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Transitive Behavior in Hippocampal-Lesioned Pigeons

Rosemary Strasser[a] Joyce M. Ehrlinger[b] Verner P. Bingman[b]

[a]University of Nebraska at Omaha, Psychology Department, Omaha, Nebr., and [b]Bowling Green State University, Psychology Department, Bowling Green, Ohio, USA

Key Words
Hippocampus · Transitive inference · Birds · Pigeon · Non-spatial learning · Conditional discrimination

Abstract
The hippocampus of birds and mammals is critical for the learning of map-like memory representations of environmental space. It has been suggested that the hippocampus of rats also participates in non-spatial relational learning, including the learning of non-spatial transitive relationships among odor stimuli [Bunsey and Eichenbaum, Nature 1996]. Although transitive-like learning has been demonstrated in a variety of vertebrate species, from a comparative perspective the role of the hippocampus in this form of learning has not been tested in other amniote groups. We trained control and hippocampal-lesioned homing pigeons on a series of visual, non-spatial, go/no-go conditional discriminations and then tested them on novel transitivity probe trials. The hippocampal-lesioned pigeons were as successful as control pigeons in responding appropriately to correct and incorrect transitivity pairs. The finding that the homing pigeon hippocampal formation is not necessary for solving this serial, conditional discrimination task is important for further understanding hippocampal function across species, and represents one of the few studies that have attempted to localize a brain region responsible for the phenomenon of transitive behavior learning.

Introduction

The spatial ability of animals, including the ability to successfully navigate among desired locations in the environment, is vital to the fitness of an individual and is likely substantially shaped by ecological and evolutionarily forces. The mammalian and avian hippocampus (Hp) are homologous structures [Bingman et al., 1995; Colombo and Broadbent, 2000; Puelles et al., 2000] that display a remarkably similar functional role in the learning of map-like memory representations of environmental space [O'Keefe and Nadel, 1978; Eichenbaum et al., 1990; Nadel, 1991; Bingman et al., 1995, 2003; Gagliardo et al., 1999]. It has recently been suggested in some rodent and non-human primate studies that Hp participates not just in the representation of space, but in a range of spatial and non-spatial learning processes [Eichenbaum et al., 1994; Bunsey and Eichenbaum, 1996; Dusek and Eichenbaum, 1997; Wood et al., 1999; Day, 2003; but see O'Keefe, 1999 for challenge to this position]. For example, Hp-

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Rosemary Strasser, PhD
Psychology Department, University of Nebraska at Omaha
418 Allwine Hall
Omaha, NE 68182-0274 (USA)
Tel. +1 402 554 2705, Fax +1 402 554 3121, E-Mail rstrasser@mail.unomaha.edu

lesioned rats display deficits in tasks of non-spatial transitive learning among odor stimuli [Bunsey and Eichenbaum, 1996; Dusek and Eichenbaum, 1997; but see Van Elzakker et al., 2003 for a challenge to this interpretation]. As described by Piaget [1928], the ability to display transitive learning is based on understanding and drawing inferences about the relationship among stimuli that share common element(s). Performance on transitive inference tasks is typically modeled to depend on the ability of a subject to develop a mental representation, or schema, of the stimulus elements necessary to deduce ordinal relationships between items [Halford, 1993; also see Wynne, 1997]. There is now evidence supporting the hypothesis that, under some conditions in rodents, Hp is critical for its expression.

For some comparative psychologists, the ability to infer transitive relations is important for understanding cognitive learning and language function in human and non-human primates [Bryant and Trabasso, 1971; De Boysson-Bardies and O'Regan, 1973; McGonigle and Chalmers, 1977]. Other researchers have noted that social animals might also use transitive relations to make judgments about group members [Cheney and Seyfarth, 1990; Hogue et al., 1996; Wynne, 1997]. For example, if an animal observes that individual A is dominant to individual B, and B is dominant to individual C, it could conclude that A must also be dominant to C without observing any interactions between them. It is easy to see how this ability could be highly adaptive and it has been found to occur in several animal species that live in social groups [Wynne, 1997; Bond et al., 2003].

