Possible cues driving context-specific adaptation of optocollic reflex in pigeons (*Columba livia*)

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Gioanni H, Vidal PP. Possible cues driving context-specific adaptation of optocollic reflex in pigeons (*Columba livia*). *J Neurophysiol* 107: 704–717, 2012. First published November 2, 2011; doi:10.1152/jn.00684.2011.—Context-specific adaptation (Shelhamer M, Clendaniel R. *Neurosci Lett* 332: 200–204, 2002) explains that reflexive responses can be maintained with different “calibrations” for different situations (contexts). Which context cues are crucial and how they combine to evoke context-specific adaptation is not fully understood. Gaze stabilization in birds is a nice model with which to tackle that question. Previous data showed that when pigeons (*Columba livia*) were hung in a harness and subjected to a frontal airstream provoking a flying posture (“flying condition”), the working range of the optokinetic head response [optocollic reflex (OCR)] extended toward higher velocities compared with the “resting condition.” The present study was aimed at identifying which context cues are instrumental in recalibrating the OCR. We investigated that question by using vibrating stimuli delivered during the OCR provoked by rotating the visual surroundings at different velocities. The OCR gain increase and the boost of the fast phase velocity observed during the “flying condition” were mimicked by body vibration. On the other hand, the newly emerged relationship between the fast-phase and slow-phase velocities in the “flying condition” was mimicked by head vibration. Spinal cord lesion at the lumbosacral level decreased the effects of body vibration, whereas lesions of the lumbosacral apparatus had no effect. Our data suggest a major role of muscular proprioception in the context-specific adaptation of the stabilizing behavior, while the vestibular system could contribute to the context-specific adaptation of the orienting behavior. Participation of an effertent copy of the motor command driving the flight cannot be excluded. Muscular proprioception; vibratory stimuli; vestibular stimulation; flying posture; lumbosacral apparatus

Reflexes, once believed to be “hard-wired,” turned out to be extremely variable during the preparation, realization, and aftermath of a given motor behavior. This variability may correspond in some cases to mechanisms defined as context-specific adaptation by Shelhamer and Clendaniel (2002). To quote these authors, reflexive responses can be maintained with different “calibrations” (such as gain and phase) for different situations (contexts). Context cues are associated with each adapted state, and the context cues themselves [rather than error feedback, as is the case, for instance, for the adaptation of the vestibulococular reflex (VOR)] instantaneously invoke the proper adapted state. Different types of contextual cues could be at play: exteroceptive cues issued from the environment, proprioceptive information generated by a given behavior, and internal representation of the different phases of the motor behavior to achieve (efferent copies of motor commands). Which cues are crucial and how they combine to evoke context-specific adaptation is not fully understood. Gaze stabilization in birds is a nice model with which to tackle that question.

When flying or walking, birds stabilize their gaze (head + eye position) by combining visual (optokinetic) and vestibular reflexes that limit retinal slip and therefore avoid visual blurring (Dickman et al. 2000; Fite 1968; Fukuda 1959; Gioanni 1988a, 1988b; Mowrer 1936; Türke et al. 1996; Wallman et al. 1982). Optokinetic responses are triggered by retinal slip and are more efficient (higher gain) during low-frequency or constant-velocity displacements, whereas the vestibular reflexes are optimal during high-frequency head movements. In head-restrained pigeons submitted to visual rotatory stimuli, the ocular response is sufficient to stabilize the image of the world on the retina for stimulation up to 20°/s (Gioanni 1988a). However, in the head-free condition, pigeons essentially use their head, that is, the optococlic reflex (OCR), to stabilize their gaze (Gioanni 1988a; Haque and Dickman 2005) in response to retinal slip.

Importantly for the study of context-specific adaptation, the OCR is heavily modulated by the behavioral context. In body-restrained pigeons, the beating field is irregular and the gain of the OCR (slow-phase head velocity/stimulation velocity) decreases for stimulation velocities higher than 40°/s (Gioanni 1988a). When the animals’ body is less restrained with the use of a harness, so that their wings, legs, and tail are free (“resting condition”), the beating field is still irregular but the gain remains close to 1 for stimulation velocity up to 60°/s (Gioanni and Sansonetti 1999). If the pigeons are additionally blown by a frontal airflow that provokes a flying posture (“flying condition”), the beating field becomes very stable and a substantial response is still present for stimuli up to 200°/s (Bilo and Bilo 1978, 1983; Bilo et al. 1985; Bilo 1992; Gioanni and Sansonetti 1999). The context-specific adaptation of the OCR is not limited to the flying posture: When pigeons are standing still on the ground or are walking on a treadmill, the gain of the OCR reaches values intermediate between those obtained in the “resting” and “flying” conditions (Maurice et al. 2006). Correlatively, the velocity of the fast phases increases in correlation with the slow-phase velocity when the animals are walking or flying (Gioanni and Sansonetti 1999; Maurice et al. 2006). Similarly, McArthur and Dickman (2011) have recently shown that vestibular eye and gaze reflexes as well as tail responses of pigeons are also enhanced in the flying condition. These responses are mostly improved within the low-frequency/velocity range of stimuli. In summary, the improvements in these
METHODS

head vibration.

