

Research report

Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons:
Possible behavioral equivalencies to the mammalian prefrontal system

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Abstract

The neostriatum caudolaterale (NCL) of birds is thought to be equivalent to the mammalian prefrontal cortex (PFC) due to its dense dopaminergic innervation, its associative structure, and its importance for cognitive tasks which are known to be affected in mammals with prefrontal lesions. The aim of the present study was to analyze the functional importance of the NCL and its main thalamic afferent structure, the n. dorsolateralis posterior thalami (DLP), in reversal and go/no-go tasks, two behavioral procedures which are often used to assess mammalian prefrontal functions. Using a multiple regression analysis in which structure-specific lesion extents are correlated with different postoperative behavioral measures, the specific contribution of the relevant structures were differentiated from the neighbouring areas CDL (area corticoidea dorsolateralis) and NC (neostriatum caudale). The analyses showed a highly significant contribution of the NCL to reversal but not to go/no-go or to visual discrimination performance, while all other structures under analysis had no impact on any behavioral measure. These results underline the specific contribution of the pigeons' NCL on a subset of cognitive tasks which are known to be affected by prefrontal lesions in mammals. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

Comparative neuroanatomical studies have demonstrated important similarities in the chemoarchitecture and connectivity of avian and mammalian forebrains [44]. However, these investigations mostly concentrated on sensory and motor pathways, with only limited emphasis on associative structures. Recently, Ivan Divac and colleagues proposed an area in the caudolateral part of the avian forebrain to be comparable to the mammalian prefrontal cortex (PFC) [10,35]. One hall-

mark of the PFC is the dense dopaminergic innervation [47,50]. Indeed several studies could show that the neostriatum caudolaterale (NCL), a semilunar area in the caudalmost subventricular part of the avian forebrain, receives a dense dopaminergic innervation comparable to the PFC [10,12,34,48,51], and displays a high density of dopaminergic D1-receptors [42]. The pattern of intratelencephalic afferents of the NCL also resembles that of the PFC and demonstrates a multisensory convergence [31,34,37]. Additionally, behavioral studies could demonstrate that lesions of the caudolateral forebrain caused deficits in spatial working memory tasks like delayed alternation [14,18,35,36], and sequential procedures like go/no-go [18], but left performance in various visual discriminations intact [14,35,36].

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Lesion studies are always faced with the problem that the lesioned area generally also includes, at least to a certain extent, neighbouring structures. This is especially problematic in studying the NCL, since every approach inevitably also damages parts of the overlying area corticoidea dorsolateralis (CDL) and the neighbouring neostriatum caudale (NC). Given the dense reciprocal connections of the CDL with the hippocampal formation [5] and the multimodal nature of the NC [37] it is conceivable that a part of the cognitive deficits after NCL-lesions is due to lesioning these neighbouring structures. One elegant way to deal with this problem is to use multiple-regression analyses based on quantitative reconstructions of structure-specific lesion extents which are correlated with different postoperative behavioral measures [21]. Using this method would allow the statistical assessment of the possibly separate contributions of neighbouring structures to different behavioral tasks.

The aim of the present study was to use multiple-regression analyses to examine the functional importance of the pigeon's NCL and its thalamic afferent structure, the n. dorsolateralis posterior thalami (DLP) [48], in further tasks which are generally associated with prefrontal functions. If it could be shown that these structures are specifically involved in the procedures examined, the idea of an equivalence of NCL and PFC could be substantiated. Four different behavioral tasks were employed. The first was a reversal procedure since deficits in this task are often observed in mammals after prefrontal [6,40] or hippocampal [3] lesions while lesions of the pigeon's caudal neostriatum are not associated with reversal deficits [32]. Go/no-go was used as a second task, since it is also often observed to be deficient after lesions of the ventromedial prefrontal cortex [25,41]. Performance attenuations in go/no-go tasks were not observed after ablations of the complete caudal neostriatum in pigeons [39] although deficits were seen after extensive NCL-lesions [18]. Finally a grain-grit and a simultaneous pattern discrimination task were employed to control two very different procedures for possible sensory deficits.

2. Method

A total of 20 adult homing pigeons (*Columba livia*) of local stock were used. They were kept in individual cages with water always available. During the experiments the pigeons were food deprived to 80% of their normal body weight. All subjects were pretrained on a daily basis in a grain-grit discrimination procedure and a simultaneous pattern discrimination task with two response keys in a conventional skinner-box for food reward.

