Exp Brain Res (1992) 92:27–38

Experimental
Brain Research

Translational head movements of pigeons in response to a rotating pattern: characteristics and tool to analyse mechanisms underlying detection of rotational and translational optical flow

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Received February 3, 1992 / Accepted August 25, 1992

Summary. Pigeons freely standing in the centre of a two-dimensionally textured cylinder not only rotate but also laterally translate their head in response to the pattern sinusoidally oscillating or unidirectionally rotating around their vertical axis. The translational head movement dominates the response at high oscillation frequencies, whereas in a unidirectionally rotating drum head translation declines at about the same rate as the rotational response increases. It is suggested that this is a consequence of charging the 'velocity storage' in the vestibulo-ocular system. Similar to the rotational head movement (opto-collic reflex), the translational head movement is elicited via a wide-field motion sensitive system. The underlying mechanism can be described as vector integration of movement vectors tangential to the pattern rotation. Stimulation of the frontal visual field elicits largest translational responses while rotational responses can be elicited equally well from any azimuthal position of a moving pattern. Experiments where most of the pattern is occluded by a screen and the pigeon is allowed to view the stimulus through one or two windows demonstrate a short-range inhibition and long-range excitation between movement detectors that feed into the rotational system. Furthermore, the results obtained from such types of experiments suggest that the rotational system inhibits the translational system. These mechanisms may help the pigeon to decompose image flow into its translational and rotational components. Because of their translational response to a rotational stimulus, it is concluded, however, that pigeons either generally cannot perfectly perform the task or they need further visual information, like differential image motion, that was not available to them in the paradigms.

Key words: Optokinetic response – Optic flow – Motion detection – Visual-vestibular interaction – Pigeon

Introduction

Animals placed in the centre of a textured drum which rotates around their vertical axis usually display a rotational nystagmus with the head and/or the eyes. By these optomotor responses the retinal slip speed is reduced. Consequences of this behaviour are minimizing image blur, enhancing visibility of object motion by reducing background motion or removal of the rotational component in the visual flow pattern which is generated by locomotion along curved paths. The remaining translational flow carries motion parallax information about the three-dimensional layout of the environment. In a variety of animals this information is used for depth estimation, and some even produce translational flow for this purpose by active head translations (e.g. gerbils, Ellard et al. 1984; locusts, Sobel 1990). However, a vast number of birds even remove this translational image flow by visually driven compensatory head movements during walking so that their head is virtually stationary in space during a significant portion of the bird's locomotion (Whiteside 1967; Dagg 1977). The function of this behaviour is still debated (Davies & Green 1988). Since image velocity caused by translation is inversely related to distance, one might speculate that such birds, like the pigeon or the chicken, which search for grains of food need to keep their head stationary in space to obtain an unblurred image of the ground close to the eye (Nalbach et al. in press).

In pigeons and chickens, it has been demonstrated that both rotational (Visser and Rademaker 1934, Mowrer 1936, Simon 1954, Fite 1979, Wallman and Velez 1985, Gioanni 1988a) and translational (Dunlap and Mowrer 1930, Visser and Rademaker 1934, Bangert 1959, Friedman 1975, Frost 1978) head movements can be elicited with the appropriate visual stimulation. Rotational head movements are under additional control of the vestibular organ (Visser and Rademaker 1934, Mowrer 1935, Huizinga and van der Meulen 1951, Wallman et al. 1982, Gioanni 1988b, Kirmse et al. 1989), and the otolith organ might assist to stabilize the head against

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translation, similar to its role in driving eye movements in mammals (Paige and Tomko 1991). However, the interaction of the systems which detect the translational or rotational components of image flow has not yet been investigated. In theoretical studies, it has been shown that decomposition of the translational and the rotational component of image flow is not a trivial problem (Longuet-Higgins and Prazdny 1980; Koenderink and van Doorn 1987) and its biological solutions are widely unknown (Collett et al. in press). Since head movements in pigeons are relatively easy to elicit and to monitor, they offer a tool to obtain some insight into such mechanisms.

In this study, head movements in response to a sinusoidally oscillating pattern are described. Such experiments have already been performed with great accuracy by Gioanni (1988a) and one might ask whether further work is required. However, during the experiments I found that pigeons only partly rotate their head in this experimental situation. Instead, they translate their head in response to the rotating visual surround, depending on the stimulus parameters. The same curiosity was independently observed by G. Marin and J. Wallman in chickens (personal communication). Previous researchers might have overlooked the translational component either because they restricted the pigeon's head movement to a rotation around the vertical axis (Gioanni 1988a) or because they only recorded the rotational component (Visser and Rademaker 1934; Mowrer 1936; Fite 1979). In this report, I will specify the conditions under which the one or the other mode of head movement can be evoked. I will exploit them to obtain some qualitative results about the mechanisms underlying the pigeon's systems used to analyse translational and rotational image flow and their interactions.

Materials and methods

Adult homing pigeons *(Columba livia)* were obtained from a local supplier and housed in an outdoor cage. During the experiments, a pigeon was freely standing with its legs loosely fastened by a ribbon of leather to a horizontal wooden bar 4 cm above the ground with the head positioned close (within a radius of 5 cm) to the central axis of a drum (diameter 64 cm, height 46 cm). Its wall carried a two-dimensional pattern of equidistantly spaced horizontal and vertical dark blue lines (2 mm wide, separated by 14 mm) on a white background with dots (diameter 6 mm) at the crossings. Such a highly redundant pattern was chosen to make visual fixation of single features of the pattern unlikely and thus obtain predominantly a response to the global image movement when the drum rotated around the vertical axis of the animal. The bottom and top of the drum were screened by stationary sheets of white paper. The pigeons were video-taped from above through a central hole in the cover (diameter 16 cm). Visibility of the head movements was enhanced by reversibly gluing a light paper cross (length 9 cm, width 6 cm, width of the paper stripes 3 mm) onto the head. The head movements were analysed either by direct inspection of the recordings or by digitizing the coordinates of the crossing, frame by frame. Only head beats were used as an index of the optokinetic response, and eye movements were not monitored. However, when pigeons are allowed to freely move their head, most of the optokinetic response is performed by head movements and eye movements contribute only little (at most 15%–20%, Gioanni 1988a). The drum was either sinusoidally oscillated by an excenter (0.006 Hz–0.7 Hz, 5 frequencies tested for each animal) or rotated by a DC motor whose speed was controlled via a tachometer attached to its shaft (1°/s–20°/s, 5 velocities tested for each animal). The experiments were performed in daylight with additional ceiling light.

