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The Economy of Winter: Phenotypic Plasticity in Behavior and Brain Structure

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Abstract. Mobile animals must learn the spatial distributions of resources. The cost of foraging increases dramatically for temperate-zone animals during the winter. Two strategies may be used to balance the energetic budget: reducing costs of foraging and reducing need to forage. Both strategies are correlated with changes in brain structure, specifically in the hippocampus, a fore-brain structure used by birds and mammals to map spatial distributions of resources. Small mammals that reduce their need to forage, through hibernation or reduction in body size, show a specific reduction in the structure and size of the hippocampus. The costs of foraging can be also decreased by migration to better foraging conditions or by food-storing, both of which decrease the temporal heterogeneity of food resources. Both of these latter strategies are associated with increased hippocampal structure; for food-storing birds, this increase is a seasonal phenomenon. Thus not only behavior, but also learning ability and even brain structures in adult animals, may be phenotypically plastic in response to the changing demands of the environment.

Introduction

To every thing there is a season, and a time to every purpose under the heaven . . .

—Ecclesiastes, 3:1

Behavior and neural structure evolve in response to changing environments, not static ones. When interactions between the environment and the genotype result

in a variety of phenotypes, this is called 'phenotypic plasticity' or "the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions." (West-Eberhard, 1989). The phenotype includes "all aspects of an organism other than the genotype, from the enzyme products of the genes to learned behaviors and the effects of disease." (West-Eberhard, 1989). Thus questions of plasticity in behavior and neural structure, usually addressed by the discipline of cognitive neuroscience, or the neural basis of cognitive abilities, may be seen as an example of phenotypic plasticity, and fit into the larger framework of evolutionary processes.

Behavior is perhaps the most plastic of phenotypic traits, and as such has long been seen as a unique agent of evolutionary change (Weislo, 1989). The neural bases of behavior, in contrast, are usually considered to be a constraint on the range of behaviors, tethering them to the information-processing capacity of a species' predetermined brain size and structure. The idea that both behavior and brain can change in response to environmental challenge is relatively new. It was first recognized in the extraordinary ability of forebrain nuclei in canaries to add new neurons in advance of the annual breeding season. This dramatic example of adult neurogenesis in response to photoperiod revolutionized our perception of adult brain plasticity (Nottebohm, 1981). Yet it can also be seen simply as phenotypic plasticity: a change in brain phenotype in response to changes in the environment. Environmental cues trigger a change in the brain structure, which is correlated with an increase in behavioral plasticity, *i.e.*, the ability to produce nuptial advertisement song. The production of song in turn creates more changes in the environment, as females arrive, attracted by the song, and as their arrival initiates the breeding process. The production of offspring, and the

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increase in individual fitness, is of course the driving force behind this remarkable phenotypic plasticity in behavior and the brain, which is subject to sexual selection (Searcy and Andersson, 1986; Jacobs, 1996).

Thus our understanding of phenotypic plasticity must include not only plastic behavior, such as learning, but must ask whether its neural basis is plastic as well. The question I would like to address in this review is whether such adaptation in the songbird is extraordinary, or whether it is simply our first example of the phenotypic plasticity of cognitive abilities and their neural basis. If the latter, then where should we search for other examples? Clearly we must first identify what animals learn about their environments, *i.e.* their 'cognitive niche' (Jacobs, 1995), and second, the conditions under which the cognitive niche changes.

It is a basic tenet of behavioral ecology that mobile animals must track the spatial and temporal distribution of critical resources, and that such spatiotemporal distributions underlie and predict adaptive patterns of behavior, such as mating systems (Emlen and Oring, 1977). Thus an animal's ability to learn about space is critical to its adaptive response to a changing environment, and spatial learning should evolve in response to the predictability of spatial patterns of resources. Theoretical models of the evolution of learning ability predict that learning evolves in response to intermediate levels of environmental predictability (Stephens, 1991). At the two extremes, the environment is either perfectly predictable or completely unpredictable, so there is no advantage to tracking and learning spatial distributions. But if the environment is predictably unpredictable, then those individuals who can learn to recognize the changes and predict the distributions will clearly enjoy a fitness advantage over their less perspicacious competitors (Stephens, 1991).

