Influence of the behavioural context on the optocollic reflex (OCR) in pigeons (*Columba livia*)

Monique Maurice[1], Henri Gioanni[1,*] and Anick Abourachid[2]

[1]*Laboratoire de Neurobiologie des Réseaux Sensorimoteurs, UMR 7060 CNRS-Université René Descartes, 45 rue des Saints-Pères, 75270 Paris Cedex 06, France and* [2]*Muséum d'Histoire Naturelle, UMR 8570 CNRS-MNHN-P6, 55 rue Buffon, 75005 Paris, France*

*Author for correspondence (e-mail: henri.gioanni@univ-paris5.fr)

Summary

We investigated the effects of several behavioural conditions on the properties of the horizontal optocollic reflex (OCR) in pigeons. The head reflex was triggered by rotating the visual surroundings at different velocities (stimuli steps of 30–300 deg. s^{-1}) and the characteristics of the slow and fast phases of the OCR were analysed during, (i) the 'resting condition', in which animals were hung in a harness, (ii) the 'standing condition', in which animals were freely standing, (iii) the 'walking condition', in which animals were walking on a treadmill at different velocities, and (iv) the 'flying condition', in which animals were hung in a harness and subjected to a frontal air-stream, provoking a flying posture.

In the 'resting' condition, irregularities were observed in the amplitude of nystagmic beats, in the beating field and in the slow phase velocity (SPV) of the OCR. These irregularities diminished progressively when the behavioural condition changed from 'standing' to 'walking', and disappeared in the 'flying' condition. Correlatively, the working range of the OCR (evaluated by its gain at the plateau of SPV) was progressively extended toward higher stimulation velocities.

The velocity of the fast phases of the OCR (measured for all the conditions except the 'walking condition') also increased in correlation with the SPV. The walking speed did not influence the OCR in the treadmill velocity range of 0.20–0.40 m s^{-1}. The presence of a frontal airstream in the 'standing condition' did not change the OCR properties. This fact (and other observations discussed in the paper) suggests that the adaptation of the OCR to the behavioural context is mediated by internal signals generated by each behavioural condition.

Key words: bird, pigeon, *Columba livia*, optokinetic reflex (OKR), behavioural context, walking, flight.

Introduction

When walking or flying, birds limit retinal slip, thereby avoiding visual blurring, by stabilising their gaze (i.e. head and eye position). Like other species, under rotational stimuli, birds stabilise their gaze by combining vestibular (vestibulo-ocular reflex: VOR and vestibulo-collic reflex: VCR) and visual (optokinetic nystagmus: OKN and optocollic reflex: OCR) eye and head reflexes (Mowrer, 1936; Fukuda, 1959; Fite, 1968; Wallman et al., 1982; Wallman and Velez, 1985; Gioanni, 1988a,b; Türke et al., 1996; Dickman et al., 2000). In pigeons and some other birds, when walking on the ground, a 'head-bobbing' reflex also stabilises the head (Dunlap and Mowrer, 1930; Friedman, 1975; Frost, 1978; Davies and Green, 1988; Green et al., 1994; Troje and Frost, 2000; Fujita, 2003). The fundamental role of the nucleus of the optic basal root (nBOR) and the pretectal nucleus lentiformis mesencephali (nLM) in the elaboration of optokinetic responses in birds is well established (Britto et al., 1981; Mc Kenna and Wallman, 1981,

1985; Morgan and Frost, 1981; Gioanni et al., 1983a,b, 1984; Winterson and Brauth, 1985; Telford and Frost, 1989; Wylie and Frost, 1990a,b, 1999; Wylie et al., 1998a; Frost et al., 1990; Fu et al., 1998a,b; Zhang et al., 1999; Wang et al., 2000a).

Optokinetic responses are usually studied by moving the visual surroundings around the stationary animal, whereas vestibular reflexes are investigated by oscillating the animal in darkness on a turntable. Most studies have used body-restrained animals. The head is also immobilised for studying isolated eye reflexes (OKN, VOR). In these conditions, birds display consistent eye reflexes. For example, in pigeons the OKN allows a good stabilisation of the retinal image for stimulation velocities up to 20 deg. s^{-1} (Gioanni, 1988a). However, when the head is free to move and the body is restrained, birds use head reflexes (OCR, VCR) to stabilise their gaze, with the eye response being weak, and variable depending on the species (Gioanni, 1988a,b; Haque and

Dickman, 2005). In these conditions, gaze stabilisation is better than for pure eye reflexes. In birds, eye and head movements strongly depend on the animal's behaviour. Pigeons display different specific eye and head movements when walking, feeding or pecking (Wohlschläger et al., 1993). The characteristics of the OCR also depend on the behavioural situation of the animal. The gain of the OCR (slow phase velocity/stimulation velocity) decreases for stimulation velocities higher than 40 deg. s^{-1} in body-restrained pigeons (Gioanni, 1988a), whereas when the animal is held in a supple harness so that its wings, legs and tail are free ('resting condition') the gain remains close to one for stimulation velocities up to 60 deg. s^{-1} (Gioanni and Sansonetti, 1999). Also if pigeons are provoked into a flying posture by a frontal air-stream ('flying condition'), the working range of the OCR extends considerably toward higher velocities (Bilo and Bilo, 1978, 1983; Bilo et al., 1985; Bilo, 1992; Gioanni and Sansonetti, 1999). In this 'flying condition' the fast phase velocity is also increased in correlation to the slow phase velocity (Gioanni and Sansonetti, 1999).

The fact that dynamic properties of the slow and fast phases of the OCR are increased in the high velocity range of visual stimuli when pigeons are in the 'flying condition' reveals a physiological reflex adaptation to the behavioural context. Indeed, the velocity of the optic flow is substantially increased when the animal is flying compared to when the pigeon is on the ground. If there is such an adaptation, the properties of the OCR should also change when the animal is walking compared to standing still. Moreover, the changes in the dynamic properties of the reflex should be adapted to the range of velocities corresponding to the different behavioural conditions.

Here, we have analysed the OCR of pigeons in the 'resting condition', which was taken as a reference. We then analysed the OCR in free animals standing still ('standing condition'), in animals walking on a treadmill ('walking condition'), and then in the 'flying condition' (as already studied) to allow a comparison of the OCR properties produced in these different behavioural contexts.

Materials and methods

The experiments were carried out on six pigeons (*Columba livia* L.). All experiments were done in accordance with the European Communities Council directive of 24 November 1986, and following the procedures issued by the French Ministère de l'Agriculture.

Experimental procedure

The OCR was recorded for each animal for the four behavioural conditions: the 'resting condition', the 'standing condition', the 'flying condition' and the 'walking condition'. For the 'resting condition' the animal was hung in a supple harness so that its head, wings, legs and tail were free (Fig. 1A). In the 'flying condition' a frontal airflow of compressed air at a constant 1.6 bars pressure (160 kPa) was delivered through a 15 mm diameter tube placed 15 cm in front
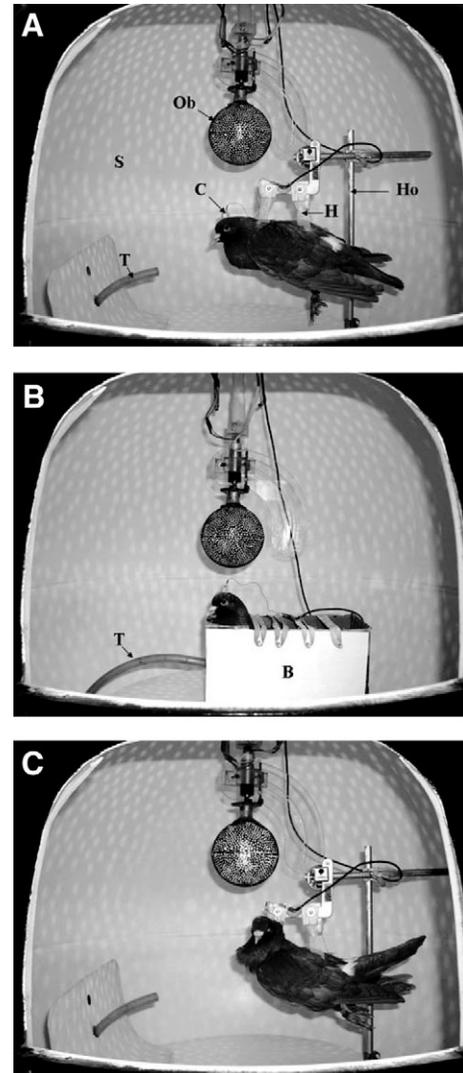