2.1. Simultaneous pattern discrimination

The patterns used were a T and a \cap which were backprojected on the two keys of a Skinner-box with the aid of multichannel microprojectors. All events within a session, consisting of 40 trials, were controlled and recorded by modular logic programming equipment. The box was illuminated by a house light. A trial began with the presentation of the stimulus pair. When the animal pecked the positive stimulus, both stimuli extinguished, food was offered for 3 s and the next trial began immediately afterwards, with the left-right positions of the stimuli being determined by a quasi-random sequence [16]. Following an error the pigeon spend 3 s in darkness, followed by a correction trial with unchanged positions of the stimuli. Correction trials were presented until the animal ceased pecking the incorrect pattern. These correction trials were not considered when calculating the discrimination accuracy measures. All animals were given one session per day, weekends excepted. The training continued until an animal made at least 90% correct responses on 2 consecutive days.

2.2. Grain-grit discrimination

Always half an hour after the pattern discrimination task the pigeons were tested in the grain-grit discrimination with the procedure being slightly altered to that described by Güntürkün and Kesch [19]. The birds had to discriminate brownish-white dari grains from similar looking small pebbles. First, 30 grains were mixed with 30 g of pebbles (about 1000 in number) in an opaque tray, which could be attached to an opening in the pigeon's home cage. Then, the animal was allowed to peck 30 times before the tray was removed. By counting the remaining grains the percentage of pecks leading to swallowing of grain could be calculated, which served as a measure for the discrimination performance. The pigeons reached stable performance for 1 week before surgery started.

After reaching baseline in the grain-grit discrimination experiment and passing discrimination criterion in the simultaneous pattern discrimination the birds were assigned to the three surgical groups (NCL, DLP and NC) based upon their performance in the latter experiment. Thus, the best three pigeons were first randomly distributed to the three groups, then the three second best and so on, until NC- and DLP-groups contained six and the NCL-group eight animals. Since four birds died during surgery, minor rearrangements had to be made such that six animals underwent NCL-ablation, five had the DLP removed and five served in the NC-group. The regression method employs data from all lesioned animals and tests the significance of structure-to-performance correlations. Therefore, there is no

Table 1
Coordinates of electrocoagulation lesions of the three groups according to the pigeon brain atlas of Karten and Hodos [27]

DLP-lesions (25 mA, 8 s) (vertical approach)	NC-lesions (25 mA, 10 s) (vertical approach)	NC L-lesions (25 mA, 10 s) (30° tilt of the tip to lateral)
A 5.25, L 2.00, D 7.50	A 6.00, L 4.50, D 5.00 A 6.50, L 4.50, D 4.50 A 7.00, L 4.50, D 5.00	A 4.00, L 4.40, D 3.20 A 4.50, L 3.50, D 3.60 A 4.50, L 5.30, D 3.10 A 5.00, L 2.80, D 3.10 A 5.00, L 4.80, D 3.20 A 5.00, L 5.30, D 4.00 and 5.20 A 5.50, L 3.80, D 3.40 A 5.50, L 5.40, D 3.90 and 5.90 A 6.00, L 4.90, D 3.50 A 6.00, L 6.00, D 5.20 A 6.50, L 5.00, D 3.60 A 6.50, L 5.80, D 5.00

For an animal of a given group, coagulations were applied at each of these coordinates in each hemisphere.

need for a control group like in traditional approaches.

2.3. Surgery

The animals were anaesthetized with equithesin (0.5 ml/kg), the scalp was incised at the midline and retracted sideways. The skull was trephined using a dental drill over the appropriate locations. For electrocoagulations a 0.25 mm thick insect needle, insulated except for 0.5 mm at the tip, was used. The electrode was introduced under stereotaxic guidance and the tissue at the target locations was coagulated for 10 s with 25 mA (8 s for DLP-group). Preliminary data had shown that a coagulation with these parameters resulted in a lesion size of slightly less than 1 mm³. Lesions were placed symmetrically in both hemispheres at the locations given in Table 1. At the same time, care was taken to leave the dorsally situated CDL and parahippocampal areas intact. The definition of the NC as used in the present study involves the neostriatum outside the NCL and caudal to A 7.00 according to the pigeon brain atlas of Karten and Hodos [27].

