14 NIKOLAAS TINBERGEN: THE STUDY OF INSTINCT

Experimental psychology around 1950 was dominated by behaviorism. Behaviorist researchers emphasized the study of behavior under laboratory conditions, with the study of *learning* a major emphasis. However, biologists and naturalists continued to investigate behavior in its natural setting, emphasizing observation before experiment. Watching what animals did in the natural world, scientists identified patterns of action that characterized the members of a species, and the patterns of stimulation that triggered these actions.

A direct challenge to behaviorist orthodoxy was the publication in 1951 of *The Study of Instinct*, by Nikolaas Tinbergen—a book that summarized much of this work. Even the title was a challenge.

Behaviorists had thrown the concept of *instinct* out the window. There were several reasons for this. First was the belief that learning could account for all the complexity of behavior. Second, instincts were unobservable, and sounded like mysterious driving forces for which science had no need. Third, it was objected that the concept was circular. Why does an animal do this or that? It is instinctive. How do we know it is instinctive? Because the animal does it. Not very helpful.

Meanwhile, however, observations of behavior in its natural setting were being made by scientists, most of them biologists and many of them European, known as *ethologists*. Their observations convinced them that there are complex actions that are not learned. These action patterns—or the interconnections within the nervous system that control them—have evolved in a given species, just as its fur or feathers have evolved. We might as well call them *instinctive*. This is not intended to explain them—no modern ethologist will ever say that an animal does this or that *because* it is instinctive to do so—but only to distinguish them from complex actions that do result from learning.

The work of ethologists was brought to the attention of English-speaking psychologists during the 1940s and 1950s, and a landmark event during this period was the publication of Tinbergen's *The Study of Instinct*.

Tinbergen (1907–88) was born in The Hague, Netherlands. As a young boy, he spent much of his time just observing the abundant wildlife of Holland (and the stickleback fish that lived in an aquarium in his backyard) rather than at his studies. He did decide to study biology at Leiden University, after which he organized a course in animal behavior for undergraduates. It was in connection with this that he made his famous observations of courtship and mating in the stickleback fish. Tinbergen later joined the faculty at Oxford University, where he published many books on ethology—the study of behavior in its natural environment.

Tinbergen's curiosity about nature led him to take observations on a wide variety of species, from digger wasps to herring gulls (Tinbergen, 1961). Of necessity, we will focus on his observations dealing with the reproductive behavior of a fish, the three-spined stickleback *Gasterosteus aculeatus*, a fish about three inches long as an adult and found in fresh- or saltwater shoals.

In the spring, the male three-spined stickleback is brought into reproductive condition by hormonal changes. These have effects on its behavior, and also on its appearance: they give the male fish a characteristic red-colored underbelly (more on this later). The male fish builds a tube-shaped nest under the water and then patrols the territory around the nest entrance.

What happens when another stickleback approaches? It depends. If another fish with a red underbelly approaches, the male treats it as a rival male and attacks it. The attack is quite constant in its form. It begins with a head-down posture and spread fins—the threat display (figure 14.1). When so threatened, the intruder usually gives up and swims away. If he does not, a full-blown biting fight is likely.

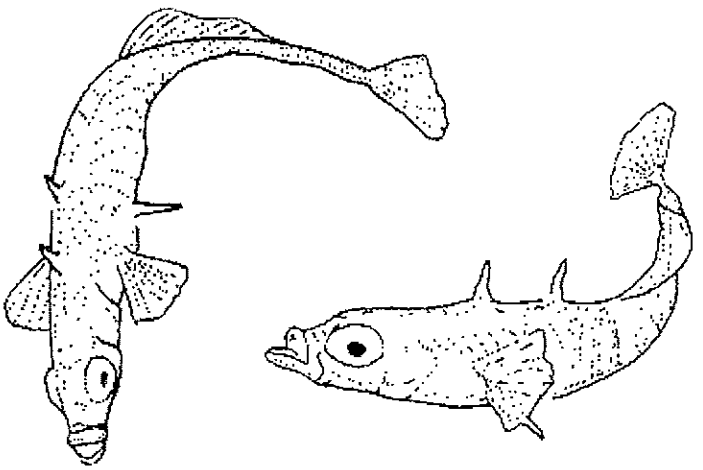
This threat pattern is so characteristic of the species that early ethologists referred to it (and other stereotyped actions like it in many species) as a *fixed action pattern*. The *fixed* was later dropped, because the actions turned out not to be as fixed as all that, but the term *action pattern* remains a handy way of referring to species-typical patterns of movement and posture.

Having identified this pattern, Tinbergen and his colleagues turned from observations to experiments. They made models of male sticklebacks, omitting or adding different features for different models. In this way, they were able to show that the male's threat display is elicited, or *released*, by a specific characteristic of the intruder—the red underbelly. Even very crude models, if lowered into the water near the male, will be threatened if their undersides are red, but only then. This one specific aspect of a male fish's appearance is a *releasing stimulus* for attack.

