

## INTER- AND INTRAOCULAR TRANSFER OF COLOUR DISCRIMINATIONS WITH MANDIBULATION AS AN OPERANT IN THE HEAD-FIXED PIGEON

HORST D. MALLIN and JUAN D. DELIUS

*Experimentelle Tierpsychologie, Psychologisches Institut, Ruhr-Universität, D-4630 Bochum, F.R.G.*

### ABSTRACT

Lower mandible abduction of pigeons was instrumentally conditioned with water as reinforcer. The subjects were restrained and their head was held fixed. The response was sensed with a piezoelectric transducer. High rates of responding could be obtained using variable ratio reinforcement schedules. Differential stimulus control with coloured lights presented in the frontal and lateral field of view was demonstrated. Interocular transfer of these visual discriminations was good when the stimuli were presented frontally and poor when they were presented laterally. Intraocular discrimination transfer, where the stimuli were shifted from a frontal to a lateral position and vice-versa within the field of view of the same eye, was poor. No evidence of a functional hemispheric lateralization was found. The method is considered useful for studies demanding precise stimulus positioning and requiring acute access to central nervous structures while learning is in progress.

Key words: colour discrimination; interocular transfer; intraocular transfer; lateralization; instrumental conditioning; mandibulation; pigeon.

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In several areas of behavioural research with pigeons there is need for an efficient instrumental conditioning method that can proceed while the subject's head is held in a fixed position. In contrast to more conventional procedures this would allow the presentation of controlling stimuli in specified positions within the animal's sensory fields and acute access to its nervous structures while learning is in progress. Besides, there is interest in expanding the repertoire of operant behaviours available for study since it can no longer reasonably be held that one of them is necessarily representative of them all. We now describe such a procedure in which beak-opening is the response instrumental for water reinforcement in thirsty pigeons whose head

is held fixed. First results concerning the intra- and interocular transfer of learned colour discriminations obtained with this novel method are reported. Such transfer is of interest in view of the pigeons restricted binocular visual field (Jahnke, 1983), the marked regional specializations of the pigeon's retina with associated central differentiations (Emmerton, 1983), the totally crossed optic nerves and the reduced development of interhemispheric visual pathways in birds (Benowitz, 1980).

#### GENERAL METHODS

##### *Subjects and surgery*

8 conventionally housed adult homing pigeons (*Columba livia*) of local origin were used. For surgery they were anaesthetized with a freshly prepared chloral hydrate (3.3%), pentobarbital sodium (0.7%) and magnesium sulphate (1.7%) solution in 10% ethanol administered intramuscularly (initial dose 0.5 ml/100 g body weight, additional doses 0.2 ml/100 g). While their head was held in a stereotactic instrument (Karten and Hodos, 1967) the crown of the skull was exposed with a slit through the scalp. Three cavities were drilled with a dentist burr, two into the alveolar bone lateral to the cerebellum and one between the olfactory nerves. The cavities were filled with liquid dental acrylic cement using a pipette and from these anchorage points a platform was built up on the dry skull surface with the same cement. A small rectangular metal block with a tapped hole uppermost was set into this platform in a standardized position. The skin was drawn together with a pair of stitches leaving the block's surface exposed. A few day's recovery followed.

##### *Apparatus*

During the conditioning sessions the animals were constrained with a tight cloth jacket and placed in a foam-rubber cradle. The head block was affixed with a knurled screw to an arm of a stand mounted on a base-plate. A small cup-shaped fountain was placed immediately below the beak of the subject with the aid of another adjustable arm. Water from a raised reservoir could be delivered to it through tubing and an electromagnetic valve. The water quantity issued was adjusted through the duration of the valve activation to be approximately 0.1 ml. A clear miniature light bulb placed next to the water-fountain could be used to signal the availability of the reward. 1.5 sec after delivery the water was withdrawn by a suction pump acting through another electromagnetic valve and a catching vessel. The airflow through this normally open suction line also provided for ventilation.

A third adjustable arm was fitted with a piezoelectric ceramic element furnished with a 100 mm long spring-wire whisker. The tip of the whisker was placed under the lower mandible of the subject. Abduction of the mandible during beak opening activated the force transducer (Fig. 2, insert). Its output was amplified and pass-filtered between 10 and 100 hz. An adjustable trigger stage converted the mandibulation signals into standard digital pulses. A double-beam oscilloscope was used to monitor the trigger threshold adjustment.