Cytoarchitectonically this region displays no obvious inhomogeneities and is largely consistent with area Ne16 outside NCL according to the quantification of grey level indices in the pigeons' neostriatum [38].

2.4. Postoperative retention

After 4–6 days of postoperative recovery, both the grain–grit discrimination as well as the simultaneous pattern discrimination were repeated as a postoperative retention test. Postoperative testing in the pattern discrimination lasted until the 90%-criterion of learning had been reached again. Grain–grit discrimination was performed for seven postoperative sessions.

2.5. Reversal learning

After successful completion of the postoperative retention tests the values of the two stimuli in the pattern discrimination task were reversed. Procedures were the same as before. Pigeons had to reach learning criterion of 90% before being admitted to the next experiment.

2.6. Go/no-go

The Skinner-box for this task contained only one pecking key in the center of the front panel. A session consisted of 40 trials, each of which lasted 20 s. During this period only one of two new stimuli, a 4 and an N, was backprojected on the key in a quasi-random sequence [16]. During a positive trial, each peck on the key was reinforced with access to food for 3 s. Immediately thereafter the same stimulus was presented again and the sequence could be repeated until the 20 s of the trial had passed. During the 20 s of a 'no-go'-trial each response of the animal was followed by 3-s time-out in which all lights were switched off. The number of correct and incorrect responses were recorded. Daily sessions were given until the subject had reached the 90%-criterion of learning.

2.7. Perfusion and anatomical analysis

After completion of all behavioral experiments the animals were perfused intracardially with saline (40°C) followed by 4% paraformaldehyde in 1.2 M phosphate buffer (pH 7.4, 4°C). Brains were removed and kept for 6 h in a 4% buffered paraformaldehyde solution containing 30% sucrose (6°C) before being transferred for 48 h to a 30% sucrose solution (6°C). With a freezing microtome sections of 30-μm thickness were cut in frontal plane. Every third section was

mounted, dried and stained with cresyl violet. Lesioned areas were measured with the image analysis system AnalySIS (Münster, Germany) in steps of 500 μm from A 3.50 to A 7.50 for NCL and NC and in steps of 250 μm from A 4.75 to 5.75 for DLP. Since the pigeons' caudal forebrain offers only limited cytoarchitectural heterogeneities which could easily be used for structure delineations, a set of landmarks including their relative topographical positions was used for the reconstructions, which had been developed according to the map of the NCL provided by Waldmann and Güntürkün [48]. Normal tissue volumes of NCL, NC, DLP, CDL, archistriatum (A), and paleostriatum augmentatum (PA) were measured along their complete rostrocaudal extension in steps of 500 μm in non-lesioned birds. From these data the percentage volume losses for NCL, DLP, NC, CDL, A and PA were calculated for each hemisphere (L% and R%) and animal. L% and R% were combined in W%, a the weighted index of bilateral damage introduced by Hodos and Bobko [20]. $W\% [W\% = (L\% \times R\%)/100]$ indicates the amount of combined damage incurred in the two hemispheres by minimizing the influence of asymmetrical lesions on the statistical analysis. It ranges from 0 to 100% and has the following properties: it is equal to zero for unilateral lesions; lesions that exhibit either nearly complete bilateral sparing or are grossly asymmetrical have W% values close to 1.0; it is equal to 100% in cases where total bilateral destruction occurred.

3. Results

3.1. Histology

Table 2 presents a summary of the quantitative analysis of the lesion reconstructions. The first six cases in the table are the NCL-animals, followed by the five NC-cases, and the five DLP-lesioned pigeons. The first three data columns give the total lesion volume in mm^3 encountered in the left and the right hemisphere, as well as the addition of these two values indicating the total lesion amount in a single animal. The remaining rows present the percentage of damage on the left (L%) and the right (R%) side of the brain for a certain structure. In addition, the weighted index W% is given which was calculated as outlined in the method section.

The NCL-group sustained bilateral forebrain damages from 35.2 to 107.3 mm^3 . Lesions to the NCL ranged from $W\% = 12.2$ to 71.2. Inevitably their lesions had also encroached on surrounding structures like the NC in which volume losses ranged from $W\% = 0.01$ to 3.64. Although care was taken to spare the overlying CDL as much as possible, all NCL-animals also had damages in this structure from $W\% = 1.2$ to 19.1. In three pigeons minor lesions in the left archistriatum

were observed.

