Presumed ‘prefrontal cortex’ lesions in pigeons: effects on visual discrimination performance

Laura Aldavert-Vera ^a, David Costa-Miserachs ^a, Ivan Divac ^b, Juan D. Delius ^{c,*}

^a *Departament de Psicobiologia i de Metodologia B, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Spain*

^b *Department of Medical Physiology, University of Copenhagen, DK-2200 Copenhagen, Denmark*

^c *Lehrstuhl Allgemeine Psychologie, Universität Konstanz, D-78457 Konstanz, Germany*

Abstract

The posterodorsolateral neostriatum (PDLNS) in pigeons may be an equivalent of the prefrontal cortex (PFC) in mammals. Here we report that lesions of this brain region in pigeons have a detrimental effect on various learned visual discriminations. Pigeons with lesions of the overlying area corticoidea dorsolateralis (CDL) served as controls. Both the postoperative re-learning to criterion of a preoperatively learned simultaneous double visual mirror pattern discrimination and the learning of a simple successive go, no-go discrimination were impaired by the PDLNS lesions. The PDLNS and CDL groups did not differ significantly in the postoperative learning of a reversal of the simultaneous discrimination. The results are discussed in relation to the presumed equivalence between the avian PDLNS and the mammalian PFC.

Keywords: Lesions; Pigeons; Posterodorsolateral neostriatum; Prefrontal cortex; Reversal learning; Visual discriminations

1. Introduction

It has recently become widely accepted that the avian neostriatum, together with some other structures (hyperstriatum, ectostriatum, nucleus basalis), is an equivalent of the neocortex in mammals [17,36]. In mammals the prefrontal cortex (PFC; we use this term only for mammals) is thought to play an important role in the control of cognitively mediated behaviour [11]. Birds have shown to be capable of cognitive performances comparable with those of mammals [34]. Some time ago one of us [6] suggested that the posterodorsolateral neostriatum (PDLNS; we use this term only for birds; some authors call the same structure neostriatum caudolaterale, NCL) in pigeons may be the structure which corresponds to the PFC. Subsequent studies have lent support to this proposal (see below and also Ref. [28]). Anatomical techniques showed that much like PFC, the PDLNS is rich in dopamine [7–10,37,39], receives affer-

ents from secondary sensory areas, and sends efferent connections to premotor structures [15,21,33]. Behavioural results also support this hypothesis: like ablations of PFC [11], lesions of the pigeon's PDLNS have been found to impair delayed responding [12,15,24,25] but not simultaneous visual discriminations [12,15,16,24,25]. However, there may also be differences in that the thalamic nuclei innervating the PFC and PDLNS are not quite equivalent [15,37].

The PFC can be variously subdivided on the basis of anatomical features [13], activation during different tasks [32] and behavioural effects of small lesions [11,19,22,30]. A gross division of the PFC into a dorsal and a ventral area, however, suffices for our purposes. The dorsal division is particularly involved in delayed responding tasks, whereas the ventral division appears to mediate the performance of tasks depending on response suppression such as discrimination reversal or go, no-go discrimination [11,23,30,31].

So far, the neurobehavioural evidence has been indecisive as to whether the PDLNS includes an equivalent of the ventral PFC. Delayed alternation impairments

* Corresponding author.

E-mail address: juan.delius@uni-konstanz.de (J. D. Delius)

have been repeatedly demonstrated [12,15,24,25], indicating that the PDLNS contains an equivalent of the dorsal PFC but the tasks sensitive to ablations of the ventral PFC have seldom been tried on birds [15,16]. One aim of the present study was to find out whether the PDLNS includes equivalents of the ventral PFC, in which case we could expect deficits in both discrimination reversal and go, no-go discrimination tasks but not in the retention of a visual discrimination. Pigeons with area corticoidea dorsolateralis (CDL) lesions served as controls. This region is unavoidably damaged during ablations of the PDLNS. Previous findings indicate that CDL lesions do not impair delayed responding, go, no-go visual discrimination, or simultaneous visual discrimination reversal performance [12,16].

2. Method

2.1. Subjects and apparatus

Fifteen adult domestic pigeons (*Columba livia*) of local homing stock were used. The birds were kept in individual $40 \times 45 \times 35$ cm metal grid cages located in a well ventilated and brightly illuminated (12 h on/12 h off) animal room. Throughout the experiment they were kept food-deprived to 80% of their normal weight. This and all other treatments that the pigeons were subjected to complied with German animal protection laws and regulations.

