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Mini-review

Behavioural–analytical studies of the role of head movements in depth perception in insects, birds and mammals

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Abstract

In this review, studies of the role of head movements in generating motion parallax which is used in depth perception are examined. The methods used and definitiveness of the results vary with the animal groups studied. In the case of insects, studies which quantify motor outputs have provided clear evidence that motion parallax evoked by head movements is used for distance estimation and depth perception. In the case of birds and rodents, training studies and analyses of the head movements themselves have provided similar indications. In the case of larger mammals, due to a lack of systematic experiments, the evidence is less conclusive.

Keywords: Depth perception; Behaviour; Motion cues; Motion parallax; Vision

1. Introduction

When one moves one's head from side to side, objects within the field of view appear to change position relative to one another, with nearby objects exhibiting a greater apparent displacement than more remote objects. This phenomenon, referred to as "motion parallax" can be used for the determination of object distances. Motion parallax generated by head movements (Fig. 1) is utilised not only in humans, but also in various other animals. In the case of humans, numerous psychophysical investigations have yielded extensive evidence, as indicated by the comprehensive literature (Cornilleau-Pérès and Gielen, 1996). However, in the case of other animals direct evidence is difficult to obtain, which has led to the use of a behavioural–analytical approach that examines motor outputs. In order to obtain definitive results, it is necessary to examine reactions triggered by motion stimuli which exhibit a quantifiable stimulus dependence. For instance, a targeted jump could represent a behavioural reaction ideally suited to such studies. Because of the largely ballistic nature of a jump, it must be preceded by an exact distance measurement so as to make possible a precise determination of the required motor output, to control the amplitude and velocity of the jump, since subsequent corrections during the jump are virtually impossible. Precision of distance estimation is particularly critical for long jumps, due to the increased expenditure of energy and the risk of injury. In experiments, jump distances and visual cues can be controlled, making it possible to arrive at conclusive results. Such definitive behavioural–analytical investigations have so far been carried out for only a few animal species.

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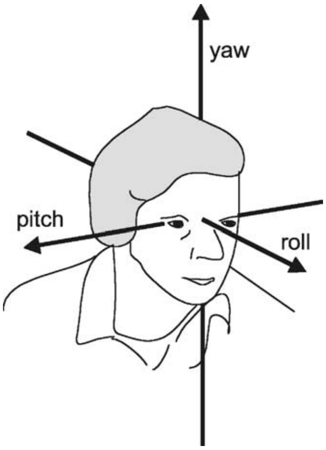

Fig. 1. Active movement of the head in space can be described in terms of three translational and three rotational components with the aid of three axes of rotation: the pitch axis, the yaw axis and the roll axis, about which the head can be rotated or along which it can be translated.

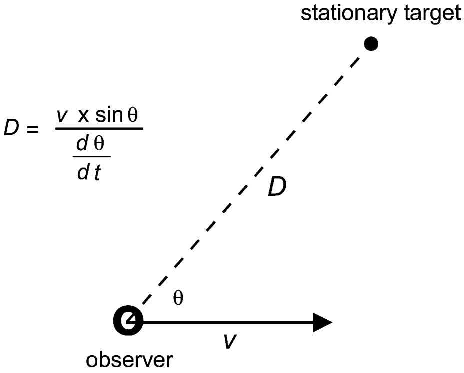

Fig. 2. Diagram illustrating how the distance to an object can be determined by means of motion parallax evoked by self-generated head movements. The distance D from the observer to a target can be determined from the relative angular velocity ($d\theta/dt$) of the retinal image motion which is induced by the lateral movement of the observer's head in the frontoparallel plane (v = velocity). [Modified from Yakovleff and Moini (1998), reproduced with permission from the authors and Kluwer Academic Publishers.]

The present review examines studies of this type in various animals (except primates), as well as studies in which the results are not as conclusive. For each group of animals, the discussion is first put into the context of why motion factors may be important for depth perception. A range of experiments which provide evidence for the use of motion parallax in depth perception is then discussed, and the significance of the findings is examined. It should be noted that some studies use the concept of "retinal image motion", to refer to the fact that the apparent displacement of an object resulting from the observer's head movements is in fact due to the motion of the image of the object on the retina of the eye of the observer (Fig. 2). Also, in studies of motion parallax, a distinction is made between the apparent motion of objects relative to one another, from which relative distances can be determined, and the absolute motion of the image of an object across the retina of the eye, from which, in combination with information about the amplitude or velocity of head motion, the absolute distance to the object can be determined. The paper then discusses broader questions arising from the studies, including possible mechanisms by which inputs from head movements could be translated into distance information, and the adaptive significance of the head movements.

