MOTOR LEARNING AND THE VALUE OF FAMILIAR SPACE

JUDY STAMPS

Section of Evolution and Ecology, University of California, Davis, California 95616

Abstract.—Judging from studies of homing and territorial behavior, many animals value familiar home ranges or territories. This article discusses a new proximate explanation for this phenomenon: individuals may learn site-specific serial motor programs that enhance their ability to move rapidly, safely, and efficiently around obstacles and barriers in familiar areas. The literature on motor learning in humans and on hurdle race training in humans and horses yields a number of specific predictions on how animals should behave, if they practice and learn serial motor programs that facilitate high-speed locomotion along complicated routes or pathways. Support for some of the predictions of the motor learning hypothesis is already available in the literature on animal play, exploration, maze learning, and spatial orientation, and other predictions of this hypothesis should be readily testable using small mammals.

Many animals do not roam randomly across the landscape but instead confine their activities to a particular region, home range, or territory (Burt 1943; Brown and Orians 1970; Kaufmann 1983). Over the years, evidence has accumulated that animals "value" familiar areas, in the sense that they are willing to incur considerable costs to regain or retain them. For instance, the homing literature shows that when animals are artificially displaced, they often travel long distances over many days to return to their old haunts (reviewed in Papi 1992). Other indications of the value of familiar space comes from territorial animals. When challenged for ownership of space, territory owners usually win contests with intruders, a phenomenon termed the "prior residency advantage" (Waser and Wiley 1969; Archer 1988; Stamps and Krishnan 1994). Experimental studies suggest that owners typically win because they attack first, persist longer during fights, or are more willing to escalate fights than are intruders (Phillips 1971; Frey and Miller 1972; Figler and Einhorn 1983; Waage 1988; Englund and Olsson 1990). One common interpretation of these observations is that territory owners value their territory more than do intruders (Maynard Smith and Parker 1976; Krebs 1982; Enquist and Leimar 1987; but see Grafen 1987).

The fact that animals are willing to incur costs to remain in a familiar area implies that experience with space enhances fitness in that space. In fact, experimental studies have shown that familiarity improves the ability of rodents to escape from real predators (Metzgar 1967; Ambrose 1972; Synder et al. 1976), mechanical predators (Renner 1988), or humans (Clarke et al. 1993). Along the

same lines, the optimal foraging literature indicates that animals forage more efficiently in familiar than unfamiliar areas (Stephens and Krebs 1986), and studies of territorial animals suggest that defense costs may be lower in familiar than in novel areas (Eason and Hannon 1994; Stamps 1994). Hence, on an ultimate level, it is often assumed (though rarely tested) that familiarity with an area improves individual growth, survival, or reproduction.

On a proximate level, the very term *familiarity* indicates that learning enhances the value of space. To date, proximate explanations for the value of familiar space have focused on knowledge that residents might acquire as a result of experience with a particular area. For instance, residents might learn about the location, type, or quality of resources, escape routes, nest sites, or other important features of the area or about the nature and location of other animals living in that neighborhood (review in Shulter and Weatherhead 1992). Indeed, many students of animal behavior view learning in general and exploration in particular as a means of gathering information about important features of the external environment (Staddon 1988; Renner 1990; Shettleworth 1993; Stephens 1993).

There is already abundant evidence that animals are capable of learning the location of salient topographic features in novel areas, and a large and growing literature considers the proximate bases of spatial representation and navigation in animals (see, e.g., Gallistel 1990; Leonard and McNaughton 1990; Papi 1992; Poucet 1993). It is easy to see how information about the nature and location of important biotic and abiotic features might increase individual fitness (e.g., how knowing the location of refuges in a home range might enhance survival when fleeing from a predator).

However, in this article I argue that an animal encountering a novel area may do more than learn about the nature and location of salient features of that area. In addition, animals may learn serial motor programs that increase their ability to move rapidly and safely in a home range. If there are ultimate advantages to moving quickly and safely around obstacles (e.g., when escaping predators, chasing conspecifics, capturing prey, or courting females), then motor learning processes could enhance the value of familiar space.