Little is known concerning the brain mechanisms responsible for complex conditional discrimination learning, especially learning thought to rely on transitive inference learning as originally proposed by Piaget [1928]. Rats with damage to Hp [Dusek and Eichenbaum, 1997] and aged monkeys [Rapp et al., 1996] are impaired in tasks that use sequentially ordered pairs of stimuli (A+B–, B+C–, C+D–, D+E–) to test for transitive learning. The authors in both studies attribute the deficit to impaired relational flexibility although a simpler explanation for this phenomenon based on the unequal distribution of excitatory weights is more likely [von Ferson et al., 1991; Van Elzakker et al., 2003; and the discussion in this article]. In another influential study, Bunsey and Eichebaum [1996] tested for transitivity in intact rats and rats with Hp damage using four concurrent, non-spatial stimulus pairs. In this design, if stimulus A was presented first the rewarded stimulus was B over Y. However, if stimulus X was presented first the rewarded stimulus was Y over B. Once learned, the rats were given a second discrimination task with either stimulus B or Y presented first and the rewarded stimulus was C and Z, respectively. On novel probe trials, intact rats successfully chose stimulus C when followed by A and chose stimulus Z when followed by X, but rats with Hp damage failed to show a preference for the correct transitivity pairs [Bunsey and Eichenbaum, 1996]. Although the authors conclude from this result that Hp is critical for the acquisition of flexible, relational representations and postulate that Hp function is conserved across species [Bunsey and Eichenbaum, 1996], it is still unclear whether other interpretations could explain their findings and if deficits in transitive learning can be demonstrated in other amniote groups.

In the following study, we are interested in examining whether the avian Hp might play a role in serial, non-spatial conditional discriminations that resemble transitive inference learning. It is uncertain whether the role of the avian Hp extends beyond the realm of spatial learning [but see Colombo and Broadbent, 2000], and whether bird/mammal differences in the role of the Hp in non-spatial cognition exist. Suggesting that the latter might be true is the finding that parahippocampal lesions in homing pigeons do not impair non-spatial, paired-associate learning [Bingman et al., 1998] as they do in rats [Bunsey and Eichenbaum, 1993]. In the following study, we trained control and Hp-lesioned pigeons on a series of visual, non-spatial, go/no-go conditional discriminations and then challenged them with novel transitivity probe trials. The results are discussed in terms of various theoretical views of transitive inference learning and possible bird/mammal differences in the role of the Hp in non-spatial cognition.

Materials and Methods

Subjects and Surgical Procedures

Fifteen adult homing pigeons of both sexes were used. Prior to training, 7 of the pigeons were subjected to Hp lesions (Hp pigeons), 4 were subjected to control lesions in the caudal neostriatum (N pigeons), and 4 served as untreated controls (C pigeons). Briefly, pigeons were anesthetized with Rompun (0.5 ml/kg body weight) and ketamine (0.5 ml/kg body weight) and placed in a stereotaxic apparatus. Electrolytic lesions were made bilaterally with electrodes with a 5.00 mm exposed tip for hippocampal lesions and a 3.00 mm exposed tip for the neostriatum lesions. The electrodes were positioned in the brain according to coordinates obtained from the atlas of Karten and Hodos [1967]. Three bilateral, electrolytic lesions were made of the hippocampal target regions and one bilateral, electrolytic lesion was made of the neostriatum, an auditory processing area. We choose this area for control lesions because the learning task has no auditory component. Further details of the procedures can be found

