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How barn owls (*Tyto alba*) visually follow moving voles (*Microtus socialis*) before attacking them

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ABSTRACT

The present study focused on the movements that owls perform before they swoop down on their prey. The working hypothesis was that owl head movements reflect the capacity to efficiently follow visually and auditory a moving prey. To test this hypothesis, five tame barn owls (*Tyto alba*) were each exposed 10 times to a live vole in a laboratory setting that enabled us to simultaneously record the behavior of both owl and vole. Bi-dimensional analysis of the horizontal and vertical projections of movements revealed that owl head movements increased in amplitude parallel to the vole's direction of movement (sideways or away from/toward the owl). However, the owls also performed relatively large repetitive horizontal head movements when the voles were progressing in any direction, suggesting that these movements were critical for the owl to accurately locate the prey, independent of prey behavior. From the pattern of head movements we conclude that owls orient toward the prospective clash point, and then return to the target itself (the vole) — a pattern that fits an interception rather than a tracking mode of following a moving target. The large horizontal component of head movement in following live prey may indicate that barn owls either have a horizontally narrow fovea or that these movements serve in forming a motion parallax along with preserving image acuity on a horizontally wide fovea.

1. Introduction

Once a predator locates a potential prey, it must follow it and time its attack to prevent the prey's escape. Vision is an important sense in following the prey, and may involve movements of the eyes, the head, or the entire trunk [1]. Birds, however, are able to follow the prey visually (and perhaps also auditorily) mainly by head movements, since their eyes are extremely restricted in movement [1]. Accordingly, owls perch motionless and move their head in order to visually and auditorily locate and follow their prey. Detailed analysis of barn owl (*Tyto alba*) behavior before swooping down on a dead prey in a laboratory setting revealed that their repertoire of movements can be categorized into three types of head movements: (i) fixations; (ii) translations (straight or curved); and (iii) rotations (yaw, pitch or roll) [2]. Nevertheless, owls in the wild frequently need to visually follow a live moving prey, for which the above types of movements, used for locating a stationary target, may not suffice. The present study therefore scrutinized in a laboratory setting how barn owls follow a live moving prey. Specifically, we exposed barn owls to live voles (*Microtus socialis*) and recorded the movements of the owls' head in relation to the voles' movements, under the working hypothesis that owl head movements reflect their capacity to efficiently follow a moving prey.

Barn owls are known to display head movements in order to assess the distance to a target [3]. Similarly, various predators perform head movements before launching their attack (e.g. [4]). These movements serve in estimating the distance and orientation of the prey by means of a mechanism termed 'motion parallax' [5,6]. In this mechanism, the predator's head movement generates an artificial change in the location of a stationary prey on the predator's retina, thus providing a better three-dimensional image, which is essential to accurately locate the prey. It was further suggested that following the prey is based on two complementary components: binocular vision, which provides a distance estimate, and horizontal movements, which provide the angular relationship between objects [7]. Studies in terns [4] and falcons [8,9] revealed that each of these species displays a unique pattern of head movements that are aimed at keeping the image of the prey in the fovea, which is a region of the retina with high neuron density. Several bird species have two foveas in each eye, and display head movements that are aimed at moving the image from one fovea to the next, or even from one eye to the other [10]. Robotic simulation of head movements revealed that horizontal movements provide a good distance estimate when the observer is stationary, whereas forward/backward head movements are more effective for estimating distance by a moving observer [11]. Here we studied which movements were executed by the barn owls before they swooped down on a live prey, and how these movements were affected by the behavior

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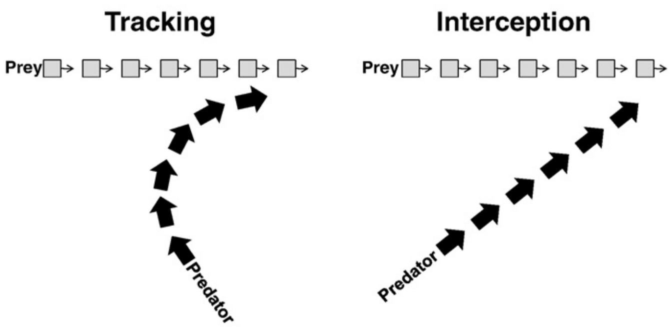


Fig. 1. Following a prey by continuously tracking its location (left) or by intercepting it at a future clash point along its path of progression (right). Based on the model of [29].

of the prey. It should be noted that the present analysis was aimed at the movements of the head, regardless of the sensory cues that stimulated these head movements. Computerized tracking of head movements was based on tracking owl eye movement, since owl eyes are fixated in their skull, and therefore, eye movement equals head movement. Moreover, the sharp contrast between dark eyes on the background of white face feathers in barn owls made it easy to track head movement via eye movement. Altogether, tracking eye movements reflects head movements but in no way implies that owl head movements were simulated by only visual cues.

