Hippocampal Subregions Related To Spatial Learning In Pigeons Of The Species *Columbo livia*: A Literature Review

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Summary

Spatial memory is an important feature of the avian brain. This type of memory is used in behaviours like migration (in migratory birds) and food hiding and retrieval (in food-caching birds). Much research has been performed on the neural and neuroanatomical features of spatial memory in mammals but research on this topic for the avian brain lacks. The current review aims to summarize what we now know about neural features related to avian spatial cognition in the case of pigeons of the species *Columba livia*. The main results of the current review include a comparison of the mammalian hippocampus and the avian hippocampal formation, a view on connectivity and neurotransmitters of the avian hippocampal formation, functions of specific subregions of the hippocampal formation and the role of another region, the nidopallium caudolaterale, equivalent to the mammalian prefrontal cortex, on spatial cognition in pigeons. The findings of the current research provide a summary of what is known about spatial cognition in pigeons and can provide a basis for future research into similar questions on spatial memory or spatial memory-related behaviour in pigeons or other birds.

Introduction

All vertebrates require strong spatial memory, for instance, to remember rich feeding grounds (Crystal, 2010; Salwiczek et al., 2010), predator hideouts, suitable nesting sites and in general to improve navigation. This field of research on learning and memory is already studied for quite some time in mammals (Moser et al., 2008; O'Keefe and Dostrovsky, 1971). For birds, this is not yet the case. Spatial memory, or functionally explained by an animal's ability to keep track of its location and to navigate through stored visual cues (Olton, 1977) is key in this. In mammals, it is long known that the hippocampus (HC) is allowing this spatial memory (Zemla and Basu, 2017). Both anatomical and functional characteristics of the mammalian HC regarding spatial cognition are known well (Morandi-Raikova and Mayer, 2022). The mammalian HC consists roughly of the dentate gyrus and the cornu ammonis (CA) and lies close to and in interaction with the subiculum and the entorhinal cortex (EC) (Anand and Dhikav, 2012). In terms of avian cognition, learning and memory in birds and in specifically the pigeon, research is scarcer. For pigeons, spatial memory is of great importance. The rock pigeon, the ancestor of the current day's homing pigeon, is used since 3000BC as a mode of communication and has been subject to artificial breeding ever since (Clarke, 1933). This long ongoing selective pressure has led to the evolutionary development of these almost perfect abilities to navigate (Hough, 2022) and shows they, homing pigeons, possess not only great navigational abilities but also their spatial memory seems to work quite well (Olson and Maki, 1983). Research has shown the linkage between hippocampal formation (HF) volume and food caching (where food-storing birds possess larger HF volumes) (Krebs et al., 1989; Sherry and Vaccarino, 1989), as well as the linkage between HF volume and migration distance (Healy et al., 1996), suggesting the great function the HF has in spatial cognition. However, there is still much less known about the hippocampal-like structure called the hippocampal formation (HF) in the avian brain. While the avian HF is functionally very much comparable to the HC, it is morphologically very different, as will be explained later in the review. Both share their main functions in (spatial) learning and memory (Bingman et al., 1988, 1985; Krebs et al., 1989; Sherry and Vaccarino, 1989). The current study deals with the case of the pigeon, the rock pigeon and its subspecies Columba livia (domestica) to be more specific. Pigeons of the species *C.livia*, the rock pigeon, include many domesticated subspecies that fall under the name of the domesticated pigeon Columba livia domestica which is found commonly across the globe, most prevalent species include the homing pigeon and the feral pigeon. The current review aims to present what is currently known about the HF in pigeons, where there is scientific consensus and where there is still space and needs for future research. This is done by answering the research question of how subregions of the HF are associated with spatial learning and memory in pigeons of the species Columba livia and how this compares to the mammalian hippocampus. The following subchapters in this review deal with different aspects of avian cognition, compare anatomical characteristics of the pigeons' HF to the mammalian HC, HF connectivity and neurotransmitters and receptors of the HF, HF subregion-specific activation during spatial testing and suggest another area possible co-responsible for spatial cognition. The findings of the current research provide a summary of what is known about spatial cognition in pigeons and can provide a basis for future research into similar questions on spatial memory or spatial memory-related behaviour in pigeons or other birds.