Several context cues could contribute to evoke context-specific adaptation of the OCR (Maurice et al. 2006). Sensory feedbacks could play a major role since they differ depending on the ongoing behavior. Proprioceptive information generated at muscular and/or articular levels are obvious candidates since they could vary to form patterns of activity characteristics of each motor behavior. In the flying (Bilo and Bilo 1983; Bilo et al. 1985) and walking conditions the skeletal muscles display various synchronized rhythmic activities, while they should be tonically active at rest to control posture. In addition, the pattern of vestibular information most probably varies according to the ongoing head movements during a given behavior. An efferent copy of the motor commands could also modulate the optokinetic responses in a predictive way depending on the type of behavior programmed by the pigeon. Finally, birds possess a specific lumbo-sacral apparatus, extensively studied by Necker and colleagues, that contributes to body stabilization (Necker 1997, 2005, 2006; Necker et al. 2000). It is constituted by bony canals and mechanoreceptors located in the accessory lobi of the ventral spinal cord (Rosenberg and Necker 2000, 2002). These cells respond very accurately to vibrations around 75–100 Hz (Necker 2002). These cells respond very accurately to vibrations around 75–100 Hz (Necker 2002) and could therefore encode high-frequency movements of the body, which in turn could modulate the OCR dynamics.

Therefore, this study was aimed at investigating which context cues could contribute to evoke context-specific adaptation of the OCR and how they combine. More specifically, we have recorded the OCR in the alert head-free pigeon while manipulating the vestibular, proprioceptive, and lumbosacral information during five types of behavioral conditions: a “resting condition,” a “flying condition,” and during body and/or head vibration.

CONTEXT-SPECIFIC ADAPTATION OF THE OCR

Forty-five adult pigeons (Columbia livia) were used. The birds’ weights ranged from 300 to 500 g. All pigeons were used in accordance with the guidelines established by the CNRS and Paris Descartes for the Care and Use of Animals in Research and those approved by the Service Vétérinaire de la Ville de Paris. The protocols used in this work were reviewed and approved by the “Direction Départementale de la Protection des Populations de Paris” with the protocol number B-75-103. Animals were housed and cared for in the certified Laboratory Animal Facilities under veterinary supervision.

Experimental Procedure

The OCR was recorded in 20 animals in three conditions: the “resting condition,” the “flying condition,” and during body vibration. For the “resting condition” the animal was hung up in a supple harness so that its head, wings, legs, and tail were free. In the “flying condition” a frontal airflow of compressed air at a constant 1.6-bar pressure was delivered through a 15-mm-diameter tube placed 15 cm in front of the animal. The airflow principally reached the front of the head, the breast, and the anterior part of the wings. In these conditions 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 their wings did not influence the characteristics of the OCR. The experimental procedure corresponding to these two conditions has been used and described in a previous study (Gioanni and Sansonetti 1999). For body vibration, pigeons were placed in the “resting condition” and submitted to a vibratory stimulation over 20–30 s once the optokinetic stimulation had begun. In a second group of 10 animals, the OCR was additionally recorded during head vibration and during body + head vibration. For the combined body and head vibration, the two different vibratory stimuli were delivered simultaneously. All these vibratory stimuli were delivered over 20–30 s once the optokinetic stimulation had begun.

Before starting the OCR recording sessions, the pigeon was placed with its head centered inside a 1-m-diameter spherical screen. During the recording sessions, gently tapping on the spherical screen maintained the animals in a high level of alertness. The order of the behavioral conditions varied from one animal to the other.

Stimulations

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 ~2–3° on the spherical screen. The optokinetic ball was rotated in the horizontal plane by a DC motor monitored by a velocity servosystem. Optokinetic stimuli consisted of constant velocity steps of 30, 60, 100, 150, 200, 250, and 300°/s. 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 (cw) and counterclockwise (ccw) directions. A new stimulation was delivered only when the postresponses were finished.

The whole body vibration was carried out, at ~130 Hz, with a homemade vibrator directly in contact with the holder so that it was mainly applied to the body of the animal. The angular amplitude of vibrations measured with a coil attached to the back of the pigeon was 0.25° in yaw and 0.1° in roll. Because the vibrator generated noise, we verified that the auditory stimulation alone did not generate any particular head movements.

The vibratory stimulation of the head was delivered, at ~110 Hz, with another homemade vibrator of circular shape, 15 mm in diameter and 4 mm thick, fixed on top of the head by adhesive tape after the feathers had been cut. The angular amplitude of head vibrations measured with a coil cemented to the skull was 0.15° in yaw, 0.6° in roll, and 0.45° in pitch. Although this stimulation may activate several receptors (see Discussion), it was first intended to activate the vestibular system.

Recording of Head Movements

Head movements were recorded by the magnetic search-coil technique (Robinson 1963) with an EPM 510 apparatus (Skalar, Delft, The Netherlands). In the “resting” and “flying” conditions as well as during the body vibration, an 8-mm-diameter coil was fixed in a rigid cylindrical piece of plastic. This piece of plastic was then firmly secured to the top of the head with double-sided adhesive tape. When animals were submitted to head vibration, in order to provide a space to fix the vibrator a coil of 18-mm diameter was glued (light paper glue) on the skin around one eye. Before each experiment, the coil was calibrated by rotating it in the horizontal plane by ± 30°, 60°, and 90°. The head position signal and the control signals of the different stimuli (velocity of the optokinetic stimulation, airflow duration, body and head vibration) were stored on a computer with the PowerLab system (AD Instruments, Paris, France). As the range of horizontal head movements can exceed the linear range of the coil system (~30°), an arccos function was applied to the head position signal to obtain a linear signal of the head position. The head position signal was then differentiated to obtain a head velocity signal.
Surgical Lesions of the Lumbosacral Apparatus

A surgical approach to the region was performed in 15 animals, allowing either a mechanical lesion of bony canals or a chemical or electrolytic lesion of the accessory lobes.