Every sequence of video-tape was inspected twice, one time head the rotations, the second time head translations were counted over at least one stimulus cycle at low and up to 10 cycles at high frequencies. The numbers then were normalized to occurrences per 10 cycles of drum oscillation. Each sequence of continuous head movement separated by saccades or by reversal of direction was counted as an occurrence. Rotation is the change in the azimuth of the head's midsagittal plane; translation is the linear displacement of the centre of the head between both eyes in the horizontal plane (Fig. 1a). The sum of elements of head rotation and head translation is called the total response. Depending on the experimental conditions, the pigeons either only rotated (Fig. 1c) or only translated (Fig. 1d) their heads in a stimulus-correlated manner, or they simultaneously rotated and translated it (Fig. 1b). Thus, one sequence contributed to the counts of rotations or translations, or to both.

In some experiments, most of the oscillating pattern was screened by a stationary white cylinder (diameter 62 cm, placed concentrically to the rotating drum) that allowed the pigeons to see the pattern only through one or two windows. They gave sight of the full vertical extent of the pattern and their horizontal width could be varied. In other experiments, a vertically-extended object or a broad stationary paper screen occluded parts of the oscillating pattern. In these types of experiments, only those sequences were evaluated during which the pigeon turned its head not more than ± 20° away from the direction of the centre of the window.

Results

The phenomenon

Pigeons standing in the centre of a textured drum that unidirectionally rotates about their vertical axis display a regular rotational optokinetic head nystagmus (optocollic response) (Visser and Rademaker 1934; Mowrer 1936; Fite 1979; Gioanni 1988a). At the onset of the pattern motion, however, they translate their head laterally to the direction of the pattern motion across their frontal visual field (Fig. 1b). In order to study this curious transient head translation without interference from frequent unspecific head movements – probably evoked by the sudden increase in motor noise or other disturbing conditions – the drum was sinusoidally oscillated. Thus, the pigeon was subjected to periodical onset and change in direction of the pattern movement.

In this stimulus condition, the pigeons both rotate and translate their head (Fig. 1a, c, d). The amplitude of smooth head rotation is, however, much lower at high than at low frequencies. The stronger the rotational response is the more frequently it is interrupted by small saccades and finally, at large oscillation amplitudes, sequences of regular nystagmus are elicited. I never observed a sequence that might be called a translational nystagmus with slow following and fast reset movements when the pigeon was standing in the centre of the drum. Probably the oscillation amplitudes of the drum were too small at the frequencies needed to evoke strong translational head movements.

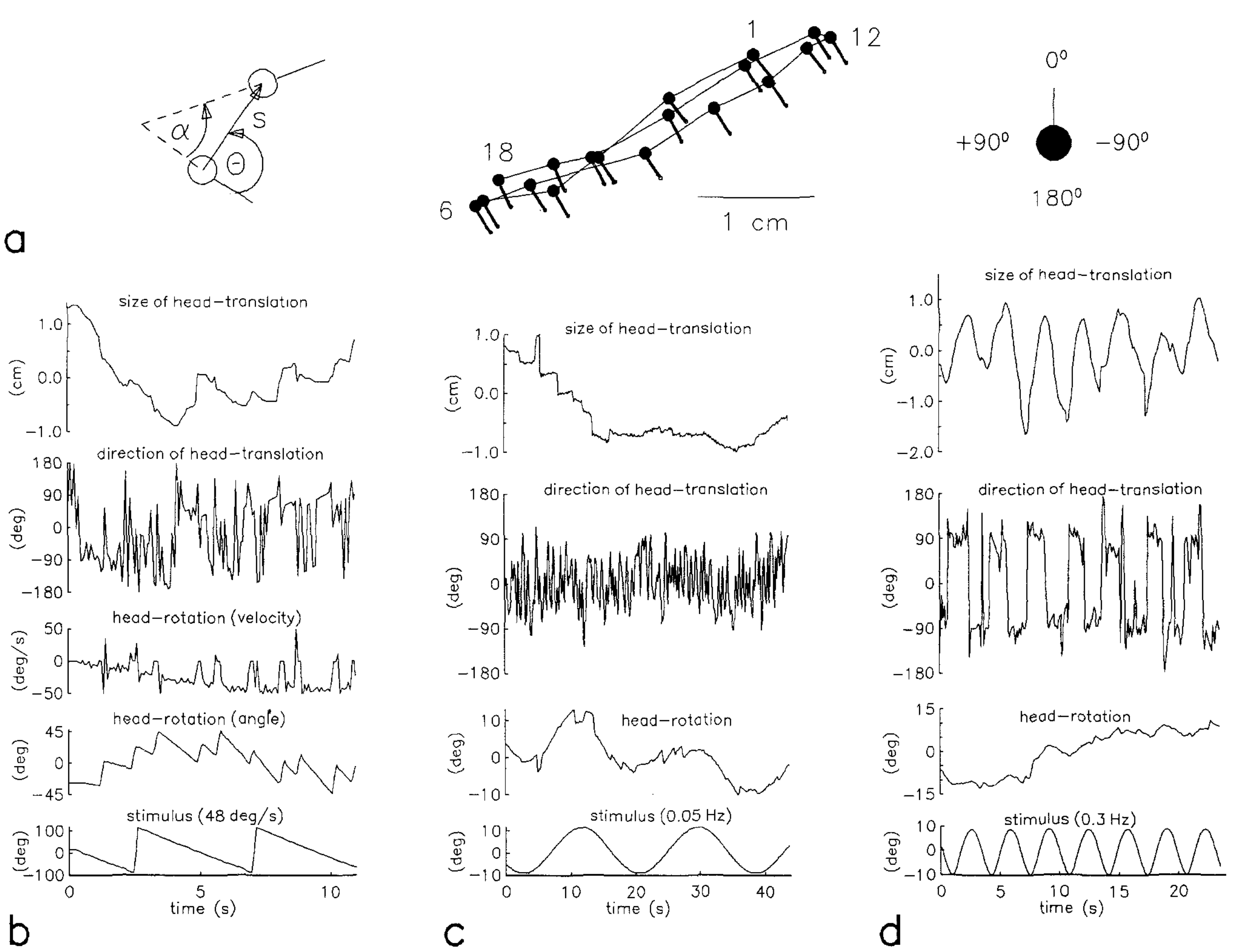

Fig. 1a–d. Sample records of translational and rotational head movements elicited from a pigeon standing in the centre of a rotating drum. **a** Movement of the head in the horizontal plane. Position of the head (midpoint between both eyes) is illustrated by the *black dot,* the *line* indicates the direction into which the bill is pointing. The *numbers* indicate 1st, 6th, 12th and 18th frame of the sequence, the interframe interval being 240 ms. Stimulus is an oscillating pattern, frequency 0.3 Hz, amplitude ±10°. Rotation (angle α) is determined by the orientation of the head's midsagittal plane; parameters of head translation are direction θ and size s. In the top traces of **b–d** the time course of the size component perpendicular to the head's sagittal plane (s cosα, positive to the right) is shown, since this represents the stimulus related head translation along the axis $\theta = \pm 90°$. The zero-position represents the average head position of a longer trace from which only a section is shown. **b** Continuous clockwise pattern rotation elicits regular rotational head nystagmus with speed increasing to the final value over about 8 s. During this initial sequence the head translates sidewards in the direction the pattern is moving across the pigeon's frontal visual field; later the head apparently drifts into some arbitrary position. **c** Sinusoidally oscillating drum, frequency 0.05 Hz, amplitude ±10°. Strong head rotation but almost no stimulus-related head translation; note noisy time course of direction of head translation although smoothed by a 7 point binomial filter. **d** Sinusoidally oscillating drum, frequency 0.3 Hz, amplitude ±10°. Almost no stimulus related head rotation but strong translation