The Economy of Winter

For animals living in seasonal environments, the changing of the season is a highly reliable predictor of a change in resource distribution. Shortening daylengths are an unmistakable predictor of a decrease in temperature and a change in the abundance and distribution of food. Thus foraging behavior, and the brain structures that support it, might be expected to show equally predictable changes in response to winter. How might such changes be organized? A simple answer is that there is a reduced energy budget for the winter economy and that to balance this budget, an animal has two options: it can decrease its costs of foraging or it can decrease its requirement for foraging.

Foraging costs could be decreased by adaptive changes in behavior, such as migration to better foraging areas or storage of food, whereas basic requirements can be altered only by changing the metabolic costs of daily activity. Reproduction is expensive; metabolic costs can be largely reduced by postponing reproduction or ceasing to reproduce. In addition, an animal can decrease basic metabolic costs through hibernation or torpor, through reduction in the absolute size of its physical structure, such as its body or brain size, or through a combination of both.

What would be the cognitive consequences of such winter strategies? One might expect to find changes in the behaviors needed to track spatial distributions. In birds and mammals, a large part of this function is mediated by the hippocampus, or hippocampal formation. This is classically defined in mammals as the Ammon's horn and the dentate gyrus; in birds the relevant brain regions are also known as dorsomedial cortex, and include the hippocampus and the area parahippocampalis (Figs. 1 and 2). The hippocampal formation (hereafter referred to as the hippocampus) is an important fore-brain structure in birds and mammals. Damage to this structure has a variety of effects; however, one of the most consistent and important side effects is loss of the ability to learn new spatial relationships among known landmarks (O'Keefe and Nadel, 1978). For example, laboratory rats with hippocampal damage can no longer create shortcuts through a complex spatial environment; every new path must be laboriously discovered rather than extracted from the rat's memory of the landscape. Invertebrate species, which do not have a hippocampus, cannot make such mental shortcuts (Dyer, 1991), which is the definition of a cognitive map (Tolman, 1948). Thus the hippocampus, in birds and mammals, is required to create cognitive maps, or flexible mental representations of spatial arrays (Bingman *et al.*, 1990; O'Keefe and Nadel, 1978). Further, as might be predicted from this function, the size of the hippocampus within and between species is directly correlated with space use. Its relative volume (volume relative to the size of the whole brain) varies among species with different foraging tactics, and between males and females of the same species when they differ in their space use. For example, a larger home range or a specialized foraging ability, such as scatter hoarding, predicts a relatively larger hippocampus. Closely related species or members of the opposite sex that face lesser spatial demands have relatively smaller hippocampi (Sherry *et al.*, 1992, 1993; Jacobs, 1995).

Because winter is a time of changed spatial distributions of resources critical to individual fitness, such as food and receptive breeding partners, one might predict that a brain structure involved in learning about these