2. Results and discussion

2.1. Head motion in insects

Insects have immobile eyes with fixed-focus optics. Thus, unlike vertebrates, they cannot estimate object distance from the degree of dynamic convergence of the lines of sight when viewing an object, nor can they determine object distance from the refractive power required to focus the image of an object on the retina. In some animals, including humans, distance information can be obtained from binocular cues, that is, by making use of the fact that different informations are received by the two eyes, due to their slightly different viewpoints. The eyes of insects, however, are positioned much closer together than human eyes and have a lower spatial acuity (Kirschfeld, 1976). Hence, the precision with which insects can estimate object distance by means of binocular cues (Rossel, 1983; see also Köck et al., 1993) would be expected to be relatively low and restricted to nearby objects, within a range of a few millimetres to at most a few centimetres.

It follows from this that at greater distances, cues other than binocular ones may play a role in distance measurement. The hypothesis that motion cues could be involved has been indicated by various studies

(Srinivasan et al., 1999). For instance Srinivasan et al. (1990) succeeded in training bees to select an object at a specific height above a structured ground from among several objects at various heights. The bees were able to select the correct object despite variations in the size, shape and position of the objects, supporting the hypothesis that they were able to monitor the apparent motion of the object relative to the ground (for review see Lehrer, 1994; see also Wehner, 1994).

In mantids, locusts and some other insects, typical self-generated side-to-side translational movements of the head in the horizontal plane along the pitch axis can be observed; these are referred to as "peering movements" (Wallace, 1959; Collett, 1978; Eriksson, 1980; Goulet et al., 1981; Horridge, 1986; Sobel, 1990; Prete, 1993; Walcher and Kral, 1994; Poteser and Kral, 1995; Kral and Poteser, 1997). Fig. 3 illustrates the object-related peering movements of a praying mantis. For *Mantis religiosa* individuals 50–70 mm in size, peering amplitudes are approximately 2–10 mm and peering velocities are approximately 6–18 mm/s.

When executing such head movements, the animal accompanies each sideways movement of the body with a compensatory counter-rotation of the head about the yaw axis, so that the head is always directed straight forward and thus remains oriented toward the edge of the object (Kral and Poteser, 1997). It is not yet clear what mechanisms control the linearity of the head movement, although there is some evidence of co-ordination between the visual system and the mechanical position and movement receptors, particularly those located in the neck, that is, the sternocervical and tergocervical hair plate sensilla (Poteser et al., 1998).

The peering movements have long been connected by researchers with motion parallax (Kennedy, 1945). By moving a square black landing target in front of a white background synchronously but counter to the peering movements, Wallace (1959) endeavoured to induce desert locusts (*Schistocerca gregaria*) to perceive the object distance incorrectly. The intention was to increase the amplitude and speed of the image motion artificially, so as to give peering locusts the impression that the object was nearer than it really was. The locusts were in fact misled, and jumped short of the target. Sobel (1990) performed similar experiments with the locust *S. americana*, using computer-controlled visual targets. He used the takeoff speed of the jumping locust, which was dependent on object distance, as a measure of the accuracy of distance estimation. In this way he was able to demonstrate and quantify the underestimation and overestimation of the distance in relation to the lateral movement of the object with or counter to the peering movements. In similar experiments performed with juvenile praying mantids (*Tenodera sinensis*, *Polyspilota* sp.; see Fig. 3), movement of the landing

