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Innovation in the Study of Social Learning in Animals: Developmental and Biological Perspectives

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It is somewhat surprising that I should have been invited to contribute a chapter to a volume concerned with methodological innovations and their use in resolution of theoretical issues in behavioral development. I have always taken a perverse pride in the fact that, despite a near total lack of technical competencies, I have been able to make empirical contributions to a field as methodologically sophisticated as developmental psychobiology has become. I can't program a computer, extirpate a gland, wire the simplest of electrical circuits, implant an electrode, assay a hormone, stain a tissue sample, or carry out any of the myriad other technical chores that today's graduate student can perform with ease. Consequently, if one defines methodological innovation in a narrow sense, this chapter is complete in a single paragraph, even in a single sentence. My methodological contribution to developmental psychobiology has been nil.

Yet it seems to me (and, I suspect, to the editors of the present volume, since they asked me to contribute to it) that methodological innovations can be conceptual as well as material. And conceptual innovations are often as important as methodological ones in advancing our capacity to study developmental problems of theoretical importance.

A scientist's most important tools are the intellectual frameworks or perspectives within which he or she works. Changes in perspective can lead to improvements in methodology as useful as those that accompany increased ability either to measure dependent variables or control the application of independent variables. Though novel perspectives on a problem are less concrete than innovations in technique, novel perspectives may lead directly to improvements in method and are, therefore, worth considering in a volume such as the present one.

Animal social learning, the research area in which I have been working for more than 20 years, is a field with a long and complex history (Galef, 1988a, 1988b). It is an

area that might be characterized, not entirely unfairly, as having produced remarkably little progress in advancing understanding of behavior, despite more than a century of experimentation and discussion.

In the late 1960s, when I first became interested in problems in social learning, the area was a subspecialty of animal learning. Most experimental work in the area—at least most such work conducted by psychologists—was concerned with demonstrating, in standard laboratory apparatus (Skinner box or T-maze), the existence of general behavioral capacities in animals (learning by imitation, social facilitation, or the use of conspecifics as discriminative stimuli) that might result in social learning. For example, in a well-known study, typical of psychological research in social learning during the 1960s, Chesler (1969) demonstrated that kittens that had observed their respective mothers press a lever to obtain food subsequently acquired the lever-press response more rapidly than did kittens that had observed strange female cats press a lever for food. In Chesler's view, this finding demonstrated that kittens could learn by imitation.

Zajonc (1969) was making much of the observations that (1) two human cyclists in competition rode faster than either did when alone (Triplett, 1897) and (2) that ants each dug more vigorously when in pairs than when in isolation (Chen, 1937). Such observations were interpreted as exemplifying social facilitation, the energizing of dominant behaviors by the presence of others.

Russell Church (1957a, 1957b), Richard Solomon (Solomon & Coles, 1954), and Vaughn Stimbert (1970a, 1970b) had conducted (or were conducting) studies demonstrating that the activities of one rat could serve as discriminative stimuli for another rat, indicating to the latter individual those occasions when a particular response would be reinforced. For example, Church (1957a) had shown that a rat could be taught to turn left or right in a T-maze by reinforcing the animal whenever it entered the same arm of the maze that had been entered by a trained, leader rat.

During the 1950s and 1960s, when general process theories of learning dominated experimental, animal psychology, advance in the study of social learning seemed to require identification of social learning analogs of such individual learning processes as operant and classical conditioning. If one could elucidate critical features of paradigmatic cases of social learning (e.g., learning by imitation, matched dependent behavior, social facilitation), then social learning could be studied in the same way and at the same level of abstraction as individual learning had been studied for decades (Jenkins, 1984).

The problem I had with such an approach was that the categories of social learning available to explain relevant phenomena seemed both arbitrary and restrictive. For example, a cyclist might ride faster when on the track with a competitor than when alone because of an increase in aerodynamic efficiency gained by using the competitor as a windbreak. Alternatively, a cyclist might ride faster in the former situation than in the latter because of increased effort in a competitive situation. If ants do dig more efficiently when in pairs than when alone, it is probably because of some form of pheromonal communication between them. Nothing appeared to me to be gained by studying an abstraction called *coaction* or *social facilitation*. The proposed explanatory terms seemed to interfere with, rather than encourage, analyses of the effects of social interaction on behavior. Furthermore, even if the existence of

social facilitation or imitation learning could be convincingly demonstrated, why should one believe that already-identified types of social learning are more important than other, as-yet-undiscovered processes?