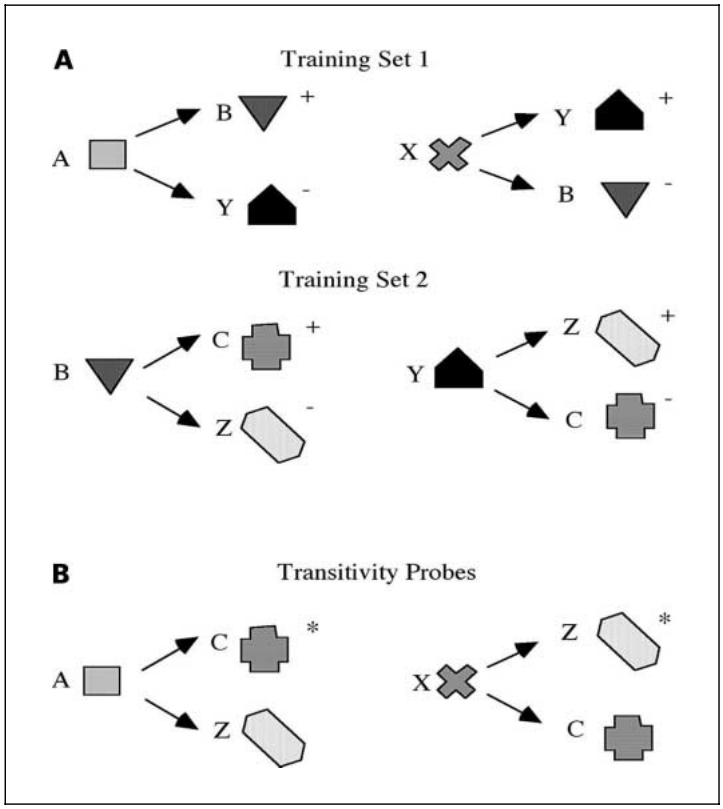

Fig. 1. A Schematic diagram of the conditional discrimination training stimuli of different shapes and colors serially presented on a monitor in an operant chamber where a plus denotes a reinforced (food) training pair and a minus denotes a punished (lights out) training pair. **B** Schematic diagram of the 4 unreinforced transitivity probe trials where * denotes a correct transitivity probe.

elsewhere [Bingman and Mench, 1990; Bingman and Hodos, 1992]. It should also be noted that 5 of the 7 Hp lesion pigeons and 2 of the 4 N lesion pigeons were used in a previous 'open field' one-trial associative task where spatial deficits were observed in the Hp lesion birds [Strasser and Bingman, 1999]. The research reported here was performed under guidelines established by the Animal Care and Use Committee at Bowling Green State University.

Training Procedures

The task employed was a visual, non-spatial, conditional discrimination task. Pigeons were brought to 85% of their free feeding body weight and then autoshaped to peck at an illuminated key for a food reward. Subsequent behavioral training took place in an operant chamber (42 × 41 × 36 cm) illuminated with an overhead incandescent light bulb (15 watts). The front wall of the chamber contained a central Perspex window (10.8 × 8.2 cm) behind which a video monitor (screen dimensions 11 × 8.2 cm) was placed. Stimuli were presented on the video monitor and pigeons could peck the Perspex window to break an electrical circuit interfaced to a personal computer. A food hopper (access hole in the front wall: 6.2 × 6.2 cm), the center of which was located 2.8 cm below the bottom of the Perspex window, was used to deliver food (mixed grain) to the pigeons. White noise was delivered continually to mask any environmental sounds. Before training on the experimental task, all pigeons were first pretrained to peck the Perspex window seven times within 10 s after a yellow circle (2.0 cm in diameter) was presented on the video monitor. The pigeons were then given a simple go/no-go discrimination task to solve. When a red cross was presented on the video monitor, seven pecks within 10 s of presentation led to a food reward. In contrast, seven pecks to a green X within 10 s of presentation led to a 5-second lights out period. All birds quickly learned the go/no-go discrimination.

Training Sessions. After completing pre-training the pigeons were trained in the same operant chamber on a transitivity task involving first the learning of a series of conditional discriminations in which for each trial two visual stimuli would be serially presented on the video monitor (fig. 1A). A pigeon needed to first peck seven times at the first stimulus within 10 s of presentation. This was followed by the removal of the first stimulus and a 1-second inter-stimulus interval. Subsequently, the second stimulus was presented and the pigeon needed to determine if responding to the second stimulus would yield a reward or a brief lights-out period. For the first series of conditional discrimination, when stimulus A was followed by stimulus B or when stimulus X was followed by stimulus Y (+ correct pairings), seven pecks to the second stimulus within 10 s activated the food hopper for 2–3 s of grain access followed by a 10-second inter-trial interval. In contrast, when stimulus A was followed by stimulus Y or when stimulus X was followed by stimulus B (– incorrect pairings), 7 pecks to the second stimulus within 10 s resulted in lights out in the experimental chamber for 5 s followed by a 10-second inter-trial interval. For both correct and incorrect trials, an absence of 7 pecks to the second stimulus within 10 s resulted immediately in the 10-second inter-trial interval and 10 s latency score recorded for that trial (the pigeons always completed 7 pecks to the first stimulus). Pigeons were given one session of 100 trials/day, with trial types equally distributed among the four possible stimulus-pair combinations. Pigeons