The pigeons were trained using horizontal conditioning platforms [40] controlled by a personal computer. The platforms (Fig. 1) were attached to the pigeons' home cage replacing their standard feeding troughs. Each platform incorporated two side-by-side transparent pecking keys (centres 5 cm apart, diameter 2.5 cm). Light-diode matrices (green, 5×7 diodes, 1.2×1.7 cm) displayed visual patterns below these keys. Two so-

lenoid feeders issued rewards of a few grains of millet onto the keys.

2.2. Pretraining

The pigeons were first shaped to peck the keys. Each trial began with the random presentation of a small pentagonal stimulus (Fig. 1, stimulus 1) for a maximum of 8 s either under the right or the left key, the other key remaining dark. A peck to the illuminated key yielded an immediate reward on the corresponding key accompanied by a 2-s feeding interval and followed by a 20-s intertrial interval. If the animal did not peck, a reward was automatically delivered at the end of the stimulus presentation. When the birds pecked in at least 80 trials of a block of 100 trials the procedure changed. A trial began with the presentation of the stimulus below the left or right key. When the pigeon pecked the key three times it was rewarded and the stimulus was extinguished. A 4-s intertrial interval followed before the next trial began. The pretraining terminated when the pigeons completed a block of 40 such trials.

2.3. Discrimination training

Daily sessions consisted of ten blocks of 40 trials each. A trial began with the simultaneous presentation of two discriminative stimuli below the keys. They were displayed until the pigeon completed a response to one of them (see below). Two mirror-image visual stimuli were used, a p-like shape and a q-like shape (1×1.2 cm in size) in either their standard 0° orientation (Fig. 1, stimuli 2 and 3; 20 trials per block) or 180° rotated on the matrix surface (looking then like d and b shapes, respectively; stimuli 4 and 5; 20 trials per block). The stimuli p and d were defined as correct (S+), the stimuli q and b as incorrect (S-). The sequencing of the stimulus pairs (p, q and d, b) and the right/left position of the stimuli was random. Three pecks delivered to the key showing an S+ resulted in the extinction of the stimuli; the issue of a reward on the corresponding key and a 2-s feeding period. Three pecks issued to the key showing an S- were defined as an error and were followed by a penalty consisting of a 4-s time-out period with both stimulus matrices fully illuminated. Both reward and penalty were followed by a 2-s intertrial interval with the stimuli off. Errors were followed by a repeated trial (correction trial) using exactly the same stimulus configurations. The correction trials procedure ended when the correct stimulus was chosen. These trials were counted but they neither entered into the discrimination scores nor into the trials-per-block count. Training ended when a criterion of 80% correct trials was achieved within a block.

Fig. 1. Conditioning platform and discrimination stimuli.

2.4. Surgery

Four to 7 days after training was completed, the pigeons were anaesthetised with an initial intra-muscular (i.m.) dose of 0.1 ml Kemint® (Alvetra, ketamine chlorhydrate 100 mg/ml) and 0.02 ml Rompun® (Bayer, xylazine 23 mg/ml) per 100 g body weight. The anaesthesia was maintained with additional 0.1 ml i.m. doses of Kemint administered at 15-min intervals. The pigeons were randomly assigned to two groups. In seven birds both the PDLNS as well as the CDL were ablated. In eight animals only the CDL was aspirated. While their heads were held in a stereotaxic apparatus, the scalp was retracted, the cranial bone was removed and the dura was retracted. The relevant brain tissue was removed by aspiration under visual microscopic control. A piece of dura substitute, Preclude® (W.L. Gore & Associates) was used to cover the lesion and the scalp was sutured over it.

2.5. Retraining and reversal

Seven days after surgery the animals underwent a retraining with the same procedure as before. Retraining ended when the animals regained the 80% correct criterion within a block of 40 trials. On the following day the birds were subjected to reversal training with the same procedure except that the previously positive stimuli were now defined as negative and vice-versa. The pigeons were trained until they completed a block with 80% correct trials.