I would attribute much of whatever progress my students and I have made in studying social learning to a recasting of the conceptual framework within which we have worked. We chose to treat social learning as an aspect of behavioral development rather than as a type of animal learning. In consequence, instead of asking whether animals have the ability to learn by imitation, to exhibit social facilitation, or to use conspecifics as discriminative stimuli, we asked whether social interactions might be important in development of adaptive patterns of behavior.

Changing the nature of the question opened up new realms of inquiry and provided new sources of both data and hypotheses. First, if one is interested in the role of social learning in the development of adaptive behavioral repertoires, the behaviors one might investigate extend far beyond the Skinner box and T-maze; foraging, predation, homing, predator avoidance, tool use, nest building—the list of behaviors of potential interest seems endless.

Second, one could make use of the field literature to identify promising behaviors to investigate. Instances in which many members of one population of a species exhibit a pattern of behavior absent in other populations of that species suggest that social influence might play a role in the development of the idiosyncratic behaviors (traditions) observed: Song dialect learning (Marler & Tamura, 1964), sweet potato washing (Kawamura, 1959), milk bottle opening (Fisher & Hinde, 1949), as well as myriad other less-well-known instances of animal tradition (Galef, 1976), are defined as phenomena that, if studied in the laboratory, might reveal behavioral processes involved in social learning.

Third, because we would be attempting to determine the causes of differences in behavior among populations, there would be no bias toward demonstrating that one process rather than another was involved in the development of the differences under investigation. Instead of undertaking demonstration experiments to prove, for example, that animals can learn by imitation, or that social facilitation is a general phenomenon, we needed only to determine the necessary and sufficient conditions for the emergence of behaviors observed in natural circumstances. Whatever the behavioral process involved in the development of behavioral differences between populations, whether social or nonsocial, new or familiar, such an approach promised unbiased, logically satisfying analyses.

Last, and perhaps most important, approaching the study of social learning as a developmental process permitted integration of psychological and biological approaches to the study of behavior. Tinbergen (1963) had indicated that four different questions could be asked about any behavior: What is its cause, function, development, and phylogeny? Looking at social learning as a factor in the development of behaviors that had functions outside the laboratory allowed us to examine behaviors of interest from both psychological and biological perspectives.

I should make clear that I can claim little originality in adopting the general perspective outlined above. I had the good fortune to complete my dissertation research under the supervision of Paul Rozin. He communicated most effectively the utility of combining biological, developmental, and psychological approaches to the study of behavior. Furthermore, by 1970, the impact of ethology was steadily growing

and the dominance of the general process approach to the study of animal learning was in decline. Analyses of, among other things, imprinting in precocial birds (Hess, 1973) and song learning in passerines (Marler & Tamura, 1964), as well as texts such as Hinde's (1966) *Animal Behaviour*, had demonstrated the heuristic value of considering learning as a factor in the development of adaptive behavioral repertoires in animals. Many others (e.g., Johnston, 1981; Kamil & Yoerg, 1982; Shettleworth, 1984) came independently to the conclusion that consideration of animal learning within a biological framework, as a developmental process, might be a fruitful way to approach the study of learning by animals.

I cannot even claim originality in application of developmental and biological approaches to the study of social influences on behavior; Harlow's (Harlow & Harlow, 1965) studies of reproductive behavior in rhesus monkeys and Marler's (Marler & Tamura, 1964) investigations into bird-song learning in white-crowned sparrows are clear antecedents. All I can claim is the good sense to follow illuminating precedent.

INVESTIGATIONS OF SOCIAL LEARNING IN MAMMALS

It is easy enough to say that investigation of necessary and sufficient conditions for the development of traditional patterns of behavior observed in field settings might provide a fruitful approach to the study of animal social learning. It is a different and somewhat more difficult matter to design such investigations in a satisfying fashion. There are problems both in finding phenomena susceptible to investigation in controlled settings and in establishing reasonable laboratory analogs of traditions observed in the outside world. All this is especially true if, as I am, one is interested in mammalian behavior.