If it is a female fish that comes along, then the homeowner male behaves quite differently. Instead of attacking, he courts. Here the action pattern is a peculiar back-and-forth swimming pattern, a zigzagging dance. Again, experiments with models can identify the releasing stimulus for this action pattern as well, It is the swollen underbelly of the female fish heavy with eggs. Even crude models with swollen undersides will be courted with the zigzag dance; good models without them will not be.

If mating occurs, it will be with a meticulously choreographed series of releasing stimuli and action patterns in response to them. The male leads the female to the nest. If she follows, he points to the nest entrance with his nose. If she swims into the nest, he nuzzles her, causing her to release her clutch of eggs. He then swims after her, depositing sperm to fertilize the eggs (fertilization takes place outside the body in this species). Experiments with models have shown that every stage of the

Figure 14.1.
Threat display by a male stickleback fish. A male stickleback near its nest (left) makes the head-downward "threat display" at an intruding male (right).



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sequence is an instinctive pattern of responses—an action pattern—triggered by certain releasing stimuli provided by the partner's appearance and/or behavior.

Finally, experiments show that the actions, and the coupling of these to releasing stimuli, are unlearned. Male sticklebacks that have been raised in isolation, never having seen another fish, nonetheless threaten or court in the normal way when the appropriate releasing stimuli are encountered for the first time. This does *not* mean that learning cannot modify these actions—a frequent source of confusion. It does mean that no specific learning experiences were required to put them there.

One more important concept came from this research. The actions of an animal are produced not just by the external stimulus situation, but also by the internal organization of a species' behavior. Only thus can we understand why a red underbelly releases attack behavior in one species of fish but not in another—and why, for that matter, it will release attack only if the internal hormonal state of the animal is right. Internal as well as external influences must be identified and understood. Watson's original program—given the stimulus, to predict the response—will not work. We need to know more than the stimulus.

All this is just one of the many analyses of instinctive behavior reported by ethologists—most of them in relatively simple animals such as fishes, birds, or insects (for it makes sense to begin with simpler cases). The impact of these ideas was severalfold. First, they did resurrect the concept of instinct from the behaviorist tomb. Second, they affected the way we study behavior. And third, they affected the way we think about it.

Most experimental psychologists studied behavior in tightly controlled environments, as Pavlov (chapter 20) and Skinner (chapter 23) did. This has the advantage, first, that the tighter control makes it easier to see the effects of experimental

manipulations, and second, that it allows us to see interesting effects of conditions that might never occur in nature. (Will a male stickleback learn to make a lever-pressing response, or equivalent, in order to gain access to a female? It will [Sevenster, 1968].) This would not have been discovered in the fish's natural environment, where there are no levers (or equivalents) that have that consequence.

On the other hand, important aspects of a species' behavior might never be seen in a controlled setting, if the experimenters did not happen to impose the right conditions. Suppose experimenters placed a male stickleback in a controlled environment and imposed various changes in conditions one at a time. They might never see the threat display. Why? Because they might never happen to present an object with the red underbelly required to elicit the action. Even if they did, they would not know what to make of the reactions they saw if they did not already know that this is *how* a male stickleback threatens an intruder. In short, there is much to be said for looking carefully at what happens in nature before experimental variations are imposed.

The arguments about these matters have largely died down. It is clear that the two approaches to research are not antagonistic but complementary. In recent years, scientists from the two traditions have cooperated in fruitful ways (see, e.g., Rozin & Schull, 1988).

Finally, the terms and concepts of ethology led us to ask whether they might apply to more complex creatures—monkeys, perhaps (chapter 13), or even humans. Notions like action patterns, releasing stimuli, and behavioral hierarchies have been useful concepts in thinking about human behavior. After all, our bodies are products of evolution, and this includes the fine-grain wiring of our brains. Why should we not, like the stickleback, have evolved certain patterns of action and their connection to appropriate stimuli?

Here is just one example. In humans, certain facial expressions have some of the properties of action patterns. Facial expressions for certain emotions, like anger, sadness, or happiness, are the same in cultures that have been separated from each other by many thousands of years. In that sense they are characteristic of the human species, just as the stickleback's attack and courtship patterns are characteristic of that species. And they are, at least initially, unlearned (though learning can modify them). The typical facial expressions of emotion are displayed by people who could not have learned them in any obvious way—for example, children born both blind and deaf. It appears that indeed we are not Lockean blank slates! (For discussion, see Pinker, 2002.)

Questions about the evolution of behavior, including human behavior, have led to the rapidly developing field of *evolutionary psychology*. It is a direct descendant of the work of the early ethologists.

For his scientific and theoretical work, Tinbergen was awarded the Nobel Prize in 1973. Two other ethologists, Konrad Lorenz and Karl von Frisch, were also awarded the prize in that year. These three were the first behavioral scientists to win that prestigious award.

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