remained on this first training set until the mean latency to respond to the second stimulus of incorrect pairings was 2.0 s greater than that of the second stimulus of correct pairings. Once reaching this criterion, pigeon proceeded to the second training set, again one session of 100 trials/day, in which the first stimulus was either Y or B and the second stimulus was either C or Z (see fig. 1A). After reaching the same criterion as the first training set, pigeons were given sessions in which both training set 1 and 2 stimulus pairs were included in a session with the 8 possible pair combinations being randomly ordered and equally frequent. Pigeons were trained on mixed training sessions until meeting the same criterion of a 2-second latency difference in completing 7 pecks to rewarded and unrewarded second stimuli.

Test Sessions. Training session trials were composed of 8 possible stimulus pairs and conditional discriminations. After reaching the training criterion, transitivity probes were inserted into the training session on the last training phase. Test sessions consisted of 100 trials, each pigeon was given 3 test sessions, with 4 non-reinforced and non-punished transitivity probe trials (once each stimulus A followed by either C or Z, and stimulus X followed by either C or Z) randomly inserted among the 96 remaining conditional discrimination training trials (fig. 1B).

Data Analysis

Analysis of variance (ANOVA) was used to determine if there were any between-group differences in sessions to reach criterion through to the last phase of training. An ANOVA was also used to determine within and between group differences in response latency to the second stimulus of correct and incorrect conditional discrimination training trials and correct and incorrect transitivity probe trials during the three test sessions only.

Histological Analysis

Following completion of training, the two groups of lesioned pigeons were deeply anesthetized with sodium pentobarbital intravenously. Birds were perfused via the left ventricle starting with 10% saline solution followed by 4% paraformaldehyde. Following fixation, brains were cut at 50 μm using a freezing microtome and every sixth section was placed on a gel-coated slide. All sections were stained with cresyl violet. The extent of the lesion damage was determined for each pigeon with a macroprojector. Additional details of the procedures are described elsewhere [Bingman and Hodos, 1992].

Results

Conditional Discrimination Training

Intact control pigeons, N- and Hp-lesioned pigeons all took approximately the same number of sessions to complete training on training set 1 (controls: mean = 8.75, SE = 1.44; N = 8.75, SE = 1.60; Hp: mean = 7.143, SE = 0.71; $F_{2,12} = 0.758$, $p = 0.4899$) and training set 2 (controls: mean = 7.5, SE = 0.87; N = 7.25, SE = 1.32; Hp: mean = 7.57, SE = 0.75; $F_{2,12} = 0.030$, $p = 0.9703$). Further, there were no significant differences in the number of sessions to reach criterion on the combined training of sets 1 and 2 together (controls: mean = 9.00, SE = 2.86; N = 8.25, SE = 1.93; Hp: mean = 7.57, SE = 1.04; $F_{2,12} = 0.168$, $p = 0.8475$). During the three test sessions with transitivity probe trials, there were also no significant differences between the two control groups with respect to differences in latency to respond to the second stimuli on correct and incorrect conditional discrimination training trials ($F_{1,28} = 0.12$, $p = 0.73$). Therefore, the data from the two groups were combined for the following analyses. A 2-factor ANOVA confirmed that there was no overall difference in response latency between combined control and Hp lesioned pigeons ($F_{1,56} = 0.01$, $p = 0.92$) and no significant group x stimulus pair/response latency interaction ($F_{1,56} = 1.4$, $p = 0.24$). However, there was an overall difference in response latency to correct and incorrect training pairs ($F_{1,56} = 2245.5$, $p = 0.00001$), as both groups responded more quickly to the second stimulus of the correct training pairs (Correct training pairs: combined controls mean = 2.59, SE = 0.08; Hp mean = 2.42, SE = 0.10; Incorrect training pairs: combined controls mean = 8.82, SE = 0.18; Hp mean = 8.97, SE = 0.16; see fig. 2). Taken together, the data demonstrate that Hp lesions do not impair learning in a non-spatial, visual conditional discrimination task.