Head translation in the horizontal plane is described by a vector that can be represented by its two components; amount of displacement of the centre of the head and direction of the displacement relative to the head's midsagittal plane (Fig. 1a). In the oscillating drum, the pigeon translates its head in a line about perpendicular to its midsagittal plane. Due to the minor displacements at stimuli of low frequency the direction of head translation can only be determined with some scatter (Fig. 1c). At high frequencies, however, the amplitude of head translation is strongly increased and its direction is well defined (Fig. 1d).

The two modes of head movement – rotation and translation – can easily be observed by direct inspection and the sections of smooth trajectories of either mode can be counted. Such counts at least partly reflect the amplitude of the head movements. Thus, they can be used to obtain an immediate impression of the responses of pigeons stimulated by a sinusoidally oscillating pattern.

Strength of head rotation and translation in response to pattern oscillation

The dependence of responses on oscillation frequency was quantified by counting the number of occurrences of both rotational and translational head movements. Both

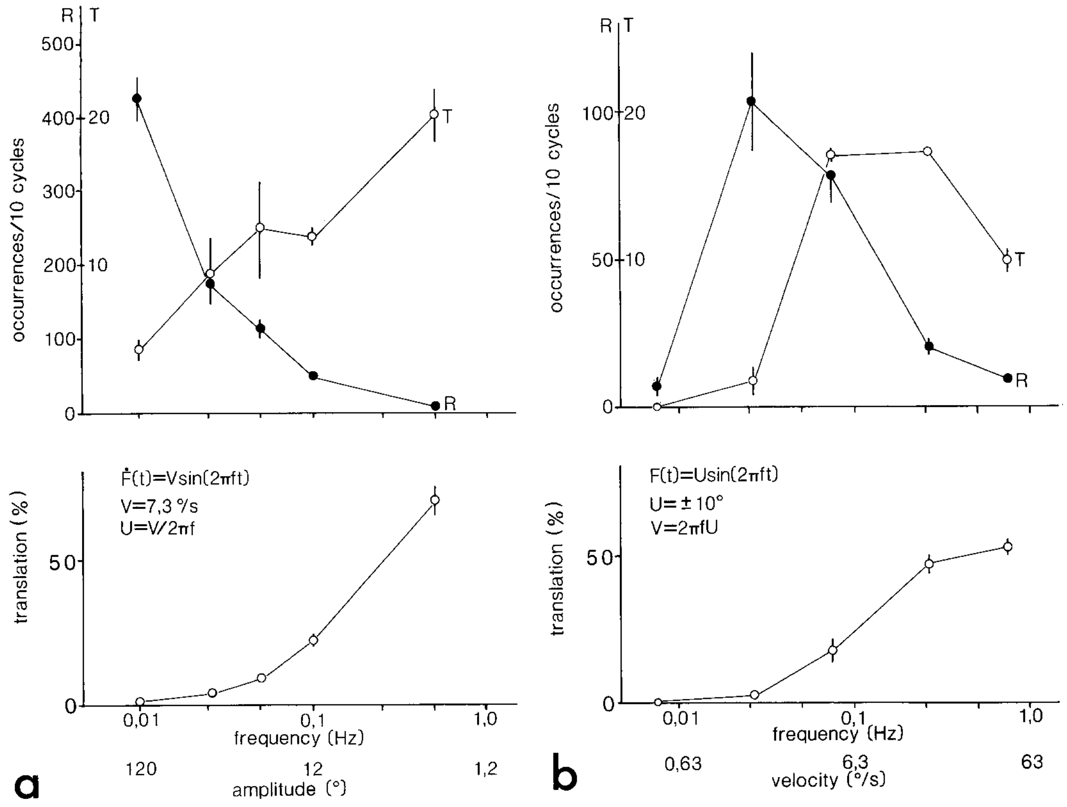

Fig. 2a, b. Number of occurrences per 10 cycles of translational (*T*) and rotational (*R*) head movements, and percentage of translational head movements contributing to the total response elicited in a drum oscillating at various frequencies (*f*) either (**a**) at constant peak velocity (*v*) and thus variable amplitude (see abscissa) or (**b**) at constant displacement amplitude (*U*) and thus variable peak velocity (see abscissa). Note different scales for rotational and translational responses. Average values and standard errors obtained in experiments with six repetitions of each situation with each of three pigeons

at oscillations of constant peak-velocity (Fig. 2a) and constant amplitude (Fig. 2b), the rotational response is stronger at pattern oscillation of low frequency and declines rapidly with increasing frequency. The opposite is true for head translations. Consequently, the percentage of occurrences of head translations relative to the total response increases from almost 0% at stimulus frequency 0.007 Hz to 60%–80% at frequency 0.7 Hz.

Under similar stimulus conditions (two dimensional pattern oscillating at different frequencies and constant peak velocity 20°/s), Gioanni (1988a) obtained a curve of closed-loop gain of head-velocity versus frequency almost identical to the count of occurrences of head rotations presented in Fig. 2a. This may be taken as a further indication that the crude measure of head movements in the present study adequately describes the opto-collic responses of pigeons in an oscillating drum.

The number of head rotations and translation seems to depend on stimulus velocity. At a low velocity (0.5°/s), the number of head rotations is low (Fig. 2b) although at about the same frequency (0.01 Hz) but faster peak velocity (7.3°/s), a maximum number of head rotations is counted (Fig. 2a). At a high stimulus velocity (50°/s), the number of head translations declines (Fig. 2b) although at about the same frequency (0.5 Hz) but moderate peak velocity (7.3°/s) the maximum number is counted (Fig. 2a).

Nevertheless, the general impression from these data is that the major stimulus parameter to shift the head movement from rotation to translation is frequency. To further test this conclusion, the drum was oscillated in that range of frequencies (0.05 Hz–0.5 Hz) where the percentage of head translations increases most significantly. At each frequency, the drum was oscillated with three different amplitudes (9.4°–22.3°) and thus a range of peak velocities and accelerations (Fig. 3). At least in the range tested, the number of rotations and of translations, and thus the percentage of head translations is almost independent of stimulus amplitude and therefore stimulus velocity and acceleration.

