



Hippocampus and Spatial Memory in Brood Parasitic Cowbirds 11

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Abstract

Natural selection can modify cognition and its neural mechanisms if these modifications enhance fitness. Brood parasites are ideal subjects to study sex-specific adaptations in cognition and the brain because it is often females that search for potential host nests, and some species as a result show a reversal of sex-typical space use usually seen in mammals. Research from North and South America shows that female brown-headed (*Molothrus ater*) and shiny (*M. bonariensis*) cowbirds have a larger hippocampus than males, and female brown-headed cowbirds exhibit more hippocampal neurogenesis than males. Female cowbirds have better spatial memory than males in some tasks, especially tasks requiring long-term spatial memory in an ecologically relevant context. The hippocampus and spatial memory in cowbirds appear to be specialized for brood parasitism. Because of their diversity and unusual breeding biology, brood parasites offer many opportunities for investigating general questions about the adaptive modification of cognition and the brain.

11.1 The Evolutionary Importance of Spatial Memory

Natural selection produces adaptations that increase reproductive success. Spatial memory, for example, can promote individual survival and reproduction (Sherry 2006; Roth and Pravosudov 2009). Brood parasites like brown-headed cowbirds

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(*Molothrus ater*) remember the locations of suitable host nests in which to lay their eggs (Sherry 2006). Presumably, female brood parasites that failed to remember the locations of target nests were less successful at reproducing than those that remembered. If such variation in spatial memory has a genetic basis, the outcome would be selection for enhanced memory for host nests. In other words, spatial memory may evolve because of the fitness-promoting effects of improved recall of spatial information (Nairne and Pandeirada 2008). The exact mechanisms by which selection affects spatial memory, however, are not always clear.

11.2 Cowbird Neuroecology

11.2.1 Ecology and Space Use in Cowbirds

Cowbirds (*Molothrus* spp.) and other brood parasites are ideal models for testing ideas about the adaptive specialization of memory and the brain because some species exhibit both sex and seasonal differences in how much they rely on spatial memory for host nests. The five parasitic species of cowbirds (*Molothrus ater*, *M. aeneus*, *M. bonariensis*, *M. oryzivora*, *M. rufoaxillaris*) form a monophyletic group that excludes all other non-parasitic icterids and the non-parasitic grayish baywing (*Agelaiodes badius*; previously bay-winged “cowbird” or *Molothrus badius*; Johnson and Lanyon 1999; Lanyon and Omland 1999). Icterids in the genera *Agelaius* and *Quiscalus* are more closely related to *Molothrus* than grayish baywings are (Johnson and Lanyon 1999; Lanyon and Omland 1999). Grayish baywings belong to a South American icterid clade that is a sister clade to both the *Molothrus* and *Agelaius* clades (Johnson and Lanyon 1999; Lanyon and Omland 1999). Comparative analyses incorporating grayish baywings, parasitic *Molothrus* species, and non-parasitic icterid species (*Agelaius* and *Quiscalus* spp.) make for ideal comparative research as described by Garland and Adolph (1994).

Brown-headed cowbirds and the ecologically similar South American shiny cowbird (*Molothrus bonariensis*) show a female-biased sex difference in space use, with females searching for host nests in the breeding season unassisted by males (Rothstein et al. 1986; Mason 1987). Both species of cowbird are extreme host generalists. Female brown-headed and shiny cowbirds parasitize nests during a brief 1-h window before sunrise, when it is still quite dark, so they are not searching for new host nests at this time (Gloag et al. 2013). Instead, they find suitable host nests at least 1 day before parasitizing them (Rothstein et al. 1986; Scardamaglia et al. 2017).

Brown-headed and shiny cowbirds are rare examples of species in which females—because they search for host nests—experience greater demand on spatial memory than males, a reversal of the sex difference often found in mammals, in which males experience greater demands on spatial memory as a result of greater male range size (Sherry et al. 1992). Female shiny cowbirds, in fact, have smaller home ranges than males (Scardamaglia and Reboreda 2014). Any sex difference in spatial ability favouring female shiny cowbirds, as described below (Astié et al. 2015), would thus

not be associated with spatial mapping of a larger home range but instead with remembering the locations of multiple host nests (Scardamaglia and Reboreda 2014).