2.6. Successive discrimination

Three to 5 days after completion of the reversal phase the pigeons were trained on a successive discrimination. Daily sessions consisted of ten blocks of 40 trials. After an inter trial interval of 2 s, trials began with the randomised presentation of one of two stimuli under one of the two keys. The key used was randomly chosen and the unused key remained deactivated and dark. The stimuli were l- and t-like patterns (Fig. 1). Stimulus 6 was defined as positive (S+), stimulus 7 as negative (S-). Either stimulus was presented for 10 s and three or more pecks during that period triggered one of two consequences at the end of the period. The response to the S+ led to an extinction of the stimulus, the issue of the grain reward, and a 2-s feeding time. The response to the S- led to a 3-s time-out penalty with the diode matrix entirely lit up. In the latter instance, the trial was repeated. Trial repetitions followed until the pigeons refrained from responding to the S- for its 10-s presentation. The repetition (correction) trials were counted but did not contribute to the performance score. When the animals completed a block with 75% or more correct trials on both negative

and positive trials the experiment ended. A lower criterion than for the earlier simultaneous tasks was chosen because preliminary experiments had indicated that some pigeons would not reach the higher criterion with this task even after extended training.

2.7. Histology

After the behavioural procedure was completed, the birds were anaesthetised and perfused transcardially with saline and a 4% formaldehyde solution. The brains were removed and postfixed in the latter solution. Before sectioning they were placed in a 30% saccharose solution for at least 2 days. After mounting and freezing in a cryotome they were cut at 40-µm intervals under a $\times 10$ magnifying lens. Every fifth section containing the lesion was mounted. These sections were examined under a microscope with dark-field illumination. The extent of the lesions was transferred to standard sections taken from a pigeon brain atlas [18].

3. Results

3.1. Histology

Examination of the sections showed that the lesions had generally affected the areas targeted. Fig. 2 shows the extent of the lesions on frontal brain section diagrams. The lesions directed at the PDLNS of each pigeon affected between about one-third and three-quarters of this area, as delimited on the basis of anatomical criteria [15]. They inevitably had also damaged about three-quarters and four-fifths of the overlying CDL. In some PDNLS-lesioned birds the damage also extended to minor fractions of either the non-PDNLS portions of neostriatum caudale, the area parahippocampalis or the area temporo-parieto-occipitalis [18]. The control lesions all affected about three-quarters of the CDL and in some birds a very small fraction of the PDNLS.

3.2. Behaviour

None of the lesioned pigeons displayed any obvious changes in overt behaviour after surgery. The number of blocks that each pigeon needed to reach in the preset criteria during the various discrimination learning tasks were compiled. They are presented averaged for the PDNLS and CDL groups in Fig. 3. There was no significant difference between the two groups of pigeons in the number of blocks needed to reach the 80% pre-operative correct criterion. Table 1 shows that there were pre- to postoperative performance decays in both PDLNS and CDL ($F_{1,13} = 92.05$, $P < 0.001$) but that the difference in decay between the two groups was

Fig. 2. The extent of the lesions in the pigeons of the PDLNS (experimental) and the CDL (control) group on standard brain section drawings [15,18]. The dark areas indicate the volume lesioned in all pigeons, the shaded areas encompass the lesion extents across all pigeons.

small and not significant. However, regarding the re-attainment of the 80% correct criterion after surgery the PDLNS group needed on average more than twice as many training blocks as the CDL group and this re-acquisition difference was significant (Fig. 3; 10.0 and 4.8 blocks; $F_{1,13} = 6.47$, $P < 0.05$).

In the reversal training on the same discrimination (i.e. the previous negative stimuli were now positive and vice-versa) the two groups did not differ significantly from each other. However it is fair to point out that this was probably so because in this instance the control CDL lesioned pigeons yielded relatively variable results (large standard error, Fig. 3). For the acquisition training of the successive discrimination, the PDLNS pigeons needed more than twice as many blocks on average (14.0 blocks) to reach the 75% criterion on both S+ and S- trials as the CDL

Fig. 3. Acquisition and re-acquisition during the various phases of the experiment. Shown are the mean number of blocks ($\pm$ S.E.) which the CDL group (clear columns) and the PDLNS group (shaded columns) needed to reach the performance criteria (see text).

pigeons (6.6 blocks). This difference is significant ($F_{1,12} = 7.61$, $P = 0.01$). One of the PDLNS pigeons in fact, ceased to respond altogether after the 12th block of training without having reached criterion and thus could not be included in the analysis. The difference between the groups on this latter task was wholly due to the fact that the PDLNS group pigeons had on average more difficulties in learning to suppress responses to the negative stimulus than the CDL group pigeons did (Table 2). Only the group difference concerning the S- trials is significant ($F_{1,12} = 5.26$, $P < 0.05$); there was in fact no group difference concerning the S+ trials.

Very similar group differences and statistical significance patterns (not detailed here) emerged when the total average number of trials to criterion, rather than the blocks to criterion was analysed. This information is not wholly redundant because the standard blocks of 40 trials on which the above analysis is based did not include counts of the additional correction trials.