Anatomical correlates of the avian HF versus the mammalian HC

The HF in pigeons is rather different compared to the HC in mammals. The mammalian hippocampus consists of clearly distinguishable subregions, the DG, CA1-3 (sometimes considered CA1- CA4) and a subiculum (Amaral and Witter, 1989; Amunts et al., 2005; Insausti, 1993). Information processing of the hippocampus starts with DG (Jonas and Lisman, 2014). The DG mostly consists of granule cells (Claiborne et al., 1986) allowing information reception and processing from the entorhinal cortex (EC) in the DG, where it is subsequently processed towards the spatially specific place cells of the CA (Jonas and Lisman, 2014). The granule

cells of the DG rive rise to the so-called mossy fibres, unmyelinated axons (Frotscher et al., 2012). These mossy fibres form large presynaptic axon terminals that project to the CA pyramidal neurons and in that way act as a precursor for the CA (Sloviter and Lømo, 2012). The CA fields consist of densely packed pyramidal neurons (Witter, 2007), the CA1 is responsible for memory retrieval (Suthana et al., 2015) and the CA2 and CA3 regions are involved in the formation of new memories, specifically connections between a location and an object or a reward (Rolls, 2013; Scoville and Milner, 1957; Suthana et al., 2015). The CA, in general, encodes spatial representations (Muller et al., 1991), that are received from the DG. This complete pathway from EC to CA allows for the formation of episodic spatial memories. The mentioned projections and connections of and within the HC can be seen in Figure 1.

Morphological and functional characteristics are much less known in the pigeon HF. The distinguishable regions of the HC are much less clear and are overlapping in a way in the avian HF. To be able to compare the mammalian hippocampus to a pigeon's HF it is important to understand the anatomical characteristics of the HF. Up till now, research has characterized HF by looking at either intrinsic and/or extrinsic connections (Atoji and Wild, 2006, 2004; Kahn et al., 2003; Székely and Krebs, 1996) or receptors in receptor binding studies (Herold et al., 2014). The most widely used HF map is made by Atoji and Wild (2006). The pigeon's HF can be subdivided into seven subregions, dorsolateral (DL), dorsomedial (DM), triangular (Tr), V-shaped (V), magnocellular (Ma), parvocellular (Pa), and a cell-poor region (Po). Some of the latter subregions are further divided into sub-subregions, based on their position (dorsal, ventral, lateral, medial) in the HF. All these subregions are visualized using Nissl-staining (Atoji and Wild, 2006) and can be seen in Figure 2.
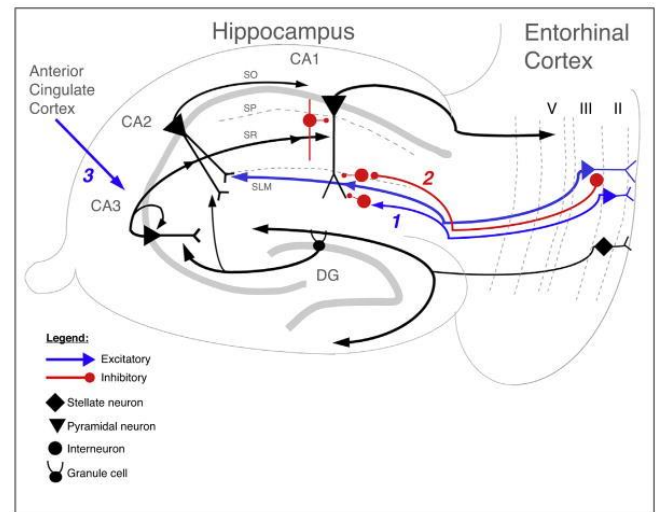

Figure 1 Schematic drawing of morphological and functional characteristics of the mammalian HC (Image source: Zemla and Basu, 2017)
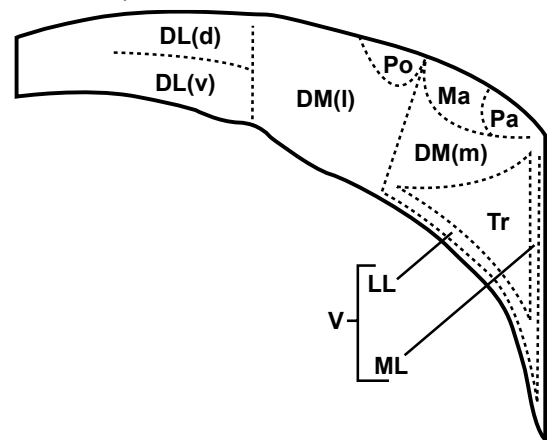