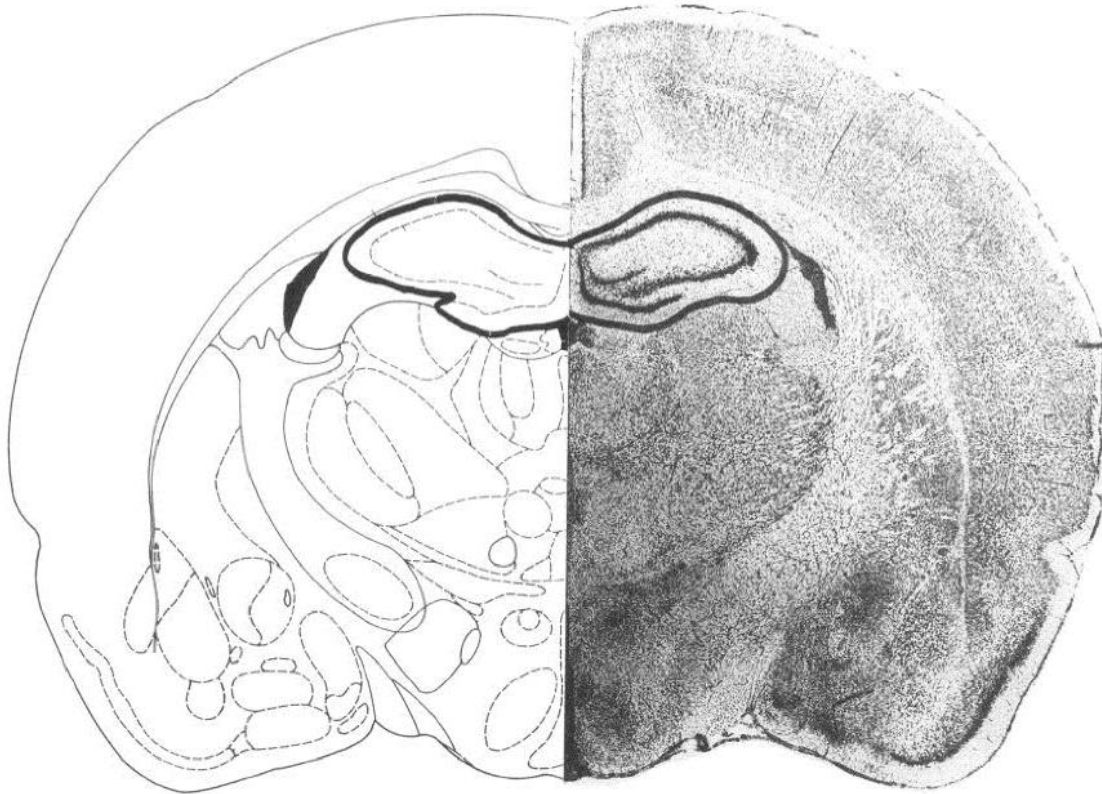


Figure 1. Diagram of a coronal cross-section of the hippocampal formation in the laboratory rat. The right side of the figure shows the Nissl-stained brain section; the left side of the figure shows the boundaries of brain regions. The hippocampus (Ammon's horn and dentate gyrus) are outlined. Adapted from Paxinos and Watson (1986).

distributions would also change with the seasons. It should again be noted that the hippocampus is also involved in nonspatial brain functions, such as the ability to discriminate odors (Eichenbaum *et al.*, 1992) and is not involved in some spatial abilities, such as the ability to remember the location of an object (Cave and Squire, 1991). However, structures may have more than one function, and we would not expect that the size of a structure could be predicted from each of disparate functions, but only from its primary function. In rodents and birds, the evidence strongly favors the hypothesis that the primary function of the hippocampus is to create mental representations of space (Nadel, 1991). Thus I will limit the following discussion to the question of how spatial behavior and the hippocampus may adapt to winter in temperate-zone birds and mammals, according to the two types of winter strategies: reduction of foraging need and reduction of foraging cost.

Reducing foraging requirements

An important strategy in reducing the need to forage is to decrease body size and hence decrease absolute en-

ergetic needs. Many small mammals such as the meadow vole (*Microtus pennsylvanicus*) show reductions in body weight of up to 20% in winter or in short daylengths (Dark and Zucker, 1985).

Another winter strategy employed by small mammals in the temperate zone is to undergo hibernation, dropping their body temperature to a few degrees Celsius (Carey, 1993). This considerable savings in metabolic expense might be expected to have dramatic effects in the brain. Because a hibernating animal lives in an environment that requires no processing of new spatial information, one might expect concurrent decreases in the allocation of brain space used for such processing. Although this conjecture may seem far-fetched, such changes have been demonstrated in hibernating Siberian ground squirrels. The dendritic structure of hippocampal neurons changes dramatically between the state of torpor, an awakened state (such as 2 h after provoked arousal) and a spontaneously active state (between torpor bouts, after spontaneous arousal). In the middle of hibernation, dendrites are significantly shorter and less branched, and they have fewer dendritic spines than dendrites in squirrels who become spontaneously active between hiberna-

