BINOCULAR FIELD IN PIGEONS: BEHAVIORAL MEASURES OF STIMULUS DETECTION AND CODING

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INTRODUCTION

It has been claimed that pigeons possess an ovoid binocular visual field, with its absolute amplitude along the vertical axis. There is, however, disagreement on the size of the binocular window, partly because of the different pigeon breeds and the particular techniques used in the experiments. Walls (41) stated that pigeons have a binocular field 24° width. More recently, optical techniques on alert pigeons, indicated an extension of about 110° along the vertical axis with an absolute horizontal amplitude of 41° at an elevation of 25° below the bill (22, 31). On the contrary, ophthalmoscopic reflex techniques on anaesthetised birds provided measures of the binocular window ranging from 110° to 135° on the vertical axis and from 22,5° to 37,4° on the horizontal axis (29, 33, 36). Also the estimate of the meridian position of the absolute horizontal amplitude differed among the authors. Martin and Young (29) as well as Nalbach *et al.* (36) reported that it was above the bill of about 20° and 15°, respectively; whereas McFadden and Reymond (33) derived a measure of about ± 5° around the eye-beak axis. In addition, anatomical measures from the eye-cup provided a computed binocular field of 18° around the eye-beak axis (18).

Taken together all these measures provide an indicative evaluation of the actual extent of binocular field. However, they are far from being exhaustive since they represent theoretical estimations not supported by a functional correlate, especially considering the role played by the eye movements, responsible for a significant shift in the binocular overlap (3, 17, 18, 20, 28, 30, 36).

Unfortunately, the few studies carried out with behavioral perimetry using head fixed pigeons were not aimed to map and value the extent of binocular field (16, 27). In addition, the unique investigation on visual detection in free moving animals (43) did not provide any estimation of the field.

It has been demonstrated that during pecking response the approaching to the target is successive to head fixation stops (F1-F2), in which the decision to peck and the coding of stimulus properties have been made (1, 16, 19, 39, 44, 45). Thus, taking advantage of motor stereotype of the pecking response and improving the "behavioral fixation" procedure (2), we attempted to bring together the requirements of a perimetric measure with a free moving experimental condition (9). By videorecording pigeon pecking responses to a spot displayed at different positions in the frontal field, we suggested that binocular field was a round area about 24° width, and centred on the eye-beak axis.

Inside this area, pigeons performed the pecking after a single head fixation stop to the stimulus, whereas outside it pigeons needed a second head fixation stop, following movements of rotation and/or transport of the head towards the stimulus to accomplish the response.

We considered the maximum spot distance requiring only one head fixation before pecking to be the boundary of the functional binocular field. This was in agreement with the observations that a stimulus detected in the lateral visual field was unable in producing an appropriate pecking behavior (3, 14, 21, 26, 37).

However, since pigeon eyes worked at their near point of accommodation this probably limited the focusing field, thus the stimuli still displayed within the field of binocular overlap could be detected but blurry perceived. If this had been the case, we would have obtained an underestimate of the binocular field. The present paper deals with experiments aimed to determine the extent of binocular overlap by founding the monocular limits of visual detection in the frontal field.

METHODS

Subjects. - The present study used four pigeons maintained at 80% of their free feeding weight. Before the experimental stage, thin rings of Velcro had been permanently fastened around the eyes. To yield monocular vision, during each concerning block of trials, light metal half-caps (300 mg) were coupled on the rings adjusted to hide the distal portion of lateral visual field to the looking eye as well as the frontal field to the occluded eye. Binocular condition was realised coupling the half-caps on both rings to leave out lateral fields in order to balance monocular and binocular viewing conditions (Fig. 1, B and C).

