. One theoretical possibility is that observers might be able to judge their destinations from a single brief sample of the flow pattern rather than needing to compare two or more samples taken at different times. In this context it has been suggested that observers can locate the focus of expansion from a single sample of the visual flow pattern (7–9). This suggestion can be tested empirically. We found that translational motion of the retinal image severely degrades a subject's ability to locate the focus of expansion in a 20° by 16° field (1); on this basis we suggested that observers would not be able to use the focus to accurately guide locomotion except in the restricted conditions set out above. Other authors have come to similar conclusions from their experimental results (10–12).

Evidence against one specific implementation does not, of course, rule out Gibson's general suggestion. We discussed (1) a second hypothetical method for extracting guidance information that is based on the progressive geometrical distortion of the visual image caused by self-motion (8), rather than on the focus (5). Our stimulus was designed to dissociate visual sensitivity to flow pattern focus and visual sensitivity to local maxima in magnification rate [also called "local maxima in div **V**" (13, 14)]; previous experimental studies have confounded these two factors (15). A focus differs from a div **V** maximum in important ways; in particular, focus can be shifted by translational motion (1), whereas div **V** is unaffected (13, 14). The human visual system is specifically sensitive to div **V** independently of translational motion (14), and this sensitivity is adequate to locate the focus of one kind of flow pattern (16). However, because computations show that div **V** is not always maximal along the direction of motion [reference 6 in (1)], sensitivity to local maxima of div **V** does not provide a sufficient explanation for real-world directional judgments (4). The two algorithms discussed so far start with a single sample of a local property of the flow pattern (either focus or div **V**). Alternative kinds of candidate procedure involve several momentary samples of the flow pattern rather than one, and a large-field rather than a local property. Template-matching is one alternative procedure. A suitable template might be a neural mechanism that summed the outputs of many detectors of local radial motion distributed over an extensive area of the visual field (17). For some environments, exploratory eye movements would produce the largest response when the fovea was maintained centered on the destination because, for that unique direction of gaze, the retinal flow pattern would correlate most closely with the template [figure 1 in (1)]. It remains to be shown, however, that this means of extracting guidance information would be accurate in asymmetric environments.

Torrey (12) correctly points out that we leave open the possibility that observers might be able to judge the location of the focus provided that any translational motion is generated by eye movements rather than by moving the physical stimulus pattern as in our experiments; I know of no data to resolve that point.

I do not agree with Priest and Cutting's statement (3) that our conclusions (1) imply that pilots could not make accurate visual judgments of self-motion. Rather, they imply that a complete explanation for this evident ability is not yet established. Elsewhere we compared quantitative data on pilots' remarkable visual judgments while landing and in other flying tasks in simulators and high-performance jet aircraft (18) with visual discrimination of flow patterns. In view of the theoretical interest in the general rotating-eye case, quantitative data on human performance are surprisingly sparse; it has not been experimentally ruled out that a partial or even complete failure of directional judgment might occur when the eye rotates (19). Comparisons between different models of extracting guidance information from the optic flow pattern are currently constrained by the shortage of empirical knowledge about human performance.