Surgery was performed under general anesthesia (40 mg/kg ketamine hydrochloride im). After a local subcutaneous injection of lidocaine (2%), feathers were removed and a midline incision of the skin was achieved to expose the synsacrum. The outer lamella of the bone was removed to uncover the bony canals between L2 and S2 segments. In five pigeons, canals were mechanically removed with a fine drill. In three pigeons, a canal was opened on one side and a small volume of 30% neomycin saline solution was injected through the canal aperture to allow chemical lesion of the accessory lobes bilaterally. In seven pigeons, the electrolytic lesions of the accessory lobes were achieved after the opening of several canals (2–6) on the two sides. A small electrode (silver ball tip) was introduced through the ventral hole of the canal and placed on the surface of the lobe, whereas a reference electrode was placed on the skin. A negative DC current of 500 μA was then injected for 15–20 s. This high level of intensity was necessary to obtain correct lesions and was probably due to a partial diffusion of the current through the cerebrospinal fluid. Lesions involved two or three accessory lobes. The destructed bone was then replaced by low point fusion paraffin and the skin was sutured.

Data Analysis

All the parameters were analyzed with PowerLab dedicated software (AD Instruments). In the “resting condition,” the slow-phase amplitude and velocity (SPV) of the OCR for a given velocity of the visual surround were measured once it reached a plateau. As shown in Fig. 1, when a behavioral condition was shifted to another condition, the transition time to reach a steady-state response was within seconds. The analysis was systematically started once the steady-state period was reached. The slow-phase amplitude and SPV were averaged over 20 s of stimulation.

Head vibrations could not be detected at the level of the head position and velocity traces during the body vibration. On the other hand, vibrations could be detected at the level of the head position and velocity traces during the body vibration.
hand, head vibrations were observable when the vibrator was applied directly to the head. In that condition, in order to analyze the head movements, the head position and the head velocity signals were smoothed with a triangular window (method of Bartlett) of 3 points and 41 points, respectively, to filter out the head vibration signal. Data obtained for cw and ccw stimulations in each behavioral condition were pooled after a statistical analysis demonstrating a lack of difference between these two sets of data. The OCR gain values (SPV/stimulation velocity) were calculated.

The fast phases of the OCR were quantified by measuring their peak velocity (PV) and amplitude. These measurements were made in five animals. About 10 fast phases were quantified for each stimulation velocity (30, 60, 100, 150, 200, 250, and 300°/s) in the cw and ccw directions. The velocity of the slow phases preceding and following each fast phase was also measured in order to investigate the relationship between fast- and slow-phase velocity.

The beating field of the head was quantified in the following way: During a given stimulation, the deviation of the head relative to the straight-ahead position was calculated at the midexcursion of each recorded fast phase and averaged. This averaged value was taken as an index of the mean orientation of the beating field, and the standard deviation (SD) was used as an index of its variability. Statistical analyses of data relative to the slow phase of the OCR or to the beating field consisted of two-way analysis of variance (ANOVA) with the amplitude, the frequency, the gain, the head position, or the SD of the beating field as the dependent variable and the behavioral condition and the stimulation velocity as the factors of variation. Once the normality test (Shapiro-Wilk) and the equal variation test were passed, a global analysis was performed to determine the sources of variation. A comparison between the behavioral conditions was then done for each stimulation velocity (Holm-Sidak method). The parameters \( t \) and \( P \) indicated below corresponded to the comparison between the different behavioral conditions for the stimulation velocities showing a significant difference. All comparisons were achieved with paired tests except when comparing the effects of head vibration or body + head vibration with the other conditions, where unpaired tests were used.

The amplitude and the PV of fast phases along with the neighboring SPV were plotted for each condition. The fit equation corresponding to a linear correlation of the three parameters was calculated, and the corresponding plane was drawn on the plots. Parameters \( R \) and \( p \) of the correlation and the parameter \( F \) (analysis of variance) were calculated and indicated together with the plots on Figs. 3 and 8.

### Histological Control

Animals with lesions (canals, accessory lobes, or spinal cord) were anesthetized with an overdose of ketamine (80 mg/kg ketamine hydrochloride i.m) and then perfused intracardially with saline, which was followed by fixative (4% paraformaldehyde). The spinal cord was removed and postfixed at 4° centigrade overnight (4% paraformaldehyde in 0.1 M phosphate buffer solution, pH 7.4). The tissue was then stored at 4° centigrade for a day in a 0.2 M phosphate buffer solution, pH 7.4. After inclusion in tissue freezing medium, cryostat sections of 50 μm were made and mounted on gelatin-coated glass slides. Sections were stained according to the cresyl violet method. The lumbarosacral column was also removed to control the section or opening of canals.

### RESULTS

The optocillic responses (OCR) recorded during the five different behavioral conditions (“resting condition,” “flying condition,” body vibration, head vibration, and body + head vibration) were analyzed by measuring the amplitude and the frequency of the slow phases and by calculating the gain of the OCR for each visual stimulation velocity tested (30–300°/s) in the cw and ccw directions (\( n = 40 \)). The “resting condition” was regarded as the reference condition in all measurements. The influence of the different behavioral conditions on the head beating field was evaluated by calculating the mean orientation of the head and its variability during each type of stimulation (see METHODS). Raw data of the OCR during different types of stimulation are illustrated in Fig. 1.