Launching an attack on a moving prey requires the processing of visual (sometimes also auditory) information in order to plan the spatial clash point. There are two modes by which predators follow a moving prey: (i) interception, and (ii) tracking (Fig. 1). In interception, the predator fixate its glance on the target and moves directly toward the future clash point [12], much as dogs do when they intercept a Frisbee [13]. In tracking, the predator continuously follows (or chases) the current location of the prey (not its future location as in interception), resulting in a curved path, similar to carnivore beetles [14]. The present study on how barn owls follow live moving prey was thus intended to elucidate whether owls track or intercept their prey.

When barn owls were challenged to catch a simulated moving prey (dead mouse or chick that was pulled away by means of a transparent string), they showed a high success rate in catching those prey that moved directly away from, rather than towards the owls (50% and 18%, respectively), but failed in catching food items that were pulled sideways [15]. It was suggested that while the difference in successful catch of a prey moving toward or away from the owl could be merely kinematic, the failure to capture a food item that was dragged sideways could reflect a difficulty in following prey horizontally [15]. Indeed, in a laboratory setting it was found that spiny mice (*Acomys cahirinus*) displayed a preference to escape sideways in order to evade an attacking barn owl [16]. Accordingly, another target of the present study was to test whether barn owls have a different capacity in following a prey that moves sideways compared with a prey that moves either toward or directly away from them.

2. Methods

2.1. Subjects

2.1.1. Barn owl (T. alba)

Five barn owls that had hatched at the research zoo of Tel-Aviv University were hand-reared to adulthood and used in the present study. Each barn owl was kept individually in an $80\times60\times60$ cm cage. These cages were placed in a large aviary ($6\times6\times4$ m), where each owl was released separately once a week for 24 h. Like the other zoo predators, owls were fed with freshly killed (and sometimes also live) chicks and mice (1 mouse/day/owl), obtained from surplus stock from the animal quarters and from chicken-hatcheries. Thus, these captive barn owls were accustomed to preying on live rodents. The hand-reared owls were habituated to humans by being held in the hand daily for 15 min. Owls were also accustomed to day-time feeding, and no food deprivation was required in the present study.

2.1.2. Social (Guenther's) vole (Microtus socialis guentheri)

Social voles (weight 37–50 g, length 11 cm, plus a 2-cm tail) are burrow-dwelling rodents. High year-round fecundity and early maturation result in large vole populations that are heavily predated upon by owls and other predators. Indeed, voles comprise 40–70% (sometimes over 90%) of the diet of barn owls and tawny owls (*Strix aluco*) [17–19]. Fifty captive-bred voles (males and females), were kept in groups of 5–15 in metal cages ($64\times121\times43$ cm). They were fed *ad-libitum* with standard rodent pellets, sunflower seeds and fresh vegetables. Each vole was tested once in the following procedure.