The experiments with the sinusoidally oscillating drum demonstrate that the critical stimulus parameter for switching from rotation to translation is not stimulus acceleration or velocity or displacement amplitude, but frequency. An oscillating pattern movement does not, however, allow one to decide whether the switching is due to the change in direction, the dynamical properties of the rotational and translational system or the onset of movement. Therefore, the drum was moved with velocity pulses. Drum rotation was periodically interrupted by pauses after which the drum continued to rotate either in the same or the reverse direction (see inset in Fig. 4a).

Independent of the stimulus conditions, there was no difference in the percentage of head translations elicited by the two types of drum movement (Fig. 4, see open and filled circles). Therefore, the periodical change in direction of pattern movement can be excluded as an important parameter to favour either a rotational or a translational response.

The percentage of head translations is widely independent of the duration of pauses between two velocity pulses (Fig. 4a). Only at very short pauses of less than 0.15 s does the percentage of head translations become reduced. When the drum moves continuously in one

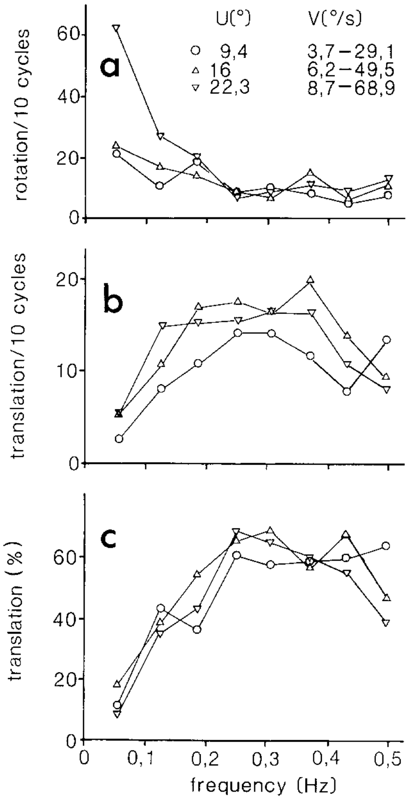

Fig. 3a–c. Number of occurrences of (**a**) rotational and (**b**) translational head movements, and (**c**) percentage of translations contributing to the total response as function of oscillation frequency with 3 different displacement amplitudes (*U*) and thus a range of peak velocities ($V = 2\pi f U$) as indicated by the inset. Average values from experiments with two pigeons

direction ($T_0 = 0$ s), almost no translation is seen while the number of rotations is maximal; there are 24.8 ± 1.91 ($n = 6$) rotations per 10 cycles at $T_0 = 0$ s and on the average 14.67 ± 1.52 ($n = 24$) rotations per 10 cycles with pauses from 1.5 s to 21 s ($P < 0.005$, two-tailed t-test). Thus, at least a short pause is needed to evoke a substantial percentage of head translations and to simultaneously reduce the number of head rotations.

Furthermore, these experiments allow us to determine the influence of pattern velocity on the percentage of head translations independently of angular displacement. The pigeons more often translate their head when velocity is increased in experiments with constant displacement amplitude (Fig. 4b) or when angular displacement amplitude is decreased in experiments with constant velocity (Fig. 4c). This suggests that the critical stimulus parameter is duration (equal to displacement amplitude divided by velocity) of pattern displacement. At duration of movement $T_m = 0.5$ s, about 70% of the head movements are translational (Fig. 4b), while at $T_m = 30$ s they contribute to less than 10% of the responses (Fig. 4c). However, a stimulus velocity faster than 2°/s is needed to evoke a substantial number of head translations (Fig. 4b). At about the same duration of pattern movement of 5 to 6 s, with a velocity of 2°/s, only 7% of head translations can be evoked (Fig. 4b) while with 7.5°/s (displacement 47°), 34% of the responses are translational (Fig. 4c).

In summary, these results (Figs. 2–4) demonstrate that stimulus parameters like acceleration, velocity and displacement amplitude only play a minor role in switching the pigeon from one mode of head movement to the other. They suggest, however, that head translation is a transient phenomenon that is elicited at the onset of pattern movement while head rotation slowly develops during ongoing stimulation. This phenomenon is illustrated in Fig. 1b. In this example, the pigeon translates its head in a stimulus-related way only during the initial 8 s in which rotational head velocity builds up. The time constant of decay of the translational response can be estimated from Fig. 4c after converting displacement into duration of pattern movement. The time constant amounts to roughly 10 s since, after that time, the response has declined to 37% of the initial percentage.

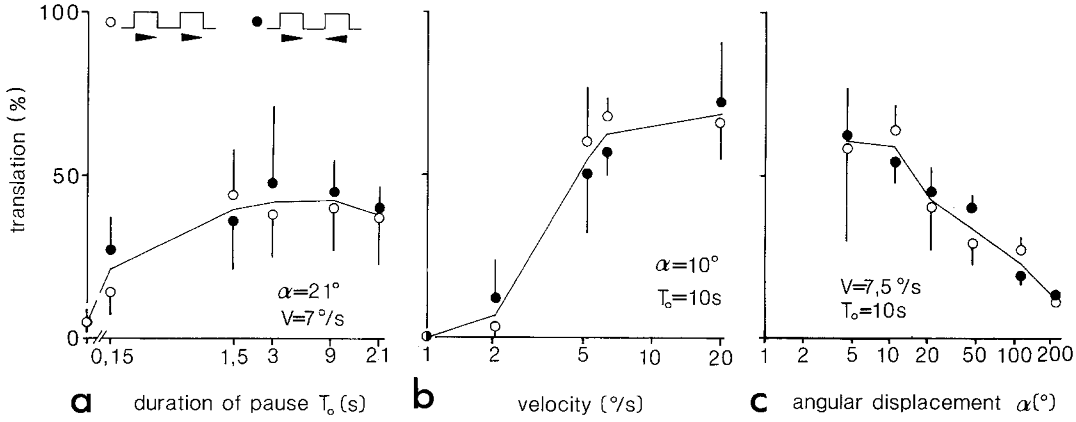

Fig. 4a–c. Percentage of head translations contributing to the total response elicited in experiments with drum moving stepwise (see inset). The drum either moves in the same direction during each velocity pulse *(open circles)* or the direction is periodically reversed *(filled circles)*. Either the duration of the pause between two drum movements (**a**), the velocity of the movement (**b**) or the angular displacement (**c**) is varied. Parameters were either angular displacement (α), velocity (v) or duration of pause (T_0) as indicated in the figures. Note that the duration of pattern movement T_m is given by the division of angular displacement α by velocity v. Average values and standard error obtained in experiments with three pigeons