The NC-animals had bilateral forebrain lesions reaching from 6.8 to 31.5 mm^3 . The volume loss in the target area ranged from $W\% = 0.7$ to 1.53. In animal 471 the NCL had also sustained a small lesion of $W\% = 0.4$. Several pigeons of this group also had small A and/or PA-damages. Overall, the W% values of the NC were in this group much smaller than those for the NCL in the NCL-group. When evaluating this difference, it has to be considered that the NCL is much smaller than the NC as defined in the present study. In addition, however, the absolute values of the volume losses were also larger in the NCL- than in the NC-group. Therefore, a part of the following statistical analysis was devoted to the possibility that the extent of the behavioral deficits were a mere effect of lesion size.

The pigeons with damage of the DLP had bilateral thalamic lesion volumes ranging from 2.0 to 4.97 mm^3 . The specific extent of volume loss in DLP took values between $W\% = 0.84$ and 60.1. Fig. 1 presents reconstructions of the lesions of an NCL-, an NC-, and a DLP-animal. In the following statistical analysis W%-values of NCL, NC, DLP, and CDL were employed. The data for A and PA were not used, since these structures were only damaged in very few animals and to some extremely limited extent.

3.2. Behaviour

Postoperatively, none of the animals displayed any obvious sensory or motor deficit. The sensory aspect was quantitatively tested in the grain-grit discrimination and the retention of the simultaneous pattern discrimination task. For the pre- to postoperative comparison of the grain-grit task the discrimination accuracy of the pigeons was not significantly altered ($t_{15} = 1.5$, n. s.). The absence of sensory deficits was even more obvious in the retention of the simultaneous pattern discrimination in which all animals reached criterion in the first postoperative session.

3.3. Group results, correlations and multiple regression analyses

Multiple-regression analyses were carried out to separate the contribution of each structure to the deficits of the behavioral tasks. Since all animals had reached criterion in the first postoperative session of the simultaneous pattern discrimination, this variable was discarded from further analyses. The three remaining tasks for which structure-deficit relations were analyzed were the grain-grit discrimination, the reversal task and the go/no-go paradigm. Performance in the grain-grit discrimination accuracy (GGD) was calculated with the grain-grit index: $\text{grain-grit index} = \text{GGD}_{\text{post}} - \text{GGD}_{\text{pre}} / \text{GGD}_{\text{post}} + \text{GGD}_{\text{pre}}$.

Table 2
Lesion volumes and percent structure losses for all experimental animals and lesioned areas in the left (L%) and the right hemisphere (R%)

Group	Case	Total lesion (mm ³)		NCL			NC			DLP			CDL			A			PA				
		L	R	both	L%	R%	W%	L%	R%	W%	L%	R%	W%	L%	R%	W%	L%	R%	W%	L%	R%	W%	
NCL	470	48.9	58.4	107	52	56	29.1	13	15	1.95	0	0	0	39	49	19.1	2.1	0	0	0	0	0	0
NCL	478	30	30.2	60.2	34	40	13.6	12	8	0.96	0	0	0	12	23	2.76	2.96	0	0	0	0	0	0
NCL	481	48	35.1	84.2	45	27	12.2	13	28	3.64	0	0	0	38	7	2.66	9.15	0	0	0	0	0	0
NCL	474	53.7	44.9	98.5	56	42	23.5	14	9	1.26	0	0	0	42	28	11.8	0	0	0	0	0	0	0
NCL	679	14.9	20.3	35.2	49.1	41.4	20.3	2	0.05	0.001	0	0	0	8.5	17.6	1.5	0	0	0	0	0	0	0
NCL	13	30.2	26.1	56.3	86.2	82.6	71.2	4.7	4.3	0.2	0	0	0	11.4	10	1.2	0	0	0	0	0	0	0
NC	678	2.6	4.2	6.8	0	0	0	3	4	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	27	9.25	9.88	19.1	0	0	0	8	80	0.64	0	0	0	0	0	0	7.1	6.9	0.49	3.03	9.65	0.29	0.29
NC	480	5.31	5.79	11.1	0	0	0	5	6	0.3	0	0	0	0	0	0	1	0	0	0.35	1.86	0.01	0.01
NC	96	12.2	6.98	19.1	0	0	0	12	7	0.84	0	0	0	0	0	0	1.27	0	0	2.1	1.61	0.03	0.03
NC	471	10.4	21.1	31.5	4	10	0.4	9	17	1.53	0	0	0	0	0	0	1.1	0	0	0	0	0	0
DLP	472	2.17	2.8	4.97	0	0	0	0	0	0	68	88.4	60.1	0	0	0	0	0	0	0	0	0	0
DLP	324	1.84	2.24	4.08	0	0	0	0	0	0	53.5	92.6	49.5	0	0	0	0	0	0	0	0	0	0
DLP	460	1.32	1.13	2.46	0	0	0	0	0	0	68.6	57	39.1	0	0	0	0	0	0	0	0	0	0
DLP	95	79	2.48	3.27	0	0	0	0	0	0	25.9	77.3	20	0	0	0	0	0	0	0	0	0	0
DLP	476	0.9	1.1	2	0	0	0	0	0	0	4.57	18.3	0.84	0	0	0	0	0	0	0	0	0	0