The ''motor learning'' hypothesis differs from previous proximate explanations for the value of familiar space in that it emphasizes the motor rather than the sensory or cognitive side of learning processes. It implies that knowing the location of important topographic features may be a necessary but not sufficient condition for rapid, accurate locomotion in a given area. Instead, this hypothesis argues that rapid, safe locomotion around obstacles is likely to require physical practice and that practice along one route is unlikely to improve locomotor performance along routes with other spatial configurations. In this situation, motor learning would enhance the value of familiar space, by increasing an animal's ability to move rapidly and safely around that area in the future.

More formally, the motor learning hypothesis rests on the following five assumptions:

1. Individuals live in topographically complex home ranges that contain many obstacles and barriers to locomotion.

2. The configuration of obstacles in a home range remains relatively stable over the period that an individual inhabits that home range.

3. Selection favors individuals that are able to move rapidly and safely around the barriers and obstacles in their home range.

4. An animal's ability to move rapidly and safely along a given route in a topographically complex area improves with practice.

5. Practice is at least partially site specific, such that an animal must practice locomotion along a particular route in order to move rapidly and safely along that route in the future.

The first three conditions specify the type of animals most likely to benefit from learned site-specific motor programs. These conditions are probably satisfied in many small mammals. For instance, chipmunks (*Tamias striatus*) inhabit long-term home ranges in topographically complex habitats, in which they escape predators by running along particular pathways to safe refuges (Bowers and Ellis 1993; Clarke et al. 1993). Other possible candidates include lacertid lizards (Stamps 1977) or butterfly fish (Reese 1989) that use predictable routes when traveling around spatially complex home ranges. In the aerial domain, many bats and birds live in cluttered habitats with many obstacles to flight (Griffith 1958; Avery et al. 1978; Norberg 1983; Martin 1986). Recent studies have shown that starlings (*Sturnus vulgaris*) are sensitive to obstacles in their flight paths and that they avoid using aerial routes near obstructions unless rewarded for doing so (Cuthill and Guilford 1990).

The last two conditions form the heart of the motor learning hypothesis. The first goal of this article is to determine whether these conditions might apply to the types of locomotor patterns that animals use when moving at maximum velocity around obstacles and barriers within familiar home ranges. To my knowledge no one has explicitly tested these conditions in free-living animals. However, a rich literature on motor learning in humans and other animals bears on these questions. Since this literature is probably foreign to most readers of this journal, I have briefly summarized the principles and results that are most germane to the motor learning hypothesis. The relevant studies fall into two groups: a general literature on motor skills acquisition in humans, and an applied literature that focuses on training programs for human and equine hurdle races, sports that require motor skills comparable to those used by animals traveling at high speed in topographically complex home ranges.

In addition to showing the importance of practice in the acquisition of complex motor programs, the motor learning literature offers a number of specific predictions about how free-living animals should behave, if they learn site-specific motor programs after moving into a novel home range or territory. My second goal is to outline specific predictions of the motor learning hypothesis and review data from the play, exploration, and orientation literatures that support these predictions. Finally, I consider how one might test the motor learning hypothesis, by highlighting predictions of this hypothesis that differ from those generated by alternative explanations for the behavior of animals in novel habitats and spatial configurations.

MOTOR LEARNING IN HUMANS

Because of a long-standing interest in teaching humans particular motor skills, the literature on motor learning in humans contains a number of insights relevant to the motor learning hypothesis. Of special interest are serial motor programs, in which a group of discrete motor patterns are strung together in a temporal series and the order of the actions is important (Lashley 1951; Rosenbaum 1985; Schmidt 1988; Mazur 1990). From the perspective of a rabbit escaping from a predator, a serial motor program might consist of a dash to the nearest familiar escape route, followed by abrupt changes in direction, jumps over obstacles, and low runs under barriers, and ending with a dive into a burrow.

For practical reasons, most studies of human skill acquisition have focused on the early phases of motor learning, when a relatively small number of practice sessions has a dramatic effect on the speed or accuracy of a motor program. In addition, college undergraduates are frequently used as experimental subjects in human motor learning studies. These subjects are already proficient at the motor patterns required for the task at hand (e.g., they are able to run, jump, throw or manipulate objects). They are then asked to learn skills that combine familiar motor patterns in novel ways or that refine motor patterns already in the behavioral repertoire.