Fig. 1. Experimental set-up used to record head movements during optokinetic stimulation delivered on a spherical screen. (A) 'Resting condition'; (B) 'standing condition'; (C) 'flying condition'. B, box; C, coil with its support; H, harness; Ho, holder; Ob, optokinetic ball; S, spherical screen; T, tube delivering the frontal airflow.

of the animal (Fig. 1C). The airflow principally reached the front of the head, the breast and the anterior part of the wings. In these conditions, the pigeons adopted a flight posture: the legs were moved to the rear, the tail was opened and the wings were beating or remained spread without beating. Whether or not the pigeons beat its wings did not influence the data. The experimental procedure corresponding to these two conditions has been previously used and described (Gioanni and Sansonetti, 1999). In the 'standing condition', the pigeon was placed in an open box so that its head extended from the top of the box (Fig. 1B). The animals could not turn round in the box. The effects of the airflow in this condition were tested by connecting the tube delivering the compressed air to the front of the box. The pigeon was placed with its head centred inside a 1 m diameter spherical screen before starting the OCR
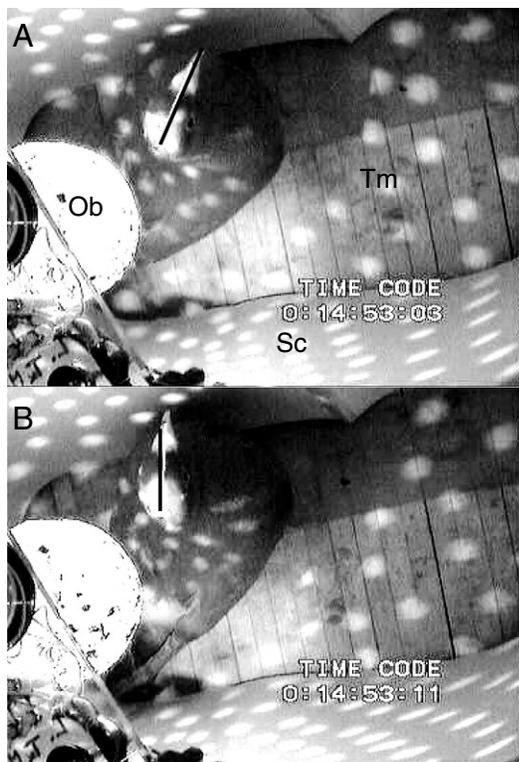
Fig. 2. Experimental set-up used to study the head movements during the 'walking condition'. The black line drawn along the sagittal axis of the head allows angles corresponding to each nystagmic beats of the OCR to be measured. The corresponding duration is given by the time code. (A) Onset of a slow phase triggered by an anticlockwise stimulation; (B) end of the slow phase. Ob, optokinetic ball; Sc, screen; Tm, treadmill.

recording sessions. During the recording sessions, gently tapping on the spherical screen maintained the animals in a high level of alertness.

For the 'walking condition', pigeons were previously trained for 4–6 weeks to walk on the treadmill, with and without optokinetic stimulations (Fig. 2). The OCR was first studied on the unmoving treadmill ('standing condition'). The treadmill was then started in the dark and optokinetic stimulation began once the animal was walking normally. The OCR was tested for increasing velocities of the treadmill (0.2, 0.3, 0.35 and 0.4 m s^{-1}). The treadmill was stopped for a few minutes between each test.

The OCR was recorded for the four behavioural conditions for all the animals. Each animal was submitted to no more than one test a day. The order of the behavioural conditions varied from one animal to the other.

Optokinetic stimulation

Whole-field optokinetic stimulation was delivered by a light source within an opaque metallic sphere (11 cm in diameter). The sphere was pierced with numerous holes and located above the pigeon's head. The ball projected a pattern of spots of about 2–3 degrees either on the spherical screen (Fig. 1) for the 'resting', 'standing' and ''flying' conditions, or on an ellipsoidal screen (25 cm×60 cm), perpendicular to the treadmill plane, for the 'walking condition' (Fig. 2). The optokinetic ball was rotated in the horizontal plane by a DC motor, monitored by a velocity servo-system. Optokinetic stimuli consisted of constant velocity steps of 30, 60, 100, 200 and 300 deg. s^{-1}. The optokinetic ball was set in motion in the dark. Stimulation began when the light was turned on, and terminated when the light was turned off. Each stimulus was given in clockwise and anticlockwise directions. A new stimulation was delivered only when the post-responses were finished.

Recording of head movements

In the 'resting', 'standing' and 'flying' conditions head movements were recorded using the magnetic search-coil technique (Robinson, 1963) with an EPM 510 apparatus (Skalar, Delft, Netherlands). An 8 mm diameter coil was fixed in a rigid cylindrical piece of plastic. Before each experiment, the coil was calibrated by rotating it in the horizontal plane by ±30, 60 and 90°. As the range of horizontal head movements can exceed the linear range of the coil system (±30°), an arcsin analog device was used to obtain a linear signal of the head position. The coil system was firmly attached to the animal's head (Fig. 1) with adhesive tape. The head position signal was electronically differentiated to obtain a head velocity signal. These signals, the velocity control of the optokinetic stimulation and the onset and end of the optokinetic stimuli were stored on a computer using the PowerLab system (ADInstruments, Paris, France).

In the 'walking condition', the head movements were filmed by a video camera in the dorsal view at 25 frames per second.

Data analysis

For head responses recorded using the search-coil technique ('resting', 'standing' and 'flying' conditions), the slow phase velocity (SPV) of the OCR was measured, once it had reached a plateau, by averaging the velocity of the slow phase during 10 s of stimulation or more when required. Corresponding gain values (slow phase velocity/stimulation velocity) were calculated. The fast phases of the OCR were estimated by measuring their peak velocity (PV) and amplitude, according to the classical relation between these two parameters ('main sequence'). The data obtained from the video camera ('walking condition') were analysed using Colorvision I and Sigmascan Pro 5 software. A reference axis, corresponding to the middle line of the head, was drawn between the top of the head and the front of the beak. This allowed the angle of the head rotation corresponding to each slow phase of the OCR to be measured (Fig. 2A,B). Values were measured for at least 10 slow phases produced in the clockwise and anticlockwise directions. The SPV and gain values were then calculated. Data obtained for clockwise and anticlockwise stimulations in each behavioural condition were pooled.

ANOVA statistical analysis was used for the gain curves (study of the slow phase of the OCR) and linear correlation for the fast phases of the OCR.

Results

We will present the results from the 'resting', standing' and 'flying' separate from the 'walking condition' as the experimental set-ups were different.

Influence of the 'resting', standing' and 'flying' conditions on the OCR

Slow phase analysis

In the 'resting condition', the optokinetic stimuli triggered a head reflex (OCR) composed of irregular nystagmic beats (their amplitude and their frequency varied during a same stimulation) (Fig. 3A). The beating field (eccentricity of the head movements) was also irregular since the nystagmic beats were not centred around a constant axis. As is usually observed, the SPV increased progressively to reach a plateau, but the time course of the rising phase and of the plateau were irregular. The mean gain measured in the plateau was close to 0.8 for a visual stimulation of 30 deg. s^{-1}, and decreased considerably for stimuli greater than 60 deg. s^{-1} (Fig. 4A).

