

spatial lag of the strobed segments, which increases with the angular velocity of the line (b in the figure).

How might this effect be explained? I believe the answer lies in the predictability of the continuous segment and the unpredictability of the strobed segments resulting in a differential processing delay. The continuous segment is illuminated for a long enough time for it to be represented cortically. Furthermore, as the angular velocity of this segment is constant, there is information at time t as to where the segment will be at $t + \tau$ ms. It is proposed that in order to overcome the transmission delay, an 'early' visual mechanism corrects the spatial lag by extrapolating the moving object's instantaneous location. Thus, the perceived location, which incorporates the input from this mechanism, is closer to the object's physical location than might be expected from neurophysiological estimates¹ of the delay. The perception of the strobed segments is also contingent on the retinal signal triggering a cortical neural representation, but owing to the unpredictability of the stroboscopic event, the visual system cannot overcome the transmission delay in this case.

If an equal delay for both the moving and the strobed segments is assumed, one could account for the present 'flash-lag' effect in terms of visual persistence of the strobed segments for about 100 ms after their off-set, and the 'deblurring' of the continuous segment by the motion system^{3,4}. But according to this account, the strobed segments should appear aligned with the continuous segment at the instant of strobe onset. While observers report that the large visible misalignment (of up to 25°) is already present at the instant of strobe onset.

The present findings suggest that in the case of moving objects the visual system overcomes at least some of the transmission latency through extrapolation. Future experiments will reveal the discrepancy, if any, between the extrapolated and physical locations of moving objects. In this context, it is interesting to note that the computed average (angular deviation ÷ angular velocity) of the time delay of the strobed segments is approximately 82 ms, which is not too different from typical estimates of about 100 ms. Thus, the error between the physical location and the extrapolated location may not be very large.

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Ant sex ratios

SIR — Sundström¹ reported that colonies of the ant *Formica truncorum* on islands in southern Finland produce sexual broods with a bimodal distribution of sex ratios. Colonies headed by queens that Sundström inferred had mated multiply (based on intra-colony allele frequencies at 3–4 allozyme loci) rear significantly more males than females, indeed sometimes only males, whereas colonies headed by putatively monogamous queens do the reverse. Sundström argued that sex specializations result from workers first assessing their relatednesses to male versus female brood, relative to average worker-relatedness asymmetries in other colonies of their population, and then adjusting the sex ratio in their own reproductive interests (specializing on females when relative relatedness asymmetry is high, and on males when it is low).

The hypothesis of genetic-relatedness asymmetry^{2,3} requires that worker ants: (1) assess the total number of different males with whom their mother mated (which conceivably exceeds the number of patrines active during any one worker's lifetime) relative to the mean frequency of polyandry in their local population; and (2) recognize the sex of eggs or larvae, and behaviourally bias their colony's sex ratio, for example via neglect or siblicide; but (3) do not distinguish full sisters from half sisters among eggs or larvae (because discriminative nepotism would always result in female-biased broods). Because Sundström^{1,4} provided no evidence that *F. truncorum* workers are altering their queen's preferred sex ratio, it is not possible to judge the plausibility of the mechanisms underlying her interpretation.

An alternative hypothesis to explain bimodal sex ratios in ants² is that queens themselves sometimes lay predominantly male (haploid) or female (diploid) eggs, with the workers caring for all the brood. This hypothesis implies synonymy of queen and worker sex-ratio preferences, a possibility that has apparently not been investigated for any species. A direct test would be to compare primary versus secondary sex ratios — that is, samples of reproductive-destined eggs versus alates, controlling for workers' elimination of inviable eggs.

Queens and workers would benefit from manipulating the sex ratio in that outbreeding would be optimized. Colonies of social insects are frequent targets of debilitating parasites and pathogens^{5,6}, and dispersal from infected areas and genetic variability among progeny might thwart such biotic enemies. Multiple queens, multiple mating by queens and outbreeding all enhance genetic variability^{5,6}. Male-biased broods promote both extreme dispersal and out-

breeding, especially since male ants are typically much smaller and lighter than reproductive females.

We suggest that queens adjust their mating frequency and, in collaboration with workers, their progeny sex ratio in response to the local severity of parasites and pathogens. If this hypothesis were correct for Finnish *F. truncorum*, queens from islands where diseases are prevalent, where there are local pockets of disease within islands, or where there are survivors from individual diseased colonies, would mate multiply and produce male-biased, dispersive broods. Queens from relatively disease-free localities (for example where the success of daughter colonies is high), in contrast, would mate monogamously and produce female-biased, philopatric broods. This suggestion is an alternative explanation for Sundström's¹ fascinating results.

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SUNDSTRÖM REPLIES — Sherman and Shellman-Reeve offer constructive suggestions for further investigation, together with some new ideas on causes of sex ratio specialization in ants. I agree that queens may gain at least partial control by adjusting the primary sex ratio, and this is clearly the next question to address. In colonies headed by a multiply mated queen, they propose that workers and queen mutually agree to produce a male-biased sex ratio. This is also fully consistent with worker control according to current sex ratio theory, because the optimal sex ratio for workers and queen converge in colonies headed by a multiply mated queen^{7,8}.

However, for the colonies headed by a singly mated queen, Sherman and Shellman-Reeve make some predictions which are not supported by the data. First, if females disperse less than males, as they suggest, local resource competition among females would ensue, with selection for male-biased population-level sex ratios⁹. This stands in contrast to my results, which demonstrate a female-biased population-level sex ratio. Moreover, under local resource competition only small colonies may be expected

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