The goals of many human motor skills are speed, accuracy, and consistency of performance. A basic truism of motor learning theory is that practice is critically important to achieve these goals (Adams 1987; Schmidt 1988; Mazur 1990; Ericsson et al. 1993). Many studies have confirmed the "law of practice" (Snoddy 1926), which states that performance first increases rapidly, and then gradually levels off as a function of the time spent in practice (Annett 1985; Lane 1987; Schmidt 1988). A saturating functional relationship between practice and performance is general, though the exact shape of performance curves depends on the motor pattern involved and the criteria used to assess performance (Lane 1987).

During the acquisition period in experimental studies of skill acquisition, there is frequently a trade-off between speed and accuracy (Hancock and Newell 1985; Schmidt et al. 1985), a phenomenon familiar to anyone who has learned to type. Speed and accuracy may both approach asymptotic values after moderate amounts of practice, but additional practice may be required to produce other important attributes of well-learned motor programs (Namikas 1983; Schmidt 1983, 1988). After intensive practice, motor programs may become "automatic," in the sense that individuals can perform parallel (usually nonmotor) tasks at the same time as they are running off the motor program (Hirst et al. 1980; Schneider and Fisk 1983; Annett 1985). In addition, intensive practice may improve retention, so that well-learned motor patterns can be produced with speed and accuracy months or even years after they were last practiced (Fleishman and Parker 1962; Ryan 1962; Meyers 1967; reviewed in Schmidt 1988). In the jargon of cognitive psychology, well-learned motor patterns are examples of "procedural" knowledge—that is, knowledge that is not under conscious control and that is relatively automatic, inflexible, and situation-dependent (Eysenck 1991).

A key assumption of the motor learning hypothesis is that practice is site

specific, such that learning a serial motor program for one route would have little effect on an animal's ability to move rapidly and safely along another route with a different spatial configuration (see above). In fact, experimental studies suggest that learning one motor program usually has little if any effect on the performance of another motor program. That is, transfer across motor skills is usually low (Cormier and Hagman 1987). Not surprisingly, the extent of transfer across motor tasks depends on both practice schedules and the degree of similarity between the tasks, although the nature of these relationships is still under dispute (Magill and Hall 1990; van Rossum 1990; Chamberlin and Magill 1992).

For our purposes, the most relevant examples from this literature involve serial motor programs that require subjects to move in space using a sequence of different motor patterns. As is true for motor learning in general, in this situation positive transfer can occur, but only if the spatial topography of the two situations is very similar (Hay and Schoebel 1990; Wood and Ging 1991; Wood and Magill 1991).

Of special relevance to serial motor programs is the concept of "part-whole" transfer. The question here is whether practice of a portion of a serial motor task is likely to enhance performance when the entire program is performed. Over the years, studies of humans have shown that effective learning of serial motor programs may not require that the entire program be practiced in its entirety. Instead, it may be more efficient to practice the most difficult portions of the sequence, and then string the portions together to form the final motor pattern (Seymour 1954; Wrightmann and Lintern 1985; Schmidt 1988).

Generally speaking, the efficacy of part-whole transfer depends on the nature of motor patterns in the sequence. If a series of motor patterns follow one another in quick succession, they may interact with one another, such that the outcome of one motor pattern affects the beginning of the next component of the series (Schmidt 1991). For example, in a gymnastics routine, the velocity and position at the end of one turn is likely to affect the muscle contractions required to produce the next movement in the routine. If the components of a serial motor pattern are highly dependent on one another, then practicing each component in isolation may have a negligible or even a negative impact on performance when the complete motor sequence is performed (Sheppard 1984; Schmidt 1991).

One method that is often used for learning serial motor skills is backward chaining, in which the subject begins by learning the last portion of a sequence, and then systematically adds on earlier and earlier motor patterns until finally the entire sequence has been assembled (Wrightmann and Lintern 1985). Backward chaining is especially useful when the final goal of a serial motor pattern is important, since it ensures that the final component in the series is practiced most, and it maintains performance of the last component as preceding components of the motor program are gradually added to the sequence.

<p style="text-align:center">HURDLE RACES IN HUMANS AND HORSES</p>

The applied literature on hurdle racing in humans and horses offers additional insights about how animals might learn to move quickly and accurately along

familiar routes. The goals of these sports are similar to those envisioned for free-living animals: fast, safe, and consistent locomotion around obstacles (humans, Cretzmeyer et al. 1974; Doherty 1980; horses, Smith 1970; Chamberlin 1973). Human and equine jumpers are first asked to learn the basic components of the motor program (e.g., how to jump safely, how to run and then jump, how to jump over obstacles of different heights). Initially, the obstacles are low and few in number, and there is little pressure for maximal speed. Gradually, speed, height, and the level of difficulty are increased, and motor patterns are strung together into sequences that reflect those used during the competitive event. The final step is extensive practice on courses that are as similar as possible to those that will be encountered during the race.