The subject with all the ancillaries was placed inside a sound-insulating box. The interior of this box was painted buff-black and was illuminated with a frosted 25-W bulb located behind and above the animal. A loudspeaker broadcast white noise at 80 db SPL. A small one-way window allowed viewing of the animal. Modular digital equipment was used to register and program all relevant events. Counters and a cumulative recorder recorded the operant behaviour.

#### EXPERIMENT I: INSTRUMENTAL CONDITIONING

This experiment was intended to establish the replicability of preliminary experiments that had suggested the feasibility of an instrumental conditioning of the mandibulation response of pigeons.

##### *Methods*

##### *Procedure*

The animals were deprived of water for 23 h and 20 min before each session. This induced an individual water debt of approximately 20 ml. Sessions lasting about 30 min were conducted daily except weekends. In an initial session the baseline mandibulation under no-reinforcement conditions was recorded for each subject. In the following sessions the pigeons were shaped by intermittently offering them water. As they drank the animals triggered further reinforcements. Gradually the reinforcement ratio was increased up to VR 20. Finally each reinforcement was accompanied by a blocking period of 1.7 sec during which mandible responses had no consequences whatsoever. 3 to 6 daily 28-min sessions were needed to establish steady responding in all animals. Each animal was then run for 2 sessions under the final conditions.

##### *Results*

The unconditioned, spontaneous drinking of the pigeon has been described in great detail by Zweers (1982). For our purposes it is important that the pigeon makes some preparatory beak movements, involving mainly the lower mandible, before dipping the beak tip into the water. It then suction-pumps the water into its gape and swallows it. This involves small amplitude mandibulatory movements. After actual water ingestion has ended a few further larger amplitude lower mandible movements are shown. Early during shaping the beak movements issued after drinking were the ones that triggered reinforcement. As the partial reinforcement schedule and the blocking period came into force the reflexive vicious circle was interrupted. Having obtained reinforcement the animals drunk immediately but the postdrinking mandibulation now fell well within the blocking period that was empirically and conservatively set to 1.7 sec. The preparatory movements turned pro-

gressively more exaggerated and frequent as they became instrumental in yielding reinforcement.

The subjects adapted well to the conditioning situation. Some restlessness evident in early sessions disappeared in later sessions. The reinforcement of mandibulation lead to a dramatic increase of its rate of occurrence (Figure 1). The deprivation

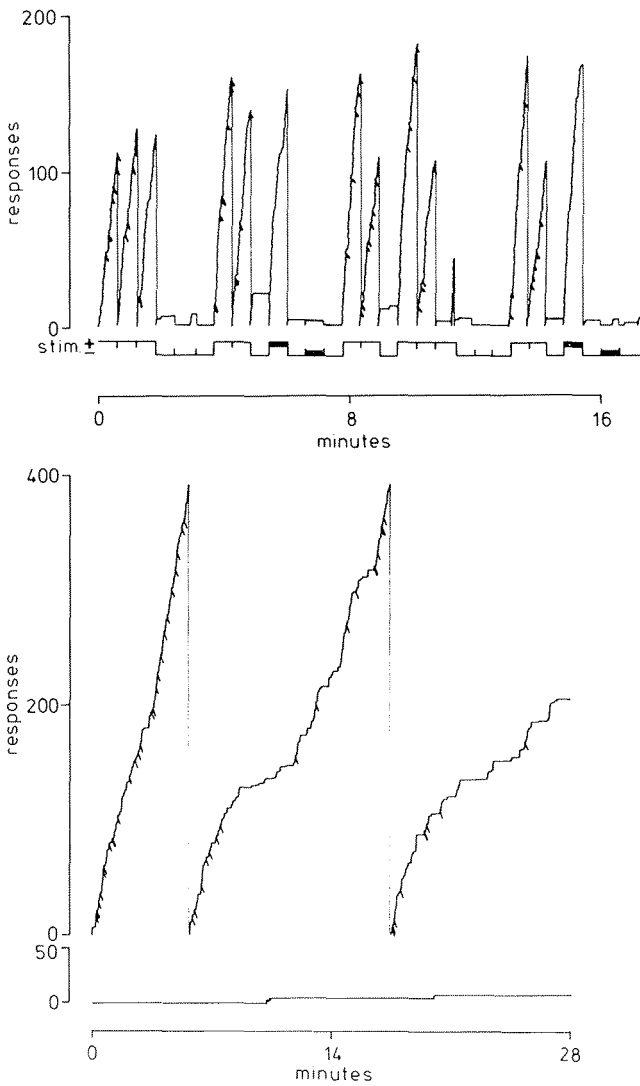


Figure 1. Typical cumulative records of baseline mandibulation responding (bottom) and conditioned mandibulation responding (VR 20) of a water deprived pigeon (middle). Differential mandibulatory responding of a pigeon to visual discrimination stimuli placed frontally (top; see text). Oblique strokes mark water reinforcement delivery; responses during concurrent blocking period were not recorded.