Figure 2 Map of a pigeon's hippocampal formation (A5.75), subdivided into seven subregions, further subdivided according to dorsal, ventral, lateral or medial location of the sub-subregion. DL(d) = dorsal side of dorsolateral HF; DL(v) = ventral side of dorsolateral HF; DM(l) = lateral side of dorsomedial HF; DM(m) = medial side of dorsomedial HF; Tr = triangular region; V = V-shaped structure; LL = Lateral Layer of V-shaped structure; ML = Medial Layer of V-shaped structure; Po = cell-poor region; Ma = magnocellular region; Pa = parvocellular region.
Figure adapted from Atoji and Wild (2006).

Regions of the avian HF, although structurally and morphologically quite different, can be compared to regions of the mammalian hippocampus via staining and looking at connectivity. Although a full comparison is still missing, research seems to unanimously relate the avian DL to the EC (Kahn et al., 2003), further supported by evidence showing the DL receives input from parts of the hyperpallium and nidopallium, higher orders in the visual system, comparable to the EC (Husband and Shimizu, 1999; Shimizu et al., 1995). Also, the DM region of the HF seems to correspond to both the CA regions as the subiculum of the HC (Atoji and Wild, 2006; Kahn et al., 2003). Homology in this is found in

glutamatergic projection fibres originating from pyramidal neurons of the CA and subiculum ending in the lateral septal nucleus (LSN), the HF shows similar projection from the DM to the LSN (Atoji and Wild, 2004). Besides this, DM also projects to the hypothalamus (Atoji and Wild, 2004). This is also found in the HC, where the CA/subiculum projects to the hypothalamus. Whether there is a functional or morphological similar structure to the DG raises more question marks but is hypothesized to correspond to the V-complex. This is due to the intrinsic character of the V-complex, meaning the V-complex only connects to other regions within the HF, not throughout the brain. This is similar to the DG in the mammalian HC which also only connects to other subregions within the HC and not outside of the HC (Atoji and Wild, 2004). However, A difference from the HC is found in the absence of a mossy fibre structure (or equivalent) in the avian HF, this is hypothesized in the pigeon's brain and already proven in the zebra finch and chicken (Faber et al., 1989; Montagnese et al., 1993; Tömböl et al., 2000). Besides the latter, the V-complex shows reciprocal connections with the DM while the DG only has one-way connections with the CA(3) region of the HC (Atoji and Wild, 2004). But this does not necessarily mean that the V-complex is not complementary to the DG.

Connectivity of the HF

Information processing of the HF in the pigeon starts with the higher level region hyperpallium apicale (HA) that passes information to the DL(d) and the DM region through the hyperpallium densocellulare (HD) (Atoji and Wild, 2019). The downstream pathway that starts in DL and DM contains (within HF) connections that show both reciprocity and nonreciprocity. The following intrinsic connections of the HF have been investigated extensively by Atoji and Wild (2004). While information, received in the DL(d) and projected to the DL(v) region, exits the DL(v) in a one-way route to the DM(l), just like de DL(d) does to the V, other connections of the HF go in both directions. Both DL subregions are connected, Both DL(d) and DL(v) are reciprocally connected to the DM(m), which is reciprocally connected to Ma, the Ma projects to the DL(d) and the other way around. DM(l)