The trade-off between speed and accuracy has long been acknowledged in the applied literature, in which it is thought that pushing for maximal speed too early in a learning program may lead to falls or other accidents (Doherty 1963; Gordon 1972). Aside from the obvious risk of injuries, accidents early in a training program may also lead to motivational changes that prevent athletes from ever attaining maximal performance levels (Cretzmeyer et al. 1974). In addition, survey data from humans suggest that the intensity (e.g., speed) of practice has less impact on final performance than does the volume (e.g., duration) of practice (Hopkins 1991). Hence, human and equine athletes often practice at something less than maximal velocity, especially when they are first learning a motor program.

Although the training programs for human and equine jumpers are similar in many respects, only the former are allowed to practice the serial motor program that will eventually be used during competition. In humans, each hurdle race has a fixed number, height, and placement of hurdles, so that athletes practice on training courses that are virtually identical to the course they will later encounter during competition. In this situation, athletes and their trainers plan a serial motor program in excruciating detail; such plans include the exact number and placement of every footstep during the running phases of the race, the exact location of the takeoff for each jump, the position of the legs and body during each jump, and so on (Robison 1974; Doherty 1980). This serial motor program is then practiced repeatedly, eventually producing a smooth alternation of high-speed runs and jumps that can be automatically and reliably produced during the competitive event (Schoebel 1985; Hay and Schoebel 1990).

In contrast, steeplechase and cross-country events for horses originated from sports in which riders and their mounts ran and jumped over obstacles while chasing foxes or other prey. To this day, tradition favors the design of a novel course for each equestrian event (Carruthers et al. 1978), and horses are usually not permitted onto these courses prior to the race. Hence, in contrast to the situation with humans, equine jumpers are required to move quickly and accurately over obstacles in unfamiliar terrain. Training programs involve practice using barriers, courses, and conditions that are similar to those likely to be encountered in the final race, but horses cannot practice the exact motor program that they will use in the competitive event (Chamberlin 1973; Clayton and Barlow 1989).

Interestingly, even though horses are excluded from competitive arenas, their riders often engage in a form of "mental practice," in which specific details of a complicated series of motor patterns are planned ahead of time (Clayton and Barlow 1989). For instance, one Olympic cross-country rider reported that she walked the course a total of five times before the race. During the first few trips, she noted the location and types of obstacles and the distances and angles between them, as if assembling the equivalent of a "map" of the course. During the final walk, she mentally ran through a detailed motor program for the entire race, including her mount's gait at various locations, the takeoff and landing points for each jump, and the location and angle for each change in direction (Dawson 1989). Experimental studies with humans have shown that mental practice can improve the performance of complex motor skills, although not as much as physical practice (Adams 1990; Hall et al. 1992).

Because horses are not allowed to practice the serial motor programs specific to a given race, their performance in cross-country and steeplechase events illustrates the potential risk of traveling at high speed over obstacles in unfamiliar terrain. In contrast to human hurdle races, falls and injuries are relatively common during equine jumping events. For instance, in the years from 1837 to 1849 a total of 218 horses ran in the Grand National, the most famous steeplechase race in Great Britain (Smith 1970). Of these competitors, more than 15% fell during the race, and 2% died. Although these figures are impressive enough, it is worth noting that when fleeing from predators, any fall might be fatal.

PREDICTIONS OF THE MOTOR LEARNING HYPOTHESIS

The literature on motor learning in general and hurdle racing in particular implies that locomotion along a topographically complex route is likely to improve with practice and that practice along one route would have little or no positive effect on locomotion along other routes with different spatial configurations. Hence, this literature supports the assumption that animals fitting the conditions outlined earlier might benefit by practicing route-specific locomotor programs and that the value of a familiar home range would increase as animals perfected route-specific serial motor programs. In addition, the motor learning literature offers a number of suggestions about how animals ought to behave, if they learn site-specific locomotor programs for moving along particular routes in familiar areas.