4. Discussion

The results of the experiment have only partially answered the question of whether the PDLNS corresponds to the entire PFC or only its dorsal division. The PDLNS group was impaired in a go, no-go discrimination and in the re-learning of a complex simultaneous visual discrimination task. The postoperative

Table 1
Simultaneous discrimination performance (mean % trials correct per block $\pm$ S.E.) for the CDL and PDLNS groups of pigeons during the last two preoperative and first two postoperative blocks

Blocks	-2	-1	+1	+2
CDL	70.0 ($\pm$ 2.6)	83.2 ($\pm$ 0.9)	64.5 ($\pm$ 2.9)	68.1 ($\pm$ 3.6)
PDLNS	69.7 ($\pm$ 2.1)	83.2 ($\pm$ 0.9)	61.7 ($\pm$ 1.5)	63.7 ($\pm$ 3.4)

Table 2

Average number of blocks ($\pm$ S.E.) needed to reach the 75% criterion within the successive discrimination task, reported separately for S+ and S- trials and for the PDLNS and CDL groups

Trial type	S+	S-
CDL group	1.5 ($\pm$ 0.2)	6.6 ($\pm$ 1.1)
PDLNS group	1.5 ($\pm$ 0.2)	11.0 ($\pm$ 1.2)

reversal of the latter discrimination, however, was not impaired.

The marked difficulty that the PDLNS-lesioned pigeons had with relearning of the simultaneous discrimination was not anticipated since in previous studies PDLNS ablations had practically no effect on simultaneous discriminations involving a variety of cues [12,15,16,24,25]. Simultaneous visual discriminations have been found to be at most only transiently affected by PFC lesions, regardless of the area ablated [14,27,29,31,35]. The reasons for these slight deficits remain obscure but it may be that the nature of the discrimination stimuli and the level of the acquisition criteria played a role. It is thus possible that either the special discriminanda, the b, d and p, q shapes and/or the relatively low learning criterion used in the present study may have amplified the dysfunction induced by PDLNS lesions. It is known that intact mammals have difficulties with distinguishing such mirror-symmetric stimuli [2], but there is no data on what effect PFC lesions have on their discrimination. Intact pigeons appear to find such mirror-symmetric stimuli not too difficult to distinguish [5] but it is still possible that the relatively low acquisition criterion employed made the discrimination especially susceptible to PDLNS lesions.

The effect of PFC lesions on discrimination reversals depends on the duration of initial training and of postoperative recovery, together with the discriminability of, and the familiarity with the stimuli, as well as the precise location of the lesions [20,22]. This complexity is illustrated by the fact that PFC ablations in rats resulted in impairments from the first reversal onward [1], whereas in cats impairments only became evident after the third reversal [38]. Simultaneous discrimination reversal thus seems to be a less reliable index task than delayed responding is for dorsal PFC functioning. Our results may be interpreted analogously, but alternative interpretations for the lack of a discrimination reversal deficit are also possible. The absence of a significant difference between the PDLNS- and the control CDL-lesioned pigeons could be due to the comparatively large variance affecting the scores of the latter group (Fig. 3). This in turn, may relate to the possibility that the CDL tissue is part of the avian hippocampal complex. Lesions of the pigeon hippocampus have previously been found to increase the variability of visual

discrimination reversal performance in pigeons [26]. CDL lesions have not been found to interfere with the performance of other behavioural tasks [12,16] but they may not be suitable controls for PDLNS lesions in the context of this particular task. In any case, it has been demonstrated that the extent of PDLNS but not of CDL lesions correlates with reversal learning deficits of a simultaneous shape discrimination [16].

The effect of the PFC lesions on go, no-go successive discrimination tasks, like their effect on simultaneous visual discrimination reversal, depends on several variables: the species under study, the precise location of the PFC lesions, the localisation of the stimuli and responses, the discriminability of the stimuli, the duration of the intertrial intervals and on whether a reward is given also for the correct no-go responses [3]. Manipulations of task parameters can switch the discrimination deficit on or off in animals with PFC lesions [31]. Impairment in go, no-go discrimination was found in the present study as well as an earlier one [15] but not in a very recent study [16]. Possible reasons for this disagreement are discussed in the latter paper. The large number of relevant variables in this task (see above) requires further research in order to establish whether PDLNS is a full equivalent of the mammalian PFC. Neighbouring but more anterolateral areas of the avian neostriatum [4] may also need to be considered in this context.

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