schedule used yielded adequate responding although there was some decay in the second half of some sessions, presumably due to satiation. This explains some of the variability in the number of responses per session that oscillated between some 300 and 2000. Over and above that there was a good deal of individual variation, some birds for example consistently yielding more than 1000 responses per session, others repeatedly emitting less than 500.

## DISCUSSION

There is little doubt that mandibulation can be conditioned instrumentally in restrained pigeons whose head is fixed. The ease with which this can be done almost certainly has to do with the fact that beak movements are a natural component of the drinking response. We were now interested to see whether the conditioned mandibulation could be brought under stimulus control.

## EXPERIMENT II: INTEROCULAR TRANSFER

The experiment was specifically concerned with whether visual stimulus control over the mandibulating response could be obtained and whether the control would transfer when the stimuli were moved from the field of view of one eye to that of the other.

## METHODS

### *Subjects and apparatus*

The same pigeons and apparatus used in Experiment I were employed.

### *Stimuli*

Stimuli were presented with the aid of two-colour (red and green) light-diodes (2.5 mm diameter). They were mounted on an adjustable 120 mm radius perimeter halfcircle, centered on the pigeons' between-eyes point. The lights had an intensity of approximately 1 mcd and were grossly estimated to be of similar subjective brightness for the pigeons by reference to Blough's (1957) comparative spectral sensitivity functions. However, no careful adjustment in this respect was attempted. Stimulus positions in angular degrees are given with reference to the pigeons' interocular midpoint as coordinate origin, the mid-sagittal plane (azimuth, beak tip = 0°, clockwise +) and the plane defined by the beak tip and the interocular line (elevation, the plane = 0°, upwards +). To ensure exclusive monocular viewing during stimulus presentations in the narrow frontal binocular field (see also later) a blind that blocked the binocular field of one eye was mounted on the head holding arm and before one eye as required. Naturally, no such blind was necessary when the stimuli were placed in the monocular field of an eye. The low intensity of the stimuli and the buff-black interior of the chamber prevented the presence of unintended reflections.

### *Procedure*

The discrimination paradigm used was of the successive free-operant type. Within a session there were 24 presentations of the S+ and 24 of the S- in a quasi-random sequence (Fellows, 1967). Each stimulus presentation lasted a standard 35 sec. Between presentations there was a pause of 0.1 sec. Responses during the S+ yielded reinforcement, now without a signal light but still accompanied by a 1.7-sec response blocking period, according to a VR 5, increasing over successive sessions to VR 30. Responses during S- periods had no consequences except that from the 25th sec onwards each response entailed a further 10-sec S- presentation, thus extending the standard 35-sec presentation. For scoring purposes however only responses within the initial standard 35-sec were counted. In selected critical sessions we interspersed 3 S+ and 3 S- presentations where responses had no programmed consequences whatsoever except that they were counted separately. These fair catch trials allowed a performance assessment uncontaminated by reinforcement feedback. Discriminative performance was gauged by computing the percent responses emitted during the S+ periods, correcting where relevant for the reinforcement blocking time during which responses were not recorded, of the total number of responses during the standard presentation periods for each subject and session.

During the transfer test sessions the responses issued by the subjects had no scheduled consequences except that they were counted, that is the subjects run under extinction conditions. The discriminative stimuli were located either in the frontal (0° azimuth, -25° elevation) or the lateral (+ or -75° azimuth, +15° elevation) visual field. The allocation of the subjects to the various conditions is listed in Table 1.