The most basic tenet of the motor learning hypothesis is that animals should spontaneously and repeatedly move back and forth along unfamiliar routes, and the speed and accuracy of locomotion should asymptotically improve over the course of these "practice trials." Because of the potential trade-off between speed and accuracy, initially these trips should occur at less than maximal velocity. At the same time, they should occur at speeds high enough that the same types of motor patterns are used as would be used when moving over those pathways at maximal speed. For instance, if walking and running involve different motor patterns (as in humans; see Shapiro et al. 1981), initial practice sessions should involve slow running rather than fast walking.

Many workers have observed mice, rats, and other small rodents spontaneously dashing back and forth along routes in novel habitats, and, on at least a descriptive level, these animals behave as if they were practicing site-specific motor programs. For instance, domesticated rats placed in a novel habitat typically begin in one location (often a refuge), venture slowly forth to another point, and then immediately return to the refuge. Gradually, the speed of movement increases, and the animals begin to run rapidly back and forth between the refuge and other points in the area, generally behaving as if they were "laying down" routes and pathways around the area (Carr and Watson 1908; Dasliell 1930; Timberlake 1983; Leonard and McNaughton 1990).

The spontaneous nature of rapid locomotion in novel habitats is shown by experiments using unrewarded mazes, in which the animals receive no food or other reward at the goal box. Even in this situation, rodents eventually negotiate mazes quickly and accurately (Tolman and Honzig 1930; Haney 1931; Glanzer 1961; Brant and Kavanau 1964, 1965; Kavanau 1969; Timberlake and Lucas 1989; Timberlake 1990). As predicted by the motor learning hypothesis, both running time and the number of errors decline curvilinearly as a function of the time rodents spend in unrewarded mazes (Battig and Schlatter 1979; Timberlake 1983). Brant and Kavanau (1964, 1965) tested a variety of rodents in large complex mazes, and in each case the speed of locomotion increased asymptotically as a function of the amount of practice. For instance, when confronted with a maze with 67 m of tunnels, 313 right-angle turns, and 148 blind alleys, a *Mus musculus* required 30 min to reach the end of the maze on its first trial, but after 15 trips the time from start to finish was down to 2 min (Brant and Kavanau 1964).

More recently, Timberlake (1983) investigated the behavior of domesticated rats released into straight alleys in the absence of food or other conventional rewards. As in previous studies, there was an asymptotic relationship between trial number and running speed, with the rats achieving maximal speeds in about 18 trials. As the trials progressed, the subjects ran more quickly down the alley and spent more time running back and forth along the alley than in earlier trials. Initially the rats ran relatively slowly down the alley and completed relatively few round trips, but after a number of trials they were repeatedly galloping back and forth from one end of the alley to the other.

A second prediction of the motor learning hypothesis is that repeated practice should lead to automatic motor programs that can be produced while the animal engages in other tasks. Under natural conditions, automatic motor programs might allow animals to monitor the position of predators, prey, or conspecifics while moving as quickly as possible in familiar terrain (see, e.g., Ellard 1993). Hence, we can ask whether animals continue to practice moving along familiar routes even after speed and accuracy have reached asymptotic levels and whether animals develop automatic motor programs after repeated trips along the same route.

With respect to the first prediction, unrewarded maze studies show that rodents continue to gallop down mazes even after their speed and error rates show no further improvement (Brant and Kavanau 1964, 1965; Timberlake 1983; Timberlake and Lucas 1989). The development of automatic motor programs has

been investigated more formally in experiments in which rats and bats are allowed ample time to learn routes around barriers and pathways, and then barriers are placed in the middle of a previously well-used pathway. In this situation, the subjects often crash headlong into the barrier. For instance, Carr and Watson (1908) trained domesticated rats to run a maze until they did so rapidly and without error, and then placed a wall across a previously open route. On the first few trials following this change, the rats ran into the wall, often hitting it so hard that their bodies flattened up against it. It took one or two such trials before they began to move in a more cautious and exploratory fashion, after which they worked out new pathways around the barrier. The development of new routes followed the same pattern as described above: a gradual increase in speed and accuracy across successive trials, until the animals were running at high speed along the new pathways. Similar results have been obtained with bats (*Megaderma lyra, Eptesicus fuscus*) that were allowed to establish regular flight paths around obstacles in experimental rooms, after which wires were placed in a previously open flight path. As in the case of Carr's rats, the bats crashed into the wires, even though they were producing the ultrasonic cries that should have allowed them to detect them (Möhres and Oettingen-Spielberg 1949; Griffith 1958; Neuweiler and Möhres 1967).