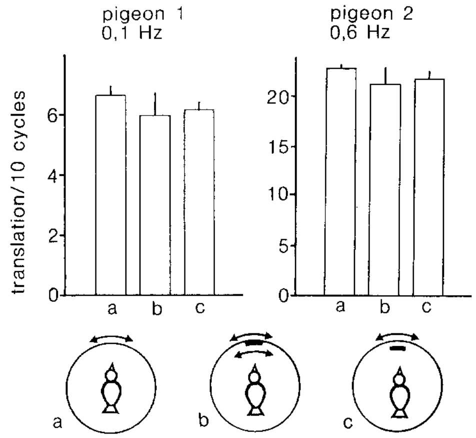

Fig. 5. Number of translational responses per 10 cycles in experiments with two pigeons standing in an oscillating drum (frequency 0.1 Hz or 0.6 Hz as indicated, displacement amplitude 10°) without additional object (*a*), an object (10° wide) oscillating in common with the drum (*b*) or stationary in front of it (*c*) as illustrated by the insets

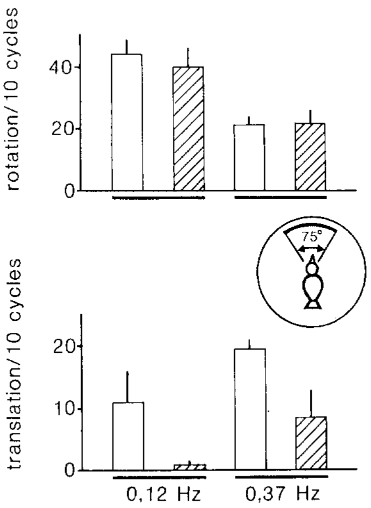

Fig. 6. Number of rotational and translational head movements per 10 cycles in an oscillating drum (frequency as indicated, displacement amplitude 10°). *Open bars:* Drum without screen, *hatched bars:* a stationary white screen, 75° wide, was inserted to occlude the moving pattern in the pigeon's frontal visual field (see inset). Average values and standard error obtained from experiments with three pigeons

Head translation: fixation of features in the frontal visual field or response to global image motion?

The pigeon placed in the centre of the drum can reduce global image motion of the rotating visual surround by a rotational head (and eye) movement only. The translational head movement perpendicular to the sagittal plane of the head merely reduces image motion over the frontal visual field, at the expense, however, of increased flow elsewhere in the image. This would be meaningful if the pigeon fixates a certain feature of the pattern in its specialised frontal visual field (Nalbach et al. 1990) similar as it does during pecking of a grain of food (Goodale 1983; Martinoya et al. 1984; McVean and Davieson 1989).

In order to test whether the translational head movements do indeed serve to fixate the pattern in the frontal visual field, responses of pigeons in three situations were compared (see inset Fig. 5): (a) The drum carried the standard pattern; (b) A vertical white stripe, 10° wide, with hand-painted, irregular black dots (diameter roughly 0.9°, spacing about 2.7°) was fastened to the drum in front of the pattern. It would be expected that this arrangement facilitates fixation of a single feature and thus evokes more translational head movements. (c) The same stripe was fastened stationary in front of the oscillating pattern. If translational head movements in experiment b do indeed indicate fixation of the stripe then, in the present case, they should be strongly reduced. In these experiments only those sequences were evaluated when the stripe was approximately in the pigeon's frontal visual field. However, neither absence nor presence of the additional stripe, whether it is stationary or moving, alters the number of occurrences of translational head movements (Fig. 5). Under all conditions, the pigeons moved their head sidewards.

This result was further substantiated in experiments where a broad, homogeneous, white, stationary screen (75° in horizontal width, in the vertical completely occluding the pattern) was placed in front of the pigeon (Fig. 6). This screen covers that part of the oscillating pattern which might be stabilised by the translational head movements. Indeed, at the low stimulus frequency, the lateral head movements almost disappear. At the high stimulus frequency, however, which favours strong translational responses (Figs. 2, 3), the pigeons displayed a substantial amount of head movements which were directed sideways as in the situations without the screen. Under both experimental conditions, the number of rotational head movements remained almost equal.

These experiments exclude the possibility that the translational head movements of pigeons in response to a pattern oscillating at high frequency are due to fixation of a feature in front of them. Thus, they are responses to the global image motion which also underlies the rotational opto-collic nystagmus.

Regional variation of sensitivity to translational and rotational components of image motion

These results indicate an imbalance in the translational system which makes the pigeon respond with lateral head movements even to a whole field rotational stimulus. The underlying reason might be a regional variation in sensitivity to image motion which elicits either predominantly translational or rotational responses. To explore the pigeon's visual field, a set of experiments was designed where a stationary drum of opaque homogeneous white paper occluded large parts of the oscillating pattern except for one or two 'windows' of variable position and horizontal width.

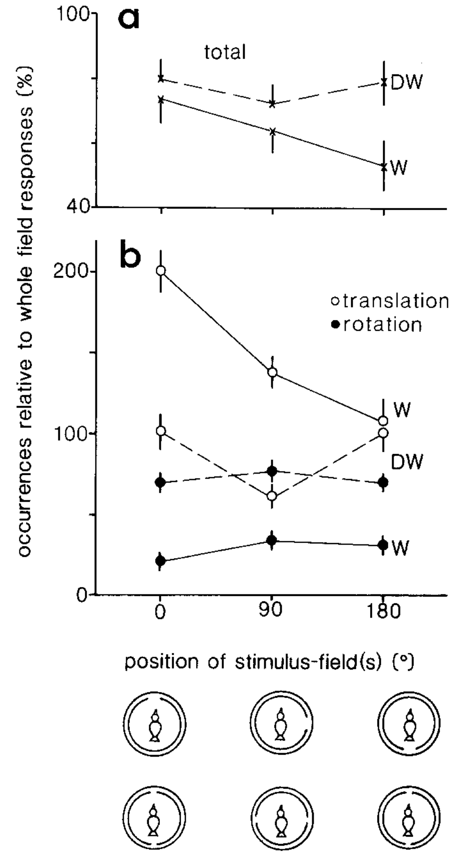

Fig. 7a, b. Percentage of (**a**) total responses, and (**b**) translational *(open circles)* and rotational *(filled circles)* head movements *(lower diagram)* relative to their occurrence during whole field stimulation. The pigeon either viewed the pattern through a window of width 60° in front of it, to its side or behind its ('window experiments' *W*), or the window was split into two (each 30° wide, 'double-window experiments' *DW*) at the indicated positions. The drum oscillated at frequency 0.6 Hz, displacement amplitude 10°. Average values and standard deviation from experiments with three pigeons with three repetitions of each situation

When the window was placed in front of the pigeon (0°), at its side (90°) or at its back (180°), always both translational and rotational head movements were elicited (Fig. 7). Independent of the position of the window, the head rotated in the same direction as the pattern, but the direction of head translation changed. The pigeon always translates its head about parallel to the visible part of the moving pattern. Thus, during a clockwise turn of the drum, the pigeon translates its head to the right when the window is in its front but to the left with the window in its back, and it translates forwards when the window is on its left and backwards when the window is on its right side. When the window is in the 90° position, the ipsilateral eye either sees the pattern moving from front to back or from back to front. Earlier studies describe a marked asymmetry in the rotational head movement for both cases when the pattern is continuously rotating (Mowrer 1936; Huizinga and van der Meulen 1951; Gioanni 1988a). Since this asymmetry was not so obvious in our experiments with oscillating patterns, we did not evaluate the responses to both directions of pattern movement separately.