In addition to finding host nests, female brown-headed cowbirds monitor hosts' nesting and laying to ensure that parasitism occurs by early incubation, allowing enough time for the cowbird eggs to hatch (White et al. 2009). Although shiny cowbirds rarely return to nests they have already parasitized, they will visit target nests and puncture host eggs before and/or during the laying event (Gloag et al. 2014; Scardamaglia et al. 2017). Female brown-headed cowbirds likely also make repeated visits to host nests although previous research has not examined the behaviour of individually marked females (Sealy 1992). Female cowbirds may thus make multiple visits to host nests and are under strong selection pressure to remember the locations and nesting stages of potential hosts to ensure that their eggs hatch and that their young are successfully raised (Rothstein et al. 1986; Gates and Evans 1998; White et al. 2009).

11.2.2 Cowbird Mating Systems

A long history of field research on brown-headed cowbirds has shown that their mating system varies among populations and can be monogamous, promiscuous, polygynous, or polyandrous (Lowther 1993; Woolfenden et al. 2002; Strausberger and Ashley 2003). Available data indicate that shiny cowbirds are polygynous and promiscuous and only females search for nests of multiple host species, whereas screaming cowbirds are socially monogamous and both sexes search for the nests of their single host species, the grayish baywing (Fraga 1986; Mason 1987; Scardamaglia and Reboreda 2014).

11.2.3 Sex and Species Differences in the Cowbird Hippocampus

The hippocampus processes spatial information in both birds and mammals (O'Keefe and Burgess 1996; Smulders 2006; Moser et al. 2008; Pravosudov and Roth 2013). Sex differences in the volume of the hippocampus have been reported in some cowbirds (Table 11.1). The avian hippocampus is located on the dorsal surface of the brain, and its boundaries can be identified by changes in cell size, density, and distribution in Nissl-stained tissue or tissue immunolabelled for the neuronal marker NeuN (Fig. 11.1; Sherry et al. 1989, 1993; Guigueno et al. 2016). Consistent with sex differences in spatial behaviour observed in the wild and spatial memory for host nests, females have a larger hippocampus than males in brown-headed cowbirds (Sherry et al. 1993; Guigueno et al. 2016) and shiny cowbirds (Reboreda et al. 1996; Clayton et al. 1997). No sex difference in hippocampal volume was reported in two other South American species, the monogamous host specialist screaming cowbird and the non-brood parasitic grayish baywing, (Reboreda et al. 1996; Clayton et al. 1997). Mean hippocampal volume was larger in parasitic species (shiny and screaming cowbirds) than the non-parasitic species (Reboreda et al. 1996). Sherry et al. (1993)

Table 11.1 Summary of sex and seasonal differences in the hippocampus of brown-headed, shiny, and screaming cowbirds, and grayish baywings, common grackles, and red-winged blackbirds (F=female, M=male, B=breeding, NB=non-breeding)

Sex differences in the hippocampus				
Species	Hippocampus volume	Hippocampal neurogenesis	Substance P terminal field volume	
<i>Brood Parasites</i>				
Brown-headed cowbird	F > M Sherry et al. (1993)	Guigueno et al. (2016)	F > M	Guigueno et al. (2016)
Shiny cowbird	F > M Reboreda et al. (1996)	Clayton et al. (1997)		F = M Nair-Roberts et al. (2006)
Screaming cowbird	F = M Reboreda et al. (1996)	Clayton et al. (1997)		F = M Nair-Roberts et al. (2006)
<i>Non-parasites</i>				
Grayish baywing	F = M Reboreda et al. (1996)	Clayton et al. (1997)		F = M Nair-Roberts et al. (2006)
Red-winged blackbird	F = M Sherry et al. (1993)		F = M	Guigueno et al. (2016)
Common grackle	F > M Guigueno et al. (2016)			
	F = M Sherry et al. (1993)			
Seasonal differences in the hippocampus				
Species	Hippocampus volume	Hippocampal neurogenesis		
<i>Brood Parasites</i>				
Brown-headed cowbird	B = NB Guigueno et al. (2016)		NB > B	Guigueno et al. (2016)
Shiny cowbird	B > NB Clayton et al. (1997)			
Screaming cowbird	B > NB Clayton et al. (1997)			
<i>Non-parasites</i>				
Red-winged blackbird	B = NB Guigueno et al. (2016)		B = NB	Guigueno et al. (2016)