Another prediction of the motor learning hypothesis is that animals must be able to perform basic motor patterns before stringing these together to form site-specific motor programs. Over the years, many behavioral biologists have suggested that play is one way that young mammals practice motor skills required at older ages (Brownlee 1954; Fagen 1982; Chalmers and Locke-Haydon 1984; Martin and Caro 1985), and locomotory play often includes the types of motor patterns required for rapid, accurate movement in any home range (review in Fagen 1981). As predicted by the motor learning hypothesis, play involving basic motor patterns (e.g., running, jumping, climbing, abrupt changes in speed or direction) typically occurs before young mammals begin to move at high speed around barriers and obstacles in their natal home range. For instance, young rhesus monkeys between 6 and 12 wk of age first perform simple motor patterns (lurches, hops), then engage in more elaborate motor "projects," such as repeatedly leaping up to a particular branch (Simpson 1976). Eventually, many infants develop complicated serial motor patterns involving runs, leaps, and climbs, with which they repeatedly trace particular routes around their natal area (Simpson 1976).

Another insight from the motor learning literature is that rapid, safe locomotion along a complicated route is likely to require two different serial motor programs: one for each direction of travel. In fact, there are already hints that bats and rodents learn two different motor programs for a given pathway. For instance, Hall and Coulter found that nets made of fine threads often catch *Myotis lucifugus* as they are flying into the mouth of a mine tunnel, whereas when the same bats are flying out they usually detect the net and fly away from it (cited in Griffith 1958, p. 161). This phenomenon was tested more formally in an experiment by Neuweiler and Möhres (1967), in which largewinged bats (*Megaderma lyra*) were trained to avoid an obstacle (a 120-μm thread), and then the obstacle was removed. While some bats immediately noticed that the thread was no longer there,

some of them continued to avoid the nonexistent thread for days. More important, the bats sometimes stopped avoiding the thread going in one direction several days before they stopped avoiding it coming the opposite direction.

Blodgett (1929) approached the same question using domesticated rats and a different technique. He trained rats to run in one direction through a maze, and then compared their performance traveling in the reverse direction with that of naive animals. In this situation, the experienced animals ran as slowly and made as many errors as the rats with no experience in the maze, which implies that learning an "outgoing" route between two points had no effect on the subjects' ability to move quickly and accurately along that same pathway in the "incoming" direction.

The motor learning literature also specifies the conditions in which animals would be most likely to practice and use learned motor programs when moving in topographically complex habitats. In the field, repeated spontaneous bouts of apparently purposeless, high-speed locomotion along particular routes should be most obvious among the age classes and at the times of year when animals first encounter novel home ranges or territories. For instance, in birds or mammals with strong site fidelity among adults, one might expect two peaks of spontaneous route-learning behavior: one for juveniles in their natal home range and another after dispersers settle into their final adult home range or territory. If the timing of these events is predictable within a species, then one might also expect ontogenetic changes in the extent to which individuals rely on well-learned motor programs for spatial orientation. For instance, wild rats follow the typical vertebrate pattern, in which juveniles disperse whereas adults are sedentary and site faithful (Barnett 1975). Interestingly, experimental psychologists working with domesticated rats have found that old rats are more likely to depend on learned motor programs for navigation than are younger individuals (Barnes et al. 1980).

The literature on motor learning also specifies the techniques animals might use when assembling routes requiring a complicated series of different motor patterns. Individuals might employ backward chaining when learning serial motor programs in which the timing and accuracy of the final component is especially important (e.g., an escape route that ends with a dive into a burrow). Alternately, partial practice might be used for particularly demanding portions of longer serial motor programs or for sequences whose performance is not affected by preceding and following motor patterns. For instance, a run followed by a jump should probably be practiced together, since the height and takeoff position for the jump would depend on the positions of the feet at the end of the run (Schmidt 1991). In contrast, it might be possible to practice a complicated sequence of turns separately from a straight run along unobstructed ground.