Apparatus. - The conditioning box was a modified Skinner box, built in Plexiglas (13.5x50x40 cm), the inner sides of which were covered with black adhesive velvet, exception for a small window that allowed the TV camera recording. A VGA 9" b/w monitor set at 10 cm above the floor of the box on the frontal wall and 45° outward sloped, displayed the stimuli generated by the computer (Fig. 1, A). Below the monitor there was a small Plexiglas container where the pellet dispenser released the rewarding food. Conditioning box was diffusely illuminated by two rows of four lamps (3 W) located at the basis of lateral sides. An exhaust fan provided continuous background noise and Skinner box ventilation.

Procedure. - Pigeons had to respond to the positive between a pair of stimuli displayed in succession on the monitor, according to a Go-Nogo procedure. Stimuli were a black spot on a white background (positive) and white background alone (blank).

The spot (3,8 mm diameter) randomly occurred on one position out of 21 (Fig. 1, A, inset). Spots lay at increasing distances (3.8 - 7.6 - 15.2 - 22.8 and 26.6 mm) along two Cartesian axes centred on the "0" point (x 320, y 210 pixel). Sometimes pigeons performed few control blocks in which the spot occurred along the two diagonals, crossing the centre of the axes. Pigeons got the stimuli displayed by pecking a small starter stimulus (black square of 5 mm by side) presented in the same position of "0" point (behavioral fixation). Stimuli remained on the screen one second. A single peck to the spot caused a single pellet reward, while a peck to the blank produced a 3 s black-out. Pecks were detected by a microphone and fed into a 80286 AT computer which drove the set-up and collected reaction times by means of the dedicated software Te.Re.S.A.(10).

Spots, blank screen, starter and grey background during the intertrial interval were 640x480 16 colour PCX files. A b/w PAL TV camera acquired and recorded on the same frame of a SVHS
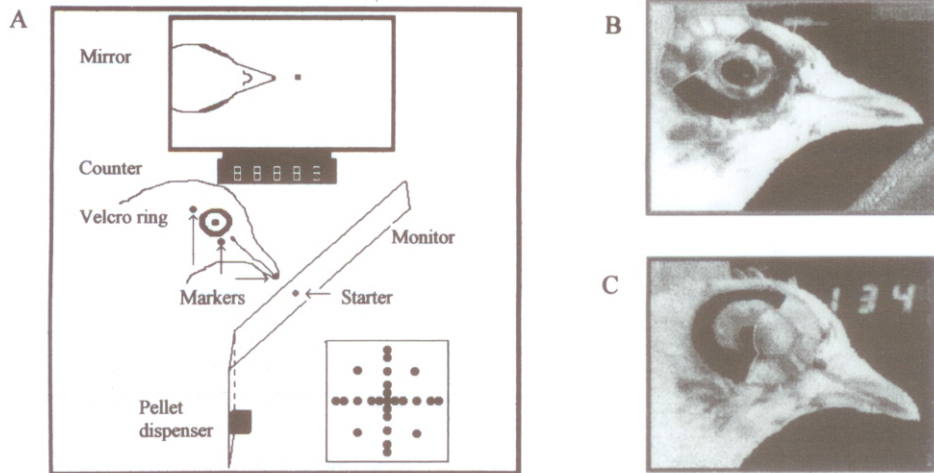
Fig. 1. - *Schematic representation of the main features of the Skinner box and drawings of pigeon's viewing conditions.*

A: Scheme of the frontal panel of the Skinner box, as seen by the TV camera. All the 21 positions of the spot along the two Cartesian axes as well as the 4 positions along the diagonals are shown in the inset. **B**: Digitised image of the pigeon performing under binocular viewing condition. Note the thin cap fastened on the posterior portion of the velcro ring. **C**: Digitised image of the pigeon performing under monocular left condition. Note that the frontal visual field of the right eye is occluded by the thin cap.

cassette a side view, an overhead view of the pigeon (via a 45° mirror mounted on the Skinner box ceiling) and a 50 Hz digital counter. Images were successively frame-by-frame analysed at 20 ms rate by means of a digitizer card (Matrox mod. Marvel 32K). Passive markers (white blots) painted around the eye, at the tip of the beak and at the centre of the skull were identified as VGA co-ordinates (calibration bar : 10 pixel = 4.56 mm) to estimate the time of stimulus fixation as well as the head position. Viewing distance was measured as the length between the centre of the eye and the origin of the Cartesian axes on the monitor. Measures were corrected for nodal posterior point (PNP - 3.55 mm behind the centre of the cornea), according to Macko and Hodos (25).