The total number of head movements was reduced by occluding most of the moving pattern with slightly more responses when the area of the window (W) was split into two (double window, DW) with each separated by 180° in azimuth (Fig. 7a). Stimulation of the frontal visual field elicits most head movements, and when the window is placed behind the pigeon, the number is strongly reduced. This result may be expected from the visual field of the pigeon with its frontal binocular overlap in the horizontal plane of 22° and the blind area of 44° at the rear of the head with the eyes in their resting position (Martin 1984). Responses to pattern motion across a window at the back of the pigeon may be evoked at all because of eye movements which narrow the blind area (Bloch et al. 1984), and also, because the pigeon's head turned, the window was not presented strictly at 180° (see Materials and methods).

When, however, translational and rotational head movements are evaluated independently, a completely different picture emerges (Fig. 7b). In the single window situation (W), rotational head movements are strongly reduced compared to whole field stimulation. They are weakest when the frontal visual field is stimulated (significantly less than with window position 90° or 180°, both $p<0.005$, two-tailed *t*-test). However, in the double-window situation (DW), more than twice the number of rotational responses could be elicited than in the window situation (W) and attained roughly 75% of the number observed during whole field stimulation.

The opposite is true for the translational responses (Fig. 7b). When visibility of the oscillating pattern is restricted to one window (W), the percentage of head translations is larger than in the double window experiments (DW) and during whole field stimulation. Pattern movement across the frontal visual field elicits even twice as many head translations as during whole field stimulation. In the experiment with a window on the left and the right side of the pigeon (position of the stimulus fields ±90°), one would expect no translational response at all. Sixty per cent of the number of translations of the whole field stimulation were, nevertheless, counted. This can be partly attributed to the interval of head orientations of ±20° around the desired position that had to be tolerated and to the asymmetric orientations of the eyes. Therefore, one eye would be stimulated in its more frontal and the other in its more backward visual field which differ in their contribution to the translational response. Furthermore, during continuous pattern motion there exists a clear asymmetry in the strength of responses of the translational system to a front-to-back and a back-to-front movement of the pattern (Nalbach and Wallman 1991). Although not obvious in the present experiments, this asymmetry may contribute to the remaining number of translational head movements counted in the present situation.

These results demonstrate that the pigeons respond to stimulation of the frontal visual field predominantly with translational head movements, but that these are reduced when strong rotational responses are elicited – either

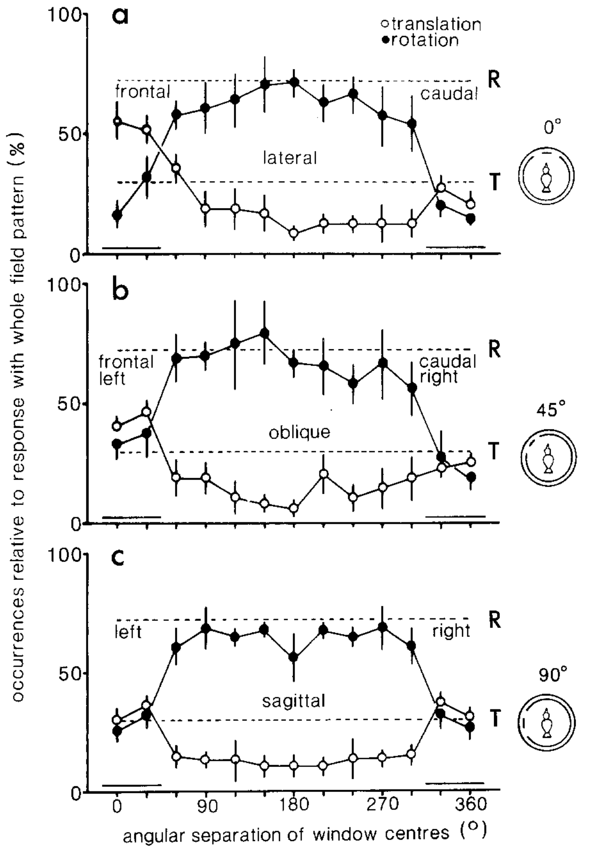

Fig. 8a–c. Percentage of translational *(open circles)* and rotational *(filled circles)* head movements in double-window experiments, each window 30° wide, contributing to the total response with whole field stimulation. The drum was oscillated at frequency 0.6 Hz, displacement amplitude 10°. Average values obtained in experiments with three pigeons with two replications of each situation. Windows are separated starting (**a**) from the frontal position 0°, (**b**) an oblique position 45° and (**c**) a lateral position; here, data obtained with symmetrically placed double windows on the right and left side of the pigeon are averaged. Angular separation of the two windows of 0° and 360° actually means a single window 30° wide, separation 30° and 330° results in a single window 60° wide (indicated by the *horizontal bar* along the abscissa). Otherwise the two windows are truely separated by a stationary screen. *Dashed lines* indicate contribution of rotation (*R*) and translation (*T*) during whole field stimulation

during whole field stimulation or in experiments with two windows separated by 180°.

To further examine these dependences, the separation of the two windows was systematically increased. The windows were placed symmetrical to one of three planes; the pigeon's sagittal plane, its transverse plane or an oblique plane (see insets in Fig. 8). This allowed us to study the influence of window separation independently of position in the visual field and symmetries in the nervous system.

In all combinations, the number of translational responses was larger when the pigeon viewed a contiguous pattern (situations indicated by horizontal bars along the abscissa in Fig. 8). As soon as the two windows were separated, their number decreased and the number of rotational responses dramatically increased almost to the same level as observed when the pigeon could see the total pattern. Separations of 60–90° of the window centres were about as effective as 180° in eliciting large rotational responses and suppressing translational head movements. The angular position of the windows did not alter this general result although the absolute number of translational and rotational head movements changed. Specifically, the number of translational head movements was particularly large when the moving pattern was seen through the single window in the frontal visual field. Furthermore, there was no qualitative difference in the responses whether the two windows were placed only on one side of the pigeon (Fig. 8c) or one on the right and the other on the left side (Fig. 8a). Also, symmetrical placing of the windows relative to a major body axis of the pigeon (Fig. 8a, c) yielded similar results to placing them at oblique angles to the pigeon (Fig. 8b).