If further experimental studies support the motor learning hypothesis, then it might be worthwhile to pursue comparative questions about the evolution of site-specific motor learning in animals. All else being equal, site-faithful species that evolved in topographically stable habitats should be more likely to learn site-specific motor programs than species that evolved in habitats with shifting barriers and obstacles to movement or species in which individuals rarely remain in the same place for long. Similarly, species with small home ranges might rely

more heavily on learned motor routes and pathways than closely related, otherwise comparable species with much larger home ranges. If animals escape from predators, aggressive conspecifics, or other danger by racing to a safe refuge, then species with only one refuge per home range might rely more heavily on learned motor routes than otherwise comparable species with many refuges per home range.

<div align="center">ALTERNATIVE HYPOTHESES</div>

As was emphasized earlier, motor learning is only one of several different processes that occur as animals become familiar with novel areas or spatial configurations. The motor learning hypothesis makes a number of predictions about how animals should behave in this situation, but some of these predictions are shared with alternative explanations for the behavior of animals in unfamiliar space. For example, locomotion around a novel home range may help a newcomer learn the location and nature of salient features of that area, while movement along specific routes might aid in the formation of mental maps (see above; also Gallistel 1990; Poucet 1993). Hence, tests of the motor learning hypothesis require identification of predictions that are unique to this hypothesis.

One unique prediction of the motor learning hypothesis is that animals should spontaneously travel at high speed in unfamilar areas. If a newcomer's primary goal is to acquire knowledge about the nature and location of important features in a habitat, then it would not be expected to travel at high velocity while becoming familiar with that habitat. Indeed, given the potential trade-offs between speed and safety (see above), exploration and spatial orientation should occur at the lowest speeds compatible with efficient information gathering. In contrast, the motor learning hypothesis argues that spontaneous locomotion at high (if not maximal) velocities should be observed relatively soon after animals settle into novel habitats or encounter obstacles that require a change in a familiar route or pathway.

Students of spatial orientation have suggested that the typical back-and-forth locomotion rats exhibit in novel areas functions in map construction, providing the animals with estimates of the distances and angles between important topographic features (Gallistel 1990; Poucet 1993). However, it is not apparent why a repeated series of galloping runs would provide more accurate information than a few deliberate trips through the same area. Indeed, domesticated rats can orient themselves in space without previous experience along a given route, use different motor programs than were employed for previous trips through an area, rely on distal or proximate environmental cues rather than motor experience, and exploit an impressive array of different maze-learning strategies (reviews in Gallistel 1990; Leonard and McNaughton 1990; Papi 1992; Poucet 1993). Hence, repeated high-speed trips back and forth along particular pathways are clearly not required for spatial orientation in rats, although such learning might be an incidental benefit of this behavior.

Another novel prediction of the motor learning hypothesis is that in situations calling for high-speed locomotion, animals should prefer to use well-practiced

routes rather than less familiar pathways. This prediction follows from the assumption that the speed, accuracy, consistency, and automaticity of serial locomotor programs increase as a function of the amount of practice. In contrast, if locomotion along particular pathways primarily functions in information acquisition or map construction, then once the home range was familiar there would be little reason for animals to favor highly practiced routes when fleeing from predators, chasing conspecifics, or handling other situations requiring rapid, safe locomotion around obstacles. Indeed, much of the current orientation literature focuses on the formation of "cognitive maps," mental representations that allow individuals to use completely unfamiliar routes when traveling between important points within a familiar area (Gallistel 1990; Poucet 1993). But even in species capable of true navigation, the motor learning hypothesis predicts that individuals offered a choice between a well-practiced route to a refuge and a less familiar (but shorter) route would choose the former when challenged to run as quickly as possible from a predator or other escape-eliciting stimuli.

The motor learning hypothesis also differs from alternative hypotheses in predicting that animals learn two serial motor programs for each route, one for each direction. As noted above, there is already some evidence favoring this prediction for bats and rats. In contrast, bidirectional route learning is not expected if one assumes that the primary function of locomotion is information acquisition or spatial orientation. For instance, Gallistel (1990, p. 152) attempted to explain the bidirectional route formation of *Megaderma* in terms of map formation, suggesting that for each route they regularly fly, these bats "construct a detailed map of the terrain immediately surrounding that route, somewhat like the route-specific maps that an automobile club supplies to tourists." Presumably, these detailed maps were so direction specific that the bats failed to recognize the landmarks for one direction when flying the opposite direction. However, other experiments have shown that *Megaderma* can orient correctly even when they deviate from previously familiar routes and, conversely, that their orientation is disturbed by the displacement of objects far from their habitual flight paths (Neuweiler and Möhres 1967). Hence, these bats are clearly capable of using cues distal to familiar flight paths for orientation, and they need not rely on direction-specific, route-specific maps to navigate in familiar areas. Taken together, these experiments imply that bidirectional route formation in *Megaderma* increases the efficiency of locomotion rather than the efficiency of orientation.