Pigeons performed daily sessions of 600 trials divided in 5 blocks of 120 trials, in which either 60 Go and 60 Nogo stimuli were displayed according to a semirandom Gellermann sequence (15). In the first block ("warm up" block) the spot was presented on "0" position, whereas, in the successive four blocks it occurred on one position out of 5: "0" point and 4 positions (up, down, left and right) equally distant from the "0". Within each session birds performed their discriminations in three viewing conditions: binocular, left monocular and right monocular. Blocks differed each other in the viewing condition used, and over the sessions the number of blocks for each condition was the same.

RESULTS

1. *Performance.* - The effect of spot distance on the percentage of correct GO responses is shown in Figure 2. As regard to the two monocular conditions, a high performance level is maintained along the vertical axis (on the right). However,
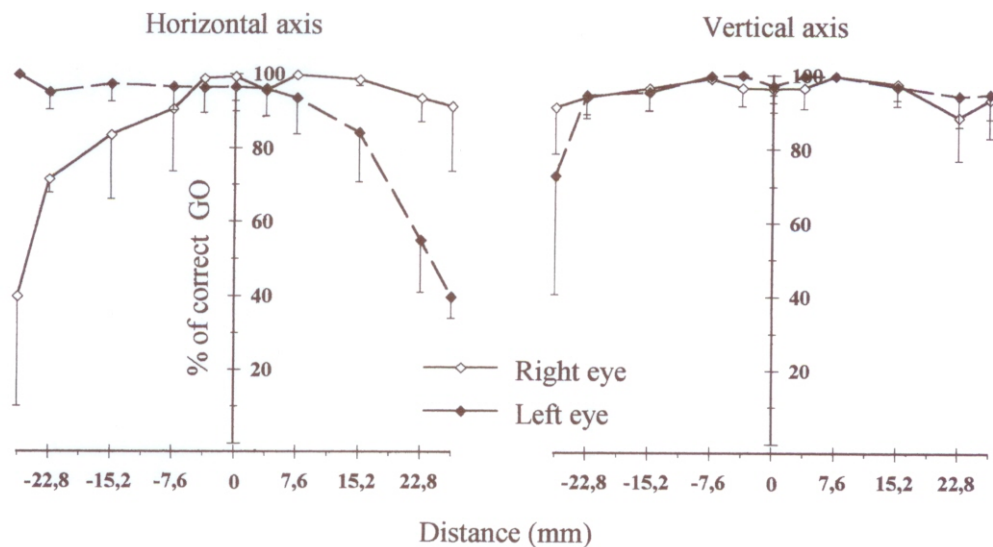
Fig. 2. - *Diagrams of monocular percentages of correct Go responses as function of spot position.*

The diagrams derived from spots displayed along the two Cartesian axes are plotted separately: horizontal axis on the left and vertical axis on the right. Each symbol represents the averaged value of the percentage of correct GO responses across the subjects. Bars plotted downwards indicate the standard deviation. The abscissae points out the spot position; negative numbers indicate positions on the left of and downward from the origin for the horizontal and vertical axis respectively.

data show an evident and progressive drop in performance on spots displayed at the contralateral side along the horizontal axis, from 7.6 mm onwards (on the left). Binocular viewing condition always performs at level greater than 90% (data not shown), except for P907 whose performance begins to go down at 26,6 mm on the vertical axis (see Table I).