Species differences in the hippocampus	
Hippocampus volume	
Brown-headed cowbird > red-winged blackbird	Sherry et al. (1993), Guigueno et al. (2016)
Brown-headed cowbird > common grackle	Sherry et al. (1993)
Shiny cowbird > grayish baywing	Reboreda et al. (1996)
Screaming cowbird > grayish baywing	Reboreda et al. (1996)
Hippocampal neurogenesis	
Brown-headed cowbird > red-winged blackbird	Guigueno et al. (2016)
Substance P terminal field volume	
Shiny cowbird > grayish baywing	Nair-Roberts et al. (2006)
Screaming cowbird > grayish baywing	Nair-Roberts et al. (2006)
Shiny cowbird > screaming cowbird	Nair-Roberts et al. (2006)

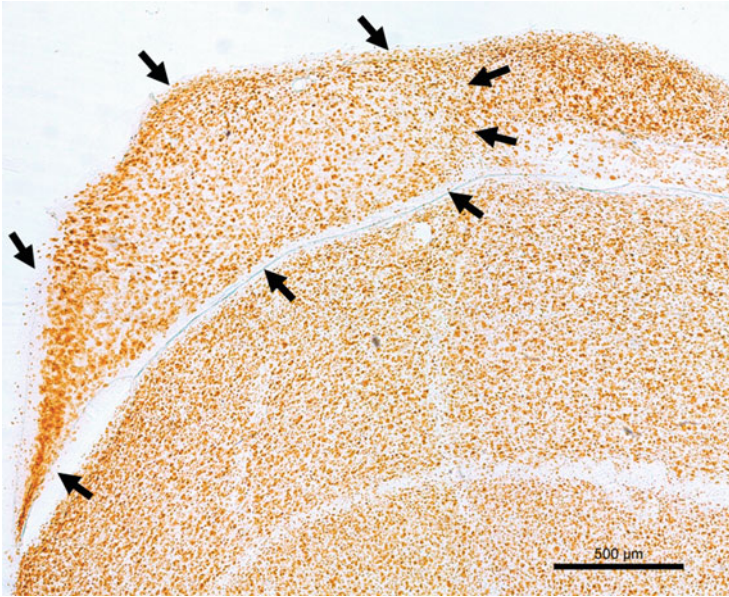


Fig. 11.1 A coronal section of the hippocampus in the right dorsomedial forebrain of a brown-headed cowbird (*Molothrus ater*), with hippocampal boundaries indicated by arrows. Mature neurons have been labelled for NeuN immunoreactivity. Figure modified from Guigueno et al. (2016)

previously reported no sex difference in the volume of the hippocampus of non-brood parasitic relatives of cowbirds, the red-winged blackbird, and the common grackle (*Quiscalus quiscula*). The results of studies of hippocampus volume, however, have not all been consistent. No sex differences in hippocampus volume were detected in a subsequent study of all three South American cowbird species (Nair-Roberts et al. 2006). In addition, Guigueno et al. (2016) found a sex difference favouring females in the volume of the hippocampus in red-winged blackbirds.

Some studies have examined the cowbird hippocampus in more detail (Table 11.1). Immunohistochemical labelling of neural proteins has been used to determine the size of regions within the hippocampus (Nair-Roberts et al. 2006) and to describe adult neurogenesis in the cowbird hippocampus (Guigueno et al. 2016). Neuropeptide substance P (SP), which has memory-promoting effects (Huston and Hasenöhr 1995), was measured in the hippocampus of two South American cowbird species and the non-parasitic grayish baywing (Nair-Roberts et al. 2006). Nair-Roberts et al. (2006) described an area within the hippocampus rich in SP which they named the hippocampus SP terminal field (SPh). The two parasitic species (shiny and screaming cowbirds) had a larger SPh than the non-brood parasitic grayish baywing, consistent with the idea that SPh may promote memory in the parasitic species that rely on spatial memory to find and return to host nests (Nair-Roberts et al. 2006). In addition, the generalist shiny cowbird had a larger SPh than the specialist screaming cowbird, indicating that SPh may be increasingly involved in