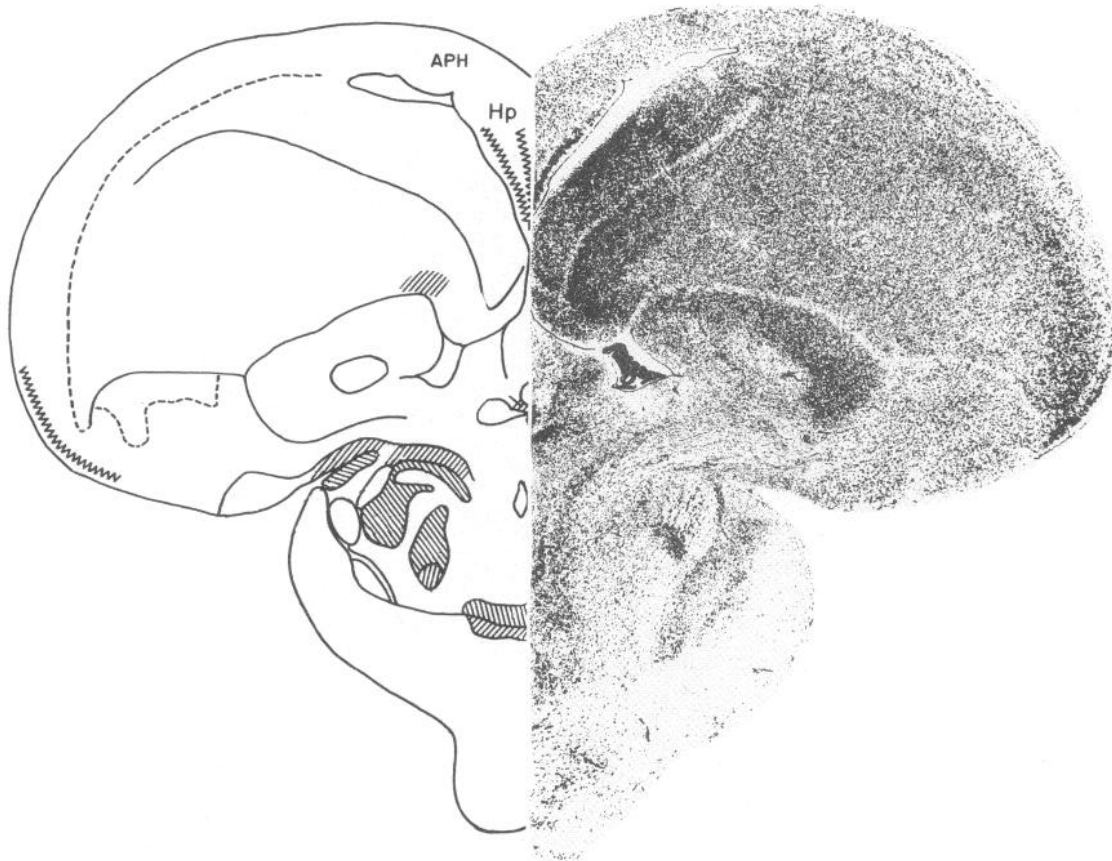


Figure 2. Diagram of a coronal cross-section of the hippocampal formation (HP, APH) in the laboratory pigeon. The right side of the figure shows the Nissl-stained brain section; the left side of the figure shows the boundaries of brain regions. The hippocampus (HP) and area parahippocampalis (APH) are labeled. Adapted from Karten and Hodos (1967).

tion bouts. Most remarkably, the changes in dendritic structure occur within 2 h of a squirrel's arousal from torpor, and it is suggested that such changes must therefore occur repeatedly throughout hibernation, with cyclic changes occurring with each bout of spontaneous activity (Popov and Bocharova, 1992; Popov *et al.*, 1992). Of course, it is possible that this remarkable process was occurring throughout the squirrel brain; other regions were not assessed in these studies. Future work should address this question, but nonetheless, such plasticity does exist in the hippocampus.