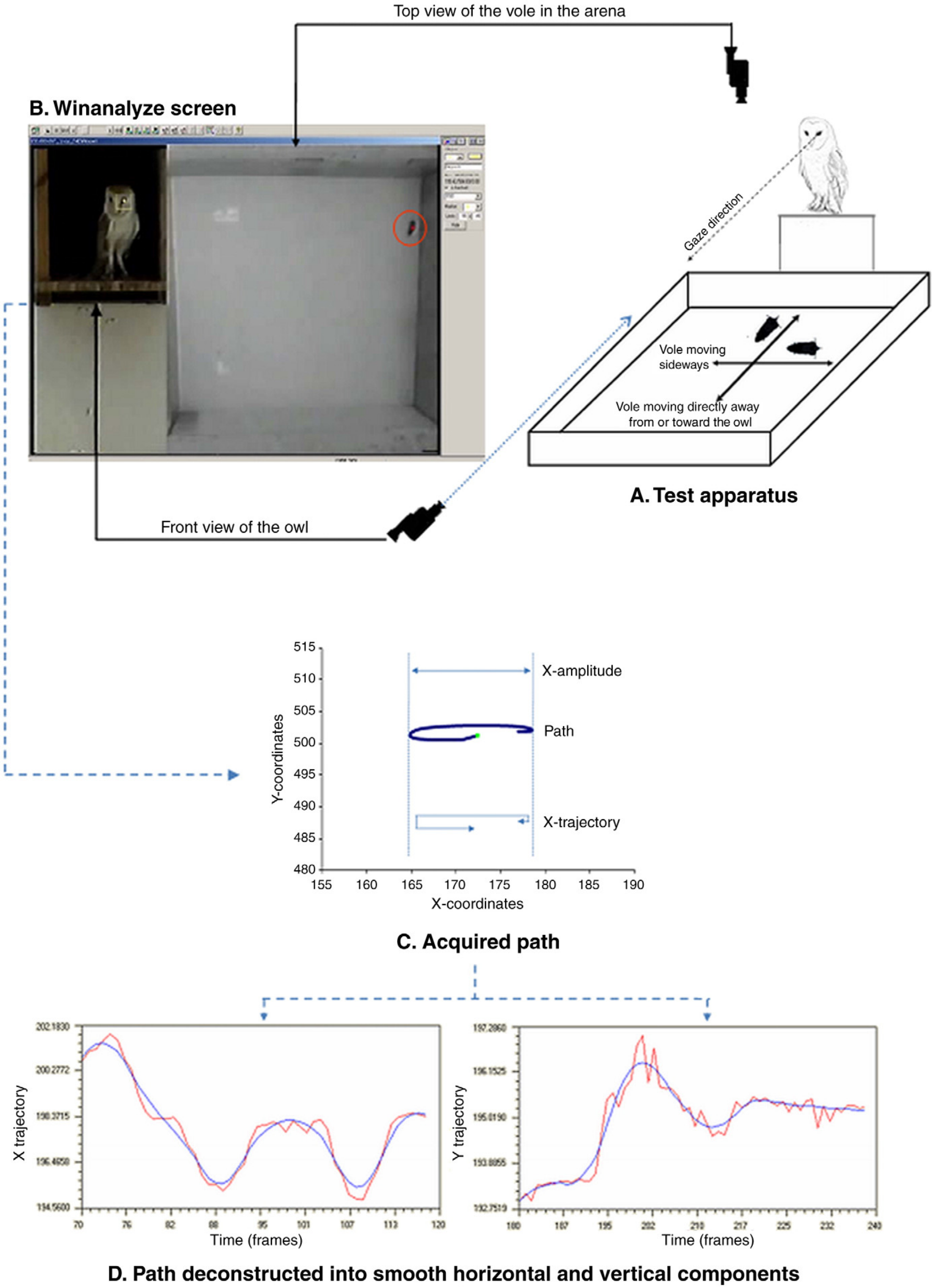
2.2. Apparatus

Experiments took place in a $6.0\times4.5\times3.0$ m cage next to the owl colony, and in which a vole was able to travel freely in a 2×2 m arena with 0.35 m high walls (Fig. 2A). Arena walls were opaque, except for a transparent Plexiglas front wall that faced the owl, providing it with full vision of the arena with no dead spots. The arena floor was covered with white PVC in order to sharply contrast the dark color of the vole and background. This contrast is necessary for computerized video tracking of the vole. A box with a roost was located 1.7 m above the arena. The box had a front door facing the vole arena and a rear door that led to the owl cage. One video camera (Ikegami B/W ICD-47E) was mounted above the vole arena to capture the progression of the vole within the arena. Another camera (Sony TRV e23) was placed in front of the owl box, providing a close view of the owl when the front door was opened (Fig. 2A). The owl and vole video signals from both cameras were simultaneously placed side by side by a mixer (Panasonic WJ-AVE5) and then recorded and digitized by means of a tracking system (Winanalyse by ARGUS) at a rate of 25 frames/s. It was thus possible to simultaneously observe both owl and vole (Fig. 2B).

2.3. Procedure

Before testing, each barn owl was trained for several weeks in the same procedure but with dead mice, in order to habituate it to the test environment and prey location. Testing the owls commenced only when they had become accustomed to the test apparatus and procedure, and attacked the food item within 20 min of it being introduced into the roost. At the beginning of the experiment, an owl was introduced through the rear door into the roosting box, facing the closed front door. It was left for 1–3 min in the box with both front and rear doors closed. During this time, a vole was gently placed in the center of the arena and video recording was initiated. The front door of the box was then quietly opened by means of a pulley, exposing the vole and the owl to one another. Once the owl had launched the attack, the experimenter re-entered the test cage, causing the owl to cease the attack and return to the roost. The arena was then wiped down and another test session commenced. Each of the five owls

Fig. 2. Test and data acquisition. The test apparatus comprised an arena in which a vole could spontaneously move in any direction, while exposed to an owl located in a box above the side of the arena (A). Signals from two video cameras were integrated into the picture in a tracking system that provides *X,Y,T* coordinates of the vole and the owl's eye (B). These coordinates could be plotted to represent the trajectory and amplitude of owl and vole movement (C). Each such plot was then deconstructed into the horizontal (*X,T*) and vertical (*Y,T*) projections of the path (red lines in D), and underwent filtration of noise (blue lines in D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)


Top view of the vole in the arena
B. Winanalyze screen
Gaze direction
Vole moving
sideways
Vole moving directly away
from or toward the owl
A. Test apparatus
Front view of the owl
515
510
505
500
495
490
485
480
Y-coordinates
155
160
165
170
175
180
185
190
X-coordinates
X-amplitude
Path
X-trajectory
C. Acquired path
X trajectory
Time (frames)
Y trajectory
Time (frames)
D. Path deconstructed into smooth horizontal and vertical components

underwent 10 test sessions, with one session per test day, at intervals of 1–3 days between successive tests. This randomization was necessary to prevent the owls from learning that the experimenter was about to interfere during test days. Tests were carried out under natural daylight, at the owls' regular feeding times (10–14 h).