is connected to the V which is, both laterally and medially, connected to the Tr. A map of all of these intrinsic connections shows a rather complex structure of connections, which can be seen in Figure 3.
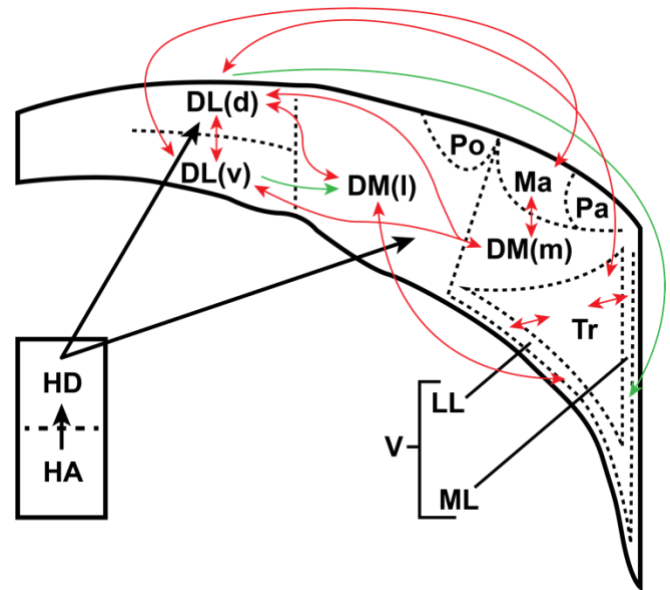

Figure 3: A map of intrinsic connection of the pigeon's HF. Note the reciprocal character of multiple connections, contrasting to intraregional connections of the mammalian HC, which are nonreciprocal.

Neurotransmitters and receptors of the HF

Subregions of the HF show rather different receptor densities compared to the mammalian HC. Research by use of quantitative in vitro receptor autoradiography performed by Herold, et al (2014) has visualized receptor densities and distribution within the HF. The $GABA_A$ receptor for inhibitory neurotransmitter ɣ-aminobutyric acid (GABA), a mediator of inhibitory postsynaptic transmission in the HC (Isaacson et al., 1993), shows high representation in the V (especially V(ML)) and the Tr, a semi-high density is found in the DL and the lowest densities are observed in the DM. The serotonergic $5\text{-HT}_{1\alpha}$ receptor for serotonin (or 5-HT), in the mammalian HC responsible for inhibition of pyramidal neurons, is generally low in the avian HF but is represented right on the border between the two subregions of the DM. Glutamatergic receptors AMPA, NMDA and kainite receptor for the neurotransmitter glutamate, an excitatory neurotransmitter key in the process of learning and memory formation (Stanley et al., 2017), all show high representation in the V/Tr. Kainate and AMPA densities both are high in the DL and all three are lowest in DM. NMDA interestingly is

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distributed rather homologous across the HF. For acetylcholine-sensitive muscarinic receptors M_1 is less represented in the HF, M_2 is found in the HF but only well represented in the DL. Nicotinic acetylcholine receptors are found in the HF, notably this receptor is the sole receptor that has its highest density in the DM. In the mammalian HC, the function of acetylcholine is to mediate memory formation of the hippocampus (Haam and Yakel, 2017). Noradrenergic $\alpha 1$ receptor for noradrenaline, in the HC noradrenaline works as a pointer to important experiences to remember (Bacon et al., 2020) and is found in the highest density in the Tr and lower in the DL. The least represented receptor the is dopaminergic $D_{1/5}$ receptor, sensitive to the versatile neurotransmitter dopamine that promotes focus, episodic memory formation, spatial learning, and synaptic plasticity (Kempadoo et al., 2016). This receptor shows a similar pattern as the M_1 receptor and is found mostly in the DL subregion of the HF.

Subregion-specific activity during spatial testing

Studies on subregion-specific testing of spatial memory in specifically the pigeon are scarce, but subregion-specific activity during spatial testing has been investigated in other species of birds. A study which is for the case of the pigeon (Coppola and Bingman, 2020), investigated the activity (or use) of subregions of the HF by measuring activity-dependent expression of the immediate early gene c-Fos. The given that an old pigeon's HF shows higher HF volume and neuron count compared to young individuals (Meskenaite et al., 2016) allows the determination of the size of subregions after spatial testing in young individuals. This study showed the laterality of the pigeon's HF, in accordance with previous studies (Kahn and Bingman, 2004; Tommasi et al., 2003), the left HF is sensitive to detection and navigation based on landmark cues within a testing arena (Kahn and Bingman, 2004) while the right HF does this based on global cues (Prior et al., 2002; Tommasi and Vallortigara, 2001). The pigeon's visual system itself is also lateralized with a left hemispheric dominance, first though only present in humans (Vallortigara et al., 1999), explained by an asymmetry in visual memory capacity(Güntürkün et al., 2000; von Fersen