### RESULTS

The acquisition of the red-green discrimination with the animals seeing monocularly is shown as mean learning curves in Figure 2. The results of the catch trials are included. The cumulative record of a criterium session of one pigeon shown in Figure 1 documents the degree of stimulus control achieved. The apparent advantage of mean learning curve of the frontal group over the lateral group is not significant (Anova;  $F = 3.62$ ; d.f. = 1,6;  $P > 0.05$ ). The initial training proceeded until each animal reached a criterion of 75% or more correct responses in three consecutive sessions. The frontal group required a mean 12.5, the lateral group 15.5 sessions to reach this criterion. The difference is not significant (Mann-Whitney;  $U = 4$ ;  $n_1, n_2 = 4,4$ ;  $P > 0.05$ ). However, since originally the target had been a higher criterion, some animals were overtrained for a few sessions. This overtraining, on average 3.0 sessions, was equated for both groups. As the total number of sessions varied individually, separate mean learning curves synchronised with respect to the first and the last training session are shown in Figure 2.

The subjects were then tested for interocular transfer. They now saw the stimuli

at homologous positions with the non-trained eye. As the animals were tested under extinction conditions the number of responses fell off rapidly. Because of this no meaningful percent correct scores could be computed beyond the 5th transfer session. The mean discriminative performance during these testing sessions is depicted in Figure 2. A relative transfer coefficient (t.c., equal to: mean % correct responses during first 3 test sessions minus 50%, all divided by mean % correct responses during last 3 training sessions minus 50%) was calculated for each subject. The better interocular transfer of the frontal group (mean t.c. = 55.6) over the lateral group (mean t.c. = 18.3) as indexed by the coefficient was significant (Terry-Hoeffding;  $SNR = 2.27$ ;  $N, n = 8, 4$ ;  $P \approx 0.05$ ).

### Discussion

It is obvious that the mandibulation response can be brought under the control of visual stimuli. Compared with earlier attempts (Kowal, 1962; Catania, 1965; Nye, 1973; Martin and Muntz, 1979; Blough, 1978; Bloch and Martinoya, 1982; Goodale and Graves, 1982; but see Uhlrich et al., 1982) to present stimuli at defined locations within the visual field, the present method has definite advantages in that it ensures a positive positioning rather than an estimated one and in that it allows the presentation of virtually any type of visual stimuli.

The interocular transfer of a hue discrimination presented frontally is better than that of one presented laterally. This conforms with the conclusions reached by Goodale and Graves (1982) in a review of earlier work, most of which, however, involved methods that ensured a less definite location of stimuli within the subjects' visual field. Functionally this difference in transfer makes some sense in as far as

TABLE 1  
ALLOCATION OF SUBJECTS (DIGITS) TO THE VARIOUS CONDITIONS OF EXPERIMENTS I AND II (SEE TEXT FOR FURTHER DETAILS)

#### Experiment I: Eye (interocular) transfer

Stimulus locus	Right → left		Left → right	
Frontal	red +	1	red +	5
	green +	2	green +	6
Lateral	red +	3	red +	7
	green +	4	green +	8

#### Experiment II: Locus (intraocular) transfer

Eye stimulated	Front. → lat.		Lat. → front.	
Right	yellow +	6	yellow +	8
	blue +	7	blue +	5
Left	yellow +	4	yellow +	2
	blue +	1	blue +	3

the frontal field is the binocular field of the pigeon (Emmerton, 1983; Delius et al., 1982) which doubtlessly supports precise depth perception mediated by binocular disparity (Martinoya and Bloch, 1981). This necessarily involves intensive interocular communication which could also support the interhemispheric transfer of visual information required for the present task. The lateral monocular fields that at all times process non-coherent visual information do not require such coordination and may thus lack elaborate interhemispheric pathways that could mediate transfer. Such difference in connectivity between the central projections of the

