

Chapter 15 Cognition

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15.1 Introduction

Poeciliids have colonized a wide range of environments from the equator to temperate regions of both hemispheres, in some cases occupying extreme habitats such as caves, hot springs, or brackish waters (e.g., see Tobler & Plath, chapter 11). While some species are adapted to a particular habitat, many others are able to live in extremely different conditions, and when introduced into different continents they often rapidly adapt to the new conditions to the point of displacing native species (Courtenay & Meffe 1989; Stockwell & Henkanaththegedara, chapter 12). Although the key to the poeciliids' success undoubtedly lies in their physiological adaptations (above all, viviparity), a further contribution to their adaptability is that they are equipped with a complex behavioral and cognitive repertoire—attributes that have made the family excellent subjects for cognitive research over the last fifteen years.

Poeciliids have only recently become the focus of cognition research, and most studies have primarily focused on only a few selected topics such as social learning and information transfer, predator-prey interactions, social cognition (individual recognition, cooperation, etc.), numerical cognition, and the lateralization of cognitive functions. The first three of these topics are covered elsewhere in this volume (Krause et al., chapter 13; Kelley & Brown, chapter 16; Webster & Laland, chapter 14; Druen & Dugatkin, chapter 20). In this chapter I summarize the available information on learning, memory, and spatial orientation and navigation. Then I focus on two very specialized topics, numerical abilities and lateralization of cognitive function, subjects that

in recent years have been the main focus of research in my laboratory. For a more general treatment of cognition in fishes, I refer the reader to Brown et al. 2006a.

15.2 Learning, memory, and spatial cognition

Learning influences almost every aspect of the life of poeciliids. Newborns are equipped with a behavioral repertoire that allows them to find food, avoid predators, and interact with conspecifics (Magurran & Seghers 1990a; Magurran 2005). Nonetheless, they possess the ability to modify their behavior in relation to both individual experience and information obtained from conspecifics. For example, guppies (*Poecilia reticulata*) can rapidly learn an antipredator response when exposed to a novel, simulated predation hazard in the presence of experienced conspecifics (Kelley et al. 2003; see also Kelley & Brown, chapter 16) and learn routes of escape from predators and new foraging sites from conspecifics (Reader et al. 2003; see also Webster & Laland, chapter 14). They also learn to recognize individuals on the basis of previous experience. In guppies this familiarity develops gradually over a period of 12 days (Griffiths & Magurran 1997a) and has important consequences for social dynamics (Croft et al. 2006a; see also Krause et al., chapter 13).

Poeciliids can gain information passively by observing social interactions among conspecifics. For example, in the green swordtail, *Xiphophorus hellerii*, male bystanders consistently modify their behavior toward individuals that they have witnessed winning or losing a fight (Earley & Dugat-

kin 2002). This behavior seems to represent eavesdropping, since bystanders do not modify their behavior toward naïve individuals (Earley et al. 2005; see also Druen & Dugatkin, chapter 20). In at least two species, the guppy and the sailfin molly (*Poecilia latipinna*), females alter their individual mate preferences after witnessing a male being chosen by another female (Dugatkin 1992a; Schlupp et al. 1994; see also Rios-Cardenas & Morris, chapter 17). A number of studies have shown that early social experience can influence male and female mate preferences (Ferno & Sjolander 1973; Breden et al. 1995). Sexual experience also plays an important role in species recognition. Inexperienced male guppies offered either hetero- or conspecific females mate indiscriminately, but males allowed prior interactions with females of both species learned to distinguish conspecific females in about a week (Haskins & Haskins 1949; Magurran & Ramnarine 2004).

15.2.1 Orientation and spatial cognition

Poeciliid habitats typically exhibit variability in the spatial and temporal distribution of resources and hazards. Numerous laboratory and field studies reveal that poeciliids are equipped with multiple, highly flexible orientation mechanisms that allow them to exploit information from their environment. For example, many poeciliids preferably inhabit shallow waters along the shorelines of rivers and lakes or areas of dense vegetation where they are less exposed to predators (Barney & Anson 1921; Mattingly & Butler 1994). Nevertheless, fish may move temporarily into open water, either individually or in schools, to escape aerial predators, avoid sexual harassment, find more favorable temperatures, or reduce competition for food (Maglio & Rosen 1969; Goodey 1973; Darden & Croft 2008) and thus need to find the route back to favorable locations.

Goodey and Ferguson (1969) found that when mosquitofish (*Gambusia affinis*) were displaced to unfamiliar locations, they use a sun compass to reach the shore from which they were captured. This movement toward shallow water seems to function principally as a mechanism of predator avoidance since it was absent in mosquitofish captured from environments lacking predators. Goodey (1973) found that mosquitofish could also orient to shore using local landmarks when available. However, when both sources of information were available, most individuals oriented by sun compass (Goodey 1973). Bisazza and Vallortigara (1996) tested wild-caught eastern mosquitofish (*Gambusia holbrookii*) in a circular tank with a light placed in the middle. Females (but not males) swam in different directions with respect to the light depending on whether they were tested in the morning or the afternoon. This pattern was not observed under diffuse light or among females

raised in captivity—a result suggesting that swimming direction in the laboratory is primarily determined by a sun compass direction learned prior to capture.