These results demonstrate that by separating the patches of moving pattern in the visual field, the number of rotational responses is dramatically increased. It saturates, however, at the level observed during whole field stimulation. To examine this phenomenon more closely, the width of a window was varied (Fig. 9). When the width of the window – in front of the pigeon, to its side or at its back was increased, the number of rotational and, to an even lesser degree, translational head movements only slightly increased. This suggests under-linear summation of the information of the increasing number of local movement detectors that feed into the rotational and translational system. Besides regional variation in sensitivity to pattern movement (Figs. 7–9) this might be caused by lateral inhibition. When, however, the pigeon could view the oscillating pattern through two narrow windows (width 30°) which subtend an angle equal to the broadest of the contiguous windows (120°), the rotational response was dramatically increased – and the translational reduced – although the moving field as halved ("DW" in Fig. 9). The rotational response could be even larger than that expected from the sum of the responses obtained in experiments (Fig. 8b) where the windows were presented separately at the appropriate positions (45° and/or 135° relative to the pigeons sagittal plane; "2*W" in Fig. 9). Only when both windows were situated in the frontal visual field did prediction ("2*W" in Fig. 9) and experimental data ("DW" in Fig. 9) coincide.

In order to calculate the number of translational responses in the double-window experiment from the results obtained to the two single windows at the appropriate positions, one needs a model of how the translational system might work that integrates movement perceived over a large visual field. As will be argued in the discussion, it is plausible to assume that, in mathematical terms, the velocities of local patches are vector integrated over the visual field to build the resulting translational vector of the head movement. When we accept that the number of occurrences represents the strenght of the responses, and that a pigeon translates its head approximately parallel to the patch of the pattern it is looking at, we have an estimate of the (average) translational response vector in the single window situation. Since, in the present experiments, the two windows are separated by 90°, the

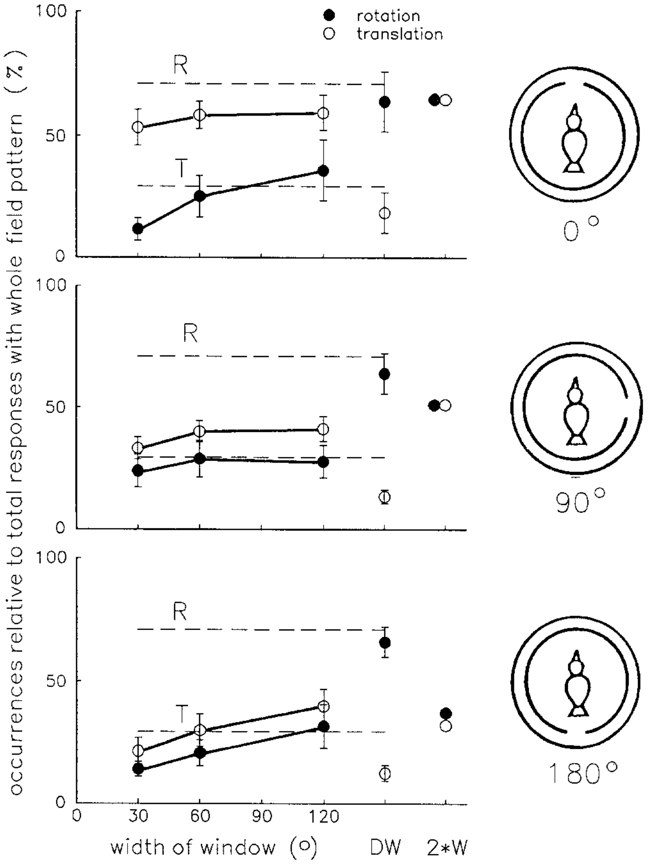

Fig. 9. Percentage of translational *(open circles)* and rotational *(filled circles)* head movements contributing to the total response during whole field stimulation when the width of a window is varied. This is compared to the responses in a double window experiment (*DW*) where the two single windows were 30° wide each and their centres subtended an angle of 90°. Thus, the outer borders of the double-window arrangement were separated by 120°, as in the experiment using the broadest window. This in turn is compared to responses that are calculated from the responses in experiments (Fig. 8b) where the single windows were in the same position as in the double-window experiment (*2*W*). The values expected for the rotational responses were calculated from the algebraic sum of the responses to the single windows, the translational responses as the absolute value from the vector summation of the responses to the two single windows. The (double-) windows were presented either in the frontal, the lateral or the rear visual field of 3 pigeons as indicated by the insets

value of the integral vector can be calculated as the square root of the sum of the squared number of responses to the single windows. In all three constellations, the calculated translational response ("2*W" in Fig. 9) is much larger than the one actually measured ("DW" in Fig. 9). Thus there is true suppression of the translational response.

This suppression should not be confounded with the reduction of the translational response from the level recorded in the window-experiments to the level recorded with whole field stimulation. In the latter case, patches of the oscillating drum move into opposite directions over the eyes which are separated by 180°. In a clockwise rotating drum the head translates to the right when the window is placed frontally, and translates to the left when the window is placed in the back of the pigeon. Since both signals are counter-directed, they should cancel each other out when both patches are visible. Because of the dominant input from the frontal visual field, the pigeon will nevertheless translate its head into the direction of frontal stimulation with, however, a reduced amplitude.

Discussion

Pigeons, like chickens (G. Marin and J. Wallman, personal communication), rotate, but also translate, their head in response to a pattern that is rotating about their vertical axis (Fig. 1). Translation is, however, a transient phenomenon that vanishes during ongoing rotation but dominates the response at repeated onset of pattern motion (Figs. 2–4). From Fig. 4c, a time constant of the decay during uni-directional pattern rotation may be estimated as about 10 s at stimulus velocities 7.5°/s–20°/s. This is consistent with the result that at oscillation frequencies above 0.1 Hz the translational head movements dominate the responses (Figs. 2, 3). The time-constant of decay of the translational response is similar to the time-constant of 7.1 ± 3.3 s that characterises the increase in rotational head velocity after onset of continuous pattern rotation with a speed of 20°/s (Gioanni 1988a). Thus, decay of the one and build-up of the other head movement might have a common origin. Gioanni (1988a) suggests that at the onset of pattern motion a neural velocity storage needs to be charged. This storage is thought to play an important role in the interaction of the vestibular and the visual system which both contribute to the same task, namely the stabilisation of eyes, head and body against rotational disturbances (review: Carpenter 1988).