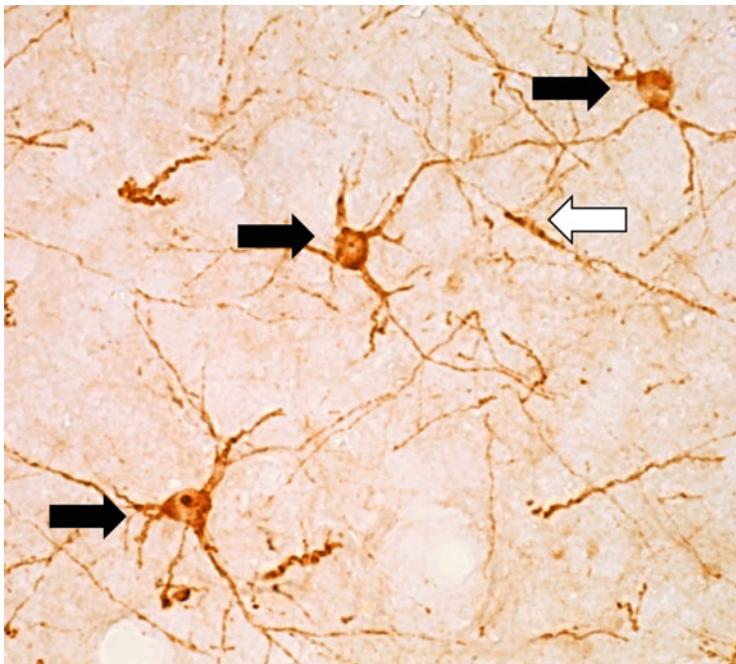


Fig. 11.2 Doublecortin (DCX) immunoreactivity in the brain of a brown-headed cowbird (*Molothrus ater*), with white arrow indicating an immature migrating cell and black arrows indicating immature differentiating cells

behavioural and cognitive processes as the number of different species of hosts that are parasitized increases (Nair-Roberts et al. 2006). Although Nair-Roberts et al. (2006) found robust species differences in SP labelling, they did not find sex differences in any of the cowbird species they examined.

Doublecortin (DCX) is an endogenous marker of neurogenesis. It is a microtubule-associated protein only expressed in immature neurons, specifically in migrating and differentiating neurons (Francis et al. 1999; Gleeson et al. 1999). DCX is a reliable marker of neurogenesis in birds (Balthazart and Ball 2014a, b), although some limitations have been discussed (Vellema et al. 2014). Guigueno et al. (2016) found greater DCX+ labelling in the hippocampus of cowbirds compared to blackbirds (Table 11.1; Fig. 11.2). There was a significant interaction between sex and species with neurogenesis being greater in female than in male cowbirds with no sex difference in blackbirds. This significant sex by species interaction in adult hippocampal neurogenesis provides strong support for the idea that the hippocampus is specialized in female brown-headed cowbirds.

11.2.4 Seasonal Differences in the Cowbird Hippocampus

The cowbird hippocampus has been shown to vary seasonally in volume and in neurogenic plasticity (Table 11.1). Shiny and screaming cowbirds had a larger hippocampus in the breeding season than in the non-breeding season (Clayton et al. 1997). Although breeding condition did not affect the volume of the hippocampus in brown-headed cowbirds, it did affect hippocampal neurogenesis (Guigueno et al. 2016). Neurogenesis peaked in non-breeding condition, when cowbirds are not searching for host nests and any associated memory demands are low. Seasonal changes in hippocampal neurogenesis in cowbirds described by Guigueno et al. (2016) resemble patterns exhibited by polygynous Richardson's ground squirrels (*Urocitellus richardsonii*; Burger et al. 2014). Although home ranges are larger in the breeding season, especially for males that mate with multiple females, hippocampal neurogenesis is at a peak in non-breeding condition (Burger et al. 2014). Heightened hippocampal neurogenesis in post-breeding cowbirds may prepare their brains to acquire, process, and retain new spatial information in the upcoming breeding season. Hippocampal neurogenesis may facilitate the forgetting of past memories, such as the locations of past host nests (Akers et al. 2014; Epp et al. 2016; Guigueno et al. 2016).

11.2.5 Cognition in Cowbirds

Spatial cognition, presumed to be hippocampus dependent, and nonspatial cognition have been studied in both shiny and brown-headed cowbirds. This research shows a complex pattern of results.

In a first study on shiny cowbirds, Astié et al. (1998) tested whether females or males would more quickly learn that one site in an 8×8 array, either in a specific location or identified by a specific colour, was baited with food. Birds had to learn to associate the baited site with a colour or with a location that remained constant between trials. No sex difference was observed for the spatial task. Females, however, learned to recover food faster than males when it was associated with a colour. A female-biased sex difference was thus observed for the task in which a sex difference was not expected (colour task), but no sex difference was found for the task in which a female-biased sex difference was expected (spatial task).