It is an unhappy fact that there are even today no mammals that are good subjects for both laboratory and field work, at least not if one is working on a modest budget. Outside the laboratory, rodents, such as rats, mice, gerbils, and hamsters, so admirably preadapted to laboratory existence, are either shy, nocturnal and subterranean, or indigenous to distant lands. Those mammals easily observed in the wild are too expensive for most researchers to acquire and maintain in captivity in numbers adequate for analytic research. Compromises have to be made. My own choice has been to work with Norway rats, members of that much-maligned, near-perfect species for behavioral research in the laboratory. The cost has been a need to depend, perhaps too heavily, on fragmentary, often anecdotal, field reports and the face validity of laboratory analogs of events presumed to occur in nature.

It is sometimes relatively easy to create a compelling analog of naturally occurring events. More frequently one must be satisfied with the knowledge that, in spite of inadequacies, one has done one's best to capture important features of the natural world while maintaining enough control over a situation to permit experiments to proceed. The important thing is to keep clearly in mind that the goal of a study is to cast light on processes that, in natural circumstances, lead to development of behaviors of interest. One hopes that even a dim light falling on an intriguing object is of more value than greater illumination of less interesting things.

In the present section, I briefly outline the methods and results of three research programs conducted in my laboratory, each concerned with the role of social learning in the development of behavior. All are, I believe, examples of the utility of studying

social learning within a biological framework, as a problem in behavioral development. In each case, my strategy was similar: Begin with field observation of a possible case of animal tradition. Bring the phenomenon into the laboratory. Attempt to determine the ways in which social interaction influences the course of development of the behavior in question.

Case 1: Following Adults to Food

Some years ago, Fritz Steiniger, an ecologist, was working for the German government as a rodent control officer. His job was to exterminate populations of wild Norway rats by poisoning them. In the course of his work, Steiniger discovered that if he used a poison bait in an area for an extended period of time, despite initial success, with the rats eating lots of poison and dying in large numbers, later acceptance of the bait was very poor. Steiniger (1950) observed that young born to those rats that had, by chance, survived their initial ingestion of poison rejected the poison bait without ever even sampling it. These offspring of survivors fed exclusively on safe diets available in the territories of their respective colonies. Steiniger attributed such "traditional" poison avoidance by the young to the effect of urine and feces deposited on the poison bait by those surviving adults that had learned to avoid it.

My coworker, Mertice Clark, and I were fortunate in that the phenomenon is robust and readily observable in captive wild rats living in the laboratory in small (1- by 2-m) enclosures (Galef & Clark, 1971b). By introducing nonlethal but nauseating concentrations of poison into one of two foods (Diets A and B) presented for 3 hours a day to our wild rat subjects, we could easily train them to avoid eating the poisoned food. Soon the adults would not eat the poisoned food even if offered uncontaminated samples of it. Next, we had to wait till the adults in a colony produced a litter and the litter grew to weaning age. Finally, we could observe the pattern of diet selection exhibited by weanlings born to colonies trained to eat only Diet A or only Diet B.

As Steiniger would have predicted, as long as the young were left in contact with adults, those young wild rats raised by colonies of adult wild rats poisoned when eating Diet A ate only Diet B; those raised by colonies poisoned when eating Diet B ate only Diet A. Both groups of young rats continued for a week or more after removal from contact with their parent colony to prefer the food the parent colony had eaten.

Steiniger (1950) had proposed that urine and feces deposited by adults in or near a food dissuaded their young from eating that food. However, when we conducted an experiment in which we offered young rats samples of Diets A and B uncontaminated by adult droppings, the young continued to eat only the diet that the adults of their colony were eating (Galef & Clark, 1971b). Furthermore, we found that rat pups reared by adults fed only Diet B, when offered a choice between Diets A and B, were just as biased in their preference for Diet B as were rat pups reared by adults that had learned to avoid Diet A and eat only Diet B. Not only were pups not avoiding a diet because the adults had marked it, the pups were not even learning to avoid the diet the adults of their colony were avoiding. Instead, pups were learning to eat the food the adults of their colony were eating.

Further studies revealed that young wild rats moving from nest site to feeding site

were strongly biased to approach adults or sibs and to begin eating in their immediate vicinity (Galef & Clark, 1971a). The simple physical presence of a conspecific at one feeding site rather than another biased the young to eat the food located there.