#### Effects of Body Vibration Compared with “Resting” and “Flying” Conditions

**Amplitude and frequency of slow phases and gain analysis of the OCR.** The amplitude of the slow phases (Fig. 2A) was larger in the “flying condition” than in the “resting condition” (\( t = 3.48, P < 0.001, n = 40 \)) only for high-velocity stimuli (200–300°/s), whereas their frequency (Figs. 1C and 2B) was augmented over the whole velocity range (\( t = 23, P < 0.001, n = 40 \)). As a result, the OCR gain was increased by the “flying condition” for all visual velocities tested (Fig. 2C). The body vibration produced a large increase in amplitude (\( t = 9.80, P < 0.001, n = 40 \); Figs. 1A and 2A) and a smaller increase in frequency (\( t = 14.30, P < 0.001, n = 40 \); Figs. 1A and 2B) of the slow phases over the whole velocity range of the optokinetic stimuli, that difference being larger in the higher-velocity range (150–300°/s). As a consequence, the OCR gain increased during body vibration (Fig. 2C) for stimulation velocities ranging from 100 to 300°/s (\( t = 12.88, P < 0.0001, n = 40 \)), to reach values statistically similar to that obtained during the “flying condition.”

**Fast phase analysis.** We measured the amplitude and PV of the fast phases to build the main sequence. The SPV occurring just prior and after each fast phase was also measured, since our previous studies (Gioanni and Sansonetti 1999; Maurice et al. 2006) revealed a correlation between the PV of fast phases and the SPV in the “flying condition.” The relationship between the amplitude of fast phases, their PV, and the accompanying SPV is illustrated as tridimensional plots using a multiple linear regression analysis in Fig. 3A (\( n = 700 \)). The equation defining each plane of correlation as well as the results given by the statistical analyses are indicated for each condition. The equations are under the form \( PV = a \cdot \text{amplitude} + b \cdot \text{SPV} + c \), where coefficient \( a \) reflects the “main sequence” and coefficient \( b \) the relationship between the velocity of fast phases (PV) and the SPV of the accompanying slow phases (Fig. 3). Constant \( c \) corresponds to a theoretical PV value of fast phases when both their amplitude and the SPV are null, i.e., it can be envisioned as a boost to the fast phase generator in some behavioral conditions.

To facilitate the comparison between data obtained in the different behavioral conditions, the planes of correlation are plotted two by two without data points in Fig. 3, B and C. As predicted by the classical “main sequence,” the PV of fast phases increased linearly with their amplitude in all conditions (Fig. 3). The slope (coefficient \( a \)) varied from 6.61 deg.s \(^{-1}\)/deg during body vibration to 10.58 deg.s \(^{-1}\)/deg for the “flying condition.” These values correspond to mean durations of fast phases of 151.3 ms and 94.5 ms, respectively. Compared with the “resting condition,” the mean duration of the fast phases was increased by the body vibration and decreased in the “flying condition” (Table 1).
In the “flying condition” (Fig. 3B) the value of c was augmented (c = 120°/s) compared with the “resting condition” (c = 67.4°/s). This increase was even higher than that obtained during the “flying condition” (c = 120°/s). However, the PV of fast phases was practically not influenced by the SPV (b = 0.6) during body vibration. The fact that the main sequence had a lower slope during body vibration than at rest (as mentioned above) explains that the two planes of correlation are not parallel (Fig. 3C). Consequently, the difference in PV in these two conditions decreased when the amplitude of fast phases increased.

These data suggest that proprioceptive signals contributed to the boost of the fast-phase velocity (c) observed during the “flying condition” and the body vibration. However, the increase in PV and its correlation with the SPV, observed in the “flying condition” but not during body vibration, cannot be solely attributed to these muscular proprioceptive signals.

Beating field analysis. The mean eccentricity of the head was calculated (n = 40) for each behavioral condition. A mean negative value indicated an average head deviation toward the apparent origin of the optic flow (the direction of the fast phase): The pigeon is looking where it would go with a free body. This will be called the “orienting direction.” A mean positive value indicated an average head deviation in the direction of the optic flow (the direction of the slow phase): The pigeon is looking where it would come from with a free body. This will be called the “stabilizing direction.”

As a rule, the head deviation (Fig. 4A) shifted progressively from the “resting condition” toward more positive values (i.e., toward the “orienting direction”) during the body vibration (t = 5.15, P < 0.001, n = 40) and then in the “flying condition” (t = 7.90, P < 0.001, n = 40). There was also a significant difference between data obtained for the body vibration and the “flying condition” (t = 2.81, P < 0.05, n = 40). The orientation of the beating field was also influenced by the velocity of the optokinetic stimulation. The mean orientation of the head was toward the “orienting direction” for the low velocities of stimulation (30–60°/s) and was progressively displaced toward the “stabilizing direction” when the stimulation velocity was increased (150–300°/s). As a result of this double influence (velocity of the visual flow and experimental conditions), the velocity of the optokinetic stimuli for which the orientation of the head moved from an “orienting strategy” to a “stabilizing strategy” varied from 40 to 100°/s when the experimental condition changed from the “flying condition” to the “resting condition.”

The regularity of the beating field during optokinetic stimulations was evaluated by the standard deviation (SD) of the mean head position (see METHODS). As shown in Fig. 1, A and C, and Fig. 4B, the body vibration and the “flying condition” provoked a significant reduction of the variability of the beating field (except for the 30°/s stimulus). The lowest values of SD were obtained in the “flying condition” for optokinetic stimuli delivered in the 100–300°/s range.