2. *Frame by frame analysis*. - The frame by frame analysis assesses the role played by the starter in compelling a behavioral fixation: after the pecking to the starter, pigeons *draw back* and the average withdrawal time is 56 ± 6 ms, independently of the viewing condition. Then, they stop their head in a position that remains unchanged from trial to trial and they spend a short time with the bill pointing to the "0" point (*fixation*) either with or without the spot and for any position of it. The eye-beak axis lies about 28° below the horizontal meridian, showing a steeper slope in binocular condition. The pecking takes place soon after the *fixation (F1)* for spot positions close to the central point (Fig. 3, at the top and in the middle); otherwise movements of *transport/rotation* of the head followed by an additional *fixation (F2)* are necessary before the pecking output (Fig. 3, at the bottom).

Table I shows individual times of head fixations at all spot positions and for the three viewing conditions along horizontal and vertical axis. The outstanding result is the slowing of F1 at increasing spot distances in any case. An analysis of

Table I. - *Individual head fixation stops for each spot position along the two Cartesian axes in the three viewing conditions.*

Each value of both first fixation (F1) and second fixation (F2) is the averaged from at least 20 observations. Note that data on the 0 point are shown either for the horizontal and for the vertical axis and they are pooled together with data obtained at ± 3.8 for they do not differ. Asterisks indicate erroneous trials. # symbol indicates data not available. —— symbol indicates that the second fixation is not present.

		Left eye								Binocular								Right eye							
Subjects	spot	P6		P905		P907		P913		P6		P905		P907		P913		P6		P905		P907		P913	
		F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2	F1	F2
Horizontal axis	-26,6	129	120	136	144	153	90	151	173	128	110	123	114	149	80	140	189	180	*	171	*	166	*	205	*
	-22,8	131	117	128	140	110	80	157	171	110	93	117	143	120	83	130	135	157	*	166	*	372	*	351	*
	-15,2	112	110	140	135	103	80	160	150	126	96	120	120	120	104	143	111	129	128	167	152	130	120	273	*
	-7,6	109	——	107	——	108	——	168	145	123	——	123	100	90	——	187	148	127	107	133	127	133	103	196	160
	0	87	——	126	——	79	——	140	——	91	——	103	——	78	——	129	——	91	——	109	——	79	——	182	——
	7,6	117	113	133	157	130	107	146	128	114	80	111	136	100	108	151	127	109	——	110	——	110	90	197	203
	15,2	130	*	163	*	150	100	223	220	110	113	117	140	112	93	140	130	131	115	143	107	110	90	147	135
	22,8	150	*	169	*	120	*	264	*	113	120	129	140	110	100	140	128	134	114	129	120	120	110	177	226
	26,6	187	*	160	*	176	*	191	*	132	150	113	180	126	100	160	180	130	125	117	140	137	110	167	193
Vertical axis	26,6	131	137	132	156	149	120	120	140	140	111	105	128	123	100	137	169	164	150	125	151	153	148	170	157
	22,8	140	110	134	134	116	92	170	155	132	116	143	140	127	83	134	146	134	117	131	131	103	100	154	191
	15,2	113	107	146	143	147	103	117	143	109	87	129	133	120	107	120	127	143	115	127	132	117	110	136	155
	7,6	#	——	127	100	90	——	120	123	97	——	83	106	93	——	126	109	120	130	107	130	108	130	283	——
	0	87	——	126	——	79	——	140	——	91	——	103	——	78	——	129	——	91	——	109	——	79	——	182	——
	-7,6	83	——	90	——	110	——	123	——	106	——	86	——	100	70	146	——	103	——	103	——	108	——	217	——
	-15,2	123	——	160	150	106	88	157	160	120	93	100	——	113	83	123	127	123	——	127	——	130	100	150	180
	-22,8	147	117	151	145	133	70	171	151	123	107	146	114	113	93	137	140	123	114	183	147	113	90	163	207
	-26,6	167	140	175	180	189	*	200	*	149	150	133	124	150	*	203	236	140	143	196	173	153	140	190	176