Wild Norway rats are known to exhibit great hesitancy to eat any food they have not previously eaten (Barnett, 1958; Galef, 1970). In consequence, biasing the young to start feeding on one diet greatly reduces the probability they will eat available alternatives.

In our experiments, young rats only gave the appearance of having learned to avoid the diet that the adults of their colony had learned to avoid. In fact, as a consequence of a tendency to affiliate with adults, pups had eaten and had become familiar with the food that the adults of their colony were eating. As a result of a hesitancy to eat unfamiliar foods, the pups were ignoring available alternative foods.

Shortly after I completed these studies, I was describing the results to a colleague at a conference. She responded, "So, baby rates follow adult rats. What's new?"—a remark I felt completely missed the point. What was new was that we could now describe in detail behavioral processes sufficient to support the development of an adaptive, traditional pattern of poison avoidance in rats. It is true that nothing like imitation may have been involved, but that matters only if you are trying to demonstrate the existence of imitation learning, not if you are interested in the role of social influence in the development of animal behavior. We had been able to show that development of an apparently complex tradition of poison avoidance rested on humble foundations. The tendency of young rats to approach adults could function to produce poison avoidance in the laboratory and possibly in the field.

Case 2: Diving for Food

In the early 1970s, a group of researchers working at the University of Parma reported that many members of some colonies of wild rats living along the banks of the Po River in northern Italy dove for and fed on freshwater clams inhabiting the river bottom. No members of nearby colonies, with equal access to mollusks within their home ranges, fed on mollusks (Gandolfi & Parisi, 1972, 1973; Parisi & Gandolfi, 1974).

These observations were interpreted as indicating that predation on submerged prey spreads through a wild rat colony as the result of naive rats observing and imitating their diving fellows. If discovery of mollusks on the riverbed by colony members is a rare event and if naive colony members learn to dive as the result of observing diving individuals, then one would expect the observed bimodality in frequency of individuals diving in various colonies. The central question, of course, is what explains the occurrence of diving in some populations of rats but not in others. Is social learning actually involved?

Once again, my coworkers and I brought the phenomenon into the laboratory in an attempt to determine whether a traditional pattern of behavior, observed in a free-living rat population, might develop as the result of social learning of some kind. Because we lacked access to either freshwater clams or the Po River we had to exercise our imaginations a bit in constructing a laboratory analog of the situation in Italy. We studied development of the behavior of diving for plastic-film-wrapped chocolates in

20-gallon aquaria (Galef, 1980). Despite possible inadequacies in our attempt to capture the real world in microcosm, I think we learned some interesting things about the development of diving behavior in rat populations.

First, we were unable to induce naive rats to dive in 15 cm of water for chocolates by letting them interact for a month with trained, diver rats recovering chocolates from beneath the water's surface. Neither adult nor juvenile, wild nor domesticated rats, that had interacted freely with a conspecific that dove 100 times or more learned to dive. Naive adult rats were extremely reluctant even to enter the water and swim. They never put their heads under the surface. About 20% of juveniles learned to dive whether they had interacted with a diving conspecific or not (Galef, 1980).

The question that arises following a negative outcome like that just described is what to do next. It is here that one's perspective on a problem is particularly important. If our goal had been to demonstrate the importance of imitation or of social facilitation in the acquisition of diving behavior in rats, we would have abandoned the project. However, because we were interested in the possible role of social influence in the development of adaptive behavioral repertoires, our negative result was almost as interesting as a positive one would have been. Regardless of the outcome of the first experiment, we still have a phenomenon to explain—Why do members of some colonies of rats and not of others dive for mollusks along the banks of the Po River?

Further studies (Galef, 1980) revealed that, if reared until 2 months of age with access to water, both wild and domesticated rats will spontaneously enter the water and swim before reaching maturity. We also found that swimming rats will, with high probability, spontaneously dive and retrieve food from beneath the water's surface. These were surprising findings in that they suggested that what needed to be explained was not the development of diving in some colonies along the Po but the absence of diving in other colonies found there. Results of additional studies suggested that although almost all rats reared with access to water will learn spontaneously both to swim as juveniles and to dive for food as adults, even animals trained to swim and dive for food would prefer not to engage in those activities. Both swimming and diving for food could be greatly inhibited by the presence of adequate rations ashore.