Transitivity Probes

On the transitivity test trials (fig. 3), both combined controls (4.71 s, SE = 0.78) and Hp-lesioned pigeons (4.38 s, SE = 0.85) took about 4.5 s to complete 7 pecks to correct, transitive second stimuli and about 7 s (combined controls: 7.19 s, SE = 0.73; Hp: 6.97 s, SE = 0.91) to respond to incorrect, non-transitive second stimuli. Indeed, a 2-factor ANOVA revealed no overall difference in response latency between combined control and Hp-lesioned pigeons ($F_{1,56} = 0.12$, $p = 0.74$) and no group × transitivity trial/response latency interaction ($F_{1,56} = 0.005$, $p = 0.95$). However, there was an overall difference in response latency to correct transitivity pairs and incorrect non-transitivity pairs ($F_{1,56} = 9.5$, $p = 0.0032$), as pigeons from both groups responded more vigorously to correct, transitive second stimuli (fig. 3). In summary, the Hp-lesioned pigeons solved novel transitivity pairings in a manner indistinguishable from controls.

Histology

Figure 4 summarizes the lesion damage to the Hp- and N-lesioned pigeons. Hp lesions resulted in almost complete damage to the hippocampus proper with less consistent damage to the neighboring parahippocampus [Karten and Hodos, 1967]. Some small damage to the hyper-

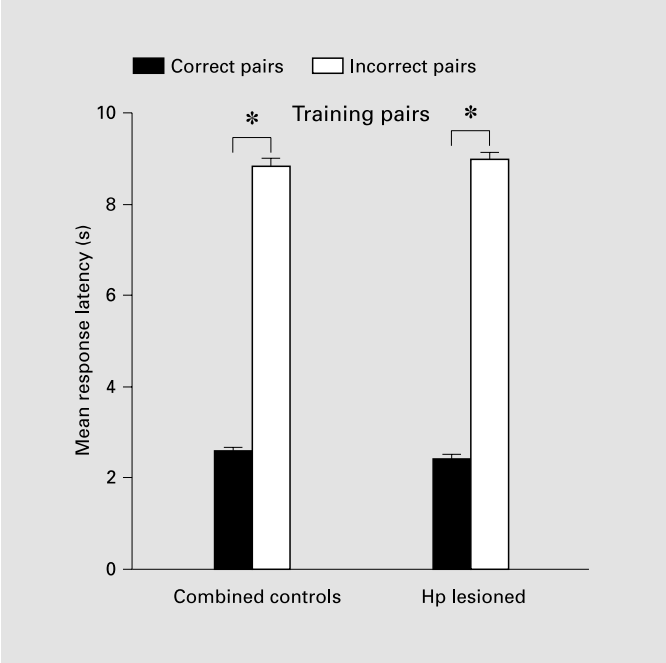

Fig. 2. Mean response latency, with standard error bars, to correct and incorrect second stimuli on conditional discrimination training trials during the 3 test sessions that included transitivity probe trials. The significant difference in response latency (indicated by *) suggests that both groups learned to discriminate between correct and incorrect training pairs (p = 0.00001).