The combined structure loss is additionally expressed as W%, a weighted index of bilateral damage. A (archistriatum), DLP (n. dorsolateralis posterior thalami), NC (neostriatum caudale), NCL (neostriatum caudolaterale), PA (paleostriatum augmentatum).

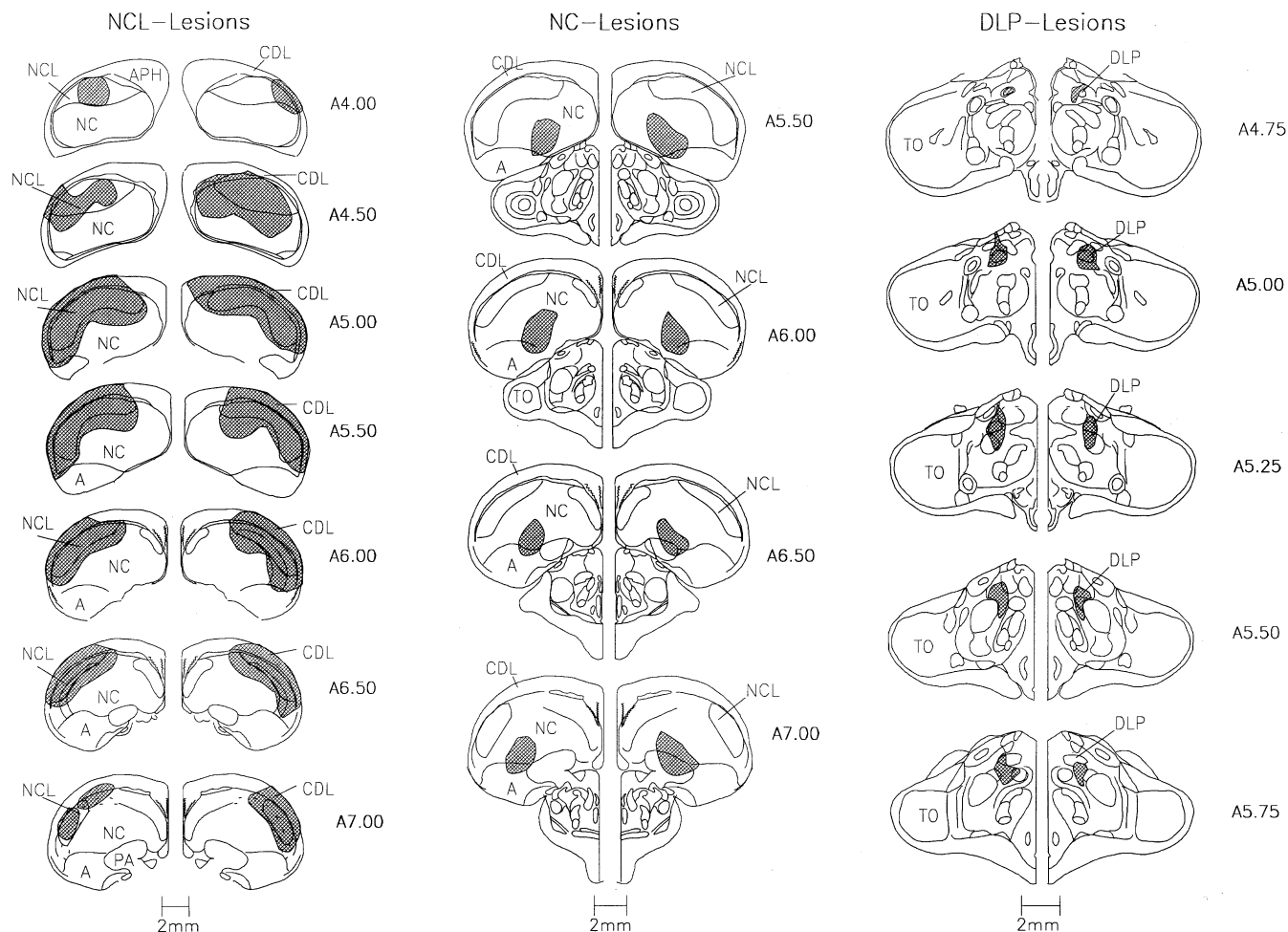


Fig. 1. Lesions locations (hatched areas) depicted on frontal sections in three representative animals from the NCL-, the NC-, and the DLP-group. Coordinates are from the pigeon brain atlas of Karten and Hodós ([27]). Abbreviations: A (archistriatum), APH (area parahippocampalis), CDL (area corticoidea dorsolateralis), DLP (n. dorsolateralis posterior thalami), NC (neostriatum caudale), NCL (neostriatum caudolaterale), PA (paleostriatum augmentatum), TO (tectum opticum). Bars below the sections indicate the length of 2 mm.

This measure varies between -1 and $+1$. A score of zero indicates no discrimination accuracy changes after surgery, negative scores show a performance decline while positive scores indicate higher postoperative achievements.

Before starting with the analyses of the lesion effects of different structures, first the effect of the total lesion extent had to be evaluated. Therefore, correlations between total lesion volumes irrespective of anatomical boundaries and the grain-grit index ($r = 0.01$), reversal learning ($r = 0.18$), and go/no-go performance ($r = 0.40$) were calculated. None of these correlations approached significance. The same was true when analyzing correlations with the total lesion volume of only the left (grain-grit index: $r = -0.06$, reversal learning: $r = 0.18$, go/no-go: $r = 0.39$), or only the right hemisphere (grain-grit index: $r = 0.09$, reversal learning: $r = 0.17$, go/no-go: $r = 0.39$). Thus, the behavioral results did not depend on the overall magnitude of the lesions.