and Güntürkün, 1990). The functional advantage of the asymmetries of the visual system is increased computational speed of object recognition, by focusing fully on one hemisphere while interference of the other hemisphere is prevented to prevent conflicting search processes to occur (Güntürkün et al., 2000). With the more recent study of Coppola and Bingman (2020) into spatial testing of the different subregions, delayed nonmatch-to-sample task testing, it was found that the Left TrV (an overarching name for Triangular region and V-complex) shows increase c-Fos (and thus activity) exposure after spatial testing together with the left DM, and Right DL, with generally higher activation of the right hemispheric HF. Lower c-Fos expression was found in hippocampal neurons of older subjects which correlates with decreased HF activation during spatial learning (Coppola and Bingman, 2020), this could suggest the possibility that older pigeons use different brain regions for allocating food or need less activation for similar performance since they did not perform worse compared to the younger subjects. However, in some spatial tasks older subjects to perform worse in HF-dependent spatial memory tasks (Coppola et al., 2014). Another interesting case is the case of head direction cells (HDC), cells that encode a neural compass (Rubin et al., 2014; Taube et al., 1990) which are key in navigation and underlie the directional sense of animals. These cells are therefore important for goal-targeted navigation and behaviours that are spatially coordinated. Research has been performed on HDCs in the HF of Japanese quails (Ben-Yishay et al., 2021). Here it was found that the Japanese quail also possesses HDCs. Most of the cells are located in the DL and DM regions of the avian HF (Ben-Yishay et al., 2021). These findings show that the DL and DM regions could be homologous in function to the Para-hippocampal structure of mammals. HDCs have also been shown in bats (Ulanovsky and Moss, 2007; Yartsev et al., 2011), barn owls (Agarwal et al., 2023), non-human primates (Killian et al., 2012), rats (McHugh et al., 1996) and humans (Ekstrom et al., 2003). Interestingly the DL and DM receive input from the visual wulst (Shanahan et al., 2013), avian equivalent to the mammalian visual cortex (Bischof et al., 2016), and the dorsal thalamus, this could suggest

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these areas work together to achieve optimal navigation, but this should be subject to future research to know this for sure. Besides HDCs also place cells, neurons that are triggered in response to specific places in an environment (O'Keefe, 1976). Presence of place cells in the avian HF has been showed in a research into place cells in the brain of the Barn owl (*Tyto alba*) (Agarwal et al., 2023). These neurons are present not only in the HF but also in the HA region of the owls. The latter supports the suggestion that it is likely that more brain areas are involved in spatial cognition. This case is supported by the fact HF lesioned pigeons in an open-field spatial maze test, while in the beginning unable to complete the task, are eventually able to complete the task with a small number of errors (Colombo et al., 1997). This is complementary to research in rats that has shown that hippocampal lesioned rats are impaired in the radial-arm maze but eventually solve the task to even difficult levels (Harrell et al., 1987). In the case of both rats and pigeons, this appears to be result of an alteration of response (to a task) strategy (Colombo and Broadbent, 2000).

Other brain areas linked to spatial cognition

Another region in the avian brain is called the nidopallium caudolaterale (NCL). The NCL is parallel to the mammalian PFC in terms of connectivity, neurochemical regulation and function (Güntürkün, 2012, 2005). Both PFC and NCL, are higher-order areas that are connected to lower-level sensory systems and other brain areas relating to memory (Kröner and Güntürkün, 1999; Leutgeb et al., 1996; Shanahan et al., 2013). Research into other regions but the HF responsible for spatial memory is already performed in carrion crows (*Corvus corone*). This research (Rinnert et al., 2019) found a high percentage of NCL neurons (41%) encode the location (or locations) of memorized cues. Furthermore, the NCL neurons not only do the latter but also represent information that is necessary to guide and control future spatial behaviour, to an extent where it is possible to predict future spatial decisions. These results are complementary to similar research into the primate PFC (Rainer et al., 1998) and show the similarity between the PFC and NCL. The function of the NCL in spatial memory can also be an explanation for the decrease in c-Fos expression as pigeons age, suggesting a shift of brain region used for tasks requiring spatial cognition. In pigeons specifically the NCL received input via similar regions as HF, but this pathway to the NCL is inversed compared to the HF. The HD projects to the HA (Funke, 1989) and subsequently the HA projects to the NCL (Wild, 1987). Interestingly, other research has shown the NCL shows weak projection to the posterior pallial amygdala (PoA) (Atoji and Wild, 2006; Bingman et al., 1994), which shows to be reciprocally connected to the DM of the HF (Atoji and Wild, 2006), this could suggest collaboration between the two areas in spatial cognition, but further research is needed to conclude this case