Many poeciliids can learn to orient themselves using local features of the environment (*Girardinus falcatus*; Sovrano et al. 2005; *P. reticulata*: Burns & Rodd 2008; *Brachyrhaphis episopi*: Brown & Braithwaite 2005; *P. latipinna*: Creson et al. 2003). For example, Sovrano et al. (2005) have shown that goldenbelly topminnows, *G. falcatus*, are able to combine geometric with nongeometric information from the environment to locate a goal. Previously, this capacity was shown to be present in human adults but absent in preverbal children and in rats, leading to speculation that the ability to combine different types of spatial information was somehow related to development of human language or other higher functions (Cheng 1986; Hermer & Spelke 1994). However, the ability of poeciliids and other fishes (Sovrano et al. 2002; Vargas et al. 2004) to use information in the same way as humans suggests that interspecific differences in spatial abilities probably reflect specific ecological adaptations rather than different levels of complexity of the nervous system (Sovrano et al. 2002; Vallortigara 2004).

15.2.2 Other learning studies in poeciliids

A few studies have employed operant conditioning to train poeciliids to discriminate between stimuli (Rensch 1956; Agrillo et al. 2009b; Dadda et al. 2009). Cantalupo et al. (1995) provide an anecdotal example of place avoidance learning in poeciliids. They examined the direction of escape by young *G. falcatus* in response to a simulated approaching predator. The stimulus was presented to individual fish when they were swimming in the center of the tank and their bodies were aligned with the stimulus predator. After repeated testing, the subjects tended to avoid the center of the tank and, if they moved through the center, tended to avoid alignment with the predator. Furthermore, guppies that witnessed the behavior of adults under attack during the first 48 hours of life were more likely to escape attacks by cichlids 10 weeks later than those that lacked this early experience (Goodey & Liley 1986). This appears to be an example of procedural memory, since fish were apparently learning how to escape from a predator rather than learning the characteristics of the predator itself.

15.2.3 Memory

Memory has rarely been investigated in poeciliids, and our current knowledge of memory processes and their neural bases in fishes comes from other species (for a review, see Rodriguez et al. 2006). Learning studies show that poecili-

ids can retain memories for varying lengths of time, depending on the task and the information required. In guppies and sailfin molly females, observation of a sexual interaction between a male and a female can influence subsequent mate-choice decisions after 24 hours (Witte & Massmann 2003; Godin et al. 2005). Guppies trained in a spatial-memory task continued to perform well when retested two weeks later (Burns & Rodd 2008). In a visual-discrimination learning task (two vs. four dots) Rensch (1956) found that the majority of guppies and swordtails (*X. hellerii*) retained the discrimination after 30 days. Goodey and Ferguson (1969) reported that western mosquitofish that learned the direction of the shore when young retained this knowledge when tested two weeks later, while fish that learned this as adults lost their shoreward orientation more quickly. Feral eastern mosquitofish females apparently retain a sun compass direction more than two months after capture (Bisazza & Vallortigara 1996).

Research on numerical abilities (see section 15.3.3) suggests that poeciliids can keep at least short-term track of a small number of objects. Griffiths and Magurran (1997b) found that female guppies living in schools with more than 50 individuals do not develop schooling preferences, suggesting that this is approximately the upper limit of the number of different individuals a female can memorize.

15.2.4 Intraspecific variation

Most studies on learning and cognition involve subjects of one sex only, and differences between the sexes in these abilities are rarely considered. However, Laland and Reader (1999a) found that female guppies were more likely to be innovative foragers than males, and in a subsequent study they observed that novel foraging information was transmitted at a faster rate among females than males (Reader & Laland 2000). As mentioned above, female but not male mosquitofish showed evidence of a learned sun compass route when tested in the laboratory (Bisazza & Vallortigara 1996). To date, however, there is no clear evidence that male and female poeciliids differ in learning and memory, and all the reported variation could be explained by other factors such as sex differences in risk sensitivity (Magurran et al. 1992), feeding strategies (Dussault & Kramer 1981), or schooling tendencies (Griffiths & Magurran 1998).

Two studies have compared cognitive abilities among populations that differ in the level of predation. Burns and Rodd (2008) found no effect of predation intensity on the time necessary to learn a spatial task in guppies. However, distinct strategies were used by high- and low-predation guppies, the latter being more inclined to make quick but inaccurate decisions than their high-predation counterparts. Brown and Braithwaite (2005) investigated

differences in a spatial task in *B. episopi* from populations with different predation regimes (see also Kelley & Brown, chapter 16). Low-predation fish learned spatial tasks about twice as quickly as high-predation fish. The causes of these differences are not known, but high- and low-predation populations also differ in temperament and in the pattern of cerebral lateralization, two factors that are known to affect learning (Sneddon 2003; Rogers et al. 2004). Direct evidence of the influence of cerebral lateralization on learning was reported in a study on *G. falcatus* in which fish artificially selected for a high degree of lateralization (see section 15.4.1) performed significantly better than fish selected for low lateralization in two tasks (Sovrano et al. 2005).