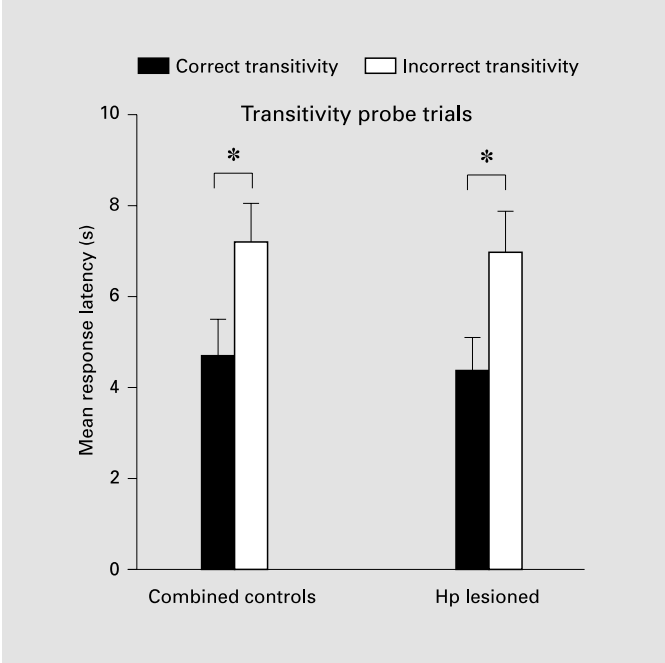

Fig. 3. Mean response latency, with standard error bars, to correct and incorrect (both unreinforced and unpunished) transitivity probe trials during the 3 test sessions. The important finding is that Hp-lesioned pigeons did not behave differently than controls during the probe sessions (p = 0.74). Further, there was a significant difference in response latency (indicated by *) to correct transitivity pairs and incorrect non-transitivity pairs (p = 0.0032), as pigeons from both groups responded more vigorously to correct, transitive second stimuli.

striatum accessorium and hyperstriatum ventrale was also observed. N lesions resulted in consistent damage to central portions of the neostriatum.

Discussion

All pigeons, including pigeons with Hp lesions, responded more vigorously to the second stimuli of correct transitivity probe trials compared to the incorrect transitivity probe trials (fig. 3). Although transitive-like learning has already been examined in birds [von Fersen et al., 1991; Couvillon and Bitterman, 1992; Wynne et al., 1992; Zentall and Urcuioli, 1993; Steirn et al., 1995; Wynne, 1997; Bond et al., 2003], this study is the first to examine the possible role of the avian hippocampus in this phenomenon. The most important finding of this study is that homing pigeons with Hp lesions were able to learn a series of non-spatial, conditional discriminations and behaved appropriately in a novel stimulus context. It should be emphasized that the lesions sustained by the Hp pigeons of the present study were essentially identical to lesions that produce robust deficits in spatial learning studied both in the field [Strasser et al., 1998; Gagliardo et al., 1999] and in the laboratory [Strasser and Bingman, 1999]. As such, the results of this study suggest that unlike the rodent Hp, which some have suggested is critically involved in transitive learning as well as memory beyond the representation of space [Eichenbaum et al., 1994; Bunsey and Eichenbaum, 1996; Dusek and Eichenbaum, 1997; Wood et al., 1999], the avian Hp plays no apparent role in non-spatial, conditional discriminations and transitive-like behavior based on learning.

Another point worth considering is how does this study differ from previous studies that have used 4 or 5 sequentially ordered pairs of stimuli (A+B–, B+C–, C+D–, D+E–) to examine transitive inference learning and just what type of representational mechanism(s) might support these possibly different types of learning? In previous research with hippocampal damaged rodents [Dusek and Eichenbaum,