Starter peck   F1   Transp./rot.   F2   Peck

Fig. 3. - *Sequences of outstanding stages of a pecking response to spots at different positions along the horizontal axis.*

The sequences of digitised images obtained during pecking behaviour in binocular condition are shown for three different spot positions: "0" point at the top; 7.6 mm in the middle and 22.8 mm at the bottom. The distance between the frames gives an idea of the time lag between the stages. The solid lines join the final stage.

variance using spot distance and viewing condition as sources shows an effect of both distance ($p < 0.001$) and viewing condition ($p < 0.01$); the interaction between the sources is not significant. A post hoc t-test for paired samples indicates a significant increase of F1 moving from 0 to 7.6 mm ($p < 0.02$) and from 15.2 to 22.8 mm ($p < 0.04$). In addition, a t-test matching the viewing conditions shows that binocular vision is significantly faster than left and right monocular ($p < 0.01$ and $p < 0.004$, respectively). The comparison between the two monocular conditions fails to attain any significance. An additional analysis of variance restricted to monocular visions compares F1 between ipsilateral and contralateral position of the spot with respect to the looking eye (i.e., left-eye on left horiz. and right-eye on right horiz. vs. left-eye on right horiz. and right-eye on left horiz.). The outcome of the test indicates a significant effect at 0.001 level from 7.6 mm onwards. As expected, spot along horizontal axis requires a longer F1 when it is displayed contralaterally to the looking eye. The second fixation (F2), when present, lasts as

long as the first fixation. For spots occurring on the outer positions on the horizontal axis there is no pecking within the maximum useful time for response (1 second). Really, pigeon makes several head movements to draw apart from the monitor as it has considered the stimulus like a nogo stimulus (asterisks in Table I). During F2 the animal places itself with the bill toward the stimulus at a distance from the monitor which is not different than in F1. The distance can be derived only for spots along the vertical axis; whereas, for spots lying upon horizontal axis only the direction of the bill can be assessed.

The time spent in movements of *transport* and *rotation* increases with the spot distance in each viewing condition, but it does not attain any significance. The average time measured is 69 ± 15 ms. The final stage of the response to go trials is the *ballistic output* towards the spot, whose average duration is 60 ± 7 ms. There is no difference whether it takes place after F1 or F2.

For NOGO stimulus, the pigeon accomplishes the trial after a fixation (F*nogo*), that lasts 139 ± 13 ms on average, and after drawing apart from the monitor by means of avoiding movements of the head and the neck until the occurrence of intertrial background. Then, the animal restores its initial position waiting for the appearance of the starter.

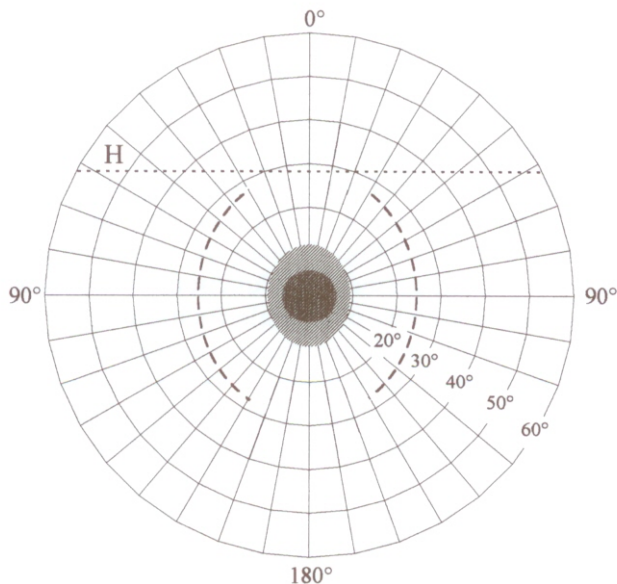3. *Computation of binocular field.* - The extension of binocular field is computed

