other applications, as Crick readily admits, Crick's criticisms do not apply.

"Even if the brain makes no use of backprop, there is no reason why we should not use it as a mathematical tool," says Sejnowski. "Nature does not have calculus, but we use it to understand nature."

The goal of much neural net research is to understand complex human performance, such as how people learn to play the flute. "Even the simplest models are providing insights into how that learning occurs," says Sejnowski. "So even if back-prop has nothing to do with it in the brain, the fact that we can create models with similar performance means you can use it to understand psychology."

"This approach allows me to study aspects of the mind that can't be touched from the neuroscientist's approach," agrees David E. Rumelhart of Stanford University, a mathematical psychologist and one of the leading modelers in the field. The danger in that approach, says Crick, is that without a few reality checks in the brain, such investigations may yield exquisite theories that have no correlation with reality, like phlogiston, the early explanation of fire.

Rumelhart concedes that some neural net researchers may not be paying enough attention to neuroscience in developing their models. "Crick is nudging people like me, saying you can do better on the brain end. He is probably right."

Crick's closing plea is, "Why not look inside the brain, both to get new ideas and test existing ones?" Such work is getting under way, if belatedly. The delay was not just because modelers and neuroscientists have been wearing blinders, says Sejnowski, but because the tools simply did not exist to test some of these ideas experimentally. Sejnowski is setting up a computational neurobiology lab at the Salk Institute with just that goal: to test some of the theoretical predictions in the nervous system.

History gives some grounds for hope. In 1949 Donald Hebb predicted a synaptic mechanism that would explain learning and memory. Neuroscientists have recently discovered a mechanism—the NMDA receptor—that behaves just that way. In his article, Crick calls on neural net researchers to develop models that embody the principle of the NMDA receptor.

Sejnowski and his colleagues have just uncovered another synaptic mechanism, known as long-term depression, that also seems to be involved in memory. "These are two examples of abstract ideas being tested in parts of the brain. They are harbingers of the progress that can be made once models and the experimental work come together." **LESLIE ROBERTS** **Inbreeding Costs Swamp Benefits**

Inbreeding can have a variety of important genetic consequences, good and bad. For instance, a female that mates with a relative benefits because the offspring have additional copies of her genes (those she shares with the relative): and the closer the relationship, the greater the potential genetic benefit. However, the closest possible mating pairs—parent-offspring and sibling-sibling—are apparently rather rare in nature, an observation that is usually explained by the disadvantages of close matings. These disadvantages, collectively known as inbreeding depression, include reduced viability and fecundity of offspring. Biologists are therefore very interested in the effects of inbreeding, for genetic theory and in the practical consequences of maintaining captive populations. Until recently, however, there were very few good data on the effects of inbreeding in populations, but a study by Katherine Ralls and Jonathan Ballou of the National Zoological Park, Washington, D.C., and Alan Templeton of Washington University has now provided some.

Two striking observations resulted from a survey of juvenile survival from parentoffspring and sibling-sibling matings in 40 captive populations belonging to 38 species. First, in all but four of the populations there was some reduction in juvenile survival. Second, the variation in reduced survival was great, ranging from just a few percent to 100% in one case. The average reduction was 33%. This latter figure just happens to match the potential genetic advantage of parent-offspring and siblingsibling matings, and so it might seem that the costs and benefits of such matings are finely balanced.

Ralls and her colleagues note, however, that the figure for costs is probably too low. For instance, it measures only juvenile viability, but does not include increased embryonic death or survival of juveniles to maturity; nor does it take into account reduced fecundity or increased susceptibility to disease, both of which are known consequences of inbreeding. These extra costs would swamp the 33% genetic advantages of close inbreeding, and thus account for its virtual absence in natural populations.

The disadvantages of inbreeding are assumed to result from the expression of deleterious recessive genes that occur in double doses. (In large, outbreeding populations these genes will usually occur only in single doses, and thus be masked.) If there is considerable variation among populations in the extent of such genes, then this could account for some of the variation in the severity of inbreeding depression observed by Ralls and her colleagues. A reduction in incidence of deleterious recessive genes can occur, for instance, if a population successfully goes through a bottleneck: the population crashes to a few individuals, genetic variance is greatly reduced, and deleterious recessives might be quickly lost through high mortality. There is considerable debate about the genetic effects of population bottlenecks, but it is clear that many populations would become extinct under such circumstances, an issue of particular interest to conservationists who must maintain small populations, either in natural habitats or in captivity.

ADDITIONAL READING

K. Ralls et al., "Estimates of the cost of inbreeding in mammals," Conserv. Biol. 2, 185 (1988).



No inbreeding here. Animals in natural populations avoid close genetic matings.