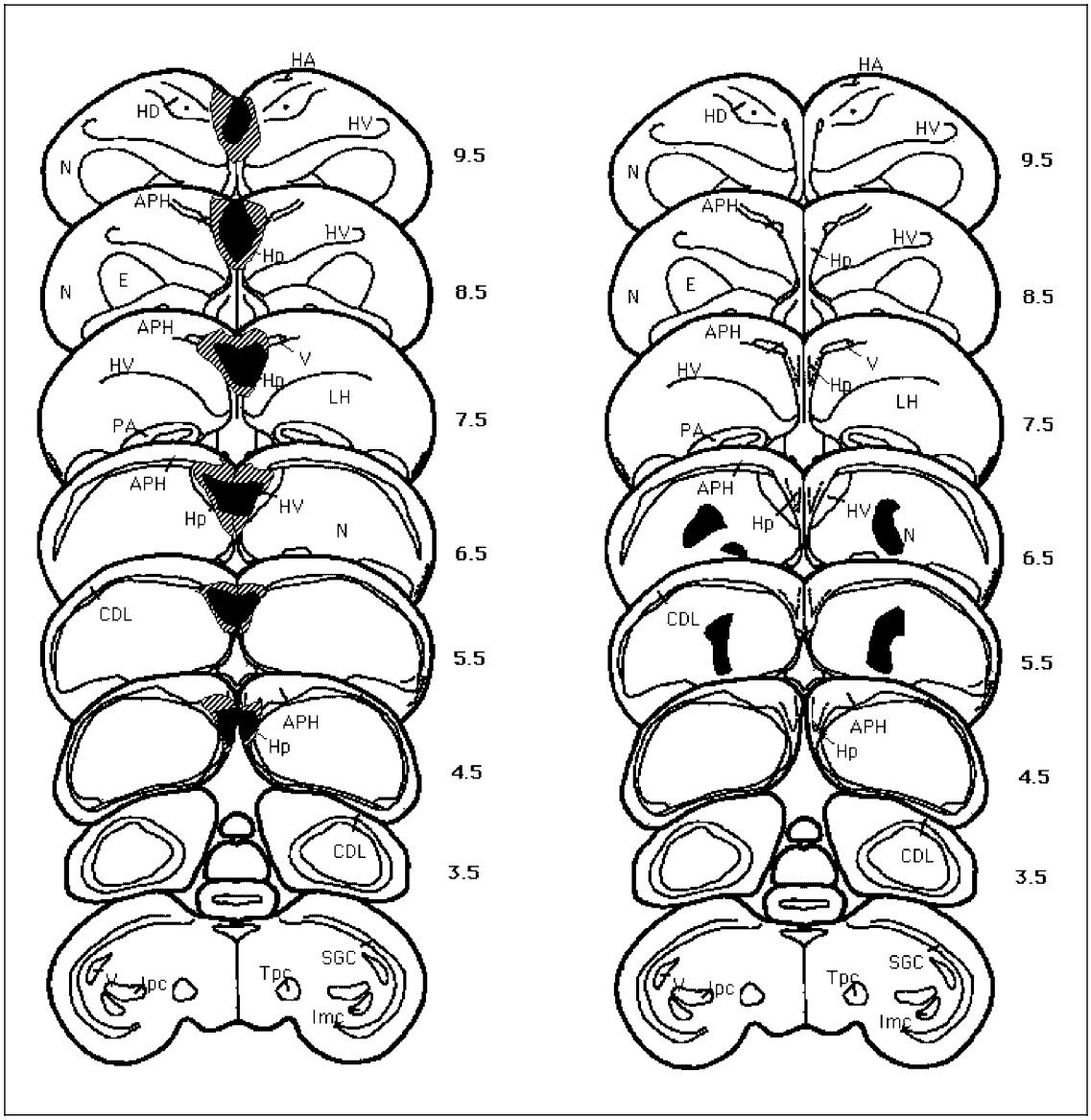

Fig. 4. Left Reconstruction of the lesion damage sustained by the Hp pigeons plotted on plates adapted from the pigeon atlas of Karten and Hodos [1967]. The pigeons sustained extensive damage to the hippocampus (Hp) with less extensive damage to the neighboring parahippocampus (APH). The black areas represent damage shared by at least 6 out of 7 Hp-lesioned birds. Gray areas represent damage seen in at least 4 out of 7 Hp-lesioned birds. Abbreviations taken from Karten and Hodos [l967]: parahippocampus (APH), corticoid (CDL), ectostriatum (E), hyperstriatum accessorium (HA), hyperstriatum dorsale (HD), hippocampus (Hp), hyperstriatum ventrale (HV), nucleus isthmi, pars magnocellularis (Imc), nucleus isthmi, pars parvocellularis (Ipc), lamina hyperstriatica (LH), neostriatum (N), paleostriatum augmentatum (PA), stratum griseum centrale (SGC), nucleus tegmenti pedunculo-pontinus, pars compacta (TPc), ventriculus (V). **Right** Reconstruction of the lesion damage sustained by the N pigeons. Damage was concentrated in the central portion of the neostriatum. The black areas represent damage shared by at least 3 out of 4 N-lesioned birds.

1997] and aged primates [Rapp et al., 1996], deficits in transitive-like learning were found using sequentially ordered pairs of stimuli (A+B–, B+C–, C+D–, D+E–), which the authors attributed to deficits in the formation of flexible, relational memory representations among the stimuli. Value Transfer theory [as described by von Fersen et al., 1991], however, could explain performance on these sequentially ordered pairs of stimuli based on the unequal distribution of excitatory weights of the test stimuli without relying on the interpretation that animals are drawing logi-

cal inferences about the relationships among stimuli. As a further indication that sequentially ordered pairs of stimuli might not require true transitive inference learning, a recent study by Van Elzakker et al. [2003] demonstrated that rodents can indeed base their choices on the absolute excitatory value of sequentially ordered pairs of stimuli.