Effects of lesion of the lumbosacral spinal cord. The injection of neomycin (30%) in the peripheral space of the lumbosacral spinal cord was initially intended to make selective lesions of the accessory lobes. However, the histological controls showed that the accessory lobes were either partially...
touched or spared while, in most cases, the dorsal part of the lumbosacral spinal cord was destroyed on both sides (Fig. 5A). The ventral part of the spinal cord and in particular the motoneurons were only slightly or not affected, and consequently the pigeons were not paralyzed. Therefore, this lesion turned out to be interesting to assess the role of the lumbosacral proprioceptive afferences in the context-specific adaptation of the OCR.

The OCR gain was calculated in the “resting condition,” during the body vibration, and in the “flying condition,” before and 15 days after neomycin injections in five pigeons. The OCR gain was clearly decreased by the lesions for responses obtained with stimuli at 100–300°/s, with a maximal effect during the body vibration (Fig. 6, A and B; \( t = 5.51, P < 0.001, n = 10 \)), a lower effect in the “resting condition” (Fig. 6, A and B; \( t = 2.97, P < 0.05, n = 10 \)), and a minimal effect, only significant for stimuli of 250–300°/s, in the “flying condition” (Fig. 6, C and D; \( t = 2.30, P < 0.05, n = 10 \)). Since a substantial “basal decrease” in the OCR gain was provoked by the lesions in the “resting condition,” we compared the effects of the body vibration and the effects of the “flying condition” in the intact and lesioned pigeons. During body vibration, the increase of the OCR gain was suppressed at 250 and 300°/s and less pronounced at 100–200°/s (\( t = 4.16, P < 0.05, n = 10 \)) in lesioned pigeons (Fig. 6B) compared with intact pigeons (Fig. 6A).

These data strongly suggest that the lumbosacral afferences contribute to the OCR augmentation induced by body vibration. In contrast, in the “flying condition,” the OCR gain modulation was similar in intact and lesioned pigeons (Fig. 6, C and D). Therefore, the lumbosacral afferences are probably not mandatory for the OCR augmentation induced by the “flying condition.”

Possible role for the lumbosacral apparatus. As previously shown (Necker 2006), the unilateral or bilateral mechanical

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**Table 1. Values of coefficient a (main sequence) and corresponding fast phase duration obtained in the different conditions**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Coefficient a</th>
<th>Fast phase duration, ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body Vibration</td>
<td>6.61</td>
<td>151.3</td>
</tr>
<tr>
<td>Body + Head Vibration</td>
<td>6.92</td>
<td>144.5</td>
</tr>
<tr>
<td>Resting Condition</td>
<td>8.66</td>
<td>115.5</td>
</tr>
<tr>
<td>Head Vibration</td>
<td>8.76</td>
<td>114.1</td>
</tr>
<tr>
<td>Flying Condition</td>
<td>10.58</td>
<td>94.5</td>
</tr>
</tbody>
</table>

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Fig. 3. Three-dimensional representation of the peak velocity (PV)-amplitude relation as a function of the slow-phase velocity (SPV) for the fast phases of the OCR. A: data points and corresponding plane of correlation for the “flying condition.” B: planes of correlation obtained for the “resting” and “flying” conditions. C: planes of correlation obtained for the “resting condition” and during body vibration. The equations of multiple linear regressions and the corresponding statistics are indicated for each condition (\( n = 700 \) fast phases in each condition).
destruction of the lumbosacral canals of five pigeons provoked a postural instability in the light and an impossibility to stand in the dark. However, the OCR gain was not modified by these mechanical lesions, whatever the behavioral condition. Mechanical lesions interrupted the flow of cerebrospinal fluid in the canals, but a direct activation of the mechanoreceptors by vibrations could not be excluded. Thus the OCR gain was then measured before and after electrolytic lesions of the accessory lobes. Histological control confirmed the lesions (Fig. 5B). Data obtained before and 8 days after bilateral lesions performed in three pigeons are shown in Fig. 7. The OCR gain was similar before and after the lesions in the three conditions.

Therefore, the lumbosacral apparatus is most probably not involved in the context-specific adaptation of the OCR.

Effects of Head Vibration and of Body + Head Vibration

Gain analysis of the OCR. The head vibration \( (n = 20) \) did not increase significantly the amplitude of the slow phases compared with rest (Fig. 2A) but increased their frequency over the whole velocity range \( (t = 9.99, P < 0.001, n = 20 \) for head vibration, \( n = 40 \) for resting condition; Figs. 1B and 2B). Consequently, the OCR gain (Fig. 2C) was only slightly increased during optokinetic stimuli delivered at 250–300°/s \( (t = 4.14, P < 0.001, n = 20 \) for head vibration, \( n = 40 \) for resting condition). The difference in gain increase provoked by the head vibration and by the body vibration was significant \( (t = 7.36, P < 0.001, n = 20 \) for head vibration, \( n = 40 \) for body vibration). Thus, while the body vibration induced a substantial increase in gain of the OCR for the 150–300°/s velocity range, the head vibration had little effect.

The body + head vibration \( (n = 20) \) was used to test whether data obtained in the “flying condition” could be experimentally replicated by the simultaneous activation of the muscular proprioceptors and the vestibular receptors. The amplitude (Fig. 2A) and the frequency (Fig. 2B) of the slow phase showed intermediate values between those obtained in the “resting” and “flying” conditions. Consequently, the resulting values of the OCR gain obtained with combined body and head vibration turned out to be not statistically different from those obtained during body vibration alone or in the “flying condition” (Fig. 2C). That is, head vibration does not bring much compared with body vibration alone.