In a recent study, Astié et al. (2015) used an operant device with two illuminated response keys to test for sex differences in learning, reversal, and retention after extinction on colour and spatial tasks in shiny cowbirds. Astié et al. (2015) reported no sex differences in the learning and reversal phases of testing for both the spatial and colour tasks. However, during the extinction phase, up to 50 days after a correct choice was last rewarded for colour and spatial tasks, females performed significantly better than chance on both tasks (85–90% of trials were correct), whereas males did not (Astié et al. 2015). Female shiny cowbirds seem to have much better long-term memory than males for both colour and spatial cues.

A recent study suggests that female brown-headed cowbirds, unlike shiny cowbirds, do not have better colour memory than males (Guigueno et al. 2015) but

Table 11.2 Summary of sex and seasonal differences in cognition of brown-headed and shiny cowbirds (F=female, M=male, B=breeding, NB=non-breeding)

Spatial memory/learning			
Sex differences			
<i>Task type</i>	<i>Brown-headed cowbird</i>	<i>Shiny cowbird</i>	<i>Reference</i>
Food cups ^a	F > M		Guigueno et al. (2014)
Touchscreens ^{b,c}	M > F		Guigueno et al. (2015)
Testing board in cage		F = M	Astié et al. (1998)
Two response keys: learning and reversal		F = M	Astié et al. (2015)
Two response keys: extinction after 50 days		F > M	Astié et al. (2015)
Seasonal differences			
<i>Task type</i>	<i>Brown-headed cowbird</i>		<i>Reference</i>
Food cups	B = NB		Guigueno et al. (2014)
Touchscreens	F: B = NB M: B > NB		Guigueno et al. (2015)
Color memory/learning			
Sex differences			
<i>Task type</i>	<i>Brown-headed cowbird</i>	<i>Shiny cowbird</i>	<i>Reference</i>
Touchscreens ^{b,c}	F = M		Guigueno et al. (2015)
Testing board in cage		F > M	Astié et al. (1998)
Two response keys: learning and reversal		F = M	Astié et al. (2015)
Two response keys: extinction after 50 days		F > M	Astié et al. (2015)
Seasonal differences			
<i>Task type</i>	<i>Brown-headed cowbird</i>		<i>Reference</i>
Touchscreens	F: B > NB M: B = NB		Guigueno et al. (2015)

^aTask required subjects to move through space and locate a previously baited food cup

^bTask required subjects to remember a location or a colour in their immediate visual field

^cBoth females and males performed better on the spatial touchscreen task than on the colour touchscreen task

do have better long-term spatial memory (Guigueno et al. 2014). Sex differences in brown-headed cowbird spatial memory are dependent on task type (Table 11.2). Females performed better than males on a task in which birds had to move through space and remember a location for 24 h (Fig. 11.3; Guigueno et al. 2014), whereas males performed better than females on a stationary touchscreen task in which they had to remember a location on a screen for up to 60 s (Fig. 11.4; Guigueno et al. 2015). In the task that most closely resembles female search for host nests, brown-headed

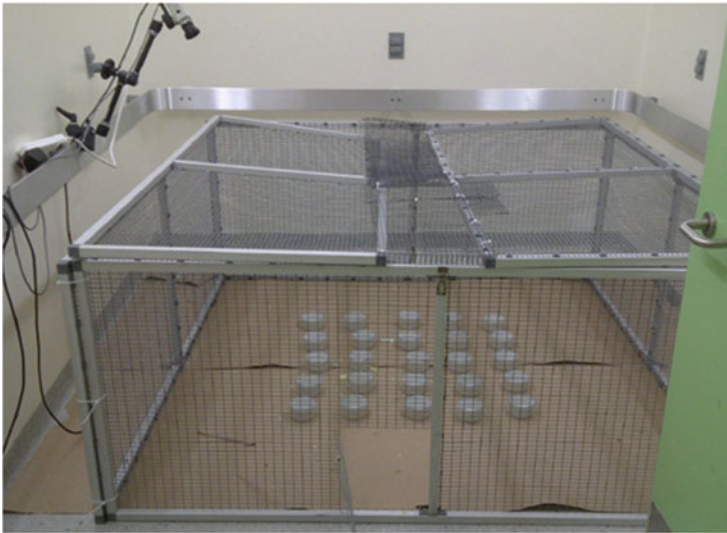
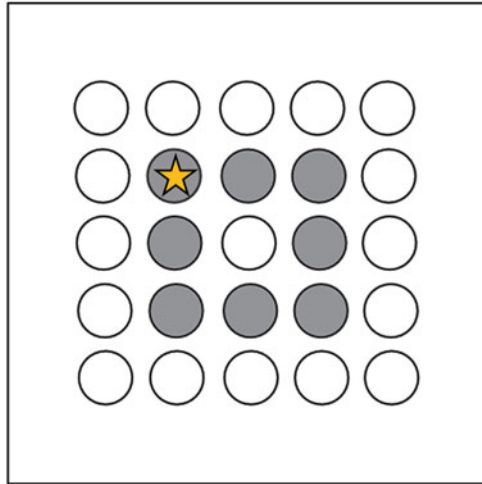