15.3 Numerical cognition

Abilities such as recording the number of events, enumerating items in a set, or comparing two different sets of objects can be adaptive in many ecological contexts. For example, wild chimpanzees enter intergroup contests only if they outnumber the opposing side by a factor of 1.5 (Wilson et al. 2001), while lions prefer to hunt smaller, rather than larger, prey groups, as smaller groups are more vulnerable (Scheel 1993). In recent years research on numerical cognition has broadened to include other mammals and a few bird species, leading to the conclusion that rudimentary numerical abilities are widespread among these two vertebrate classes (Hauser et al. 2003; Kilian et al. 2003; Rugani et al. 2008; Irie-Sugimoto et al. 2009). Despite this progress, we have yet to determine whether animals have a mental representation of numbers, whether one or several different mechanisms underlie these abilities, and whether numerical abilities are innate or learned through experience. Another question that has remained unresolved until recently is whether numerical abilities are confined to mammals and birds or are evolutionarily ancient adaptations shared by most animals.

15.3.1 Evidence for two distinct numerical systems in poeciliid fish

Some authors have contended that in primates there are two distinct nonverbal systems for representing numerosity: an object-tracking system, which is precise but has an upper limit of 3–4 units, and an analog-magnitude system, which allows approximate discrimination of large quantities (Feigenson et al. 2004; Revkin et al. 2008). Agrillo et al. (2008b) systematically investigated the limits of quantity discrimination in mosquitofish (*G. holbrooki*) using the widespread tendency of fish to choose the largest social group when placed in a new, potentially dangerous envi-

ronment (Hager & Helfman 1991; Pritchard et al. 2001). In this study, fish discriminated between two shoals that differed by one element (i.e., individual) when the choices of shoal size were 1 versus 2, 2 versus 3, and 3 versus 4, but not when the choice was 4 versus 5 elements, a limit that coincides with that observed in nonhuman primates in comparable tasks (reviewed in Feigenson et al. 2004). However, fish were able to discriminate between larger shoals provided that the number ratio was at least 1:2 (e.g., 4 vs. 8 or 8 vs. 16 fish but not 4 vs. 6 or 8 vs. 12 fish), in accordance with Weber's law. Buckingham et al. (2007) reported identical results for female green swordtails.

The study by Agrillo and co-workers (2008b) provides strong evidence for two distinct systems: one for representing exact small numbers of objects or events and one for representing large approximate numerical quantities. In accordance with Weber's law, when stimulus shoals of mosquitofish contained more than 4 fish, the comparison became more difficult as the ratio became smaller, the typical signature of the large-number system in mammals. No such relationship was found with 1 versus 2, 2 versus 3, and 3 versus 4 comparisons, where discrimination was independent of the numerical difference between groups but showed a set-size limit, the typical signature of the object-tracking system. In addition, a single mechanism obeying Weber's law can hardly explain all the results, since mosquitofish were unable to discriminate when presented with ratios of 2:3 or 3:4 in the range of large numbers, while such discrimination was possible with small numbers.

15.3.2 Estimating the number of conspecifics in other contexts

The ability to enumerate could be used in other contexts besides antipredator responses. When pursued by an active male, pregnant female mosquitofish show a tendency to join the largest shoal to dilute sexual harassment (Agrillo et al. 2006). In this situation the females' capacity to discriminate different numbers of fish is identical to that observed in the previous study, suggesting that the same cognitive systems operate in both contexts (Agrillo et al. 2007).

In many poeciliids females form shoals of varying sizes and sex ratios, and males seeking mating opportunities must often decide which group to join. Male guppies are primarily influenced in their choice by group size, whereas shoal sex ratio plays a marginal role (Lindstrom & Ranta 1993). Similar results have been found in a series of experiments conducted with male mosquitofish (Agrillo et al. 2008a). In tests with all-female shoals, males exhibited a preference for shoals rather than a single female and preferred larger shoals to smaller ones. They also preferred an all-female shoal to a mixed-sex one, even if the latter

was larger. Both preferences appear sensible, since larger groups of females offer more protection and more mating opportunities. Yet Agrillo et al. (2008a) reported that male mosquitofish did not choose shoals with more favorable sex ratios, leading the authors to suggest that there may be a cognitive limit in the capacity of males to simultaneously take into account the number of males and females in the different groups.