Fast phase analysis. Compared with the “resting condition,” the mean duration of the fast phases \( (n = 700) \) was equal during head vibration and increased by body + head vibration (Table 1).

During the head vibration (Fig. 8A), the value of \( c \) was not increased (contrary to that observed during body vibration) but rather decreased \( (c = -41.9°/s) \) compared with the “resting condition” \( (c = 67.4°/s) \). On the other hand, the PV values increased with the SPV with the same slope \( (b = 2.3) \) as in the “flying condition.” Consequently, the planes of correlation corresponding to data obtained with the head vibration and during the “flying condition” are almost parallel (Fig. 8B).

Therefore, data obtained in the “flying condition” could be explained by a combination of the effects produced by the body vibration (global increase in fast-phase velocity) and by the head vibration (correlation between the SPV and fast-phase velocity). To test further this hypothesis we compared the planes of correlation obtained in the “flying condition” with a “simulated plane” calculated by averaging the coefficients \( a \) and \( c \) and by summing the coefficients \( b \) obtained for the head vibration and for the body vibration (Fig. 8D). The simulated plane was reminiscent of the plane of correlation corresponding to the “flying condition,” which suggests that data obtained in the “flying condition” could be explained by a simple combination of the effects produced by the body and head vibrations.

The characteristics of the fast phases triggered during the body + head vibration \( (b = 1.6, c = 107.7°/s) \) appeared to be closer to those observed with the body vibration than to those observed in the “flying condition” (Fig. 8C). The plane of correlation simulated by averaging each of the three coefficients \( (a, b, c) \) obtained for the body vibration and for the head vibration was very close to the plane of correlation corresponding to the body + head vibration (Fig. 8E).

![Fig. 4. Influence of the conditions and of visual stimulation velocity on the mean orientation of the head (A) and the regularity of the beating field (B). Each point represents the mean ± SE \( (n = 40 \) for the “resting” and “flying” conditions and for body vibration, \( n = 20 \) for head and body + head vibration). A: the zero head position (dashed line) represents the straight forward orientation of the head. Head position values are positive when the head is deviated in the slow phase direction and negative when the head is deviated in the fast phase direction. The change from an “orienting” to a “stabilizing” strategy depends both on the condition and on the visual stimulation velocity. B: the regularity of the beating field is evaluated by its standard deviation (SD). The beating field is more irregular in the “resting condition” than in all other conditions.

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Beating field analysis. Compared with the “resting condition,” the head was deviated toward the “stabilizing direction” (Fig. 4A) during head vibration ($t = 2.38, P < 0.05, n = 20$ for head vibration, $n = 40$ for resting condition) and during body + head vibration ($t = 4.20, P < 0.001, n = 20$ for body + head vibration, $n = 40$ for resting condition). There was no statistical difference between data obtained with the body vibration, the head vibration, and the body + head vibration. The variability of the beating field (SD) was strongly reduced compared with the “resting condition” (Fig. 4B). The SD values obtained during head vibration and body + head vibration were comparable to those obtained during body vibration and in the “flying condition.”

DISCUSSION

We have already shown that the gain of the OCR and the velocity of the fast phases increased progressively when the behavioral context changed from the “resting condition” to standing and then to walking, the maximal response being obtained in the “flying condition” (Maurice et al. 2006). Which context cues/and or efferent copies trigger these changes and how do they combine to evoke CSA?

What Receptors Are Triggered During the Different Conditions?

Body vibratory stimuli. Preliminary experiments showed that vibratory stimuli directly applied in different parts of the body were effective to enhance the optokinetic responses. However, the vibrator was subsequently fixated on the holder that maintained the harness sustaining the pigeon because this procedure allowed more reproducible stimulations.

Muscle spindles were most probably recruited with that protocol. First, vibrations are the stimulus of choice to activate muscle spindles (Matthews 1972) contrary to Golgi tendon

Fig. 5. Histological control of a pharmacological lesion of the lumbosacral spinal cord (A) and an electrolytic lesion of the accessory lobe on one side (B); cresyl violet staining. A: the effect of a local injection of neomycin (30%) is shown on one side of the spinal cord at the $S_1$ level. The dorsal and ventral horns are delineated with a dashed line. The somas are completely destructed in the dorsal horn. In this example the accessory lobe were also destructed. B: the segmental level corresponds to $S_2$. The hole in the tissue of the dorsal spinal cord indicates the right side. The accessory lobe is intact on the right side and is completely destructed on the left side (indicated by arrow). AL, accessory lobe; TL, transverse ligament; LL, lateral ligament; DH, dorsal horn; VH, ventral horn; GB, glycogen body.