This plasticity may well be hormonally mediated because gonadal, thyroid, and adrenal hormones produce similar changes in the dendritic arbor of hippocampal pyramidal neurons in the laboratory rat (McEwen *et al.*, 1991). The hippocampus is, in fact, a remarkably plastic brain structure. As in the song nuclei of passerine birds, new neurons continue to be recruited in the granule layer of the dentate gyrus of the hippocampus in the adult laboratory rat (Altman and Bayer, 1990), and these new neurons make functional connections (Kaplan and Bell,

1983). But perhaps it is not a coincidence that such plasticity, rare in the adult brain, happens to be found in the hippocampus, a structure that plays such an important role in the neurobiology of learning.

Seasonal changes in spatial behavior and hippocampus in mammals. Evidence suggests that seasonal patterns of spatial behavior are linked to seasonal changes in the hippocampus. Voles, small rodents in the genus *Microtus* (subfamily Arvicolinae, family Muridae), are ideal subjects with which to test hypotheses on the evolution of cognitive adaptations, in particular the cognitive consequences of different mating systems (Gaulin and FitzGerald, 1986, 1989; Kavaliers *et al.*, 1993) and their underlying neural bases (Insel and Shapiro, 1992; Jacobs *et al.*, 1990; Shapiro *et al.*, 1991; Winslow *et al.*, 1993). Spatial learning, in particular, has proved an excellent model. Monogamous species, such as pine (*M. pinetorum*) or prairie (*M. ochrogaster*) voles, show little or no sexual dimorphism in space use in the field (FitzGerald and Madison, 1983; Getz and Hofmann, 1986). In contrast, among polygamous species, such as meadow

voles (*M. pennsylvanicus*) and montane voles (*M. montanus*), breeding males typically utilize a much larger home range than do breeding females (Gaulin and FitzGerald, 1988; Jannett, 1981; Madison, 1980). The presence or absence of sex differences in space use is correlated with similar patterns in spatial learning; sex differences with a male advantage (male performance superior to female performance) are present in polygamous meadow voles (Gaulin and FitzGerald, 1986, 1989; Kavaliers *et al.*, 1993), but sex differences are absent in monogamous voles (Gaulin and FitzGerald, 1986, 1989).

These patterns of space use are seasonal, however. Over the four seasons, polygamous meadow voles show marked changes in social system and space use (Gaulin and FitzGerald, 1988; Madison and McShea, 1987). In the winter, male home range decreases to a size similar to that of nonbreeding males or females; this is accompanied by an increase in social tolerance and the formation of mixed sex and lineage groups (Madison and McShea, 1987).

These behavioral changes are correlated with changes in brain structure. Under natural conditions, voles show large seasonal fluctuations in cranial volume and brain weight (Dehnel, 1949; Yaskin, 1984; Yaskin, 1989). These measures reach a maximum during the summer breeding season and a minimum in winter. The structural changes appear to be triggered by photoperiod, *i.e.* the number of daylight hours. In the laboratory, meadow vole males reared under summer photoperiod (14 h daylight) had heavier brains than males reared under winter photoperiod (10 h daylight) (Dark *et al.*, 1987, 1990). Rearing photoperiod had no effect on normal females, although females masculinized with neonatal testosterone injections also showed this effect of photoperiod on adult brain size (Whaling *et al.*, 1990). Photoperiod thus appears to be the proximate cue triggering changes in brain mass, and the response appears to be sexually dimorphic.

Such drastic changes in spatial and social ecology, accompanied by gross changes in brain volume, might be expected to modulate spatial learning ability. This has now been shown in two related species, montane voles (*Microtus montanus*) and the deer mouse (*Peromyscus maniculatus*), both of which show sex differences in natural space use (Jannett, 1981; Galea *et al.*, 1994). Rodents reared under long (*i.e.*, summer) daylengths show sex differences in spatial learning, with a male advantage, on the Morris water maze (Morris, 1984), a task that yields consistent sex differences in laboratory meadow voles (Kavaliers *et al.*, 1993). However such differences were absent in rodents reared in short (*i.e.*, winter) daylengths (Galea *et al.*, 1994; Jacobs *et al.*, unpub.).