In the 'standing condition', the amplitude of the nystagmic beats of the OCR was generally higher than for the 'resting condition' (Fig. 3B). The nystagmic beats were also more regular, but the time course of the SPV was still irregular. The maximal gain values of about 0.9 were obtained for stimuli between 30 and 60 deg. s^{-1}, and were higher than for the 'resting condition' (Fig. 4A). The gain remained up to 0.75 for a stimulus of 100 deg. s^{-1}, whereas in the 'resting condition' it dropped to 0.45. The gains observed in the 'resting' and in the 'standing' conditions were significantly

different for stimulation velocities from 30–200 deg. s^{-1} ($F_{(1-44)}$=16.6, P<0.005).

In the 'flying condition', the amplitude of nystagmic beats was higher than for the 'resting' and 'standing' conditions and had a very regular time course (Fig. 3C). The head-beating field generally extended around the sagittal axis. The SPV increased regularly to reach a stable plateau. For the lowest stimulation velocities (30–60 deg. s^{-1}), the gain values were close to those for the 'standing condition' (Fig. 4A). In contrast to the 'resting' and 'standing' conditions, the gain remained high (about 0.75) for stimuli up to 200 deg. s^{-1}. The gain values obtained in the 'flying condition' was significantly higher than
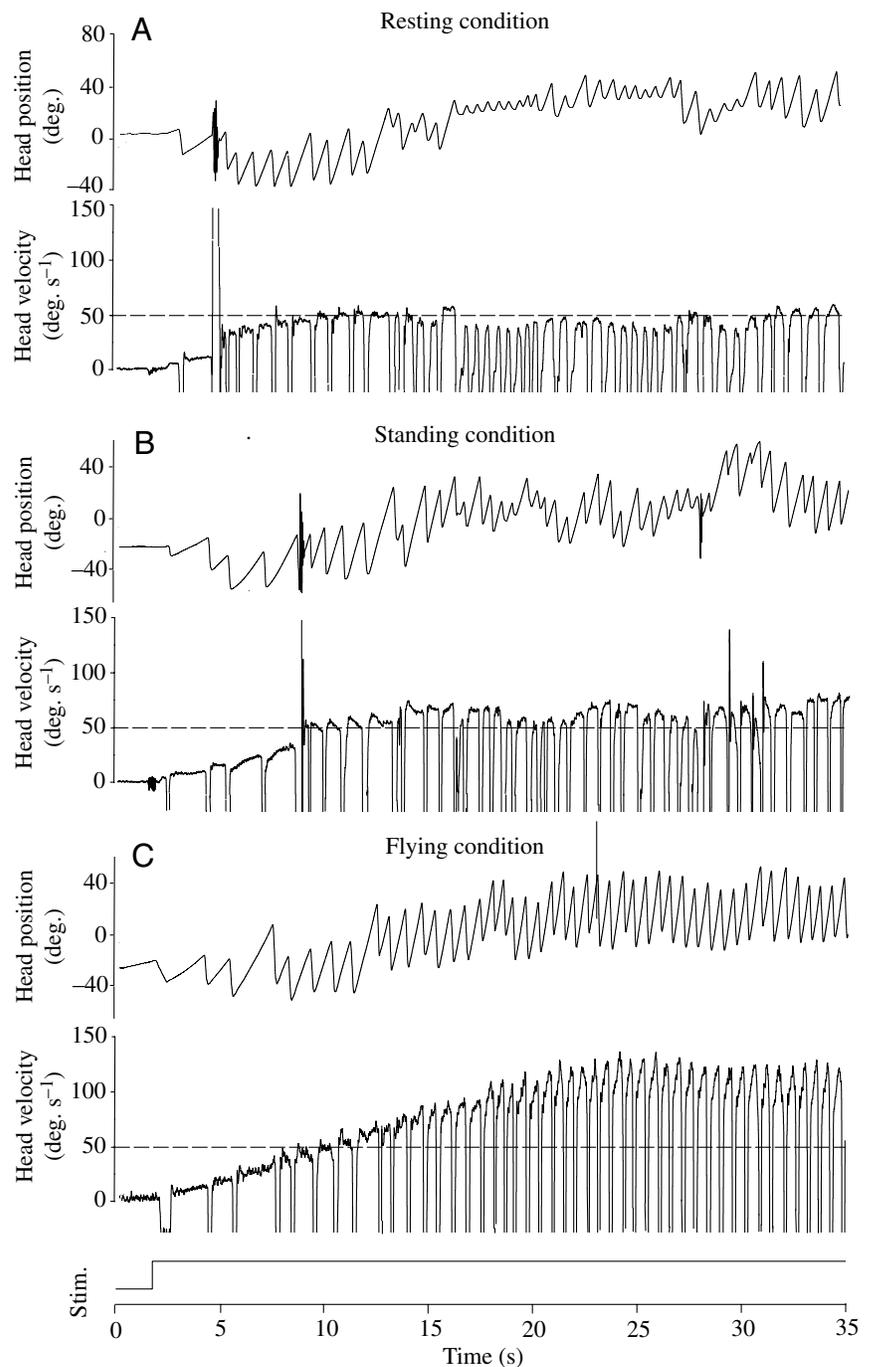

Fig. 3. Examples of optocollic responses obtained in the same animal for different behavioural conditions. The stimulation (stim.) was a velocity step of 200 deg. s^{-1} delivered clockwise. Upper traces, head position; lower traces, head velocity. A broken line has been drawn for a head velocity of 50 deg. s^{-1} to aid comparison of the maximal slow phase velocity obtained for the three conditions. The time course of the stimulation and the time scale are indicated at the bottom of the figure. (A) 'Resting condition'. Note the irregular time course of nystagmic beats and of the slow phase velocity. (B) 'Standing condition'. Nystagmic beats are larger and more regular, and the slow phase velocity is higher than in the 'resting condition'. (C) 'Flying condition'. Nystagmic beats are regular and centred around the axis of the body. The slow phase velocity is higher than in the 'standing condition'.

those obtained for the 'resting condition' for stimulation velocities from 100 to 300 deg. s^{-1} ($F_{(1-44)}$=115.73, $P<0.001$), and were significantly higher than for the 'standing condition' for stimulation velocities from 200 to 300 deg. s^{-1} ($F_{(1-44)}$=26.21, $P<0.001$).

These data show that the OCR efficiency extends to increasingly higher stimulation velocities when moving from the 'resting condition' to the 'standing condition' and to the 'flying condition'.

Influence of the air-stream

We looked at a possible role of the mechanical stimulation of feathers and skin by the airflow during the 'flying condition'. Pigeons in the 'standing condition' received a frontal airflow comparable to that used in the 'flying condition' (Fig. 1B). We found that the OCR was very similar to that observed in the 'standing condition' and that the corresponding gain curves were not different (Fig. 4B). Therefore, mechanical stimulation
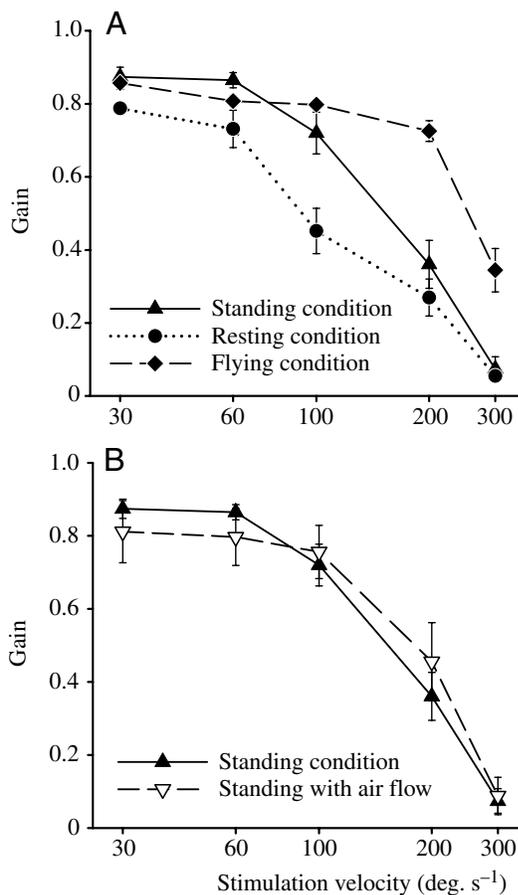

Fig. 4. Mean gain of the OCR obtained for different behavioural conditions, in response to increasing stimuli velocity step. (A) Gains obtained in the 'resting', 'standing' and 'flying' conditions. The gain was progressively increased in the higher velocity range of stimuli for each of these three conditions. (B) Mean gain obtained for the 'standing condition' in the presence of and without a frontal airflow. The corresponding gain curves were not different. Each point is the mean value ± s.e.m. (N=12) of responses obtained in the clockwise and anticlockwise directions.

from the airflow alone does not modify the optocollic response, at least when the animal is standing.