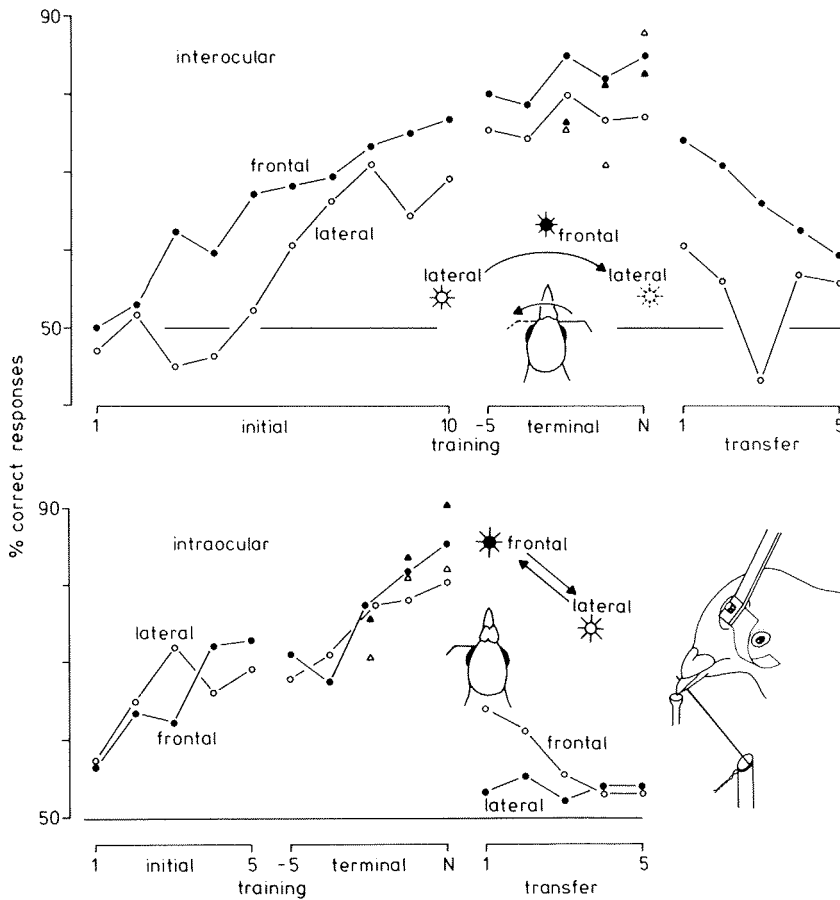


Figure 2. Top. Mean learning of pigeon discriminating hues with the frontal and the lateral visual field and extinction performance after interocular stimulus transfer. Bottom. Mean learning performance of pigeons discriminating hues with the frontal and the lateral visual field and extinction performance after intraocular stimulus transfer. Unconnected symbols refer to fair catch trials (see text). Two inserts symbolize the inter- and intraocular transfer tasks. A third insert (bottom right) illustrates the mandibulation recording set-up and the eye-blind.



binocular and the monocular retinal fields, however, has not yet been verified anatomically (Mestres and Delius, 1983).

It should not be concluded though that there is no interocular transfer of laterally learned discriminations at all since the testing under extinction which we used, probably tends to underestimate the actual transfer. For the same reason the interocular transfer of the frontally learned discrimination could be stronger than suggested by the present results. It occurs to us that a better transfer of laterally presented tasks might be obtained if rather than shift the stimuli one would turn the subjects. Doubtlessly pigeons not only learn about the intended stimuli but also about the immediate surrounding background of the stimuli. These remain unchanged with transfer between eyes under the frontal presentation condition but not with transfer involving the lateral presentation mode. More generally it also seems clear that besides the retinal locus stimulated there are other factors that determine the occurrence or extent of interocular transfer in the pigeon (see Stevens and Kirsch, 1980; Pounds et al., 1980; Mihara and Watanabe, 1982).

#### EXPERIMENT III: INTRAOCULAR TRANSFER

This experiment dealt with the transfer of a new colour discrimination task from one retinal locus to another within the field of view of the same eye.

##### *Method*

##### *Subjects, apparatus and procedure*

These were the same as those used in Experiment II.

##### *Stimuli*

They were generated with blue and yellow lacquered tungsten bulbs set in a light mixing body and radiating through a 3 mm diameter pupil covered with a diffusor. The comparatively unsaturated blue and yellow lights were adjusted to be of about equal brightness for the pigeons and of similar intensity as the lights of Experiment II. The stimuli were located again frontally at  $0^\circ$  azimuth,  $-25^\circ$  elevation and laterally at  $+$  or  $-70^\circ$  azimuth,  $+15^\circ$  elevation. An eyeblind before the irrelevant eye prevented a binocular viewing of the frontally presented stimuli. The variable of interest was the direction of the stimulus position change within the visual field of the same eye: from frontal to lateral and vice-versa. The reallocation of the subjects to the various conditions is listed in Table 1.

##### *Results*

Figure 2 shows the mean learning curves, synchronized as before one both the first and the last training session and includes the results of the catch trials. The in-

itial acquisition doubtlessly proceeded more rapidly than in the preceding experiment but in terms of sessions to criterion (three consecutive sessions with 75% or more correct responses) learning was a little slower. The frontal group needed an average of 13.5 sessions, the lateral group 24.2 sessions (one animal not quite reaching the criterion within 40 sessions). The difference between the groups, however, is not significant (Mann-Whitney;  $U=3$ ;  $n_1, n_2=4,4$ ;  $P>0.05$ ). No over-training was administered in this instance.