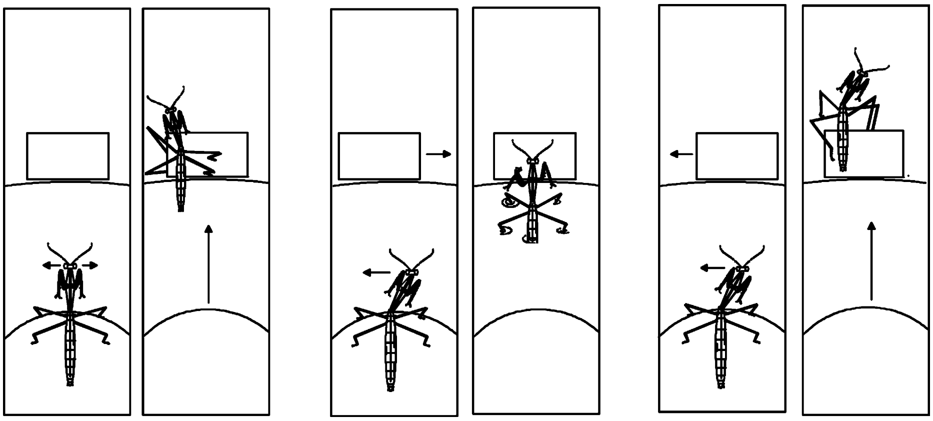

Fig. 3. Schematic representation illustrating the peering-jump behaviour of a praying mantis. Movement of the target counter to the direction of the peering movements causes the mantid to jump short of the target, as a result of underestimating the distance due to the artificially increased retinal image motion. If the target is moved in the same direction as the peering movements but somewhat more slowly, the mantid jumps too far due to the artificially decreased retinal image motion.

platform counter to the direction of peering caused the animals to jump short of the target, whereas movement of the platform in the same direction as peering caused the animals to jump too far (Poteser and Kral, 1995). Fig. 4 illustrates jumping frequency under such experimental conditions. The visual angle of the landing site was kept constant throughout the study in order to eliminate image size as a possible experience factor.

In mantids, aimed jumps that were preceded by peering movements could, however, only be elicited when both eyes were fully intact (Walcher and Kral, 1994). In contrast to mantids, locusts also jumped with one eye blinded, however unilateral blinding resulted in overestimation of the jump distance (Sobel, 1990).

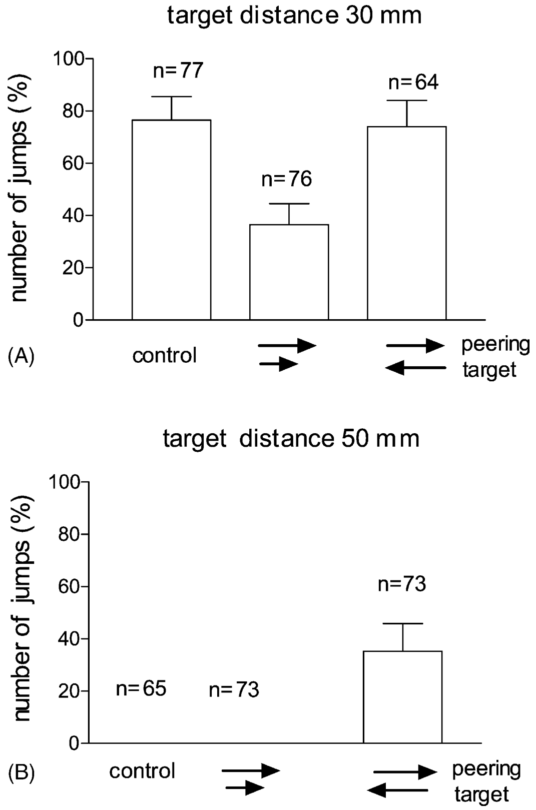

Fig. 4. Diagrams showing the percentage of jumps executed after a praying mantis has peered at a stationary object (control; no arrows), an object moving in the same direction as the peering movements (two arrows pointing the same way), and an object moving counter to the direction of the peering movements (arrows pointing in opposite directions). (A) At a distance within the optimal jump range (3 cm) and (B) at a distance at which jumps rarely occur (5 cm). The vectors (arrows) indicate the direction of motion and the velocity of the peering movement and the target. [From Poteser and Kral (1995), reproduced with permission from The Company of Biologists Limited.]

There are also insects, such as the empusid mantid *Empusa fasciata*, that exhibit peering movements which are not simple sideways translational movements of the head along the pitch axis, but rather consist of forward and backward movements containing translational components along the roll axis and rotational components about the pitch axis (Kral and Devetak, 1999). Field observations indicate that when climbing among the branches of shrubs and jumping from one branch to another, the insects use these complex head movements to estimate the distance to the nearest and most readily grasped object or landing target. In addition to absolute motion parallax, relative motion parallax also appears to be an important source of information for distance measurement. The complexity of the peering movements may be related to the complex structure of the surroundings. The translational component of the sideways movement could play a role in distance measurement. The forward and backward movements may permit targets to be fixated during peering, allowing the mantid to determine direction accurately as well as distance. By changing the peering axis, distance information about objects in a variety of directions could be obtained without the need for turning. Although the rotational component of the peering movements might interfere with the perception of parallax effects (Buchner, 1984), it could be beneficial in serving to intensify the brightness contrast, and could permit the scanning of a more extensive field of view.