Fast phase analysis

We looked at fast phases of the OCR in the 'resting', 'standing' and 'flying' conditions by measuring the peak velocity (PV) and the amplitude of fast phases, and the mean velocity (SPV) of the two slow phases occurring just before and after each fast phase (Fig. 5). As is usually observed, the PV of the fast phases increased as their amplitude increased ('main sequence') in the three conditions. In the 'resting condition', the PV of the fast phases did not depend on the SPV values. However, in the 'standing condition', the PV of the fast phases increased slightly as the SPV increased. This can be seen in Fig. 5 in which the plane of correlation is inclined along the SPV axis. Multiple linear regression analyses showed that the PV of the fast phases could be predicted from a linear combination of both the fast phase amplitude and the SPV [R=0.78 ($F_{(2-682)}$=521.77, $P<0.001$)]. In the 'flying condition', there was a much greater increase in the PV of the fast phases relative to the SPV compared to the 'standing condition' [R=0.89 ($F_{(2-686)}$=1348.66, $P<0.001$)]. Thus, the behavioural condition also influences dynamic characteristics of the fast phases, as their velocity increased with the SPV of the OCR when the animal is standing or flying.

Influence of walking on the OCR

We investigated the effect on the OCR of pigeons walking on a treadmill at different velocities (Fig. 2). The optokinetic stimuli were delivered at the same velocities (30–300 deg. s^{-1}) as for the other conditions. We also recorded the OCR while the animal was standing still on the immobile treadmill. This condition, also called the 'standing condition', allowed us to compare data obtained during walking with data obtained in the 'resting' and 'flying' conditions.

The gain obtained in the 'standing condition' had a maximal value of 0.6 for a stimulation of 30 deg. s^{-1}, which decreased regularly with increasing velocities (Fig. 6). The time course of this curve was close to that observed for the original 'standing condition' with the spherical screen. However, the gain values were lower overall, particularly the optimal gain. Walking increased the gain of the OCR over the whole velocity range of optokinetic stimuli. This increase in gain was between 0.1 and 0.2 ($F_{(3-46)}$=13.82, $P<0.001$). This increase in gain was independent of the walking speed (0.2–0.4 m s^{-1}). These data show that walking increases the gain of the OCR over a large velocity range of visual stimuli, but that walking speed does not interact with this reflex, at least over the treadmill velocities used in this experiment.

Discussion

Comparison of our results with other data obtained with pigeons

We did not test the OCR for velocities lower than 30 deg. s^{-1} since preliminary studies showed that the gain was optimal in

A — Resting condition

Fast phase PV=10.7Amp.+0.4SPV+92.9

B — Standing condition

Fast phase PV=11.6Amp.+0.97SPV+116.7

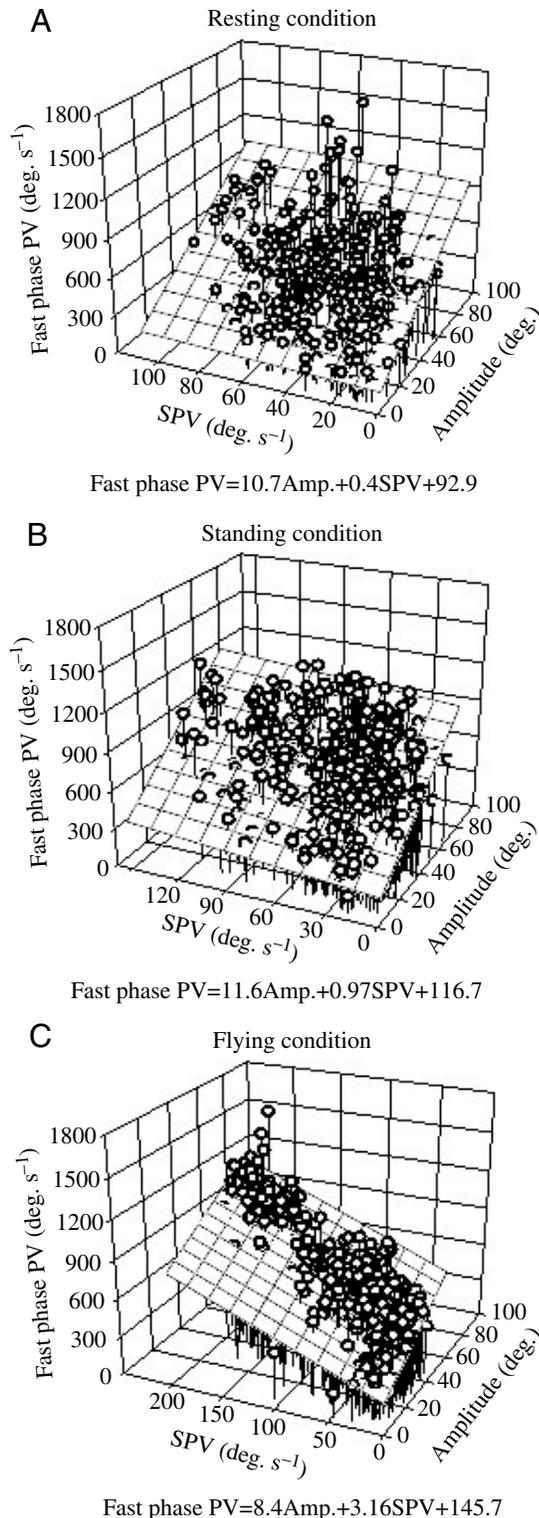## C — Flying condition

Fast phase PV=8.4Amp.+3.16SPV+145.7

Fig. 5. Three-dimensional representation of the PV–amplitude relation as a function of the SPV, for the fast phases of the OCR obtained in response to velocity step stimuli, for (A) the 'resting', (B) 'standing' and (C) 'flying' conditions. Data were obtained from the six animals. The equations of the multiple linear regressions are indicated for each condition. The PV values were independent from the SPV in the 'resting condition', whereas they increased slightly in the 'standing condition' and strongly in the 'flying condition'.
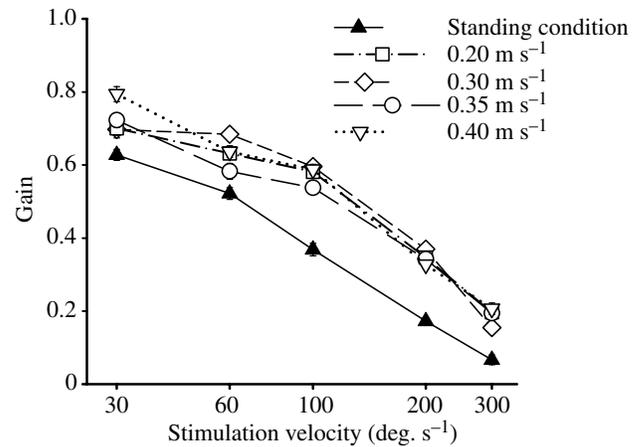

Fig. 6. Mean gain of the OCR obtained in response to velocity step stimuli for the 'walking condition' (animal on the treadmill). For the 'standing condition', the treadmill remained still. Each point is the mean value ± s.e.m. ($N=12$) of responses obtained in the clockwise and anticlockwise directions. The gain curves obtained for different treadmill velocities were not different, but the gain was systematically higher than for the 'standing condition'.

all the conditions for velocities below 30 deg. s^{-1}. As already described in many studies (Bilo and Bilo, 1978; Bilo, 1992; Gioanni and Sansonetti, 1999) the flying posture provoked by a frontal air-stream increases the gain of the OCR in the higher velocity range of visual stimuli (especially from 100 to 300 deg. s^{-1}). Also, the velocities of the fast phases are increased. Our data are consistent with previous studies for the 'resting condition' (Gioanni and Sansonetti, 1999). Türke et al. (1996) analysed the influence of different visual stimuli in pigeons standing freely and placed at the centre of an optokinetic drum with vertically striped patterns. Although the stimulating and recording methods were different to our study (head movements were recorded on video in their experiment), we can compare this to our 'standing condition'. The gain values seen in the study of Türke et al. (0.7–0.8), acquired with an optimal spatial frequency of stimuli, were similar to ours for the same velocity range of stimuli (30–100 deg. s^{-1}).