The design of the present study, however, renders it less likely that Value Transfer theory and the unequal excitatory weights of stimuli could explain successful performance during our transitivity probe trials. In the present study, stimuli C and Z, the second stimuli on the transitivity probe trials, had similar reward histories and were associated with similarly rewarded stimuli B and Y, respectively, during training. Therefore, the preference for responding to C after the presentation of A, and the preference for responding to Z after the presentation of X could be a true reflection of transitive behavior as originally described by Piaget [1928]. However, clearly, further studies are needed to test this possibility. One potential study that could resolve this issue would be to train pigeons with 8 training pairs (set 1: A B, B C, C D, D E; set 2: X Y, Y Z, Z Q, Q R) using the methods of the current study. If there were hidden, unequal distributions of excitatory weights using this method, then the Value Transfer theory [von Fersen et al., 1991] would predict differential performance on various transitivity probe trials (performance on probes BD and YQ would differ from probes BE and YR). In contrast, if the experimental design used in the present and proposed study does represent a true test of transitive (logical) inference learning, as similarly assumed in studies such as Bunsey and Eichenbaum [1996], performance on all possible probe pairs should remain relatively equal [see Van Elzakker et al., 2003].

Our results demonstrate that the avian hippocampus is not necessary for the kind of flexible, non-spatial relational learning proposed by some theorists to engage hippocampal participation in rats [Eichenbaum et al., 1992; Bunsey and Eichenbaum, 1996]. However, we must acknowledge that if certain parameters of our transitivity task were changed, the representational requirements could then possibly require participation of the avian hippocampus. For example, in the present study pigeons were tested on a go/no-go procedure, whereas in another study where a hippocampal lesion effect was found, rats were tested on a concurrent discrimination procedure [Bunsey and Eichenbaum, 1996]. Also noteworthy is that fornix-lesioned rats are impaired when trained using a simultaneous presentation of two odor cues in a go-left/go-right response choice, but actually perform better than controls if they are trained with successive odor cues in a go/no-go condition [Eichenbaum et al., 1988]. It is therefore meaningful to ask whether the properties of a behavioral paradigm used to assess transitivity can influence the kind of learning strategies used by the animals, and consequently, whether participation of the hippocampus is necessary or not? In this context, presenting pigeons with a concurrent discrimination task with transitivity probe trials could be revealing. Likewise, it is possible that the hippocampal deficits found in rodent studies of transitivity [Bunsey and Eichenbaum, 1996] are limited to odor stimuli. In rats, odors have privileged access to Hp, at least with respect to the number of synaptic crossings needed before olfactory information reaches Hp compared to other sensory modalities [Lynch, 1986]. In birds, olfactory information also reaches Hp after only a few synaptic crossings [Bingman et al., 1994]. The cognitive significance of this shorter synaptic journey is obscure, but one possibility is that hippocampal participation in transitivity is limited to odor stimuli in rodents.

Although there are many unanswered questions regarding the nature of transitive inference learning, the finding that the homing pigeon hippocampus is not necessary for solving the non-spatial, serial, conditional discrimination task used in the present study is important for comparative understanding of hippocampal function across species. This study also represents one of the few studies that have attempted to localize a brain region potentially involved in this transitive-like behavior. Interestingly, a recent study using a computational neural network model has provided some exciting predictions with which future researchers might test the role of the hippocampus in transitive-like behavior [Frank et al., 2003]. Notably, the authors suggest that, in contrast to the interpretation that the hippocampus is involved in the flexible encoding of the relational representations of the stimuli, the hippocampus might contribute to transitive-like performance when the initial associative values of sequentially ordered pairs of stimuli are being learned [Frank et al., 2003]. This is an interesting idea but the results of the present study would further suggest that if the excitatory values among the stimuli are kept equal during learning, hippocampal participation, at least in this avian species, might still not be necessary.

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