Fig. 11.3 Top: Schematic diagram of testing apparatus with potential rewarded cups shaded. Only one cup was rewarded per trial, with an example indicated by the star. Diagram modified from Guigueno et al. (2014). Bottom: The testing apparatus

cowbird females perform better than males, a reversal of the typical sex difference in spatial memory generally found in mammals (Gaulin and Fitzgerald 1986; Williams et al. 1990; Silverman et al. 2000; Postma et al. 2004).

The basis for the better performance by male brown-headed cowbirds on the touchscreen task is difficult to understand (Guigueno et al. 2015). There may be a trade-off associated with specialization in a particular form of memory, because enhanced cognitive function has energetic and life history costs, with the result that

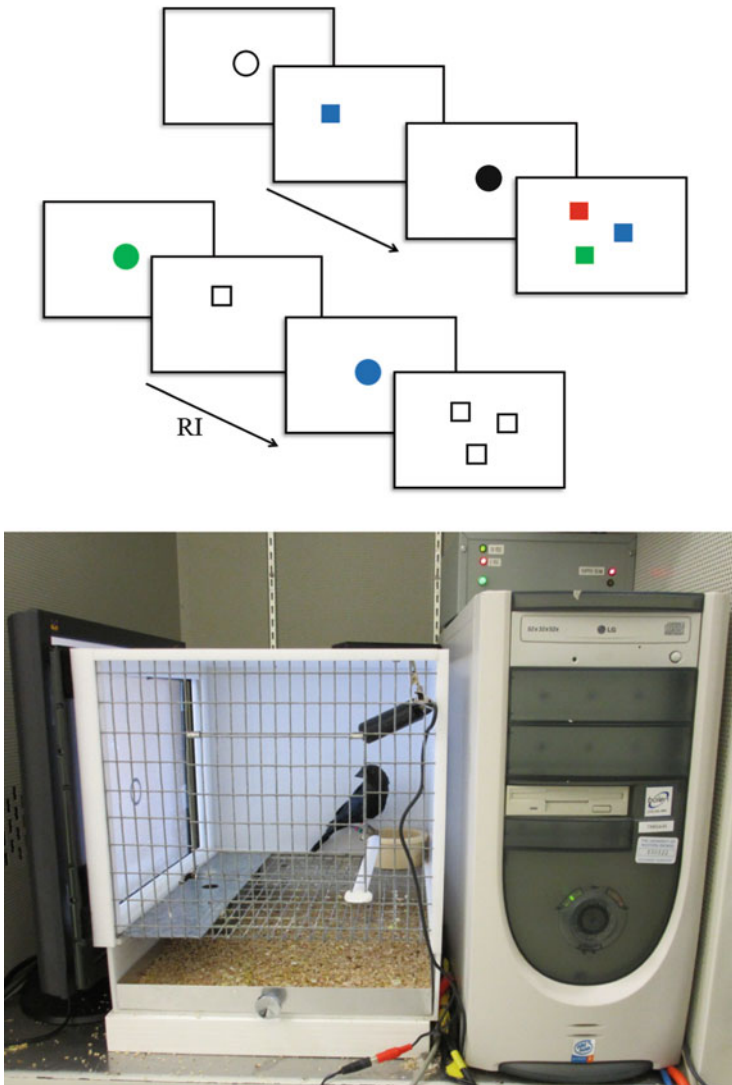


Fig. 11.4 Top: Colour (upper) and spatial (lower) delayed matching to sample touchscreen tasks used by Guigueno et al. (2015). The retention interval (RI) varied from 5 to 60 s. Bottom: Operant chamber and touchscreen