The effects of the 'flying condition' on the OCR are not seen in all other stabilizing reflexes. In particular, the optokinetic eye reflex (OKN) and the cervico-ocular reflex (COR) obtained in fixed-head conditions are not modulated by the 'flying condition'. However, when these two reflexes are combined during flying, the OKN is strongly modulated by the COR in a way that could reinforce gaze stabilisation (Maurice and Gioanni, 2004a,b). Therefore, the behavioural context can modulate isolated reflexes and affect interacting reflexes, which corresponds to more natural conditions of the animal.

Behavioural significance of data

The optokinetic stimuli delivered in our 'resting' and 'standing' conditions were somewhat artificial, as visual stimuli were not caused by the animal moving. However, this had an effect on the OCR for the 'standing condition'. In a natural

context, the improvement of the working range of the OCR in the 'standing condition' compared to the 'resting condition' cannot be interpreted as adaptation to velocity changes in the visual flow. These changes in the properties of the OCR may reflect the animal readying itself to move: even though the animal is still immobile, the system is already prepared for the perceptual adjustments that become necessary when walking begins. Also, the fact that the 'standing', 'walking' and 'flying' conditions are more natural situations as compared to the 'resting condition' may have some influence on the OCR properties.

We cannot directly compare the results from the 'walking condition' (treadmill) to those obtained in the other conditions (spherical screen) as the experimental conditions were different. Indeed, for visual stimuli of 30–100 deg. s^{-1}, the gain values corresponding to the 'standing condition' for the treadmill (Fig. 6) were consistently lower (by 0.2–0.3) than those obtained for the 'standing condition' in the spherical screen (Fig. 4A). This is most probably due to the different characteristics of the corresponding visual stimuli: the treadmill screen (ellipsoidal wall) did not allow whole field stimulation. Also, the contrast of the projected spots was lower because of the lower quality of the screen and because of the residual lighting necessary for video recordings. However, the gain values obtained in walking animals were systematically and significantly higher than in standing animals (on the immobile treadmill), revealing the effect of walking on the optokinetic response. As the gain values corresponding to the 'standing condition' in the spherical screen were optimal and similar to those obtained in the 'flying condition' for visual stimuli of 30–60 deg. s^{-1}, it seems likely that had the 'walking condition' been studied with a panoramic visual stimulation, there would have been no noticeable increase in gain for these lower velocities of visual stimulation.

The increase in OCR gain produced by walking was not modulated by the treadmill velocity, at least in the range of 0.20–0.40 m s^{-1}. We limited the velocity of the treadmill to 0.40 m s^{-1} because the combined effect of a higher speed and the optokinetic stimuli resulted in the pigeons not being able to walk normally. Davies and Green (1988) and Fujita (2002) have estimated that pigeons begin to run at about 0.75 m s^{-1}. Therefore, our velocity range corresponds approximately to normal walking.

The increasingly efficient OCR at higher velocity ranges of visual stimuli when moving from the 'standing condition' to the 'walking condition ' and then to the 'flying condition' is consistent with the increase in optic flow velocities expected in the corresponding natural conditions.

Peripheral versus internal origin of the OCR modulation

It cannot be excluded that the level of alertness could participate in the changes of the OCR properties observed in the different conditions. However, as already discussed (Gioanni and Sansonetti, 1999), several considerations strongly suggest that most of the changes are due to more specific mechanisms. Moreover, although the level of alertness is probably not different when pigeons are walking and flying, we observed that

the OCR gain was systematically higher in flying pigeons. We have also rejected the possibility that direct mechanical stimulation of feathers by the air-stream changed the OCR properties in the 'flying condition'. Indeed, tactile stimuli that did not trigger a flight posture did not produce changes in the OCR, whereas a flight posture maintained in the absence of tactile stimulation did produce changes in the OCR properties (Gioanni and Sansonetti, 1999). Data presented in this study further support this point. The 'standing' and 'walking' conditions that did not generate the mechanical stimuli seen in the 'flying condition' (stimulation of the feathers by the air-stream) did, however, modify the OCR characteristics. We have also shown that the OCR observed in the 'standing condition' was not modified by the presence of a frontal airstream. Therefore, changes observed in the OCR properties for the different behavioural conditions are most probably due to internal signals related to the behavioural state of the animal. These are probably peripheral proprioceptive muscular and articular signals produced by the different behavioural conditions. In humans, leg and neck proprioceptive stimulation modifies the optokinetic-induced quick phases (Botti et al., 2001). It is also possible that a copy of the motor command to muscles involved in each condition is sent to the optokinetic centres. Indeed, both motor commands and proprioceptive information must vary with the different behavioural conditions. In the 'resting condition', the motor command and corresponding sensorial information should be minimal, whereas in the 'standing condition', a consistent tonic command must be sent to the extensor muscles of the legs. The 'walking condition' requires rhythmic commands to be sent alternately to the flexor and extensor of the legs, as well as the tonic command. Finally, in the 'flying condition', a number of muscles related to the flight show rhythmic activities that are roughly synchronised, even when the wings are not flapping (Bilo and Bilo, 1983; Bilo et al., 1985). Therefore, each behavioural condition corresponds to a global sensory-motor pattern that could determine how much the optokinetic response should be improved. It is known that postural and dynamic reflexes (such as the OKN) are improved in elderly people by maintaining physical activity (Gauchard et al., 2003).

Structures and mechanisms underlying context-dependant changes in the OCR

We observed that, in the treadmill's velocity range in our experiment (0.20–0.40 m s^{-1}), the increase in OCR gain for the 'walking condition' is independent of the walking speed. Although we cannot exclude a larger increase in gain for higher walking speeds, our observations suggest that walking may trigger a shift from a 'low' to 'high' velocity optokinetic system. Similarly, the increase in gain of the OCR for the 'flying condition' is not related to the pressure of the airflow: once the animal has adopted a flight posture, the effects on the OCR are present and these are not increased by increasing the pressure of the airflow (H.G., unpublished results). Thus, when the animal shifts from one behavioural condition to another, the working range of the optokinetic system seems to become extended within predetermined limits.

The existence of a 'low velocity' and a 'high velocity' system has already been considered to explain the effects of the 'flying condition' (Gioanni and Sansonetti, 1999). Electrophysiological data from the analysis of the visual properties of neurones in the first stage of post-retinal relays of the optokinetic system in response to large-field gratings of varying spatial (SF) and temporal (TF) frequencies may help to explain our data. In pigeons, nBOR cells are tuned by the spatio-temporal frequency (TF/SF) rather than by their angular velocity of stimuli (Wolf-Oberhollenzer and Kirschfeld, 1990, 1994). Similar experiments using a broader range of spatial frequencies have been carried out in the nBOR, the nLM (nucleus lentiformis mesencephali) and the vestibulo-cerebellum of pigeons (Wylie and Crowder, 2000; Crowder et al., 2003a; Winship et al., 2005). These experiments led to the definition of two types of cells found in the three structures: the 'slow neurones', which are most activated by gratings of high SFs (0.35–2.0 cycles deg.$^{-1}$) and low to mid TFs (0.125–2.0 Hz), and the 'fast neurones', which are most activated by gratings of low SFs (0.03–0.25 cycles deg.$^{-1}$) and mid to high TFs (0.5–16 Hz). These two types of cells were previously identified in the pretectal nuclei (homologous to the avian nLM) of the wallaby (Ibbotson et al., 1994). It was proposed that 'fast neurones' could initiate the 'fast component' of the OKN present in the wallaby (and in most primates), and may also contribute to charging the 'velocity storage mechanism' when the retinal slip velocity is high (especially at the beginning of the response). The 'slow neurones' may become active for low retinal slip velocities, and could therefore maintain the reflex as long as the stimulation is present. Since there is no fast component of the OKN in pigeons, Crowder et al. (2003a) suggested that 'slow' and 'high' velocity neurones may be involved in charging the 'velocity storage mechanism' for low and high retinal slip velocities, respectively.