2.4. Data acquisition

Behavior was scored frame-by-frame (1 frame = 0.04 s) during playback of the video files by means of a video-tracking program (*Winanalyze 1.4*, Mikromak, Germany). The frame in which both owl legs released contact with the roost was considered as attack launch and the end of analysis; analysis was thus limited to the preceding pre-attack behavior of owl and vole. For each frame, Winanalyse provided location coordinates and time (*X*,*Y*,*T*) for the center mass of the vole and for the eye of the owl (Fig. 2C). The raw data then underwent a smoothing filtration to eliminate tracking noise (SEE Workshop program, http://www.tau.ac.il/~ilan99/see/help/ and [20]). The output of the process was smoother *X*,*Y*,*T* coordinates for the voles and owl eyes (Fig. 2D).

The behavior of the owls when following the voles was categorized according to the voles' behavior into: (i) following a moving vole; and (ii) pinpointing a stationary vole. For this categorization, a stop by a vole was defined as five frames (0.2 s) in which the vole progressed no more than 2.65 mm. This threshold was set by skimming through the video files and measuring the duration and traveled distance of obvious vole stops. According to the definition of stops, a moving bout was bounded by two successive stops. From the moving vole bouts we chose those in which they moved in a straight path, and from these straight paths selected two categories: (iii) bouts in which voles progressed sideways in relation to the owl, perpendicular to the imaginary axis of owl vision (Fig. 2A); and (iv) bouts in which voles moved toward or away from the owl, parallel to the imaginary axis of owl vision (Fig. 2A).

In the present study, analyses concentrated in the behavior of the owls when tracking the voles during their four behavioral categories (stopping, moving (regardless of direction), moving sideways, and moving toward/away from the owl). Since owl eyes are fixed in the skull, eye movement may represent head movement, which may be the product of rotation or swivel [2,21]. To reduce the effect of trunk movement on head displacement, we analyzed only bouts in which the owl did not move its legs. We included only owl head movement of 0.8 s (20 frames) or more. For each video segment of the owl's head while following the corresponding vole behavior, we measured (in mm) two parameters: (i) *amplitude*, which was the aerial distance between the start and end *XY* coordinates of the movement; and (ii) *trajectory*, which was the sum of the progression (path) between each two successive frames in the bout. Each of these parameters was independently measured on the *X* and *Y* domains, so that the path of owl head movement was deconstructed into *X*-amplitude and *Y*-amplitude, and *X*-trajectory and *Y*-trajectory, all measured over time (Fig. 2C, D).

2.5. Statistics

Unless noted otherwise, owl data were compared in a two-way analysis of variance (ANOVA) with repeated measure, where the *X*,*Y* components were the within-group factor, and the four categories of vole behavior were the between-group factor. When data deviated significantly from normal distribution (Kolmogorov–Smirnov test for normality) or when comparing proportion data, we carried out the ANOVA on arcsine- and/or square-root-transformed raw data. The alpha level was set to 0.05.

3. Results

As noted in the 'Methods', the behavior of the voles during the pre-attack period was categorized into (i) stationary or (ii) moving (regardless of the direction of progression). From the latter bouts of movement we then selected bouts of (iii) progressing sideways in relation to the owl, in a path that was perpendicular to the owl's trunk, and (iv) moving directly toward or directly away from the owl, in a path that was parallel to the owl's trunk. For each of the bouts in these four categories we measured two parameters: (i) trajectory; and (ii) amplitude. The trajectory was the length of the actual path traveled along the *X* or *Y* axes by the vole or owl's head, while the amplitude was the horizontal or vertical projection of the trajectories (Fig. 2).