15.3.3 Can fish use numerical information?

Animals can judge numerosity using cues other than the number of the items. This is because numerosity normally covaries with several other physical attributes, for example, the sum of areas or contours of the objects and the total area occupied by the set, and an individual can use the relative magnitude of these continuous variables to estimate which group is larger (Feigenson et al. 2002b). Agrillo et al. (2008b) investigated whether focal mosquitofish were still able to use numerical information when nonnumerical variables were controlled experimentally. In one experiment, the total areas occupied by stimulus (i.e., nonfocal) fish in a small and a large group were held experimentally constant by using slightly larger fish as subjects for the smaller shoal and slightly smaller fish for the larger shoal. In this way, stimulus fish occupied the same total area in both groups. Under these conditions, focal female mosquitofish did not choose the larger shoal when presented in either small (2 vs. 3) or large numbers (4 vs. 8). The total activity of fish within a shoal was also manipulated by keeping the two stimulus groups at different water temperatures. Once the total number of movements within shoals were approximately equivalent, focal fish also exhibited no preference for the larger shoal in the 4 versus 8 comparison, but interestingly they chose the larger shoal in the 2 versus 3 comparison. These results do not necessarily imply that mosquitofish are unable to discriminate two groups solely on the basis of their numerosity. Using perceptual cues of the stimuli may simply be the easiest way to obtain a quick numerosity judgment. Indeed, there is compelling evidence that species such as humans, apes, and dolphins, which have the capacity to count, typically base their quantity judgments primarily on stimulus properties such as area, contour, or density and use number only when no other cues are available (Durgin 1995; Kilian et al. 2003).

A recent study suggests that fish are capable of true numerical representation. Female mosquitofish were trained to discriminate between two quantities (2 vs. 3 small geometric figures) by reinforcing the correct choice with the possibility of rejoining their social group (Agrillo et al. 2009b; fig. 15.1). In the first experiment, during the training the figures varied in shape, size, and distance but there

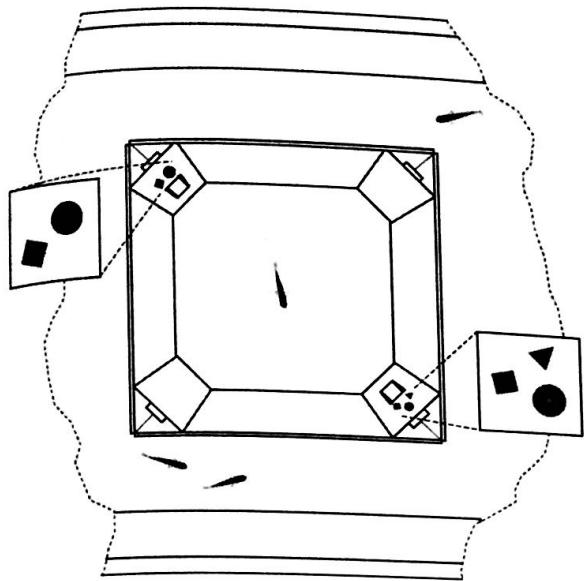


Figure 15.1 Apparatus used to train female *Gambusia holbrooki* to discriminate between sets containing different numbers of geometric figures. Subjects were placed individually in a test chamber provided with two doors (one associated with three and the other associated with two elements) and could pass through the reinforced door to rejoin shoal mates in the outer tank.

was no control for nonnumerical variables. After subjects had learned the discrimination, they were tested without reward while controlling for one nonnumerical variable at a time. A good numerical discrimination performance was maintained once the total luminance of the stimuli and the sum of perimeters of the figures were matched. Conversely, mosquitofish did not select the previously reinforced numerosity when stimuli were matched for the sum of the areas of the figures or for the total area occupied by the sets, suggesting that these two cues had been spontaneously used during the learning process. In a second experiment fish had to learn a 2 versus 3 discrimination while these nonnumerical variables were simultaneously controlled for. All fish were able to learn the task and they made approximately the same number of errors, as did the fish in the first experiment when nonnumerical cues were available. It therefore seems that fish, like mammals and birds, are able to compare two quantities using only numerical representations, although, as in the other species, this capacity is utilized only when nonnumerical cues are unavailable.

15.3.4 Development of numerical skills

As in other poeciliids, guppies shoal soon after birth (Magurran & Seghers 1990a), which makes it possible to study how counting ability develops during ontogeny. In a recent study (A. Bisazza, G. Serena, L. Piffer, & C. Agrillo, unpublished data) newborns were tested in a miniature version of the apparatus used for assessing shoal choice in adults. When offered a choice between shoals composed of "small"

numbers of fish (2 vs. 3), they chose the larger shoal significantly more often, but they exhibited no preferences when "large" numbers (4 vs. 8 or 4 vs. 12 fish) were used. The latter result was not due to newborns being motivated to avoid very large shoals, since a shoal of 8 fish was significantly preferred over shoals comprising 3 fish. Instead, this study suggests that newborn guppies have the ability to discriminate among groups comprising small numbers, while the ability to discriminate among larger shoals occurs later. To assess the relative role of maturation and experience, guppies were tested at 20 and 40 days of age after they had been raised without the possibility to count fish (i.e., with just one companion) or with normal experience (raised in a large group with some adults present). At 40 days fish from both treatments were able to discriminate 4 from 8 fish, while at 20 days this was observed only in fish that had had normal social experience. These results again suggest the existence of two separate numerical systems in poeciliids. The precise small-number system is innate and displayed immediately at birth, while the approximate large-number system emerges later as a consequence of both maturation and social experience.