In this connection, studies of the neuropteran insect *Mantispa styriaca*, similar in appearance to the mantids but not closely related to them, are worth mentioning (Eggenreich and Kral, 1990; Kral et al., 1990, 2000). In these experiments, strikes at prey, rather than jumps, were used in order to study distance determination. Since the mantispid, an ambush predator, preys on quick-moving flies, it strikes only when an item of prey is at an optimum capture distance. The strikes thus provide a good indication of the accuracy of distance measurement. The approximately 50° binocular overlap of the eyes of the mantispid, which is approximately 2 cm in length, enables it to estimate the distance to an item of prey by means of binocular triangulation as soon as the prey comes within capture range. However, if one of the mantispid's eyes is covered with a light-proof material then in contrast to its usual behaviour, immediately before striking at prey the mantispid executes characteristic head movements with translational components, similar to those executed by the above-mentioned empusid mantids. Nevertheless such movements are executed only when the item of prey remains stationary. The mantispid's success in capturing prey under these conditions is surprisingly similar to that under normal conditions. However, if the head is immobilised by being fixed to the thorax, a mantispid blinded on one side loses the ability to capture prey, evidently because it is prevented from peering. In the case of a mantispid having the use of both eyes, if the head is fixed to the thorax the ability to execute the beginnings of a strike is retained, but the strike itself is prevented (K. Kral, unpublished observations). It appears that if, due to blinding on one side, binocular triangulation cannot be used for distance estimation, it can be successfully replaced by retinal motion cues. Thus, it is evident that in this case as well, absolute distances can be measured with the aid of retinal image motion. It would appear that the visual system is remarkably flexible with regard to the use of visual cues. This raises the general question of whether in insects binocular information and retinal motion information are based on the same neuronal system. In other words, the mechanisms supporting the computation of depth from binocular cues and motion cues may not be independent of one another.

2.2. Head motion in birds

The eyes of most non-predatory birds are located in a relatively lateral position (Tables of Martin and Katzir, 1995, 1999). This provides an extensive panoramic field of view, but the small area of binocular overlap means that binocular vision is limited or non-existent. However, the precise pecking behaviour of birds such as pigeons, which have a binocular overlap of up to 30°, suggests that binocular cues may be involved in depth judgement (Martinoya et al., 1988). Nevertheless, some authors exclude binocular disparity as a possible cue (McFadden, 1993, 1994). In addition, all birds can move their eyes only to an extremely limited extent; this is compensated for by the mobility of the head. In some birds, distinct backward and forward head movements with respect to the body at the rate of a few cycles per second, referred to as "head-bobbing", may play a role in vision (Whiteside, 1967; Dagg, 1977; Frost, 1978; Casperson, 1999). In these cases head-bobbing does not seem to represent any type of social display or mating behaviour (Zocchi and Brauth, 1991).

In pigeons the visual role of head-bobbing has been extensively investigated (Dunlap and Mowrer, 1930; Frost, 1978; Davies and Green, 1988, 1991; Troje and Frost, 2000). During walking, the head movement consists of two alternating phases: a thrust phase and a hold phase. Whereas in the thrust phase the head is quickly thrust forward, in the hold phase the head remains in a fixed position in space, not only in terms of horizontal translation (along the roll axis), but also in terms of vertical translation (along the yaw axis) and rotation about the pitch and yaw axes (Troje and Frost, 2000). It is evident that the hold phase is under visual control. The head-bobbing thus constitutes an optokinetic reaction which serves to stabilise the retinal image during the hold phase, comparable to eye saccades in mammals, including humans. This may facilitate image processing, which could be important particularly for the detection of moving objects (Frost, 1978; Troje and Frost, 2000). This could also apply to the pecking behaviour observed in the ring dove, where it is postulated that the hold phases of the head could be significant for vision (Cezilly and Brun, 1989). It is unclear whether the thrust phase of the bobbing movement has a specific visual function.