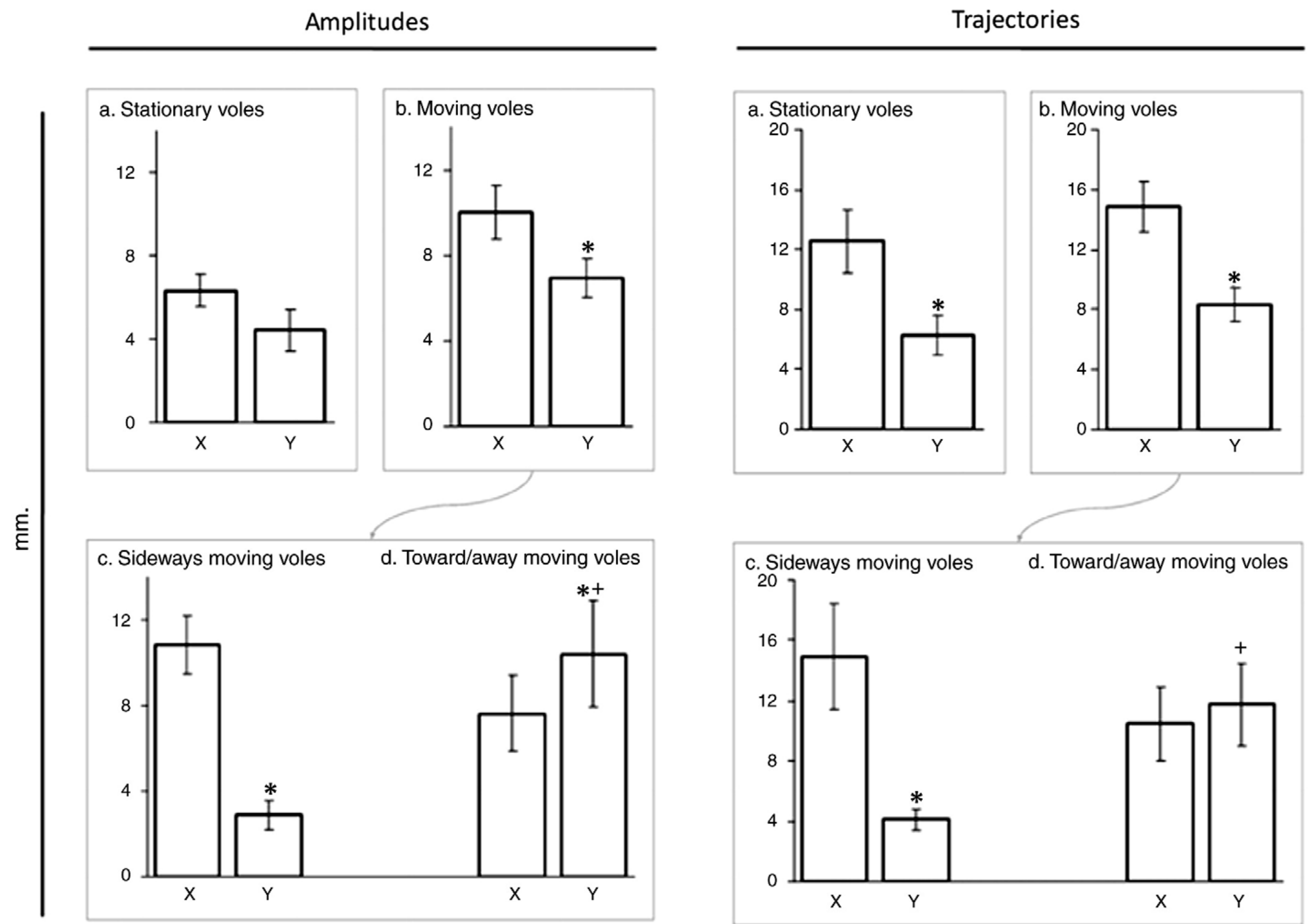
3.1. Amplitudes and trajectories of owl head movements when following the voles

A repeated measure two-way ANOVA of the owl's head movement when following voles in the four behavioral states (stationary, locomoting, locomoting horizontally, and locomoting vertically) revealed a significant difference between the *X*-trajectory and *Y*-trajectory of the owl's head movements (within-group factor; $F_{1,16}=41.37$; $p<0.0001$), and between the *X*-amplitude and *Y*-amplitude of the owl's head movements (within-group factor; $F_{1,16}=16.20$; $p=0.001$). There was no significant effect of the four locomotion types either trajectory (between-group factor; $F_{3,16}=0.42$, $p=$ ns) or amplitude (between-group factor; $F_{3,16}=2.3$, $p=$ ns) of owl head movements. Nevertheless, there was a significant interaction between the behavior of the voles and the *X*-trajectory and *Y*-trajectory of the owl's head movements ($F_{3,16}=8.38$; $p=0.001$) and the *X*-amplitude and *Y*-amplitude of the owl's head movements ($F_{3,16}=12.25$; $p=0.0002$). These interactions imply that trajectories and amplitudes of the owls' head movements were differentially affected by the locomotion type of the voles (Fig. 3).