Data on spatial learning ability in wild-caught meadow voles (*M. pennsylvanicus*) suggest that such

differences develop in response to lengthening photoperiod. Wild meadow voles captured during natural short days (early December) were housed in the laboratory under long-day conditions (14 h daylight). After several weeks of habituation under the longer photoperiod, they were tested on a series of seven symmetrical mazes (Dav-

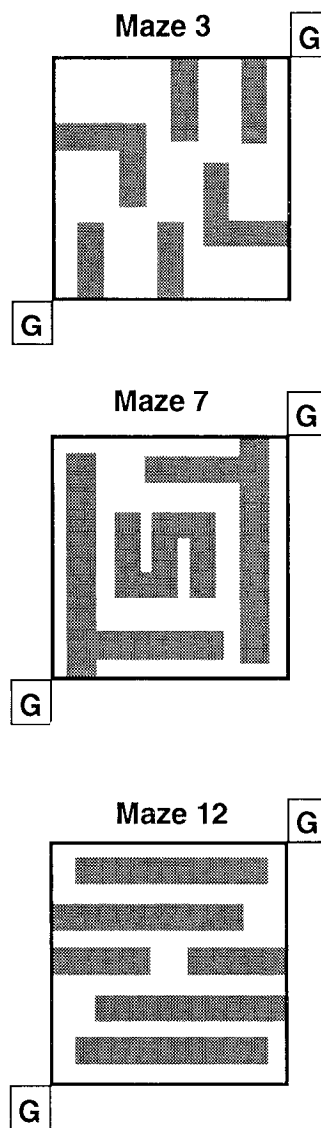


Figure 3. Schematic of symmetrical maze design, showing three of the seven maze configurations used to test meadow voles. Adult male and female voles were trapped in western Pennsylvania in late fall and brought to the laboratory. Here they were housed under long (14:10) photoperiods. Once habituated to the laboratory, food-deprived voles were required to shuttle between the two goal boxes (indicated by 'G') to obtain a food pellet. Each vole was allowed to shuttle back and forth in the maze until it had completed three error-free runs or until it had completed 12 runs. Each vole was tested only once per maze, and test periods were separated at intervals of several weeks. Performance was measured as the number of errors made; an error was defined as an entry into a blind alley. Further methodological details can be found in Gaulin and Fitzgerald (1989).

enport *et al.*, 1970; Fig. 3), at intervals of approximately 1 month (details in Gaulin, 1995). As testing proceeded on the series of mazes, the voles had thus been housed for progressively longer periods under summer photoperiods. The voles initially showed no sex differences in maze performance; however, after several months under long-day conditions, a sex difference in performance indeed developed (Gaulin, 1995; Jacobs *et al.*, unpub.; Fig. 4).

Exposure to an increased photoperiod produces significant increases in brain and body weight in meadow voles, a response that is more pronounced in males (Dark *et al.*, 1990). Therefore, one might expect that not only brain weight but also hippocampal weight would increase or decrease predictably with season, and that this response would be more pronounced in males. Vladimir Yaskin has demonstrated such a specific response in small mammals, including four species of voles and two species of shrews, in various sites in the former Soviet Union. In wild-trapped voles and shrews, many parts of the brain are larger in the summer than during the winter. The greatest relative change between seasons in the size of a major brain structure, as measured by either dry or wet weight, is seen in the hippocampus. Other structures that were measured included neocortex, striatum, cerebellum, and olfactory bulbs. In shrews, the

average adult hippocampal weight is 19.7% lighter in animals trapped in the fall than in those trapped the preceding summer, and 25.6% heavier in the spring-trapped adults than in adults trapped in the winter. Moreover, this change is sexually dimorphic both in shrews and voles, showing a greater increase in males in the spring, as would be predicted from concomitant increase in space use by males during the breeding season (Yaskin, 1984; Yaskin, 1994).