These two types of cells may correspond, for slow neurones, to a 'slow velocity system' involved during relatively slow velocity visual flow (displacement of the animal on the ground), and, for fast neurones, to a 'fast velocity system' acting during high velocity visual flow (especially during flying). The 'slow velocity system' should be involved for low retinal slip velocities, i.e. at the beginning of a slow movement like walking (closed loop situation), or when the reflex is installed with a high gain that limits the retinal slip velocity (during walking or flying at low velocity for example). In contrast, the 'high velocity system' may act at the beginning of a fast movement, like dropping from a perch to initiate the flight (closed loop situation), or when the pigeon is flying at a high velocity that provokes a consistent retinal slip velocity. This seems consistent with the spatial frequency preferences of the two cells types: for birds on the ground, the visual surroundings contain many details corresponding to a pattern of relatively high spatial frequencies. This pattern is probably well perceived by pigeons, which possess a high visual acuity for near vision, especially in the frontal field (Galifret, 1968; Bloch and Martinoya, 1982; Martinoya et al., 1983). Conversely, during flight the landscape is further away and is most likely perceived with fewer details, corresponding to a visual pattern of lower spatial frequency. In addition, the high speed movements during flying most probably provoke a blurring of high SFs.

The properties of these neurones may form a continuum, as suggested by the overlap in the mid-frequency range for the temporal frequencies of the 'slow' and 'fast' neurones. Particular subsets of neurones may be activated by stimuli containing specific spatio-temporal frequency ranges corresponding to different behavioural conditions. Moreover, some cells are probably activated when the animal is not moving, as nBOR cells also respond to stationary gratings or random-dot patterns (Gu et al., 2002).

Signals related to the behavioural condition of the animal may reinforce the visual selection of optokinetic neurones by activating or deactivating different subsets of cells. In chickens, nBOR and nLM neurones receive inhibitory projections from both local neurones that receive retinal afferents and neurones located in central structures (Zayats et al., 2002, 2003). Ariel and Kogo (2001), using a turtle brain stem preparation with the eyes attached, observed that visual stimuli provoked both excitation and inhibition of the nBOR neurones. These neurones also probably receive a tonic activation and inhibition from the retina and other cells (Kogo et al., 2002). The retinal slip signal may be due to these competing excitatory and inhibitory visual inputs. It is also probable that for a given behavioural condition, the balance between the tonic excitatory and inhibitory inputs, and a possible functional regionalisation of these inputs, may allow selection of the appropriate pool of neurones in the optokinetic system.

Anatomical data show that there are a number of connections between the optokinetic structures (in particular the nBOR and nLM), and the optokinetic system and other structures. Direct connections between the homolateral and/or heterolateral nBOR and nLM have been described (Brecha et al., 1980; Azevedo et al., 1983; Gamelin and Cohen, 1988; Wylie et al., 1997). Interactions through these connections (Gioanni et al., 1983a,b; Gioanni et al., 1984; Gu et al., 2001; Wang et al., 2001; Crowder et al., 2003b) may participate in selecting the appropriate neurones, especially concerning their directional properties. The nBOR and nLM also receive direct telencephalic projections from the visual wulst (Micelli et al., 1979; Rio et al., 1983; Wylie et al., 2005). The function of these projections is still uncertain. As the wulst also contains somatosensory neurones as well as pure visual cells (Deng and Wang, 1992, 1993), Crowder et al. (2004) and Wylie et al. (2005) suggested that the nBOR and nLM could be modulated by telencephalic somatosensory information, such as the air-stream on the pigeon's feathers during flying.

The context-dependent information may also reach the optokinetic system at a higher level than the post-retinal structures (for example, the vestibulo-cerebellum). Some major central systems may also contact the optokinetic structures through long-relayed pathways. For example, despite there apparently being no direct projections of the basal ganglia on the optokinetic centres in birds, the basal ganglia participate in the optokinetic response by maintaining the gain of the OCR at relatively high values, especially in the higher

range of stimulation velocities (Gioanni and Sansonetti, 2000). Therefore, some extra-retinal inputs reaching the nBOR and nLM probably contribute information related to the behavioural condition of the animal. In monkeys, some thalamic neurones respond in a context-dependent way during a saccadic choice task (Wyder et al., 2004).

The nBOR and nLM neurones also send axons to a number of structures that do not belong directly to the optokinetic paths, namely the cerebellar and vestibular nuclei (Wylie et al., 1997), the thalamus (Wylie et al., 1998b), the hippocampus (Wylie et al., 1999) and the nucleus rotundus (Diekamp et al., 2001). Wang et al. (2000b) have found that neurones in the nucleus rotundus are activated or inhibited by direct or indirect projections from the nBOR. These effects probably reflect a participation of optokinetic signals in the processing of visual signals (the nucleus rotundus is the telencephalic recipient of the tectofugal path) to adapt visual information to the optic flow.

Thus, although the OCR belongs to reflexive movements, it can be strongly modulated to optimise the stabilisation of the retinal image depending on the behavioural condition of the animal. As discussed by Wallman and Letelier (1993), some flexibility has been found in all classes of eye movements, which probably reflects the fact that oculomotor subsystems are driven by a complexity of inputs that subserve many different functions that depend on the behavioural context.

List of abbreviations

COR	cervico-ocular reflex
NBOR	nucleus of the basal optic root
nLM	nucleus lentiformis mesencephali
OCR	optocollic reflex
OKN	optokinetic nystagmus
OKR	optokinetic reflex
PV	peak velocity
SF	spatial frequency
SPV	slow phase velocity
TF	temporal frequency
VCR	vestibulo-collic reflex
VOR	vestibulo-ocular reflex

References

Ariel, M. and Kogo, N. (2001). Direction tuning of inhibitory inputs to the turtle accessory optic system. *J. Neurophysiol.* **86**, 2919-2930.

Azevedo, A., Cukiert, A. and Britto, L. R. G. (1983). A pretectal projection upon the accessory optic nucleus in the pigeon: an anatomical and electrophysiological study. *Neurosci. Lett.* **43**, 13-18.

Bilo, D. (1992). Optocollic reflexes and neck flexion-related activity of flight control muscles in the airflow-stimulated pigeon. In *The Head-Neck Sensory Motor System* (ed. A. Berthoz, W. M. Graf and P. P. Vidal), pp. 96-100. New York, Oxford: Oxford University Press.

Bilo, D. and Bilo, A. (1978). Wind stimuli control vestibular and optokinetic reflexes in the pigeon. *Naturwissenschaften* **65**, 161-162.

Bilo, D. and Bilo, A. (1983). Neck flexion related activity of flight control muscles in the flow-stimulated pigeon. *J. Comp. Physiol.* **153**, 111-122.

Bilo, D., Bilo, A., Müller, M., Theis, B. and Wedeking, S. (1985). Neurophysiological-cybernetic analysis of course-control in the pigeon. In *BIONA Report*, vol. 3 (ed. W. Nachtigall), pp. 445-477. Stuttgart: Gustav Fischer.

Bloch, S. and Martinoya, C. (1982). Comparing frontal and lateral viewing in the pigeon. I. Tachistoscopic visual acuity as a function of distance. *Behav. Brain Res.* **5**, 231-244.