Fig. 4. - *Bidimensional drawing of binocular visual field of the pigeon looking at its nearest point of accommodation.*

Bidimensional scheme of binocular visual field. The pole represents the direction of the eye-beak axis, lying about 28° below the horizon (H, and dotted line). The *coding area* is included within the region indicated by the two different scales of grey. The dashed line indicates the borders of the *detection field.*

by means of the two main parameters described in the present paper: the monocular performance on go responses and the frame by frame analysis of the pecking. The former measures an area of *stimulus detection* whereas the latter measures an area of *coding of the stimulus* properties. In both cases the distance of fixation derives from the average of at least six observations *in F1* for each spot position and for each pigeon. In addition, since there is not a significant difference between monocular and binocular conditions, they are pooled together, giving an overall value of 61.2 mm.

The segment of visual field useful to compute the area of detection corresponds to the range of spot positions at which the average of percentage of correct GO drops at 0%. It is separately calculated for the horizontal and vertical axis, resulting in about 45.6 mm and greater than 53 mm, respectively and providing a subtended visual angle of about 50° and more than 50°, respectively. The segment of visual field adequate to calculate the coding area is the range of spot positions at which pecking response occurs after the first fixation. As binocular and monocular ranges are not significantly different and they always include the "0" point (see Table I), the derived measure corresponds to 15.2 mm on the horizontal axis and to 22.8 mm on the vertical axis, thus giving an extension of about 18° and 24° respectively. The reconstruction of the binocular field is shown in Figure 4.

DISCUSSION

The above described results confirm and add new information to our previous data, thus suggesting to revise the concept of binocular field. Figure 4 shows a wide field of binocular vision in the centre of which a stimulus fixation area - *coding field* - can be distinguished from a surrounding area of stimulus detection - *detection field*. The *coding field* is a roughly circular area with a core of faster time of fixation (darker region in Fig. 4) than its outside edge. This area corresponds to what we previously defined as 'functional binocular field', since the stimulus was detected and coded by one single fixation stop in binocular viewing condition (9). The present paper shows that a coding area very similar in both extension and spatial position to binocular one is present also in each monocular condition. So, it seems more appropriate to rename the functional binocular field as *coding field*. It represents the maximum extension of visual focusing at a given viewing distance.

The surrounding area called here as binocular *detection field* is the peak amplitude of binocular overlap at the limit of eye convergence. Inside this area the stimulus is detected by each eye, but its properties can be coded only after an additional fixation stop. The area of detection has an ovoid-like shape with the minor axis placed on the horizontal axis. It has been possible to define the extension of just this minor axis for the level of monocular performance decreases with the contralateral increasing distance of the stimulus, until it drops down to the 0% of correct responses at a peak amplitude corresponding to 50°. On the contrary, along the vertical axis the level of monocular performance is always greater than

85% for all the spot positions we tested. Even if we have not succeeded in determining the value of the major axis, the ovoid-like shape of the field is strongly supported by the observation that the level of monocular performance is very poor on spot positions along the contralateral diagonal.

One of the most evident results of the present experiment is the great diversity of the time spent in the first fixation for the different spot positions, in both *coding* and *detection fields*. By assuming that the pigeon is looking at the 0 point with its retinal region of the best acuity and in the best focusing conditions, it is reasonable to expect a slow down of either detection and coding time for stimuli moving away from the centre. This could account for the consistent delay between contralateral and ipsilateral spot positions, since in the former case the retinal region as well as the optical system work at their utmost periphery. In addition, as the *detection field* is concerned, one of the components causing the remarkable delay may be the time spent in visual searching before saccadic head movements. However, there are no evident head or eye movements in seeking the stimulus on the screen, so that the visual searching should be confined to an attentional searching promoted by the behavioral fixation. The pigeon triggers the stimulus display and places itself according to a stereotyped mode, at the same distance from the screen, in alertness and with its visual attention straight ahead (4, 5, 17, 38, 40). The attentional searching requires a greater time to detect stimuli moving towards eccentric positions in the field; moreover, if a stimulus is as far as to be undetectable or it is absent as well, the pigeon draws back from the screen careless. This is the case of F*nogo* in which a time as consistent as for the first fixation of spots displayed in the detection field is spent.