Region of avian hippocampal formation	Abbr.	Connects to	Abbreviation	Reciprocal or One-way connection	Corresponding region of mammalian HC or surrounding structure	Abbreviation	Source:	Neurotransmitter prevalence of the avian subregion of the hippocampal formation
Dorso Lateral (dorsal)	DL(d)	V-shaped complex	V	One-way				Medium: GABA Medium: Noradrenaline Medium: Dopamine High: Glutamate (only Kainate & AMPA) High: Acetylcholine (muscarinic)
		Dorso Medial (lateral)	DM(l)	Reciprocal	Entorhinal Cortex	EC	Husband and Shimizu, 1999; Kahn et al., 2003; Shimizu et al., 1995	
		Dorso Medial (medial)	DM(m)	Reciprocal	Entorhinal Cortex	EC		
		Triangular Complex	Tr	Reciprocal				
		Dorso Lateral (ventral)	DL(v)	Reciprocal				
Dorso Lateral (ventral)	DL(v)	Dorso Medial (lateral)	DM(l)	One-way				Medium: GABA Medium: Noradrenaline Medium: Dopamine High: Glutamate (only Kainate & AMPA) High: Acetylcholine (muscarinic)
		Magnocellular	Ma	Reciprocal				
		Dorso Lateral (dorsal)	DL(d)	Reciprocal	Entorhinal Cortex	EC	Husband and Shimizu, 1999; Kahn et al., 2003; Shimizu et al., 1996	
		Dorso Medial (medial)	DM(m)	Reciprocal				
Dorso Medial (lateral)	DM (l)	Dorso Lateral (dorsal)	DL(d)	Reciprocal	Cornu Ammonis Subiculum	CA -	Atoji and Wild, 2004 Kahn et al., 2003	Low: 5-HT (serotonin) on border with DM(m) High: Acetylcholine (nicotinic)
		V-shaped complex	V	Reciprocal				
Dorso Medial (medial)	DM (m)	Magnocellular	Ma	Reciprocal	Cornu Ammonis Subiculum	CA -	Atoji and Wild, 2004 Kahn et al., 2004	Low: 5-HT (serotonin) on border with DM(l) High: Acetylcholine (nicotinic)
		Dorso Lateral (dorsal)	DL(d)	Reciprocal				
		Dorso Lateral (ventral)	DL(v)	Reciprocal				
Magnocellular	Ma	Dorso Medial (medial)	DM(m)	Reciprocal				
		Dorso Lateral (dorsal)	DL(d)	Reciprocal				
Triangular Complex	Tr	Dorso Lateral (dorsal)	DL(d)	Reciprocal				High: GABA High: Glutamate High: Noradrenaline
		Dorso Medial (lateral)	DM(l)	Reciprocal				
		V-shaped complex	V	Reciprocal				
V-shaped complex	V	Triangular Complex	Tr	Reciprocal	Dentate Gyrus	DG	Atoji and Wild, 2004	High: GABA High: Glutamate
		Dorso Medial (lateral)	DM(l)	Reciprocal				
Source:		Atoji and Wild, 2004, 2006						Herold et al., (2014)

Table 1 Summary table of intrinsic connectivity of the avian hippocampal formation, the comparison between the mammalian hippocampus and the avian hippocampal formation and neurotransmitters of the hippocampal formation.

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Discussion

The present literature review aims to present what is known about spatial cognition in the pigeon *C.livia*. This was done by investigating several parameters of spatial cognition. First, the anatomical characteristics of the mammalian HC and the avian HF were shown and both were compared to each other, subsequently, neurotransmitters and connectivity of the HF were presented followed by subregion-specific activity during spatial testing. Finally, another region of the avian brain, the NCL, is mentioned as influential on spatial cognition besides HF.