15.3.5 Cognitive limitations and decision rules

The above studies suggest that poeciliids exhibit numerical skills that closely match those found in animals such as apes and dolphins, which possess much larger and more complex brains. Indeed, in the domain of small numbers, the skills displayed by poeciliids appear to exceed those of many other vertebrates. Mosquitofish and guppies (including newborns) easily distinguish 3 from 4 items, a capacity not observed in salamanders, toads, chicks, and preverbal children (Feigenson et al. 2002a; Uller et al. 2003; Rugani et al. 2008).

Research over the last two decades has revealed that human and nonhuman primates share an object-tracking system, a mechanism that allows individuals to track up to four objects in parallel even if these are moving in space, provided they remain in view or undergo only brief periods of occlusion (Trick & Pylyshyn 1994; Scholl & Pylyshyn 1999). A considerable body of evidence suggests that the precise small-number system is based on this object-tracking system (reviewed in Feigenson et al. 2004). Recent studies indicate that similar systems may operate in other mammalian taxa and in birds (Kilian et al. 2003; Rugani et al. 2008), and the experiments with guppies and mosquitofish suggest that this system may be phylogenetically very ancient and shared by most extant vertebrates. Investigation in this area is highly desirable since cognitive limitations are likely to affect many fitness-related traits such as mate selection, foraging, antipredator responses, and so

on. Although the possibility that all vertebrates encounter similar cognitive limitations is speculative, it is intriguing to note that in the majority of species that have been studied extensively, females sample on average three to four males before making a mating decision (reviewed in Gibson & Langen 1996) and that similar effects have been observed in foraging contexts (Langen 1999). The argument that cognitive limitations can constrain comparative evaluation mechanisms can, however, be reversed. In both mate sampling and food patch selection, searching costs are normally proportional to the number of alternatives sampled, while the benefits follow the law of diminishing marginal returns (Stephens & Krebs 1986; Real 1990). Put simply, after visiting four males, sampling one or two additional males would add little to the selectivity of the female while considerably increasing her costs (risk of predation, travel time, energy consumed, etc.; see, e.g., Byers et al. 2005; Vitousek et al. 2007). It is therefore possible that selection on optimization of search rules has shaped cognition instead of the other way round.

15.4 Lateralization of cognitive functions and its ecological consequences

Hemispheric specialization refers to sensory, motor, and cognitive abilities that are specialized to either the left or right cerebral hemisphere. Lateralization of cognitive functions has traditionally been investigated in humans and in a few mammalian and avian models (Andrew & Rogers 2002). Research on fish started very recently when Cantalupo et al. (1995) documented a significant population bias to turn right during fast escape responses in young *G. falcatus* when presented with a simulated predator attack. Since this initial study, many other instances of behavioral lateralization in fishes have been reported, regarding either motor (e.g., sound production, fin use, gonopodial thrusts) or sensory biases (visual, olfactory, lateral line); for a review, see Vallortigara and Bisazza 2002. Poeciliids have quickly become a prominent group in the study of animal lateralization. Early studies, conducted mainly on two species, the goldbelly topminnow (*G. falcatus*) and the eastern mosquitofish (*G. holbrooki*), revealed a pattern of lateralization of cognitive functions similar to that observed in mammals and birds, where each hemisphere is specialized for different functions and the resulting left-right motor and sensory differences affect everyday behavior (Bisazza et al. 1997a; Bisazza et al. 1998a). Mosquitofish, for example, have a significant preference for keeping a shoal mate on their left, while they tend to inspect a potential predator with their right eye (De Santi et al. 2001). Bisazza et al. (1999) have studied the laterality of cooperative

predator inspection using a procedure introduced by Milinski (1987) in which a mirror is placed parallel to the tank during inspection so that the image appears to swim along with the fish, simulating a cooperative partner. In this experiment mosquitofish performed significantly closer inspections when the mirror was on their left side so that each of the two stimuli was seen with the preferred eye. These apparently surprising results occur because in vertebrates with laterally placed eyes, such as fish, the optic nerve fibers completely cross at the optic chiasm, and thus each eye projects almost exclusively onto the contralateral hemisphere. Since fish lack the efficient interhemispheric communication through the corpus callosum that characterizes mammals, information is primarily processed by the hemisphere that receives it.