The results of our series of studies suggest a tentative solution to the problem posed by the tradition of diving exhibited by Po River rats. Differences among colonies in frequency of diving depended not on social learning but on differences in colony access to food on land. Although the relevant experiments have not, so far as I know, been performed, the results of our analysis suggest that delivering a load of food to the territory of a diving colony would end its diving. Removing food from the territory of a nondiving colony would induce colony members to start diving. What had initially appeared to be a developmental problem turned out to be a motivational one. Resolution of the issue depended on focus on the phenomenon rather than on attempts to demonstrate the action of particular processes (Galef, 1980).

Case 3: Information Centers in Rats

The field literature provides not only traditions to analyze but also hypotheses about the development of traditions that may prove worth investigating in controlled

settings. In 1970, Ward and Zahavi published a widely cited paper in which they argued that aggregation sites of birds or mammals might function as "information centres" where unsuccessful (or marginally successful) foragers could acquire useful information from their more successful fellows about where food could be found. Individuals that were having trouble finding food might identify more successful individuals at a central site and then follow them to food. Thus, social interaction in aggregations might serve as a substrate for development of adaptive patterns of foraging.

For my purposes, the notion of an information center, of a location distant from a resource where animals might acquire information about the resource, was more interesting than the particular method of information transmission Ward and Zahavi had proposed. I had always assumed, from lack of imagination more than anything else, that mammals in general and rats in particular would be able to communicate about a resource only in the presence of that resource. Von Frisch's (1954) classic studies of dance-language communication in honeybees had clearly shown that it was possible for a successful forager bee to direct hive mates to the food source it was exploiting. Wenner (Wenner, Wells, & Johnson, 1969) had shown that odors clinging to the body of successful forager bees could serve the same function. Although I was aware of such findings, bees seemed so behaviorally specialized for communication about resource availability that it was not obvious to me that extrapolation to generalists, such as Norway rats, was warranted.

In a bit of serendipitous good fortune, Barbara Strupp, in 1980 a graduate student with David Levitsky at Cornell, came to visit my laboratory in Hamilton and told me about her thesis research on communication of diet preference among rats. Strupp had shown that a naive rat, living in a cage adjacent to a conspecific and offered a choice between two diets, one of which was the diet its neighbor was eating, would prefer its neighbor's diet (Strupp & Levitsky, 1984). The rats were communicating with one another concerning a resource while that resource was present in their shared environment. Strupp was generous in providing details of her procedures. She and Levitsky were not interested in pursuing the line of research that both interested me and seemed possible using variants of their procedure. There was lots to do.

Steven Wigmore, a graduate student in my laboratory, and I proceeded to ask whether rats could communicate information to one another concerning diets they had eaten at distant times and places. In our basic experiment (Galef & Wigmore, 1983), a demonstrator rat was fed a diet and, after finishing eating, the animal was allowed to interact briefly with a naive observer rat. Then the observer was offered a choice between the diet its demonstrator had eaten and a roughly equipalatable alternative. The results of such studies surpassed our wildest hopes. Following interaction with their respective demonstrators, observers exhibited greatly enhanced preference for whatever diet their demonstrators had eaten. The effects of demonstrators' diets on observers' subsequent diet preferences lasted for days. We now know that they can last for weeks (Galef, 1989).

Within a developmental, functionalist perspective we now had a whole series of questions to answer: How is information communicated from demonstrator to observer? How does the communicated information affect diet selection by observers? What are the implications of the ability of experienced individuals to affect the diet

preference of naive conspecifics for our understanding of the development of adaptive patterns of dietary selection? How might such a capacity function to enhance foraging efficiency and utilization of resources in natural environments?

Five years of research with a number of collaborators and students is beginning to provide some insight into the ways in which rats communicate about distant foods, insights that I believe may have important implications for a more general understanding of behavioral development in vertebrates. Below, I briefly summarize our findings (see Galef, 1986a, 1988c, for more detailed accounts) and discuss their implications for the study of behavioral development.