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4. D. Regan and K. Beverley, in *Sensory Experience, Adaptation and Perception* (Erlbaum, Hillsdale, N.J., 1984), pp. 215–240.
5. "Focus" here means a point at which velocity is locally zero while velocity vectors on opposite sides point in opposite directions.
6. W. Richards, in *Handbook of Perception* (Academic Press, New York, 1975), vol 5., pp. 351–386; J. J. Koenderink and A. J. van Doorn, *J. Opt. Soc. Am.* **71**, 953 (1981).
7. J. J. Gibson, *Br. J. Psychol.* **49**, 182 (1958).
8. ———, *The Perception of the Visual World* (Houghton Mifflin, Boston, 1950), pp. 117–144.
9. The "optic array" is a theoretical construct that, by definition, is not influenced by eye rotation. Gibson proposed that subjects can use the focus of expansion in the optic array to guide locomotion, implying that ocular rotation can be disregarded in practice. The optic array concept has been discussed elsewhere [R. M. Boynton, in *Handbook of Perception* (Academic Press, New York, 1974), vol. 1, pp. 285–307].
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11. Torrey (12) correctly points out that we unfortunately misquoted Gibson by using the phrase "retinal image" instead of "optic array." However, this should not divert attention from the empirical question whether subjects can or cannot locate the focus of expansion when the eye is rotating.
12. C. C. Torrey, *Science*, **227**, 1064 (1985).
13. For clarity in (1), we used the term "local maximum in rate of magnification" rather than "local maxima of div **V**" (vector divergence of the local velocity vector). Flow patterns have been mathematically analyzed in terms of div **V** (2, 6). The indifference of div **V** to translational motion can be intuitively understood, because div **V** expresses *relative* motion [see L. Kaufman and D. Regan, in *Handbook of Vision*, in press); (14)].
14. D. Regan and K. Beverley, *Vision Res.* **18**, 415 (1978); *J. Opt. Soc. Am.* **70**, 1289 (1980); D. Regan, *Vision Res.* in press.
15. Priest and Cutting [figure 1 in (3)] correctly show that our display did not mimic a flat plane. It was not intended to, but rather to dissociate flow pattern focus and div **V**. It is not clear what Priest and Cutting mean by "normal optic flow" because the number of real-world flow patterns is as indefinitely large as the number of different environmental geometries. For that reason we made no attempt to mimic any particular environmental geometry, preferring to search for some general property of the human visual system relevant to a wide range of possible environmental geometries.
16. D. Regan, K. Beverley, M. Cynader, *Sci. Am.* **24**, 136 (December 1979); D. Regan and K. Beverley, *Science* **205**, 311 (1979).
17. Early reports that collicular units respond best to motion away from the center of gaze [M. Straschill and K. P. Hoffman, *Brain Res.* **13**, 274 (1969); P. Sterling and B. G. Wickelgren, *J. Neurophysiol.* **32**, 1 (1969)] have not been confirmed [N. Berman and M. Cynader, *J. Physiol. (London)* **245**, 261 (1975)], but the L.P. nucleus may be radially organized [J. P. Rauschecker, *Perception* **12**, A13 (1983)].
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19. If a movie taken from a camera mounted on an aircraft during landing is projected onto a screen, subjects can judge the point of aim (8, p. 130). This might seem to show that eye rotation can be disregarded. If the camera is fixed to the aircraft (even at some arbitrary angle), however, and if the aircraft is traveling in a straight line without pitch or yaw, then by gazing straight at the projection screen the viewer can automatically ensure that the focus of expansion coincides with the destination, thus reducing the problem to the simple nonrotating eye case.
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On the Mathematical Structure of the Visuotopic Mapping of Macaque Striate Cortex

Tootell *et al.* (1) have published the results of a 2-deoxy-D-glucose (2DG) study of primate striate cortex topographic mapping. In this study, a set of logarithmically spaced rings and equiangular rays was used as a visual stimulus. The rationale for using this particular pattern is that the logarithmic rings and equiangular rays project to an approximately rectangular pattern at the level of the striate cortex (2, 3). I have used a pattern of this kind to study human striate cortex topography [using 2DG and positron emission tomography (PETT)] (4). Since the data of Tootell *et al.* (1) are of much higher spatial resolution than the analogous human PETT data, it is now possible, for the first time, to compare theoretical to experimental cortical map functions directly (Fig. 1). It is thus possible to point out a misinterpretation of the theoretical model of cortical topography (2) cited by Tootell *et al.* (1) in the analysis of their data.

Tootell *et al.* (1) found different values of cortical magnification along the vertical and horizontal meridians (the vertical meridian is longer than the horizontal). They assumed that the cortical map function that I have published (2, 3) predicts that the magnification factor should be the same along all meridians. On the contrary, this model predicts differences in cortical magnification at