15.4.1 Individual variation in lateralization

Population level analyses often mask any underlying individual variability. For example, in mosquitofish, a minority of individuals show a reverse laterality pattern to that described above, while some other individuals show little or no eye bias (De Santi et al. 2001). The significance of such individual variation in laterality has become the focus of more recent research. In two fish species, *Danio rerio* and *G. falcatus*, the degree and direction of cerebral asymmetries were found to be partly under genetic control (Bisazza et al. 2000b; Barth et al. 2005; Facchin et al. 2009), and a selection experiment was undertaken in the latter species to obtain lines of fish that either preferentially turned to the right (right detour = RD), to the left (LD), or had no turning preferences (nonlateralized = NL) when encountering a dummy predator that was visible behind a barrier (Bisazza et al. 2007). RD and LD lines significantly diverged after a few generations (fig. 15.2), and the fish from these two lines also showed an opposite direction of lateralization in many other cognitive tasks, including motor activities and visual functions as well as other sensory modalities (Facchin et al. 1999; Bisazza et al. 2001a; Bisazza et al. 2005). This suggests that LD and RD fish may be similar but with complete mirror-reversed organization of cerebral functions, while NL fish have a bilateral representation of most cognitive functions.

The discovery that lateralization is widespread and that individual differences have a genetic basis has raised new and important questions. Is there a selective advantage of lateralization of cognitive functions? Are there costs associated with having motor and perceptual asymmetries? What mechanisms maintain variability in the strength and direction of laterality? Why do population biases exist, and why is the direction of bias sometimes consistent across different species?

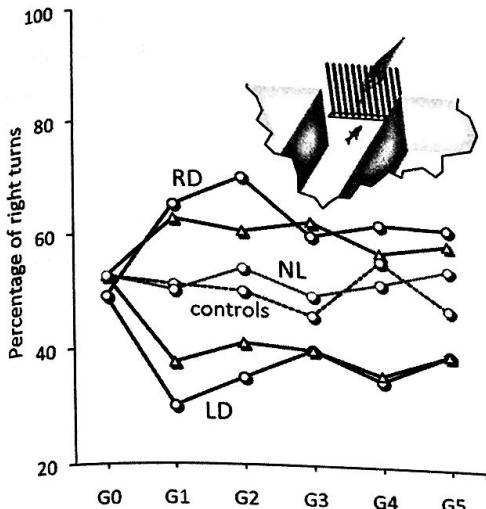


Figure 15.2 Selection experiment on *Girardinus falcatus* for turning direction when facing a dummy predator beyond a barrier. The frequency of right turns is reported over five generations for two replicated lines selected for right turning (right detour = RD), two for left turning (LD), one line selected for no turning bias (nonlateralized = NL), and one unselected control line (controls). Redrawn from Bisazza et al. 2007.

15.4.2 Selective advantages of cerebral lateralization

Animals are often constrained by how much attention they can simultaneously focus on different activities (Dukas 2004). Rogers (2000, 2002) suggested the intriguing hypothesis that hemispheric specialization evolved because it allows individuals to cope with limited attention. In her view, cerebral lateralization is one way to increase the brain's capacity to carry out simultaneous processing, by channeling different types of information into the two separate halves of the brain and by enabling separate and parallel processing to take place in the two hemispheres. To test this idea, Rogers et al. (2004) compared normally and weakly lateralized chicks (the latter obtained by incubating eggs in the dark during the final days before hatching). Chicks had to learn to discriminate between food and nonfood while a model of an avian predator was moved overhead. Lateralized chicks learned faster and were more responsive to the model predator than weakly lateralized chicks, whereas no difference in learning ability was found in the control experiment without the predator.

Dadda and Bisazza (2006a, 2006b) performed similar studies comparing lines of *G. falcatus* selected for high and low degrees of laterality (see section 15.4.1) in situations requiring the sharing of attention between two simultaneous tasks. In one study (Dadda & Bisazza 2006a) hungry individuals entered a compartment adjacent to the home tank to capture live brine shrimps in either the presence or the absence of a live predator situated at some distance. With the predator visible, fish of both lateralized lines (LD and RD, collectively called LAT) were twice as fast at catch-

ing shrimps than nonlateralized fish of the NL line, while no difference in capture rate was recorded when the predator was absent and subjects were not required to share attention between vigilance and prey capture. A more detailed analysis of fish movements in this test revealed that LAT fish tended to monitor the predator with one eye (the right eye in LD and the left in RD fish) and to use the other eye for catching prey, whereas NL fish swapped between tasks, using each eye for both functions. In the second study (Dadda & Bisazza 2006b), lateralized females proved to be better foragers than NL females when they had to share attention between retrieving food items scattered on the surface and avoiding unsolicited male mating attempts, while no difference between LAT and NL fish was evident in control tests where females could forage undisturbed.

A superior performance of LAT individuals was also shown in situations that did not explicitly involve multitasking, suggesting other possible advantages of cerebral lateralization. LAT lines of topminnows proved to be better than NL fish at using physical features or geometric cues to reorient themselves in a small environment (Sovrano et al. 2005; see section 15.2). In another study (Bisazza & Dadda 2005), schools of LAT fish showed significantly more cohesion and coordination than schools of NL fish. Moreover, in schools composed of both LAT and NL fish, the latter were more often at the periphery of the school, while lateralized fish occupied the center—a position normally safer and energetically less expensive (Bumann et al. 1997; Svendsen et al. 2003). In these experiments, fish were observed in a novel environment, so it is possible that during the test they were actively scanning the surroundings for predator presence, an additional attention task that would favor fish with specialized hemispheres.