females that perform better than males on one kind of spatial task but do less well on another (Hasenstaub et al. 2010; Burns et al. 2011; Cole et al. 2012). Alternatively, there could be functional incompatibility between these two types of spatial memory (Sherry and Schacter 1987). In addition to these functional or evolutionary considerations, there may also be proximate reasons for better male performance on

the touchscreen task: improved male spatial performance on the touchscreen task could be due to increased androgen concentrations. Male androgen concentrations increase more between non-breeding and breeding conditions than do female androgen concentrations, and it was only in breeding condition that males outperformed females (Guigueno et al. 2015). Elevated androgens have been shown to increase spatial memory performance in mammals and songbirds and may have caused male cowbirds to improve in spatial performance from non-breeding to breeding condition and outperform breeding females (Galea et al. 1996; Hodgson et al. 2008). In rodents, elevated levels of estradiol, which are produced from testosterone via the enzyme aromatase, increase the number of dendritic spines and the number of synapses on these spines in hippocampal neurons (Woolley and McEwen 1994; Murphy and Segal 1996; Yankova et al. 2001). Less is known about the effect of hormones on the avian hippocampus, but several studies have shown that aromatase is enriched in the hippocampus in songbirds (Shen et al. 1994; Saldanha et al. 1998; Metzdorf et al. 1999; Fusani et al. 2000). In sum, there are multiple possible explanations for the male-biased sex difference on the touchscreen task including trade-offs between different forms of spatial memory and changes in circulating androgen concentrations due to breeding (Guigueno et al. 2015).

Another breeding condition effect in brown-headed cowbirds was enhanced colour memory in female cowbirds during breeding when females search for host nests in the wild (Guigueno et al. 2015). Female shiny cowbirds outperformed males on visual memory tasks (Astié et al. 1998, 2015). Likewise, improvement in performance on another visual task increased from non-breeding to breeding conditions in female but not in male brown-headed cowbirds (Guigueno et al. 2015). Research on both brown-headed and shiny cowbirds thus suggests that visual memory, a form of cognition not dependent on the hippocampus, may play an important role along with long-term spatial memory in cowbirds' brood parasitic mode of reproduction.

Concluding Remarks and Future Directions

Many unanswered questions remain regarding cognition and the brain of avian brood parasites. To test whether brood parasitism has specifically caused evolutionary change in the hippocampus and hippocampal neurogenesis, it is necessary to conduct larger scale phylogenetic analyses, similar to those that have examined cognition and the brain of food-storing birds. Because the hippocampus can change seasonally, and because search for host nests is clearly associated with the breeding season, data on cognition and the brain in both breeding and non-breeding conditions are most valuable.

There is little detailed information on space use by brood parasites in the wild. Determining exactly how females perform spatial search for potential host nests and how frequently they visit host nests before, during, and after parasitism would help define the spatial problems these birds face. Techniques

(continued)

such as MRI that would allow repeatable measures of hippocampal anatomy would also make it possible to examine changes in the hippocampus within the same individuals between breeding and non-breeding or even within the breeding season. Individual differences in the hippocampus may also occur among females that make more or fewer visits to host nests or that navigate larger or smaller home ranges.

Finally, more detailed descriptions of the cowbird hippocampus could provide valuable information on species differences, sex differences, and seasonal change. Variation in hippocampal cell number, for example, may help explain subtle changes in behaviour, and many techniques are available for investigating hippocampal connectivity and plasticity.

In conclusion, shiny and brown-headed cowbirds have a hippocampus and spatial memory specialized for brood parasitism. In brown-headed cowbirds, females outperformed males on a navigational memory task resembling host nest search and had a larger hippocampus with greater neurogenesis than males. In shiny cowbirds, females had better long-term memory for spatial and visual cues and a larger hippocampus than males. Finally, brown-headed cowbirds had more hippocampal neurogenesis in post-breeding condition, indicating that hippocampal neurogenesis, if it indeed contributes to female memory for host nests, takes place in advance of the coming breeding season, or is a process of hippocampal modification that follows breeding. There is good evidence for specialization of spatial memory and the hippocampus in cowbird brood parasites, providing a strong test of ideas in neuroecology, specifically the origin of sex-specific adaptive modifications of cognition and the brain.

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