Botti, F., Anastasopoulos, D., Kostadima, V., Bambagioni, D. and Pettorossi, V. E. (2001). Proprioceptive influence on the optokinetic nystagmus. *Acta Otolaryngol.* **121**, 205-210.

Brecha, N. C., Karten, H. J. and Hunt, S. P. (1980). Projections of the nucleus of the basal optic root in the pigeon: an autoradiographic and horseradish peroxydase study. *J. Comp. Neurol.* **189**, 615-670.

Britto, L. R. G., Natal, C. L. and Marcondes, A. M. (1981). The accessory optic system in pigeon: receptive field properties of identified neurons. *Brain Res.* **206**, 149-154.

Crowder, N. A., Dawson, M. R. and Wylie, D. R. (2003a). Temporal frequency and velocity-like tuning in the pigeon accessory optic system. *J. Neurophysiol.* **90**, 1829-1841.

Crowder, N. A., Lehmann, I. I., Parent, M. B. and Wylie, D. R. (2003b). The accessory optic system contributes to the spatio-temporal tuning of motion sensitive pretectal neurons. *J. Neurophysiol.* **90**, 1140-1151.

Crowder, N. A., Dickson, C. T. and Wylie, D. R. (2004). Telencephalic input to the pretectum of pigeons: an electrophysiological and pharmacological inactivation study. *J. Neurophysiol.* **91**, 274-285.

Davies, M. N. O. and Green, P. R. (1988). Head-bobbing during walking, running and flying: relative motion perception in the pigeon. *J. Exp. Biol.* **138**, 71-91.

Deng, C. and Wang, B. (1992). Overlap of somatic and visual response areas in the wulst of pigeon. *Brain Res.* **582**, 320-322.

Deng, C. and Wang, B. (1993). Convergence of somatic and visual afferent impulses in the wulst of pigeon. *Exp. Brain Res.* **96**, 287-290.

Dickman, J. D., Beyer, M. and Hess, B. J. (2000). Three-dimensional organization of vestibular related eye movements to rotational motion in pigeons. *Vision Res.* **40**, 2831-2844.

Diekamp, B., Hellmann, B., Troje, N. F., Wang, S. R. and Gunturkun, O. (2001). Electrophysiological and anatomical evidence for a direct projection from the nucleus of the basal optic root to the nucleus rotundus in pigeons. *Neurosci. Lett.* **305**, 103-106.

Dunlap, K. and Mowrer, O. H. (1930). Head movements and eye functions of birds. *J. Comp. Psychol.* **11**, 99-112.

Fite, K. V. (1968). Two types of optomotor response in the domestic pigeon. *J. Comp. Physiol. Psychol.* **66**, 308-314.

Friedman, M. B. (1975). Visual control of head movements during avian locomotion. *Nature* **225**, 67-69.

Frost, B. J. (1978). The optokinetic basis of head bobbing in the pigeon. *J. Exp. Biol.* **74**, 187-195.

Frost, B. J., Wylie, D. R. and Wang, Y. C. (1990). The processing of object and self-motion in the tectofugal and accessory optic pathways of birds. *Vision Res.* **30**, 1677-1688.

Fu, Y. X., Gao, H. F., Guo, M. W. and Wang, S. R. (1998a). Receptive field properties of visual neurons in the avian nucleus lentiformis mesencephali. *Exp. Brain Res.* **118**, 279-285.

Fu, Y. X., Xiao, Q., Gao, H. F. and Wang, S. R. (1998b). Stimulus features eliciting visual responses from neurons in the nucleus lentiformis mesencephali in pigeons. *Vis. Neurosci.* **15**, 1079-1087.

Fujita, M. (2002). Head bobbing and the movement of the centre of gravity in walking pigeons (*Columba livia*). *J. Zool. (Lond.)* **257**, 373-379.

Fujita, M. (2003). Head bobbing and the body movement of little egrets (*Egretta garzetta*) during walking. *J. Comp. Physiol. A* **189**, 53-58.

Fukuda, T. (1959). The unidirectionality of the labyrinthine reflex in relation to the unidirectionality of the optokinetic reflex. *Acta Otolaryngol.* **50**, 507-516.

Galifret, Y. (1968). Les diverses aires fonctionnelles de la rétine du pigeon. *Z. Zellforsch. Mikrosk. Anat.* **86**, 535-545.

Gamlin, P. D. R. and Cohen, D. H. (1988). Projections of the retinorecipient pretectal nuclei in the pigeon (Columba livia). *J. Comp. Neurol.* **269**, 18-46.

Gauchard, G. C., Gangloff, P., Jeandel, C. and Perrin, P. P. (2003). Physical activity improves gaze and posture control in the elderly. *Neurosci. Res.* **45**, 409-417.

Gioanni, H. (1988a). Stabilizing gaze reflexes in the pigeon (*Columba livia*) I. Horizontal and vertical optokinetic eye (OKN) and head (OCR) reflexes. *Exp. Brain Res.* **69**, 567-582.

Gioanni, H. (1988b). Stabilizing gaze reflexes in the pigeon (*Columba livia*) II. Vestibulo-ocular (VOR) and vestibulo-collic (closed-loop VCR) reflexes. *Exp. Brain Res.* **69**, 583-593.

Gioanni, H. and Sansonetti, A. (1999). Characteristics of slow and fast phases of the optocollic reflex (OCR) in head free pigeons (*Columba livia*): influence of flight behaviour. *Eur. J. Neurosci.* **11**, 155-166.

Gioanni, H. and Sansonetti, A. (2000). Role of basal ganglia and ectostriatum in the context-dependent properties of the optocollic reflex (OCR) in the pigeon (*Columba livia*): A lesion study. *Eur. J. Neurosci.* **12**, 1055-1070.

Gioanni, H., Rey, J., Villalobos, J., Richard, D. and Dalbera, A. (1983a). Optokinetic nystagmus in the pigeon (*Columbia livia*). II. Role of the pretectal nucleus of the accessory optic system (AOS). *Exp. Brain Res.* **50**, 237-247.

Gioanni, H., Villalobos, J., Rey, J. and Dalbera, A. (1983b). Optokinetic nystagmus in the pigeon (*Columbia livia*). III. Role of the nucleus ectomamillaris (nEM): interactions in the accessory optic system (AOS). *Exp. Brain Res.* **50**, 248-258.

Gioanni, H., Rey, J., Villalobos, J. and Dalbera, A. (1984). Single unit activity in the nucleus of the basal optic root (nBOR) during optokinetic, vestibular and visuo-vestibular stimulations in the alert Pigeon (*Columbia livia*). *Exp. Brain Res.* **57**, 49-60.

Green, P. R., Davies, M. N. O. and Thorpe, P. H. (1994). Head-bobbing and head orientation during landing flights of pigeons. *J. Comp. Physiol. A* **174**, 249-256.

Gu, Y., Wang, Y. and Wang, S. R. (2001). Directional modulation of visual responses of pretectal neurons by accessory optic neurons in pigeons. *Neuroscience* **104**, 153-159.

Gu, Y., Wang, Y. and Wang, S. R. (2002). Visual responses of neurons in the nucleus of the basal optic root to stationary stimuli in pigeons. *J. Neurosci. Res.* **67**, 698-704.

Haque, A. and Dickman, J. D. (2005). Vestibular gaze stabilization: different behavioural strategies for arboreal and terrestrial avians. *J. Neurophysiol.* **93**, 1165-1173.

Ibbotson, M. R., Mark, R. F. and Maddess, T. L. (1994). Spatiotemporal response properties of direction-selective neurons in the nucleus of the optic tract and dorsal terminal nucleus of the wallaby, *Macropus eugenii. J. Neurophysiol.* **72**, 2927-2943.

Kogo, N., Fan, T. X. and Ariel, M. (2002). Synaptic pharmacology in the turtle accessory optic system. *Exp. Brain Res.* **147**, 464-472.