The above data were subsequently compared by Fisher LSD test, revealing that X-amplitudes in owls were larger than *Y*-amplitudes for locomoting voles but not for stationary voles. Similarly, in tracking voles that moved sideways, *X*-amplitudes of the owl's head movements were significantly greater than *Y*-amplitudes, whereas in tracking voles that moved either directly away from or toward the owl, *Y*-amplitudes of the owl's head movements were significantly greater than the *X*-amplitudes (Fig. 3). The Fisher LSD test also revealed a significant difference between *Y*-amplitudes but not between *X*-amplitudes of the owls' movements in following voles that moved sideways compared with those moving either directly away or toward the owl (Fig. 3). Similar results were obtained from Fisher LSD test for *X*- and *Y*-trajectories. These results are summarized as a table at the bottom of Fig. 3, and indicate that when following a moving prey, the owls primarily utilized horizontal head movement, regardless of the direction of prey movement. The vertical component of owl head movements accorded with the direction of prey movement: they were minimal for prey moving sideways and large for prey moving directly toward or away from the owl.

3.2. Ratio between amplitude of owl head movements and vole progression

The above analysis scrutinized owl head movements in relation to the direction of vole progression, regardless of the amplitude (distance) of this progression. However, the distance traveled by the vole could affect the amplitude of owl head movement. This ratio was assessed for the bouts in which the owls followed voles either moving sideways or moving toward/away from the owl. Consequently, we obtained: (i) *X*-ratio and *Y*-ratio for voles moving sideways, and (ii) *X*-ratio and *Y*-ratio for voles moving toward/away from the owl. Due to the small values of the *Y*-ratio for voles moving sideways and of the *X*-ratio for voles moving toward/away from owls, these ratios were not reliable and could greatly vary. Therefore, these two measures were omitted in order to prevent artificial bias. In other words, we confined the analysis to only the large amplitudes: the *X*-ratio between owl



	Owls' head movements			
	X-amplitude	Y-amplitude	X-trajectory	Y-trajectory
Voles moving sideways relative to the owl	Large	Small	Long	Short
Voles moving toward or away from the owl	Large	Large	Long	Long

Fig. 3. Amplitudes (left) and trajectories (right) of the owls' head movements are each depicted as four insets: for stationary voles (a), for voles moving in any direction (b), for voles moving sideways (c) and for voles moving away from or toward the owl (d). * indicates a significant difference between that bar and the other bar in the same inset, while + indicates a significant difference between the *Y*-bar for the voles moving away from or toward the owl compared with the *Y*-bar for voles moving sideways. The significant differences are summarized in the table at the bottom of the figure.

head movements and voles moving sideways, and the *Y*-ratio between owl head movements and voles moving toward/away from the owl.

Fig. 4 depicts the mean (±SEM) of the ratio for these two parameters. As shown, the *X*-ratio for following voles that moved sideways was significantly larger than the *Y*-ratio for following voles that moved toward/away from the owl (paired *t*-test between the means of horizontal and vertical components of the owls; $t_4 = 18.46$; $p < 0.0001$). This implies that horizontal movements were larger in amplitude compared to the vertical head movements of the owls. Indeed, the means shown in Fig. 4 indicate that in following a vole moving sideways at an amplitude of 100 cm, the owl moved its head horizontally at an amplitude of 1.37 cm, whereas for a vole moving 100 cm toward/away from the owl, the owl moved its head only 0.81 cm vertically.

4. Discussion

Owls are raptors that silently surprise their prey in a sudden attack. To achieve this, owls must accurately locate and follow the prey before launching the attack. The working hypothesis of this study was that owl head movements reflect their visual and auditory capacity to efficiently follow a moving prey. Indeed, by measuring barn owl head movements in a 2-dimensional (horizontal, vertical) plane, we found that when owls followed a moving vole, their head movements increased in amplitude parallel to the vole's direction of movement (sideways or away/toward the owl). However, horizontal owl head movements were also notable regardless of the direction of progression of the voles. In other words, owls performed relatively large horizontal head movements when the voles were progressing in any direction. Finally, we found that the owls

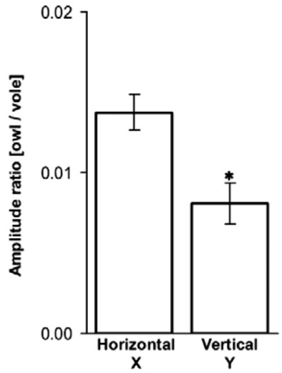


Fig. 4. Ratio between the amplitudes of owl and vole movements.

displayed large horizontal and vertical head movements when the voles were stationary. In the following, we first discuss the differences between pinpointing a stationary vole or following a locomoting vole. We then suggest that owls intercept rather than track their prey and discuss the possible reason for their large horizontal head movements.