Fig. 6. Mean gain of the OCR calculated in 5 animals, before (prelesion) and 15 days after (postlesion) the bilateral lesion of the dorsal part of the lumbosacral spinal cord. Responses produced in the “resting condition” and during body vibration are compared when obtained before (A) and after (B) the lesion ($n = 10$). Similarly, responses produced in the “resting” and “flying” conditions are compared when obtained before (C) and after (D) the lesion ($n = 10$). The increase in gain produced by the body vibration was reduced by the lesion, whereas the lesion did not modify the gain increase provoked by the “flying condition.”
The context-specific adaptation of the OCR was demonstrated through experiments in pigeons. A 500-Hz head stimulation can be used to selectively activate otolith irregular neurons (Curthoys et al. 2006). They are highly phasic and especially sensitive to vibrational stimuli, their best frequencies (low threshold) ranging from 300 Hz to ~1,000 Hz. They are located in different parts of the body but have been especially studied in the beak, the legs, and the wings (Dorward 1970a; Gottschaldt 1974; Gottschaldt and Lausmann 1974; duck’s leg: Dorward 1970b; pigeon’s wing: Necker 1990). The body vibration we used probably excited Herbst corpuscles located in the wings, the legs, and the body.

Thus both muscle proprioceptors and Herbst corpuscles were most probably excited by the body vibration and could participate in the context-specific adaptation of the OCR. However, several observations suggest that the effects observed during body vibration were mainly produced by activation of muscular proprioceptors. First, we observed in a previous work that the gain of the OCR was enhanced in standing pigeons, a situation without cutaneous stimulation, compared with the “resting condition.” In contrast, when standing pigeons were frontally blown (even strongly), a situation that most probably produced a strong peripheral stimulation, the OCR gain was not modified (Maurice et al. 2006).

Head vibratory stimuli. A 500-Hz head stimulation can be used to selectively activate otolith irregular neurons (Curthoys et al. 2010; Curthoys and Vulovic 2011). It has been shown in guinea pigs and in humans that such a 500-Hz bone-conducted vibration delivered at the midline of the forehead causes simultaneous and approximately equal-amplitude linear acceleration stimulation at both mastoids, and thus at the two labyrinths (Chiarovano et al. 2011; Curthoys et al. 2006). Therefore, it is likely that the 110-Hz stimuli we used activated the two labyrinths: In pigeons, the distance between the skull and the inner ear is shorter than in humans and roughly similar to that in the guinea pig.

Which vestibular sensors were activated in that process remains to be determined. It is generally admitted that the skull vibratory test (SVT) given at 100 Hz and used as a clinical test preferentially activates the semicircular canals, mostly the horizontal canals, at least in primates (Dumas et al. 2008; Young et al. 1977).

Finally, we cannot exclude that neck muscle proprioceptors and Herbst corpuscles were activated together with the vestibular sensors, and therefore participated in the changes observed in the properties of the OCR. It remains that vibratory stimuli did not produce the same changes in the OCR when applied to the head or to the body. Therefore, during head vibration the vestibular system was probably a major contributor to the OCR adaptation.

Head vibration caused modifications of the fast phase, but the OCR gain remained unchanged. It cannot be excluded that the retina vibration, which would decrease the efficacy of the OCR, canceled a putative augmentation of the gain caused by the vibratory stimuli. This would not be the case for the fast phases during which the visual information is suppressed (Ross et al. 2001).

Flying condition. All the receptors mentioned so far (muscular and vestibular proprioceptors, cutaneous mechanoreceptors) were most probably activated in the “flying condition” as during a normal flight.

A rhythmic and roughly synchronized activity of several muscles was present during the flying posture in pigeons, even when the wings were not flapping (Bilo and Bilo 1983; Bilo et al. 1985). This muscular activity should activate the proprioceptors, and the present study is consistent with that hypothesis: Our data showed that the increase in the OCR gain observed in the “flying condition” was mimicked by body vibration.

Hörster et al. (1983) proposed that the Herbst corpuscles located in the wings perceive oscillations on the feathers that could be generated by air currents or disturbances. Hence, these mechanoreceptors are good candidates to trigger the flight posture when the birds are subjected to a frontal airflow. The airflow could also produce vibrations at head level and activate the vestibular system. Our data showed that the correlation between the fast-phase velocity and the SPV in the “flying condition” was mimicked by the head vibration but not by the body vibration. Thus, although several cues may combine to shift the OCR gain from values...
Fig. 8. Planes corresponding to the multiple linear regression analysis of the fast phases are plotted for the “resting condition” and during head vibration (A), for the “flying condition” and during head vibration (B), and during body vibration and body+head vibration (C). The equations of multiple linear regressions and the corresponding statistics are indicated for each condition (n = 700 fast phases). D: comparison of the plane of correlation obtained in the “flying condition” with a simulated plane calculated by averaging the a and c coefficients and by summing the b coefficients of the equations obtained for the head vibration and the body vibration. The equation of the simulated plane is indicated. E: comparison of the plane of correlation obtained during body+head vibration with a simulated plane calculated by averaging each of the coefficients (a, b, c) obtained for the head vibration and for the body vibration. The equation of the simulated plane is indicated. The “experimental plane” is close to the “simulated plane” in D and E.
appropriate for the flight, our data suggest that muscular and vestibular proprioception are mainly involved.

In addition to sensory signals, an efferent copy of the motor command driving the flight could also play a major or a complementary role in the OCR augmentation observed in the “flying condition,” and a fortiori during a normal flight. Body vibrations alone are sufficient to increase the OCR gain to values obtained in the “flying condition,” which tend to confer a role of proprioception during the flight. However, it cannot be excluded that the efferent copy could totally or partially replace the effect of the muscular proprioceptive signals during the flight.