An important point to address, however, is that we do not know what savings in metabolic cost are created with decreases in specific brain structures, such as the hippocampus. In addition, the metabolic cost of the tissue itself (which may weigh only a few milligrams) is the tip of the iceberg. It is the cost of the behavior that is expensive. Thus the cost of increasing the volume of song nuclei is small; the cost of using these nuclei to attract mates is high. Consequently we must view the system as a whole and ask: what is the combined cost of this behavioral plasticity? This is the cost that influences the course of natural and sexual selection; what is surprising is that certain brain structures, such as the song nuclei and the hippocampus, are unusually plastic, as are the behaviors they mediate.

Reducing foraging costs

There are at least two good ways to reduce the cost of foraging in the winter. The first method is to escape a cold climate by migrating to a warmer one. Not surprisingly, migration is a strategy frequently adopted by flying animals such as birds and insects (Alerstam, 1990). Migration allows an animal to forage all year under summer conditions of temperature and food abundance, and thus one might expect no change in learning ability. However, the actual migration may require special spatial learning abilities. Homing pigeons, for example, have larger hippocampi than other pigeon strains, and the hippocampus is used for sun-compass orientation and for recognition of the home loft (Bingman, 1990). There is also recent evidence that passerine bird species that migrate have relatively larger hippocampi than species that do not migrate, when other ecological and phylogenetic factors have been accounted for (Healey, pers. comm.). Thus migration may require seasonal changes in cognitive abilities, such as spatial orientation, and may be accompanied by seasonal changes in the hippocampus.

The strategy of food-storing. Changes in hippocampal structure and spatial behavior are indeed seen in bird species that employ a different strategy to reduce foraging costs: storing food. Food-storing is a common strategy both in temperate-zone and tropical-zone faunas, to redistribute food surplus more evenly in time. Often the food is redistributed more evenly in space as well. For

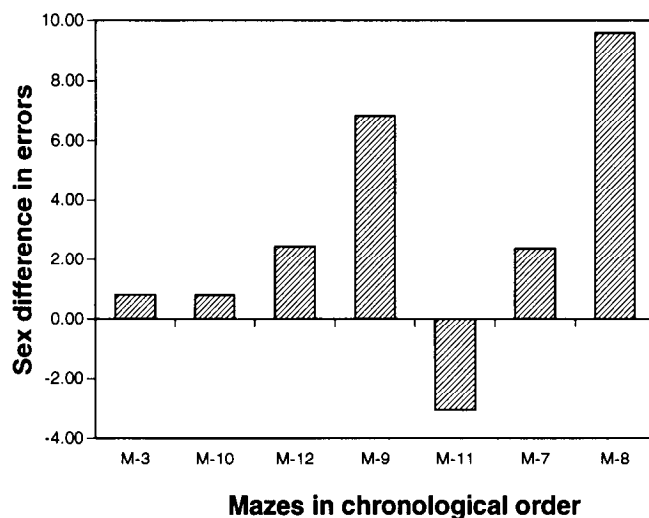


Figure 4. Changes in the sex difference in symmetrical maze performance in wild-caught meadow voles. Sex difference in maze performance is shown for a series of seven mazes. Maze performance is ordered chronologically; *i.e.* shown in the order in which voles were tested. Thus performance on the first and last maze was separated by about 7 months. Sex difference in performance was estimated as the difference (female minus male) in errors between males and females ($n = 5$ females, 4 males). There was a significant increase in the size of the male advantage in performance over the course of testing, probably related to the increased time spent housed under long photoperiods (Gaulin, 1995; Jacobs *et al.*, unpub.).

example, a gray squirrel (*Sciurus carolinensis*) may harvest 10,000 hickory nuts and cache these nuts one by one over an area of a few hectares. The squirrel then may use spatial memory to retrieve these caches (Jacobs and Liman, 1991). The use of spatial memory to retrieve caches is correlated with increased hippocampal volume in both birds and mammals (Jacobs and Spencer, 1994; Sherry *et al.*, 1992). Hence one might predict that there would be seasonal changes both in the behavior of food-storing in this manner and in the hippocampus, a structure necessary for the retrieval of food caches (Sherry and Vaccarino, 1989).