15.4.3 Costs of cerebral lateralization

In organisms such as fish with laterally placed eyes, the complementary specialization of hemispheres often translates into differential responsiveness to sensory input on the left and right side of the body (Deckel 1995; Vallortigara et al. 1998). The appearance within the visual field of biologically relevant objects such as a predator or a prey is often unpredictable, and it is easy to see the potential disadvantages arising from having side biases in the promptness or effectiveness of response to a particular class of objects, as well as the possibility for competitors, predators, or prey to exploit such asymmetries. Whether these left-right differences in the way an animal analyzes and responds to environmental stimuli also translate into a disadvantage for more highly lateralized individuals remains largely unexplored. An attempt to test this possibility involved comparing the selected lines of *G. falcatus* for their promptness in

reacting to a predatory stimulus appearing on the right or the left visual hemifield (Agrillo et al. 2009a). No difference between LAT and NL fish or between the two eyes was detected, but the setting used in this study was very simplified and the measurement technique was rather crude, so a more thorough investigation is needed before drawing further conclusions.

A recent study utilized the selection lines described above (Dadda et al. 2009) to explore the possibility that marked hemispheric functional asymmetries may interfere with a cognitive task when it relies on hemispheric communication and cooperation to be accomplished. Two situations were devised in which visual inputs were divided between the visual fields so that each eye (and contralateral hemisphere) had access to only one half of the information necessary to accomplish the task. The first experiment was an adaptation of a widely used neuropsychological test, the line-bisecting task. When right-handed human subjects are required to mark the middle points in a straight line, they tend to transect slightly to the left, an effect that is commonly ascribed to the right-hemisphere dominance for spatial tasks (reviewed in Jewell & McCourt 2000). Topminnows were required to use the middle door in a row of nine in order to join their social group (fig. 15.3). In the majority of trials NL fish correctly chose the central door, while fish from LD and RD lines made systematic errors to the left or the right of the central door, respectively.

In the second experiment, isolated individuals emerged into an unfamiliar area where they could choose between two shoals differing in quality (number and size of fish). The apparatus allowed subjects to see each shoal with a different eye prior to the choice. NL fish chose the high-quality shoal significantly more often than the lateralized fish, which in most cases chose the option seen with the eye that in their line was dominant for analyzing social stimuli, irrespective of its relative quality. Interestingly, *B. episopi*

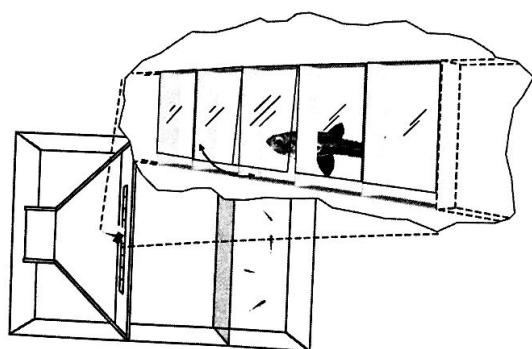


Figure 15.3 Apparatus used to study line-bisecting performance in *Girardinus falcatus*. Subjects from lines selected for high and low degrees of cerebral lateralization were trained to use the middle door in a row of nine in order to join their social group. Fish from LD and RD lines made systematic errors to the left or the right of the central door, respectively, whereas NL fish chose the correct door more often.

from high-predation populations are, on average, more lateralized than their low-predation counterparts (Brown & Braithwaite 2005) and surprisingly take longer to complete a maze task since their laterality interfered with an efficient exploratory behavior (C. Brown et al. 2004).

It is not easy to estimate the extent to which these constraints affect an individual's fitness. These experiments suggest that lateralized fish may make frequent suboptimal decisions about mates, prey, shoals, or refuges any time they need to make a rapid decision and the alternatives are placed at the opposite sides of the body. Perhaps this situation is not so uncommon in their natural habitat. Like most fish, poeciliids possess only a small overlap between the two visual hemifields, and importantly they lack the kind of mobile neck that allows them to rapidly scan relevant stimuli sequentially with the two eyes and send information to both hemispheres (Clayton & Krebs 1994).

The picture emerging from studies of *G. falcatus* is that the advantages associated with having an asymmetric brain may balance the ecological disadvantages associated with left-right differences in the response to stimuli. The relative costs and benefits of lateralization are likely to vary with ecological conditions such as predation pressure. Intuitively, better schooling performance and efficiency in multitasking (i.e., strong lateralization) should be favored under high-predation regimes, a hypothesis that recently received support from a field study of *B. episopi* (C. Brown et al. 2004; see Kelley & Brown, chapter 16). However, high predation risk should also favor fish that make quick and accurate decisions about escape trajectories. Perhaps the often-used dichotomy of high versus low predation is too simplistic, and a finer distinction is required (Botham et al. 2006; Croft et al. 2006b). For example, the capacity to mate or feed while monitoring predators should be most effective where predators are always in sight or come from predictable directions (e.g., from deep water), while ambush predators should favor fish with equal capacity to react on the left or the right side.