As shown in Table 3, none of the lesion groups displayed important postoperative declines in discrimination accuracy as measured with the grain-grit index. To analyze a possibly specific contribution of a certain brain structure to grain-grit performance, a multiple regression analysis with the $W\%$ -values of NCL, NC, DLP, and CDL as independent, and the grain-grit index as the dependent variable was conducted. The

Table 3

Means and standard errors (S.E.) of the three lesion groups for the grain-grit index (GGI) and the number of sessions needed to reach learning criterion in the learning and the go/no-go task

Group	GGI		Reversal		Go/no-go	
	Mean	S. E.	Mean	S.E.	Mean	S.E.
NCL	-0.03	0.02	7.8	1.5	8.7	1.5
NC	0.38	0.36	5.4	1.0	8.0	1.3
DLP	-0.13	0.04	6.4	0.8	7.2	1.5

result was not significant ($F(4,11) = 0.59$), and all regression coefficients between structure specific lesion volumes and the discrimination capacity as tested with the grain-grit index were very low ($\beta_{\text{NCL}} = -0.11$, $r_{\text{NCL}} = -0.13$; $\beta_{\text{NC}} = 0.36$, $r_{\text{NC}} = 0.26$; $\beta_{\text{DLP}} = -0.15$, $r_{\text{DLP}} = -0.18$; $\beta_{\text{CDL}} = -0.3$, $r_{\text{CDL}} = -0.14$; all $t_{11} < 1.1$, n.s.). The same result was observed after analyzing only left ($F(4,11) = 0.64$), or only right hemisphere structures ($F(4,11) = 1.01$). Thus, none of the lesioned structures seemed to be involved in visual discrimination performance as revealed by the grain-grit index.