First, all our data point to the conclusion that olfactory cues passing from a demonstrator rat to an observer rat carry information which allows an observer to identify the diet eaten by its demonstrator (Galef & Wigmore, 1983). Second, we have found that such diet-identifying, olfactory cues can arise both from the digestive tracts of demonstrators and from traces of food clinging to their fur and vibrissae (Galef & Stein, 1985). Thus, we have identified both the medium of communication from demonstrator to observer (olfaction) and the sources of information that allows observers to know what food their respective demonstrators have been eating.

The question of why observers prefer their respective demonstrators' diets is less fully answered. We have shown repeatedly that simple exposure of an observer to a diet is not effective in increasing an observer's preference for that diet, while exposure of an observer to the same diet in the presence of a demonstrator does increase an observer's preference for the diet. The question, of course, is why this is so. Our data suggest that, in addition to diet-identifying, olfactory cues, demonstrator rats emit contextual, olfactory cues that, when experienced by observers at the same time as diet-identifying cues, result in profound alterations in observers' diet preferences (Galef & Stein, 1985). I am currently working in collaboration with Russell Mason and George Preti at the Monell Chemical Senses Center to try to identify chemically this elusive contextual determinant of diet preferences (Russ and George look after the chemistry, I worry about the behavior).

The role of information acquired from conspecifics in the development of adaptive patterns of diet selection by new recruits to a population has been of particular interest to me. Social influences on diet selection of the type described above, can be profound. Rats that have learned an aversion to a diet will abandon that aversion following interaction with conspecifics that have eaten that diet (Galef, 1985, 1986b). Rats will greatly increase their intake of unpalatable diets following interaction with fellows that have fed on it (Galef, 1986b). Aversions are formed less readily to those novel diets that conspecifics are eating than to other novel diets (Galef, 1986c). In sum, development of feeding repertoires by rats is not just the result of individual palatability preferences and individual learning about the postingestional consequences of various foods. Each rat can and will make use of the feeding behavior of others in developing its own patterns of diet selection.

Last, rats are able to integrate the information they acquire from conspecifics with individual learning about the distribution and value of resources. A rat that knows, as the result of its individual feeding history, where a number of different foods are sometimes to be found, but does not know which food is available on a particular day, will go directly to the appropriate feeding site after interacting with a

conspecific that has eaten one of the intermittently available foods (Galef, 1983; Galef & Wigmore, 1983). A rat will more readily follow a conspecific to food if that conspecific has eaten a food known by the follower to be safe than if the conspecific has eaten a food known by the follower to be toxic (Galef, Mischinger, & Malenfant, 1987). Taken together, our results suggest not only that naive rats can extract information from conspecifics as to the food those conspecifics have been eating, but also that such information can play an important role in the development of adaptive patterns of both diet selection and foraging-site exploitation.

Conclusions

There is every reason to believe that social interactions can provide stimuli that bias the development of a wide range of behaviors. Each member of a species need not learn for itself what foods to eat, what paths to take, what potential predators to avoid. A naive individual can "assume" that live conspecifics have successfully solved many of the problems posed by an area they share. By adopting the behavior of successful others, adequate behavioral repertoires can be developed without incurring risks that are an inevitable consequence of learning on one's own.

Consideration of social learning within a biological framework, as an aspect of behavioral development with adaptive consequences, has proven a fruitful perspective, attracting a growing number of students of social learning. Curio (Curio, Ernst, & Vieth, 1978) has examined the role of social learning in the development of predator avoidance and mobbing behavior in European blackbirds. Cook and Mineka (Cook, Mineka, Wolkenstein, & Laitsch, 1985) are studying the effects of social interaction in the acquisition of snake avoidance in rhesus monkeys. Lefebvre (Palametta & Lefebvre, 1985), Mason and Reiding (1982), and Terkel and Eisner (J. Terkel, personal communication, August 1986) are examining social effects on the development of adaptive patterns of feeding and foraging in, respectively, common pigeons, red-wing blackbirds, and roof rats. Baptista and Petrinovich (1984) and West and King (West, King, & Harrocks, 1983) have increased understanding of the role of social interaction in the development of bird song.

What has been for decades a rather conservative and uninteresting subarea of animal learning is evolving rapidly into a field of both substance and intrinsic interest. Although such evolution has profited in no small measure from increased sophistication in experimental methods, progress would have been impossible without innovation in the conceptual tools, the frameworks, and perspectives used to study social learning phenomena.

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