What should it happen to the binocular overlap and to the *coding area* when the eyes are looking at from about 20 centimetres, i.e. from their usual resting position? And, what should it be the retinal area projecting to the coding field? At present it is difficult to fit our results with data in literature; however, an attempt should be made by considering the measured amplitude of vergence movements together with the models of retinal map.

The viewing distance of the first fixation reported in this paper is very similar to that found by others either in binocular and monocular viewing conditions (13, 16, 19, 25, 32). It corresponds to the closest point to the screen at which the eyelid is still fully opened and the bill closed before pecking, i.e. when the eyes are working at their near point of accommodation. In a simple approximation, by subtracting the amplitude of the eye movements as measured by Martinoya *et al.* (30) to our estimate of binocular field, we still obtain a binocular overlap of about 25-30° along the horizontal axis, which corresponds to the overlap of the farther regions of monocular *detection areas*, whereas the two monocular *coding areas* are so divergent that they do not overlap at all. The most likely retinal region providing the features of a high resolution perception is the red area in the upper temporal quadrant of pigeon retina. This area is comparable to the central fovea in the monocular field for its high density of ganglion cells (see ref. 12). Up to date, there is a general disagreement among the authors about the projection of the red area

into the visual field either during the pigeon resting condition and during vergence movements (16, 18, 36). Considering the red area as the retinal region projecting into the *coding field*, the present results seem to match the hypothesis of Nalbach *et al.* (36), according to which there is only a marginal binocular overlap of the red field in resting position, whereas the red field during frontal fixation is brought about by eye movements.

Finally, our data show a shorter time of fixation (F1) in binocular than in monocular viewing condition. This evidence is in line with previous results according to which binocular vision provides a double opportunity either to detect or recognize the stimulus with respect to the monocular vision (11, 23, 24, 42). However, binocular vision could provide further advantages than those elicited by our experimental condition, i.e. the tridimensional coding of the seed features, which are necessary to calibrate the right level of beak opening during the grasping (44). Once again, the almost complete overlap between the two monocular coding area centred on the eye-beak axis suggests that the most relevant role of binocular vision could be played by the *coding field*.

SUMMARY

The extension of the binocular visual field of pigeons is measured using a pecking behavioral method. Our estimate of the binocular field derived at the animal near point of accommodation indicates a 50° width on the horizontal axis and more than 50° on the vertical axis. Within the binocular field there is a core of about 24°, named *coding area*, in which the stimulus is detected and coded by only one head fixation before accomplishing the pecking response, in both binocular and monocular viewing conditions. Outside the coding area, lies the *detection area*, in which the stimulus can be detected, but it needs a second head fixation to be coded in all viewing conditions. Our results are in agreement with the hypothesis that the coding area corresponds to the red field projection of each retina. In binocular vision an overlap of the two areas occurs, thus promoting the image fusion useful for a stereoscopic vision during the pecking to the seed.

Post scriptum. - Altought our actual field of research is addressed to the behavioral investigation of pigeon visual system, nevertheless it still shares some of the basic features with the studies on the role of reticular formation as the regulator of instinctive activities. Some time ago, Professor G. Moruzzi published a paper entitled "Sleep and instinctive behavior" (35), in which he suggested a new hypothesis about the relationship between sleep and reticular formation: "Sleep regulation may be regarded as an aspect of a wider problem: the study of the levels of reticular activation which are required for the onset of different types of instinctive behavior" (p. 212). Pigeon was then chosen as experimental model and pecking was one of the most suitable behaviors to study the role of reticular activation (6, 7, 8, 34).

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