15.4.4 Evolutionary significance of population biases in laterality

Directional asymmetries in laterality are by far the most frequent condition in all vertebrate taxa (reviews in Rogers 1996; Bisazza et al. 1998b). Advantages in brain efficiency outlined in section 15.4.2 may explain the existence of individual lateralization but cannot account for the alignment in the direction of lateralization in most individual of a species. Indeed, consistent population biases in laterality are potentially disadvantageous since they make individual behavior more predictable to other organisms, for example, allowing predators to learn the most frequent direction of escape in their prey. Rogers (1989) has proposed

that the direction of lateralization in a population occurs as a consequence of the need to coordinate social behavior (see also Brown 2005). A game-theoretical analysis showed that population-level lateralization can arise as an evolutionarily stable strategy when the benefit to an asymmetric individual of coordinating with others with the same laterality equals the costs arising from predators having more success with the more common prey type (Ghirlanda & Vallortigara 2004). Empirical evidence in support of this hypothesis is equivocal. Rogers and Workman (1989) found that the social hierarchy was more stable in groups of light-exposed (lateralized) chicks than in groups of dark-incubated (nonlateralized) chicks. Bisazza et al. (2000a) examined 16 fish species and found some evidence that population biases were more frequent in species with a strong shoaling tendency than in solitary ones, but this result needs to be confirmed using a larger sample size and correcting for phylogeny. Nevertheless, Bisazza and Dadda (2005) found no evidence that schools composed of female *G. falcatus* with the same laterality were more coordinated than schools composed of females of mixed laterality.

15.5 Conclusions and future directions

Although classical studies on learning and memory have benefited research on other fish groups, in the last fifteen years poeciliids have emerged as important model organisms for investigating complex cognitive behaviors such as mate-choice copying, eavesdropping, recognizing individuals, social learning, and numerical abilities (see chapters 13, 14, 16, and 20). Studies on poeciliids continue to challenge the once-dominant view that a complex flexible behavior is a prerogative of mammalian and avian species, suggesting instead that these abilities are exhibited much more widely among animal taxa (see Bshary et al. 2002 for a recent discussion). As clearly highlighted here and elsewhere in this volume, in many cases complexity of behavior, learning abilities, and memory capacities of poeciliids are comparable to, and in some cases exceed, those of mammals and birds. Poeciliids can recognize up to 40 familiar individuals, remember the outcome of past cooperative predator inspections and bias behavior accordingly, exploit information obtained from observing the outcome of a fight or the mate choice of another individual, and learn new foraging and antipredator habits from an expert conspecific.

The recent rapid expansion of animal cognition studies has prompted considerable interest in understanding the selective factors that promote the evolution of specific cognitive capacities. Comparative studies have proved a useful tool to identify the ecological factors associated with variation in encephalization, brain organization, and cognition (for recent discussions, see Byrne & Bates 2007; Cunningham & Janson 2007; Healy & Rowe 2007). Poeciliid fishes appear to be an ideal group for investigating such topics using both intra- and interspecific comparative approaches. The habitats occupied by poeciliids show extreme variability in structure and complexity, and poeciliids exhibit considerable variation in diet and predation regimes (Meffe & Snellson 1989a). Pioneering studies (see section 15.2.4) have reported learning differences among populations with different predation regimes in two poeciliid species, suggesting promising directions for future studies.

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Another topic of increasing interest concerns differences in cognition that are expected to arise from the differential action of sexual selection on the two sexes and as a consequence of niche divergence that might derive from sexual dimorphism. The latter effect is expected to be particularly relevant in poeciliids, as they exhibit some of the most extreme examples of sexual dimorphism of all vertebrates (Bisazza 1993b). Yet no study has directly addressed this topic in poeciliids, although anecdotal observations (see section 15.2.4) suggest that sex differences in cognition may be present in some species.

Individual differences in cognition represent an emerging area of study that to date has been extensively examined only in humans (e.g., O'Boyle et al. 2005; Posner et al. 2007). Lateralization studies in *G. falcatus* have revealed the existence of individual differences in the organization of brain functions that appear to have a genetic basis and that exert their effects on multiple aspects of behavior and cognition (see sections 15.4.1–15.4.3). One promising area for future investigation is the potential for covariation of personality and cognitive abilities (Dugatkin & Alfieri 2003; Brown & Braithwaite 2005; see also Kelley & Brown, chapter 16). Another virtually unexplored potential source of variation in cognition is represented by differences among males in mating tactics. Since the two mating tactics of the poeciliids, sneak mating and courtship, require quite different skills (Bisazza 1993b; see also Rios-Cardenas & Morris, chapter 17, and Magurran, chapter 19), it will be interesting to see if these tactics select for different suites of cognitive abilities in poeciliids with genetically determined alternative male mating tactics (Zimmerer & Kallman 1989; Travis 1994).

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