4.1. Owls move their head when pinpointing a stationary prey, for the purpose of motion parallax and to reduce the chances of the prey suddenly disappearing

In order to follow a prey, the predator gathers information provided by that prey (e.g. — visual, auditory cues) in order to accurately estimate the location and distance to the prey, and to initiate a timely launch for a successful attack. By freezing, a prey eliminates the auditory and changing visual cues that owls use in pinpointing prey [18]. In the lack of these cues, owls must rely on the steady visual image. Nevertheless, in the visual system, a steady image fades with time since the photoreceptors receive a constant illumination signal and cease to further transmit this signal ([22], also described in humans by [23]). However, the advantage implicit in this phenomenon is that by means of visual fixation at a certain direction, the stable background fades and the image of a moving prey or predator is thereby emphasized [1]. Accordingly, when pinpointing a stationary prey, the predator is required to artificially generate a moving image of the prey by moving its own eyes or head. This displacement in the location of the predator, known as 'motion parallax' [6], results in an artificial change in the location of the prey. The change is artificial since the prey does not move, but its location on the predator's retina changes due to the predator's self eyes/head displacement. When barn owls pinpoint a stationary target, they display a rich repertoire of head movements in order to assess the location and distance to the target [2]. The present results follow up the above studies, demonstrating that in pinpointing stationary live voles, barn owls perform large horizontal and vertical head movements. These movements accord with the definition of motion parallax in other species [5], indicating that they serve the owls to accurately locate their prey.

Another potential advantage of the horizontal and vertical owl head movements in pinpointing a stationary live vole is that of reducing the chances for the vole to disappear by a sudden progression. If the owl would fixate its head on a stationary vole, the latter could suddenly move and either disappear from the visual field of the owl or force the owl to scan a large area in order to relocate it. The relatively large horizontal and vertical owl head movements cover a greater area compared to a fixated head, potentially including the area of an initial possible sudden movement of the prey and thus reducing its chances of evading the owl's attention [13].

4.2. Owls seem to intercept rather than track a moving prey

As described in the Introduction, predators may follow their prey by interception, in which they aim at a prospective interception point and move to it along a straight path. Alternatively, they may perform tracking, in which they continuously orient toward the prey, and therefore travel along a circular path (see Fig. 1). The present results reveal that the owls visually and/or auditorily follow moving voles by means of repetitive horizontal and vertical head movements, resulting in trajectories (paths) that are greater than the movement amplitude (Fig. 3). This can be interpreted as if the owl orients ahead toward the prospective clash point, and then returns to the target itself (the vole) — a pattern that fits an interception rather than a tracking mode of following a moving target. This pattern is further supported by a model suggesting that voles may evade owl attack by alternating between freezing and fleeing [24]. According to this model, when following a vole that moves and suddenly stops, the owl first continues the imaginary direction of the vole's trajectory, and only then, when realizing that the vole is no longer moving, does the owl return to where the vole was last seen. However, the owl might now not see the freezing vole that has merged into the background and does not generate visual or auditory cues. This model [24], as well as the present results, suggests that owls intercept rather than track their prey. Furthermore, in barn owls, correction of flight course is limited in the final segment of the attack [25]. Correction of the flight to a target is also limited by the lateral distance to be bridged [25], as if the final segment of owl attack is set as "launch and forget", which well fits the interception but not the tracking mechanism.

4.3. Why large horizontal head movements?

Estimating the location of a stationary prey could be made by the predator moving its head in any direction. However, it was previously found that horizontal head movements are directly linked to the success of owls in visually estimating depth, whereas vertical head movements during depth estimation are minimal [3]. In light of this finding, it was suggested that owls estimate distances by horizontal and not by vertical head displacement. This may explain the present finding that owls display greater horizontal head trajectories when pinpointing stationary live voles. Horizontal movements, termed 'peering', generate faster and larger motion parallax for close compared with distant objects, thus providing information on the location and distance of the object [5]. Other studies have also suggested that owls have a differential capacity to follow targets that move sideways compared with those that move toward or away from the owl [15]. Moreover, it was suggested that owls have four different neural circuits, each controlling a separate direction of head movement (left, right, up and down) [26,27]. In light of these past studies, we examined how the way that owls followed voles moving sideways compared with voles moving toward or away from them (Fig. 2). We found that in following voles that move sideways, the owls performed movements with minor vertical and large horizontal amplitudes and trajectories. However, in following voles that moved away from or toward the owls, the latter performed movements with large horizontal and vertical amplitudes and trajectories. Hence, the vertical component of the owls' head movement accords with the movement of the voles, whereas the horizontal component is always large, as illustrated in three actual trajectories of voles and the respective owl trajectories (Fig. 5A,B), and by a schema (Fig. 5C).