The HF and HC look rather different from each other, boundaries of subregions of the HF are less clearly defined compared to the HC and the mossy-fibre structure of the DG seems to be missing throughout the full HF. Research into HF connectivity to other brain regions has created the ability to compare HC to HF. The DG region of the HC seems to be equivalent to the DL. The HA and HD are similar to the EC, which is technically not part of the HC itself, but in close contact with the HC. The DM region of the HF shows similarity to both the subiculum and CA regions of the HC. Large differences in connectivity between the HC and HF are in the reciprocal character of many intrinsic connections of the HF, whereas in the HC most connections are one-way. C-Fos expression showed increases of left DM, Right DL and TrV after spatial testing, suggesting both that these areas are key in spatial cognition and it shows laterality of the pigeon brain. The NCL is suggested by literature as another region for spatial cognition, the NCL is functionally equivalent to the PFC. This research (Rinnert et al., 2019) concluded that 41% of NCL neurons encode locations, even to an extent where it is possible to predict a next spatial move. In the black-capped chickadee (*P. atricapillus)* is has been shown that inactivation of the HF does only impair short term spatial memory, but not visual spatial memory (Shiflett et al., 2003), this already hints towards other regions that might be of influence. All results, in the shape of a look-up-list, are presented in Table 1 on the previous page.

Similar studies have been performed in the black-capped chickadee (*Poecile atricapillus*),

where in food-retrieving birds the number of Fos immunoreactive neurons seemed to correspond to the number of remember items (Smulders and DeVoogd, 2000). This study also measured early gene expression of Zenk where it was found that the degree of neurons expressing Zenk could be related to accuracy of cache retrieval (Smulders and DeVoogd, 2000). However, in the zebra finch (*Taeniopygia guttata*) Zenk was not correlated to spatial memory performance (Bischof et al., 2016). Future research could point correlation of Zenk expression out in the case of HF-dependent spatial memory task like the spatial, delayed nonmatch-to-sample task, as stated in (Coppola and Bingman, 2020) in the homing pigeon. Zenk expression has already been related to processes of synaptic plasticity that are induced conditioned fear memory retrieval in pigeons (Brito et al., 2019), but this study did not have a spatial aspect to it.

Hippocampal formations of different species of birds do differ. For instance, the volume of the entire HF is larger for brood-parasitic species of birds (Reboreda et al., 1996; Sherry et al., 1993). Homing pigeons show larger HF volumes compared to non-homing species of pigeons, which probably require a smaller degree of spatial memory (Rehkämper et al., 2008). Food-storing birds, like chickadees, tits, nuthatches, and jays, also show higher HF volumes compared to non-food-storing birds (Krebs et al., 1989; Lucas et al., 2004; Sherry et al., 2008). Birds subspecies that migrate not only show larger HF volume (Pravosudov et al., 2006), but also higher HF neuron density (Cristol et al., 2003), compared to non-migratory subspecies. There is no literature stating differences in subregions of the HF, these seem rather homologous between avian species, and it studies rather extensively in the black-capped chickadee (see Sherry and MacDougall-Shackleton, 2015) and pigeon (present study and Atoji and Wild, 2019, 2006, 2004).

The present review gives insight into what we know, but also into what we do not know. The direction of the research is promising and research into the question of whether there are more avian brain areas, besides NCL and HF, that contribute to spatial cognition could expand our knowledge quite much. This could

be done via methods into immediate early genes (IEG) expression by looking at for instance c-FOs, Zenk or Fra-1 (see Smulders and DeVoogd, 2000) in other avian brain structures. This could for instance be avian structures that are similar to the mammalian medial temporal lobes, which in mammals play a role in spatial cognition and episodic memory in general. Hormones of the HF are outside the scope of the present study, this is already studied in the mammalian hippocampus, but literature about hormones of the avian HF is scarce, therefore could the case of hormones in the avian HF be a suggestion for future research to get a more complete picture of what is happening in the avian HF and how it compares to the mammalian HC.

Afterword and Acknowledgements

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