Martinoya, C., Rivaud, S. and Bloch, S. (1983). Comparing frontal and lateral viewing in the pigeon. II. Velocity thresholds for movement discrimination. *Behav. Brain Res.* **8**, 375-385.

Maurice, M. and Gioanni, H. (2004a). Eye-neck coupling during optokinetic responses in head-fixed pigeons (*Columba livia*): Influence of the flying behaviour. *Neuroscience* **125**, 521-531.

Maurice, M. and Gioanni, H. (2004b). Role of the cervico-ocular reflex in the 'flying' pigeon: Interactions with the optokinetic reflex. *Vis. Neurosci.* **21**, 167-180.

McKenna, O. C. and Wallman, J. (1981). Identification of avian brain regions responsive to retinal slip using 2-deoxyglucose. *Brain Res.* **210**, 455-460.

McKenna, O. C. and Wallman, J. (1985). Accessory optic system and pretectum of birds: comparisons with those of other vertebrates. *Brain Behav. Evol.* **26**, 91-116.

Miceli, D., Gioanni, H., Repérant, J. and Peyrichoux, J. (1979). The avian visual wulst: I. An anatomical study of afferent and efferent pathways. II. An electrophysiological study of the functional properties of single neurons. In *Neural Mechanisms of Behaviour in the Pigeon* (ed. A. M. Granda and J. M. Maxwell), pp. 223-254. New York: Plenum Press.

Morgan, B. and Frost, B. J. (1981). Visual response characteristics of neurons in nucleus of the basal optic root of pigeons. *Exp. Brain Res. 42*, 181-188.

Mowrer, O. H. (1936). A comparison of the reaction mechanisms mediating optokinetic nystagmus in human beings and in pigeons. *Psychol. Monographs* **47**, 294-305.

Rio, J. P., Villalobos, J., Miceli, D. and Repérant, J. (1983). Efferent projections of the visual wulst upon the nucleus of the basal optic root in the pigeon. *Brain Res.* **271**, 145-151.

Robinson, D. (1963). A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans. Biomed. Electronics* **10**, 137-145.

Telford, L. and Frost, B. J. (1989). Functional activity in the accessory optic system during visual, vestibular and visual-vestibular stimulation in the pigeon. *Exp. Brain Res.* **77**, 391-397.

Troje, N. F. and Frost, B. J. (2000). Head-bobbing in pigeons: how stable is the hold phase? *J. Exp. Biol.* **203**, 935-940.

Türke, W., Nalbach, H. O. and Kirschfeld, K. (1996). Visually elicited head rotation in pigeons. *Vision Res.* **36**, 3329-3337.

Wallman, J. and Velez, J. (1985). Directional asymmetries of optokinetic nystagmus: developmental changes and relation to the accessory optic system and to the vestibular system. *J. Neurosci.* **5**, 317-329.

Wallman, J. and Letelier, J. C. (1993). Eye movements, head movements, and gaze stabilization in birds. In *Vision, Brain, and Behavior in Birds* (ed. H. P. Ziegler and H. J. Bischof), pp. 245-263. Cambridge: MIT Press.

Wallman, J., Velez, J., Weinstein, B. and Green, A. E. (1982). Avian vestibulo-ocular reflex: adaptative plasticity and developmental changes. *J. Neurophysiol.* **48**, 952-967.

Wang, Y., Gu, Y. and Wang, S. R. (2000a). Feature detection of visual neurons in the nucleus of the basal optic root in pigeons. *Brain Res. Bull.* **51**, 165-169.

Wang, Y., Gu, Y. and Wang, S. R. (2000b). Modulatory effects of the nucleus of the basal optic root on rotundal neurons in pigeons. *Brain Behav. Evol.* **56**, 287-292.

Wang, Y., Gu, Y. and Wang, S. R. (2001). Directional responses of basal optic neurons are modulated by the nucleus lentiformis mesencephali in pigeons. *Neurosci. Lett.* **311**, 33-36.

Winship, I. R., Hurd, P. L. and Wylie, D. R. (2005). Spatiotemporal tuning of optic flow inputs to the vestibulocerebellum in pigeons: differences between mossy and climbing fiber pathways. *J. Neurophysiol.* **93**, 1266-1277.

Winterson, B. J. and Brauth, S. E. (1985). Direction selective single units in the nucleus lentiformis mesencephali of the pigeon (*Columba livia*). *Exp. Brain Res.* **60**, 215-226.

Wohlschläger, A., Jäger, R. and Delius, J. D. (1993). Head and eye movements in unrestrained pigeons (*Columba livia*). *J. Comp. Psychol.* **107**, 313-319.

Wolf-Oberhollenzer, F. and Kirschfeld, K. (1990). Temporal frequency dependence in motion-sensitive neurons of the accessory optic system of the pigeon. *Naturwissenschaften* **77**, 296-298.

Wolf-Oberhollenzer, F. and Kirschfeld, K. (1994). Motion sensitivity in the nucleus of the basal optic root of the pigeon. *J. Neurophysiol.* **71**, 1559-1573.

Wyder, M. T., Massoglia, D. P. And Stanford, T. R. (2004). Contextual modulation of central thalamic delay-period activity: representation of visual and saccadic goals. *J. Neurophysiol.* **91**, 2628-2648.

Wylie, D. R. and Frost, B. J. (1990a). Binocular neurons in the nucleus of the basal optic root (nBOR) of the pigeon are selective for either translational or rotational visual flow. *Vis. Neurosci.* **5**, 489-495.

Wylie, D. R. and Frost, B. J. (1990b). The visual response properties of neurons in the nucleus of the basal optic root of the pigeon: a quantitative analysis. *Exp. Brain Res.* **82**, 327-336.

Wylie, D. R. and Frost, B. J. (1999). Responses of neurons in the nucleus of the basal optic root to translational and rotational flowfields. *J. Neurophysiol.* **81**, 267-276.

Wylie, D. R. and Crowder, N. A. (2000). Spatiotemporal properties of fast and slow neurons in the pretectal nucleus lentiformis mesencephali in pigeons. *J. Neurophysiol.* **84**, 2529-2540.

Wylie, D. R., Linkenhoker, B. and Lau, K. L. (1997). Projections of the nucleus of the basal optic root in pigeons (*Columba livia*). *J. Comp. Neurol.* **384**, 517-536.

Wylie, D. R., Bischof, W. F. and Frost, B. J. (1998a). Common reference frame for neuronal coding of translational and rotational optic flow. *Nature* **392**, 231-232.

Wylie, D. R., Glover, R. G. and Lau, K. L. (1998b). Projections from the accessory optic system and pretectum to the dorsolateral thalamus in the pigeon (*Columba livia*): a study using both anterograde and retrograde tracers. *J. Comp. Neurol.* **391**, 456-469.

Wylie, D. R., Glover, R. G. and Aitchinson, J. D. (1999). Optic flow input to the hippocampal formation from the accessory optic system. *J. Neurosci.* **19**, 5514-5527.

Wylie, D. R., Ogilvie, C. J., Crowder, N. A., Barkley, R. R. and winship, I. R. (2005). Telencephalic projections to the nucleus of the basal optic root and pretectal nucleus lentiformis mesencephali in pigeons. *Vis. Neurosci.* **22**, 237-247.

Zayats, N., Davies, D. C., Nemeth, A. and Tombol, T. (2002). The intrinsic neuronal organisation of the nucleus of the basal optic root in the domestic chicken; a light and electron microscopic study using anterograde tracers and postembedding GABA-immunostaining. *Eur. J. Morphol.* **40**, 101-113.

Zayats, N., Eyre, M. D., Nemeth, A. and Tombol, T. (2003). The intrinsic organization of the nucleus lentiformis mesencephali magnocellularis: a light- and electron microscopic examination. *Cells Tissues Organs* **4**, 194-207.

Zhang, T., Fu, Y. X., Hu, J. and Wang, S. R. (1999). Receptive field characteristics of neurons in the nucleus of the basal optic root in pigeons. *Neuroscience* **91**, 33-40.