There seems to be a differential capacity of owls to follow prey that move sideways compared with those moving toward/away from the owl. They execute large horizontal peering movement to better estimate depth [3], they fail to follow a sideways moving prey [15], and rodents accordingly favor a sideways escape [16]. However, it is not yet known how these large horizontal head movements of the owls are linked to the structure of their retina. Moreover, head movements may also serve for sound localization [28]. On the one hand, the large horizontal compared with vertical owl head movements may indicate that the barn owl fovea is horizontally narrow compared to its vertical dimension, necessitating large horizontal head movements in order to retain the prey image on the fovea. On the other hand, it could be that owls have a horizontally

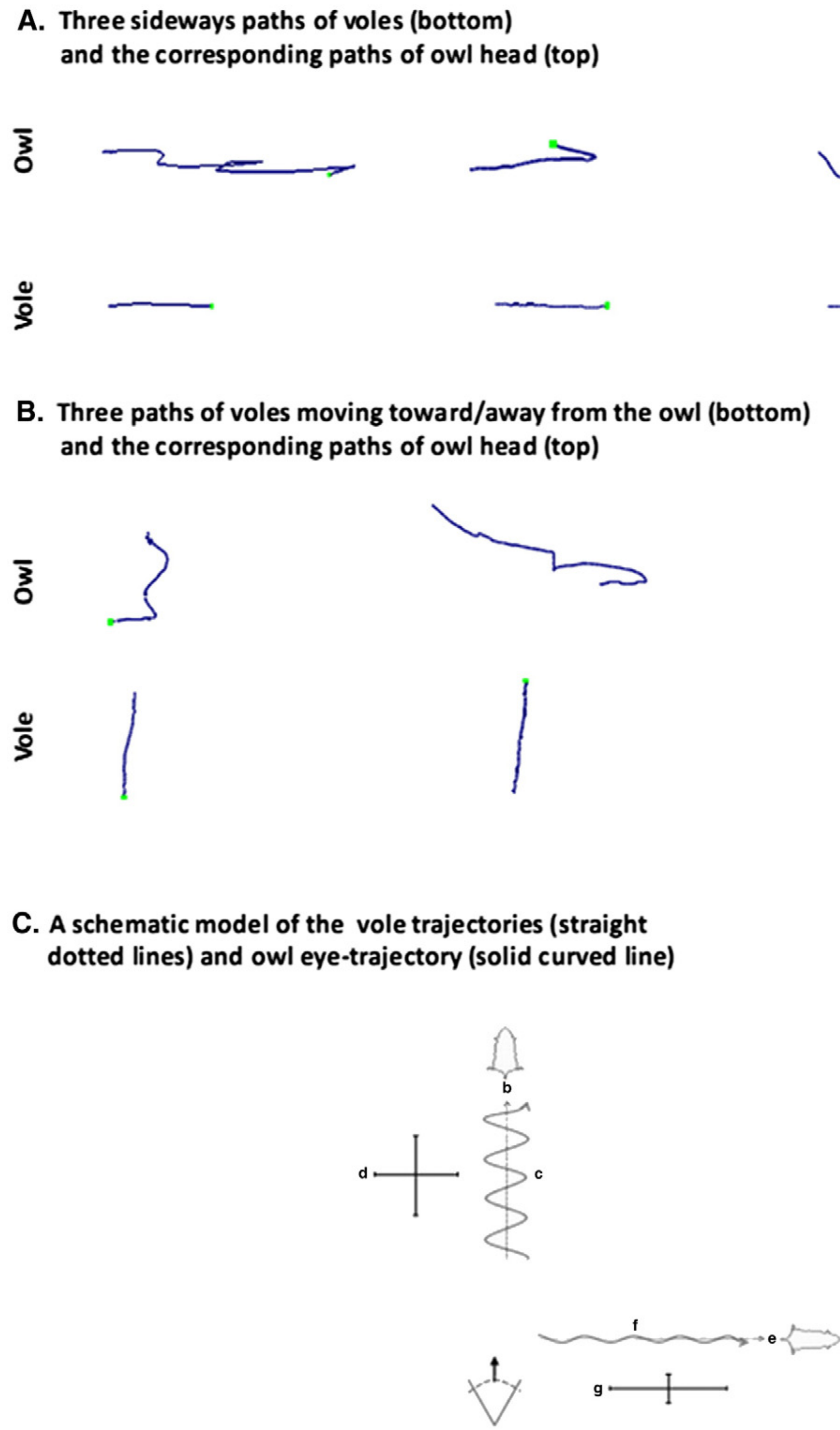


Fig. 5. Three actual trajectories of voles moving sideways and the respective trajectories of the owl's eye (A). Also depicted are three actual trajectories of voles moving away/toward the owl and the respective trajectories of the owl's eye (B). Finally, a schematic model illustrating that in following voles moving away/toward the owl (b) owl head path (c) has both large horizontal and vertical amplitudes (d). In contrast, in following voles that move sideways (e) owl head path (f) has large horizontal but minor vertical amplitudes (g).

larger fovea, and that the horizontal head movements preserve acuity during motion parallax.

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