As a next step, the number of sessions needed by the animals to reach learning criterion in reversal learning was analyzed. As shown in Table 3, the NCL-lesion group required on the average a larger number of sessions to manage this task. However, all NCL-animals also had partly substantial NC- or CDL-lesions. Since the group average thus masks the possible contribution of different structures under examination, the specific impact of NCL-, NC-, DLP-, and CDL-lesions on reversal learning performance was tested with a multiple regression analysis. This model was highly significant ($F(4,11) = 6.18$, $P < 0.01$). From the different independent variables only the standardized regression coefficient for the NCL was significant ($\beta = 0.85$, $r = 0.73$, $t_{12} = 4.5$, $P < 0.001$), while those of the other structures were not ($\beta_{\text{NC}} = -0.24$, $r_{\text{NC}} = -0.25$; $\beta_{\text{DLP}} = 0.23$, $r_{\text{DLP}} = 0.08$; $\beta_{\text{CDL}} = -0.05$, $r_{\text{CDL}} = 0.11$; all $t_{11} < 0.8$, n.s.). Partial correlations, which represent the unique contribution of the respective independent variable to the prediction of the dependent variable adjusted for other factors, also revealed lesion extent of NCL as the only significant predictive factor for reversal deficits ($r = 0.804$, $t_{12} = 4.5$, $P < 0.001$). From these data it follows that about 57% of the variance in the reversal data can be accounted by the NCL-lesion. The NCL of both hemispheres seemed to contribute to this effect. The model for both multiple regressions with lesion volumes of the left ($F(4,11) = 4.27$, $P < 0.05$), and of the right side ($F(4,11) = 4.52$, $P < 0.05$) was significant. From the different independent variables only the standardized regression coefficients for the NCL of the left ($\beta = 1.02$, $r = 0.72$, $t_{12} = 3.4$, $P < 0.01$), and of the right hemisphere ($\beta = 1.07$, $r = 0.75$, $t_{12} = 3.78$, $P < 0.005$) turned out to be significant.

As displayed in Table 3, none of the lesion groups displayed obvious group differences in the go/no-go task. The specific contribution of NCL-, NC-, DLP-, and CDL-lesions on go/no-go performance was again tested with a multiple regression analysis. The regression model was not significant ($F(4,11) = 1.05$) and all regression coefficients were very low ($\beta_{\text{NCL}} = 0.09$, $r_{\text{NCL}} = 0.23$; $\beta_{\text{NC}} = 0.37$, $r_{\text{NC}} = 0.48$; $\beta_{\text{DLP}} = -0.11$, $r_{\text{DLP}} = -0.32$; $\beta_{\text{CDL}} = 0.11$, $r_{\text{CDL}} = 0.35$; all $t_{11} < 1.2$, n.s.). The same was true for the analyses of left ($F(4,11) = 0.86$), and right hemisphere structures

($F(4,11) = 1.09$). Thus, none of the lesioned areas seemed to be involved in go/no-go achievement.

4. Discussion

The present study shows that lesion extent of the NCL is significantly related to the extent of reversal deficits in pigeons. A comparable significant relation could not be revealed for NC and CDL, which border to NCL, and for DLP, the afferent diencephalic relay of the NCL. None of the lesions produced sensory deficits as tested in a pattern and a grain-grit discrimination task. Contrary to a previous study [18] no deficits in a go/no-go task could be revealed for any structure.

The most important aspect of the present study is the finding that reversal deficits are significantly related to lesion extent of NCL but not to lesions of the neighbouring NC and CDL. Based on the pioneering studies of Divac and colleagues [10–12,35], the NCL was defined by Waldmann and Güntürkün [48] by quantifying the density of immunocytochemically labelled dopaminergic fibers. The multiple regression approach of the present study makes it likely that this anatomical definition also corresponds to a functional unit. Reversal deficits without sensory perturbations have been repeatedly obtained with prefrontal lesions in different mammals like rats [29], cats [23], old world monkeys [25,46], new world monkeys [8], and humans [6]. Thus, together with previous anatomical [10,12,48,51], biochemical [11], electrophysiological [26], and behavioral studies [14,18,35,36], the present result adds further support to the assumption that the pigeon's NCL is equivalent to the mammalian prefrontal cortex.