Rotating its head in response to the visual stimulus, the pigeon simultaneously stimulates its vestibular system. It should lead to a signal opposing the actual head movement which finally might reduce the rotational response. This can be expected to happen especially when the visual stimulus evokes high head acceleration which is the adequate stimulus for the vestibular system. The percentage of translational head movements is, however, widely independent of the acceleration of the visual stimulus and, therefore, presumably the rotational acceleration of the head (Fig. 3). Hence, the present experiments do not support the hypothesis that the translational head movement is a direct consequence of self-stimulation of the vestibular system. This interpretation gains further support from the results of Gioanni (1988a) who showed that, in experiments with a sinusoidally oscillating pattern, the gains of optokinetic head rotation and of optokinetic eye movements (measured with pigeons whose head was fixed) decline at about the same stimulus frequency; in the first situation the vestibular system is stimulated, but not in the second one. The drop in gain of the visually elicited rotational responses therefore seem to be governed by the dynamics of the underlying part of the visual system that extracts the rotational component from the image flow. However, experiments with animals whose canals have been plugged would have to be performed to provide firm evidence.

The similar time constants for the increase in the strength of the rotational and decrease in strenght of the translational response suggests that the rotational signal suppresses the translational responses. This hypothesis is supported by the fact that under all experimental conditions that elicit a strong rotational response the translational response is weak. Direct evidence for a suppression of the translational head movement comes from the comparison of results obtained in 'double-window experiments' with those expected from the responses in 'single-window experiments' (Fig. 9). Thus, the frequency dependence of the translational response (Figs. 2, 3) does not necessarily reflect the dynamic properties of the system underlying the translational response but rather is caused by the well-known dynamic properties of the rotational system (Figs. 2, 3, and Gioanni 1988a).

The really puzzling result is, however, the fact itself that the pigeon translates its head in response to a textured drum rotating about its vertical axis. It moves the head in the direction in which the features of the pattern move across its frontal visual field. Fixation of single features can be excluded as the underlying mechanism (Figs. 5, 6). Thus it has to be concluded that the translational head movement is evoked by the movement of the pattern in a large portion of the visual field, similar to the stimulus that elicits the rotational opto-collic reflex. Indeed, after occluding most of the pattern by a screen and stimulating the pigeon in restricted areas at various positions within its monocular or binocular visual field, translational head movements roughly parallel to the visible part of the moving pattern could be elicited (Figs. 7, 8). Thus, each portion of the rotating pattern evokes a translational response approximately tangential to its path. If these local contributions are integrated, preserving their directional information, this results in a net translational signal of the right direction in the 'window-experiments'. Since the frontal visual field elicits particularly strong translational responses (Fig. 7), this explains the remaining head-translation when the pigeon can see the whole pattern.

Such a translational wide-field movement sensitive system can be mathematically described as a vector-integration and can be implemented in the nervous system in a variety of ways. Present knowledge of the pigeon's accessory optic system (Wolf-Oberhollenzer 1990, Wylie and Frost 1990a) which is thought to underly the responses to whole field pattern motion (Gioanni et al. 1983a, b; McKenna and Wallman 1985) suggests that a number of topographically labelled cells with broad, overlapping receptive fields might cooperate to mediate the translational responses. The mechanism of vector-integration was first suggested to underly the control of translational locomotion in hoverflies (Collett 1980) and brazilian, stingless bees (Kelber and Zeil 1990). In the present experiments, this mechanism erroneously evokes translational head movements in response to a rotating pattern, mainly because of regional variation in movement sensitivity (Figs. 7–9). Nevertheless, under natural conditions, it would be quite appropriate to control the peculiar translational head movements (called head-bobbing) of a number of birds, among those the pigeon and the chicken (see Introduction).

Also, in the optokinetic response of the primate, there are two components; one concerned with translational and one with rotational disturbances of gaze (Miles et al. 1989). The translational component corresponds to the direct, or early component of the optokinetic response while the rotational one corresponds to the indirect, or delayed component (Busettini et al. 1991). Therefore, similarities to the present findings on optokinetic head movements of pigeons exist. The primate translational system, however, is not a wide-field system as proposed to underly the pigeon's translational head movement. Rather, wide-field motion is not the optimal stimulus for ocular following in primates, but an object moving at the centre, and the surround moving in the contrary direction (Miles et al. 1986). The authors concluded that this system is adapted to compensate for an observer's own linear motion while fixating an object. Furthermore, in the primate's translational system absolute distance information is used for scaling the gain; that is a cortical influence seems to be necessary. The mechanism proposed to underly the pigeon's responses does not need any further information than that provided by the acessory optic system.

The translational head movements elicited in a rotating drum demonstrate that the pigeon may not be able to perfectly decompose image flow into its translational and rotational components. Theoretically, it is possible to solve this problem even for restricted patches of optic flow (review: Warren and Hannon 1990). It might, however, be that pigeons need motion parallax information, such as differential image motion. This has been demonstrated to be necessary for humans to judge the direction taken in the presence of eye movements or while following a curvilinear path (Rieger and Toet 1985, Warren and Hannon 1990, Warren et al. 1992). In the present experiments, however, this source of information was not accessable to the pigeons since the drum carried a two dimensional pattern only with no depth. Currently experiments are being performed to examine whether pigeons indeed make use of relative optical motion among elements at different depths.

In any case, the present results demonstrate some elaboration of the pigeon's visual system to decompose translational and rotational image flow. One finding is that the rotational system suppresses an erroneous translational head movement (see above). It remains to be examined whether there is also an influence of the translational system to suppress erroneous rotational responses. The second elaboration is the organisation of the rotational system itself. Patches of optic flow that stimulate neighboured movement detectors are less effective in eliciting a rotational head movement than patchhes which are separated (Figs. 8, 9). A similar arrangement has been recently demonstrated in crabs and was described as a mechanism to build an efficient rotation detector (Kern et al. 1991).

Comparison of widely separated patches in the visual field simplifies discrimination of translation and rotation.

This is easiest to illustrate assuming one patch on the right and the other on the left of the path. In the case of forward translation the retinal image flows from front to back, while during rotation flow it is counterdirected for both eyes. Cells that could mediate such specificity were found in the nucleus of the basal optic root, which is a part of the bird's accessory optic system, and the vestibulocerebellum of pigeons (Wylie and Frost 1990b, 1991). These cells were characterised by their preference to respond either to binocularly delivered translational or to rotational stimuli. To date, however, no attempt has been made to investigate the neuronal substrate of the pigeon's ability to discriminate translational and rotational image flow *with one eye only,* as is suggested by the present experiments (Fig. 8).

Acknowledgements. I thank Heike Neumeister and Wolfram Türke for performing the experiments and counting head translations and rotations. Comments on the manuscript from Kuno Kirschfeld, Gerbera Nalbach and Friederike Wolf-Oberhollenzer helped to clarify several points. Discussions with Karl-Georg Götz stimulated the analysis underlying Fig. 9.

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