Another unique prediction of the motor learning hypothesis is that animals should be especially sensitive to manipulations that require a change in a previously learned serial motor program. It is a truism that changes in a familiar spatial situation elicit exploration (Thinus-Blanc et al. 1987). However, the motor learning hypothesis predicts that an object blocking a habitual route used for high-speed locomotion would have a much more dramatic effect on a subject's subsequent locomotor behavior than if the same object were placed in a less obstructive position. That is, adding a barrier to a habitually used pathway should lead to an increase in locomotory activity and the eventual emergence of an alternate locomotor route around the barrier, whereas the same object placed adjacent to the pathway should elicit less spontaneous locomotor behavior. In

contrast, if an animal's primary goal is to determine the nature and location of objects in its home range, then novel objects should elicit comparable amounts of exploratory and locomotory activity regardless of their position relative to the resident's previous routes of travel. It might be interesting to test this prediction in a species in which successive owners work out different routes when moving around the same territory (Howard 1920), such that an object placed in a given location obstructs the habitual route of one owner but not another.

CONCLUSIONS

If further studies support the hypothesis that animals learn site-specific motor programs for rapid, safe, and consistent locomotion around familiar areas, then the motor learning hypothesis would have interesting implications for a variety of problems in behavioral ecology. For instance, the prior residency advantage in territorial species is normally expressed in terms of the amount of time a resident has spent in an area (Figler and Einhorn 1983; Beletsky and Orians 1987, 1989; see also introductory text, above). If motor learning enhances the value of a territory, then the prior residency advantage in territorial animals might vary as a function of the amount of practice a resident has had traveling around the barriers and obstacles in the territory (see also Martin 1986). Locomotory practice might also provide residents with direct advantages when interacting with intruders. A number of field biologists have observed avian territory owners chasing intruders into mist nests on their territories, while avoiding these nets themselves (see, e.g., Kamil 1988; N. Nur, personal communication). In order for this strategy to be effective, the resident must not only know the location of the net but be capable of performing the aerial maneuver required to evade it at the last second. If site-specific locomotory practice gives residents an advantage over intruders, then residents might signal their superior motor knowledge of the area when interacting with intruders. For example, residents might chase intruders at high speed through complicated routes around barriers and obstacles rather than pursue them through open areas.

With respect to the animal play, the motor learning hypothesis offers some clear, testable predictions about the functional significance of certain types of locomotory play. In contrast to hypotheses that focus on the potential benefits of juvenile play for adult performance (reviews in Fagen 1981, 1982; Martin and Caro 1985), the motor learning hypothesis suggests that juvenile mammals may obtain short-term benefits from repetitive locomotory practice along routes in their natal area, in terms of improved speed, safety, and efficiency when moving along those routes in the near future. In addition, the motor learning hypothesis suggests that spontaneous, repetitive, rapid trips along complicated routes in a home range should not be confined to young animals but should occur whenever individuals move into novel areas in which they are likely to remain for appreciable periods of time.

In summary, the motor learning hypothesis is a good example of a problem in animal behavior that may benefit from simultaneous investigation at proximate and ultimate levels of analysis (Stamps 1991; Real 1992; Huntingford 1993). The

literature on motor learning in general and hurdle racing in particular suggests that animals may need to practice moving around barriers and obstacles in an area in order to become proficient at moving rapidly, safely, and efficiently in that area. This literature also makes a number of predictions about how animals should behave, if they learn site-specific locomotory programs when entering unfamiliar home ranges and territories. Indirect evidence supports some of these predictions, and most of them could be easily tested using rodents, lagomorphs, or other animals that fit the criteria for the motor learning hypothesis. If site-specific motor learning is important in free-living animals, then this proximate mechanism may help explain why many animals seem to value familiar home ranges and territories.

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