At least a part of the deficits of the NCL-lesioned pigeons in the homing experiment of Gagliardo and Divac [15] might also be due to reversal learning problems. In this study the average orientation of the vanishing bearings (170°) of the lesioned animals are well in the direction of the home loft (161°) when being released from a familiar site. At the two unfamiliar release sites, however, NCL-pigeons stuck to the south-east direction (168° and 134°), although the actual loft location was now at completely different positions (298° and 262°).

The NCL is not the only avian forebrain structure for which postlesional reversal deficits have been reported. Similar attenuations are usually observed after lesions of the hyperstriatum in chicks [4], quails [45], and pigeons [32,33]. Shimizu and Hodos [43] showed that this is specifically due to lesioning the thalamorecipient laminae of the visual Wulst. At least in one of these studies [32], the NC served as a control lesion area and, similar to the present results, no lesion-dependent reversal deficit were obtained. Thus, at least two

different forebrain structures, NCL and the thalamorecipient hyperstriatal laminae, are involved in processes which are important for pattern reversal learning. This picture resemble at least in part the situation in mammals, where beside the prefrontal cortex also different structures of the temporal lobe have been implicated in reversal tasks [1,3].

For none of the examined structures in the current study could a sensory deficit be obtained. This accords with previous studies which could not reveal visual discrimination deficits after NCL [35, 36] or NC lesions [32]. This is similar to studies using PFC-ablated animals which also generally display no or only very transitory sensory deficits [8,13].

For none of the examined structures could a significant relation to go/no-go performance be shown. This contrasts with PFC-lesion studies in different mammalian species [17,23,28,41] and also a previous experiment with pigeons [18] which revealed for the same task slight but significant deficits after NCL lesions. This last contradiction might be related to the fact that in the present go/no-go task the birds could make up to five pecks without reinforcement. This might have discouraged slightly disinhibited individuals. Additionally, the NCL-lesions in the study of Güntürkün [18] extended far more anterior along the lateral telencephalon into the area temporo-parieto-occipitalis (TPO). Lesions of this structure are known to impair the animals in intensity, hue, and pattern discriminations [7]. It is therefore possible that the go/no-go deficits obtained by Güntürkün [18] were related to the sensory and not the sequential nature of the task. However, it is also conceivable that the absence of go/no-go deficits in the present study resulted from the fact that this was the last experiment in a series of postoperative tasks so that the animals might have recovered before being tested. The pigeons of the present study had all completed well above 700 trials in more than 1 month before beginning to run in the go/no-go experiment. Behavioral recoveries in less than 700 trials have been reported for rats [49] and cats [9] with PFC-lesions, although of course the nature of the trials might considerably differ from the procedure used here. Mogensen and Divac [35,36] also observed a complete recovery of their NCL-lesioned pigeons in delayed alternation learning after 255–816 trials. Thus, although it cannot be ruled out that the absence of go/no-go deficits is due to a fast postlesional recovery, the present data clearly show that given several weeks of recovery NCL-lesions cause no deficits in a sequential go/no-go task like the one used in this study.

DLP-lesions could not be shown to affect performance in reversal- and go/no-go-tasks. In contrast, lesions of the main thalamic input source to the PFC, the mammalian nucleus mediodorsalis (MD) has been demonstrated to affect performance in these tasks [22,24,41]. The NCL in birds receives its main input from

the DLP [31,48] which itself is the projection area of different sensory pathways [30]. The DLP is thus thought to contribute to the multimodal character of the NCL. Thus, although the DLP is very likely not homologous to the mammalian MD [18] it is conceivable that DLP participates in functions equivalent to MD. This seems indeed to be true for delayed alternation but not for go/no-go (present study) and reversal learning (present study). Thus, the projection of the DLP onto NCL subserves only a subset of the functions of the MD-PFC connection.

Anatomical and electrophysiological data make it likely that the pigeons' DLP is equivalent to the mammalian posterior complex of nuclei (Po) [30]. Subnuclei of the Po project to PFC [2] in mammals, and it is possible that the DLP-NCL system is anatomically equivalent to the Po-PFC projection. Metzger et al. [34] suggest according to anatomical data the avian n. dorsomedialis anterior thalami (DMA) to be equivalent to the mammalian MD. Unfortunately, no behavioral data testing prefrontal functions are available for the mammalian Po and the avian DMA. Thus, the functional architecture of the avian thalamus has to be elucidated in further studies to clarify the issue of the prefrontal system in birds.

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