Context-Specific Adaptation of Fast Phases

The “main sequence” of fast eye movements including saccades and fast phases of optokinetic nystagmus (OKN) and optokinetic afternystagmus (OKAN) is modulated by the environmental conditions and by the behavioral task (see Jansen et al. 2009; Kaminiarz et al. 2009a, 2009b). In the present study changes in the “main sequence” occurred principally during body vibration and in the “flying condition.” In the “flying condition,” the mean duration of the fast phases was decreased compared with all other conditions, which shorten their relative duration for each nystagmic beat. For example, during a visual stimulation at 10°/s the mean duration of a fast phase represents 15% of the mean duration of the slow phases in the “resting condition” and 18% in the “flying condition.” However, if the mean duration of fast phases had the same value in the “flying condition” as in the “resting condition,” it would represent 22% of each nystagmic beat. This could be of interest, since during the fast phases (or during saccades) the gaze is not stabilized, the visual information is suppressed, and the visual perception is subjected to spatiotemporal distortions (see Burr and Morrone 2010; Ross et al. 2001). This mechanism could be especially adapted to the flight, since the frequency of nystagmic beats, and therefore the time occupied by fast phases, was maximal in the “flying condition.”

Body vibration increased the velocity of all the head fast phases by the same amount, whereas the increase in velocity produced by the head vibration was correlated to the SPV. Interestingly, these two effects combined in the “flying condition,” and our simulation shows that a simple arithmetic operation can account for this combination. However, when the head and the body vibrations were delivered simultaneously, the resulting fast-phase velocity was lower than in the “flying condition.” Our simulation shows that during body + head vibration the effects of the two stimuli are weighted rather than added. This difference could be explained by the fact that vibrations caused by the airflow and by the rhythmic activity of many muscles in the “flying condition” (Bilo and Bilo 1983; Bilo et al. 1985) are most probably cyclic at the difference of our vibratory stimuli. Also, as previously discussed, an efferent copy of the motor command present during the flight could participate in the changes observed in the fast-phase properties.

Results Obtained by Lesions Localized at the Lumbosacral Level

Bilateral lesions of the dorsal spinal cord at the lumbosacral level suggest that the lumbosacral proprioceptive afferences contribute 1) to the maintenance of the OCR gain at rest and 2) to the increase in OCR gain induced by body vibration. In contrast, these afferences did not appear to be mandatory during the “flying condition.” Hence, it seems that while the lumbosacral proprioceptive afferences are important to control the OCR during life on the ground, during flying other peripheral afferences spared by the lesion, such as the afferences from the wings and the upper part of the body, are likely to be more important.
The lumbosacral apparatus is very sensitive to vibratory stimuli (Necker 2002), and its sensory cells project mono- and polysynaptically to the neurons at the origin of the spinocerebellar tracts (Necker 1997). Therefore, it was a likely candidate to participate in the context-specific adaptation of the OCR during body vibration and in the “flying condition.” Our data showed that it was unlikely.

Context-Specific Adaptation of the Head Beating Field

The amplitude of the nystagmic beats remained limited and exhibited very low variability during the “flying condition.” Variability decreased when the velocity of the visual flow (and therefore the velocity of flight) increased. These two characteristics make sense from a functional point of view. Large and irregular head movements could pose a problem in terms of aerodynamics and maintenance of the direction of flight, whereas the numerous small slow phases of the “flying condition” would confine the portion of space monitored by the pigeon to a restricted zone in front of the animal. Conversely, the variability of the beating field was much higher in the “resting condition” than in all the other conditions. The “resting condition” is not a natural situation. However, the variability of the beating field in this condition was close to that observed in pigeons standing on the ground (see Maurice et al. 2006, Fig. 3). Thus the high variability of the beating field in the “resting condition” could correspond to an exploratory behavior adapted to the search of food, whereas such a strategy would probably be counterproductive during flight.

In the “flying condition” and during body vibration the OCR gain was similar. However, in the “flying condition,” the slow phases had smaller amplitude and higher frequency than during body vibration. Thus it could be that the burst driving neurons of the head, which trigger the fast phases (and remain to be identified), behave differently in the two behavioral conditions and therefore participate in the context-specific adaptation of the OCR.

The orientation of the head in space was also modified when the velocity of the visual flow increased or when the behavioral condition was changed from “resting” to “flying”: The pigeon shifted from an “orienting strategy” to a “stabilizing strategy.” If we assume that the “resting condition” and low velocity range of the visual flow correspond to life on the ground, the “orienting strategy” is indeed adapted to the search for food. On the contrary, during flight (high velocity range of visual flow) stabilization of the head could be the main if the only necessity, as suggested by the enhancement of visual and vestibular gaze reflexes (Gioanni and Sansonetti 1999; McArthur and Dickman 2011) and by biomechanical studies of bird flight (see Warrick et al. 2002). In the intermediate situation encountered for velocities of the visual flow around 40–60°/s, the head remained roughly oriented straight forward. This situation could correspond to a flight performed at low velocity, for example, when the animal is landing with a curved trajectory.

Concluding Remarks

This study was aimed at investigating which context cues could contribute to evoke context-specific adaptation of the OCR and how they combine. Our data suggest a major role of muscular proprioception in the context-specific adaptation of the stabilizing behavior, while the vestibular system could contribute to the context-specific adaptation of the orienting behavior.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: H.G. and P.-P.V. conception and design of research; H.G. and P.-P.V. performed experiments; H.G. and P.-P.V. analyzed data; H.G. and P.-P.V. interpreted results of experiments; H.G. and P.-P.V. prepared figures; H.G. and P.-P.V. drafted manuscript; H.G. and P.-P.V. edited and revised manuscript; H.G. and P.-P.V. approved final version of manuscript.

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