Testing under extinction proceeded after the stimulus positions were exchanged. Transfer was minimal under both stimulus translation conditions. The lateral to frontal intraocular transfer (mean t.c. = 27.6) yielded a slightly better performance than the reverse transfer (mean t.c. = 12.7) due to a reasonable transfer in one animal under the first condition. As judged by the comparison of the transfer coefficients calculated for each individual the difference is not significant (Terry-Hoeffding;  $SNR=0.699$ ;  $N, n=8,4$ ;  $P>0.05$ ).

### *Discussion*

The very weak transfer of the yellow-blue discrimination from one locus to another locus within the visual field of one and the same eye is somewhat unexpected. Although not specifically addressing this issue other research reports suggest indirectly that such intraocular transfer presents no particular difficulty for pigeons (Martin and Muntz, 1979; Bloch and Martinoya, 1982; Uhlrich et al., 1982; but see Levine, 1952). The near absence of within-eye transfer we observed must be interpreted with caution because of the testing under extinction and the possibility that the subjects might have developed a learning set through the repetition of the extinction condition. However, in another study using a different methodology (Klinkenberg and Delius, 1983) we found evidence of similar intraocular transfer difficulties. It is relevant to point out that just as interhemispheric pathways are poorly developed in birds so are lateral connections within their mayor visual central nervous structure, the tectum opticum (Hunt and Künzle, 1976). Nonetheless, in a species as mobile as the pigeon we must on general grounds expect an extensive transfer of information gained with different retinal loci. The remarks made earlier about moving around the subjects rather than the stimuli may be particularly relevant here. However, this may be, the extent of intraocular transfer in the pigeon obviously merits considerably more attention than it has hitherto received.

### GENERAL DISCUSSION

Even though the results of the experiments indicate the usefulness of the method some remarks are pertinent. Besides the piezoelectric force transducer we have recorded the lower jaw movements with electromyographic electrodes subcutaneously and chronically implanted on the surface of one of the depressor man-

dibulae muscles. This was not wholly satisfactory because some animals managed to generate unwanted signals through neck-muscle contractions which had the disadvantage of heavily straining the head anchorage. An infrared photoelectric gate has recently been used to detect the lower jaw movements and has proved to be very efficient, demanding little individual adjustment. Variable interval rather than ratio reinforcement schedules and shorter daily sessions as well as smaller rewards than those used in this study also seem to be possible improvements. The head block attachment requires much attention. A strategic lay-out of the anchorage cavities and careful cementing is essential for durability. When it is optimal one can expect about 4 months of reliable head fixation after which natural rejection mechanisms come into play.

Contrary to some earlier opinion (Nye, 1973) but in closer agreement with more recent evidence (Martin and Muntz, 1979; Bloch and Martinoya, 1982; Goodale and Graves, 1982; Uhlrich et al., 1982), Experiments I and II demonstrated that frontally and laterally presented discriminatory tasks are nearly equally well learned by pigeons (acquisition phases of both experiments). The slight non-significant, but we suspect, nevertheless, real, advantage of the frontally presented task could be due to the closer spatial contiguity between the discriminanda and reinforcement.

While specifying the positions of the visual stimuli we have disregarded eye movements. These are of relatively restricted extent in pigeons but nonetheless one must allow for movements of up to 20° amplitude, most of them of a convergent-divergent type that modify the extent of the binocular field (Nye, 1969; Bloch et al., 1981). Further more precise work may have to incorporate the measurement or suppression (see Marroco et al., 1982) of these movements.

Finally, we evaluated the acquisition data for evidence of hemispheric lateralization in pigeons. Separate mean learning curves were calculated for the subjects that had viewed the discriminanda with the left eye and those that had viewed them with the right eye, combining the data from both experiments. No difference was apparent and this also held when the data was partitioned according to whether the stimuli had been presented in the frontal or in the lateral position.

The failure to find any evidence of hemispheric lateralization is of interest because recent reports (Rogers and Anson, 1979; Rogers, 1981; Andrew et al., 1982; but see Goodale and Graves, 1980) clearly show that such specialization occurs in the context of visually controlled behaviour in birds. Indeed, current work in our laboratory (Güntürkün, 1983) suggests that in a different visual conditioning context pigeons do also evince a right eye /left brain advantage. It may be that the functional lateralization is quite task-specific in this species.

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