Seasonal changes in the hippocampus in food-storing birds. Recent evidence suggests that seasonal changes in hippocampal structure and function do occur in food-storing birds. In the fall, black-capped chickadees (*Parus atricapillus*) begin storing food in scattered locations throughout their group territory. In the laboratory, such caches are retrieved using spatial memory of locations, an ability requiring the hippocampus; chickadees with hippocampal lesions can no longer locate their food caches, although they retain other types of spatial information (Sherry and Vaccarino, 1989). The behavior of scatter hoarding itself appears to be triggered by changes in photoperiod. Wild-caught chickadees store more intensely under autumn photoperiod conditions than under spring conditions (Shettleworth *et al.*, 1995).

The seasonal modulation of food-storing behavior is paralleled by seasonal changes in hippocampal structure. Wild black-capped chickadees trapped throughout the year show a seasonal pattern in hippocampal volume, relative to the volume of the telencephalon. The greatest volume is seen in October (Smulders *et al.*, 1995). During this period, chickadees start storing seeds intensely throughout their newly expanded home range. Since increased food-storing behavior is correlated with increases in hippocampal size in young parids (Clayton and Krebs, 1995), this suggests that a similar plasticity may be seen in adults. The change in volume is also accompanied by an increase in neurogenesis in the chickadee hippocampus (Barnea and Nottebohn, 1994). The increase in neurogenesis also peaks in October, suggesting that the behavioral changes during this period are key to understanding plasticity of the adult hippocampus.

Mammalian food-storers, such as gray squirrels, also show seasonal cycles in storing behavior in the field, although not in captivity (pers. obs.). In contrast, chickadees are seasonal both in the field and in the laboratory, even under constant photoperiod (Sherry, pers. comm.). Hence it is unclear whether scatter-hoarding mammals, such as gray squirrels, would show the same changes in hippocampal size as do black-capped chickadees. In addition, male squirrels greatly increase their home range in the winter during the breeding season, which should

also be correlated with increases in hippocampal size. Seasonal changes in hippocampal size might be explained by two selective pressures: to increase the efficiency of food-storing and to increase the efficiency of breeding behavior (Jacobs, 1996). Such a pattern of combined sex and species differences in the hippocampus has already been found in kangaroo rats (Jacobs and Spencer, 1994). I am currently testing this idea by measuring hippocampal size in scatter-hoarding rodents collected at different seasons.

Conclusion

One might say that there are only two ways to face the winter: reduce costs by reducing the need to forage by opting for a more sedentary lifestyle with less cognitive capacity, or reduce costs by redefining the game, by migration or food-storing. These latter tactics appear to require more movement, more cognitive processing, and hence a larger investment in brain structure, which, it appears, can be 'bought' with the new savings in foraging costs.

Although these patterns of seasonal changes in brain structure challenge our notion of how a brain is supposed to behave, perhaps this notion has a historical explanation: most neuroscience research is conducted on animals housed under constant photoperiod. Thus the remarkable plasticity seen first in canaries and now in small rodents and food-storing birds may not be remarkable at all, but quite commonplace among species that live in seasonal environments. Seasonal changes in spatial learning have even been documented in humans, correlating with annual cycles of testosterone in normal men (Kimura and Hampson, 1994) and in patients suffering from seasonal affective disorder; these patients show deficits in spatial cognition tasks (O'Brien *et al.*, 1993). Phenotypic plasticity in learning ability and brain structure may well be a general phenomenon; it already appears to have clinical correlates in humans.

For many reasons, then, the phenotypic plasticity of learning is a problem worth further study. The implications for behavioral ecology are functional: the behavior of a winter and a summer individual may be adapted to different ecological conditions; foraging decisions in one season may be optimized relative to different cognitive capacities. Or, males or females within a species could show enhanced abilities to track resources depending on season, which would allow them to forage more efficiently than other age-sex-season classes. Future generations of foraging models might need to incorporate seasonal changes in neural and cognitive capacity to accurately describe the behavior of a species. In any case, there is no doubt that an interface is growing between cognitive neuroscience and behavioral ecology—one

that may soon change neuroscientists' ideas about the brain and its limits and capacities, as well ecologists' notions about the plasticity and evolution of complex behaviors.

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