When flying, pigeons exhibit head-bobbing during the landing approach, but not during takeoff or in steady flight (Davies and Green, 1990). During landing, in addition to ensuring image stabilisation, head-bobbing may also provide depth information via motion cues (Troje and Kelly, in preparation). A flying bird has the problem of having no direct access to information concerning its own speed over the ground. Proprioceptors can provide information concerning the velocity relative to the surrounding air, but movement of the air itself, caused by wind or convection currents, can constitute another velocity component. It is possible that during flight, differential motion parallax information could provide a solution to this problem (N. Troje, personal communication). During head-bobbing the head, as well as the eyes, moves at two different velocities. Troje and Kelly (in preparation) have hypothesised that comparing the differences between these velocities with the differences between the corresponding retinal image velocities could enable distance measurements to be carried out. These researchers have tested the hypothesis experimentally by measuring a pigeon's head movement during the landing approach to a perch. A movement component at right angles to the pigeon's line of locomotion would be required in order to evoke motion of the image of the perch on the retina. It was found that the head-bobbing does in fact contain such a movement component. In moving from one hold phase to the next, the pigeon's head travels not in a straight line, but in a curved, U-shaped path. There is thus a perpendicular movement component which could result in distance-dependent retinal motion of the image of the landing target. It seems possible that other birds with visual prerequisites similar to those of the pigeon may also use motion cues in this way when landing. During critical, fast flight manoeuvres, as in the landing approach, information obtained from motion parallax could be more useful than static depth cues, since the latter are associated with a more time-consuming approach to absolute distance measurement (Davies and Green, 1994).

In addition to these noteworthy findings for pigeons, the behaviour of some perching water-associated birds should also be mentioned. These exhibit typical head motions at constant speeds, with the head moving vertically or forward on a straight path while perching, immediately before striking or plunging into the water to capture stationary prey (Katzir and Intrator, 1987; Casperson, 1999). The cited authors found that the head movements were clearly object-related. According to Casperson, who explains his hypothesis with the aid of a plausible mathematical model, the vertical displacement of the bird's eyes brought about by the vertical head movements could provide visual information regarding the interference and distortion caused by reflection and refraction at the air/water boundary. Casperson (1999) also suggests that the head movements could give rise to motion parallax between the often stationary underwater target, such as a mussel, and the reflected image of overhead foliage. Thus, motion parallax could help the bird to distinguish between superimposed reflections and a stationary underwater target. The location and distance of the target could be estimated from the relative retinal image motion (Fig. 5).

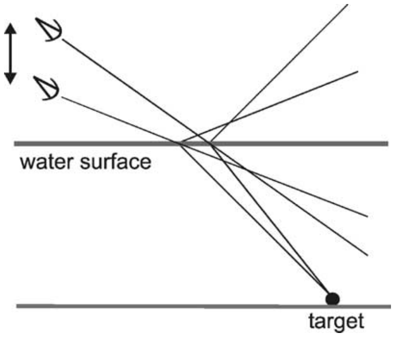

Fig. 5. Sketch showing solutions for ray trajectories from a stationary underwater target object to the eye of a seashore bird for two different eye heights. Significant changes in the directions of the rays from the target object and the above-water source of interference occur with changes in eye height. Arrows indicate vertical translational head movements having a constant velocity. [From Casperson, 1999, redrawn with permission from the author and Cognizant Communication Corporation.]

In contrast to pigeons and most other birds, raptors have relatively frontal eyes and can have a binocular visual field with a binocular overlap of more than 40°. However, some raptors have relatively small binocular visual fields, with a binocular overlap of not more than 20° (Tables of Martin and Katzir, 1995, 1999). As in non-predatory birds, the function of binocularity in raptors seems unclear. Its significance may lie not in the fact that the two eyes can image the same part of the frontal visual field simultaneously, but rather in the fact that binocularity results in the monocular fields of the two eyes projecting contralaterally (Martin and Katzir, 1999). It seems plausible that one function of binocularity may be the optimal processing of the linear optic flow which results from self-motion. Thus, stereoscopic vision, if present at all, may not be a general property of the visual system of raptors and other birds (McFadden, 1993, 1994; Davies and Green, 1994). In this connection the most recent behavioural studies of owls are interesting.

The barn owl (*Tyto alba*), a highly adaptable, cosmopolitan raptor, executes head movements when perching (Wagner, 1989), which interestingly enough are very similar to the peering movements of empusid mantids (Kral and Devetak, 1999). In addition to an excellent auditory system, owls also have good vision. Behavioural experiments carried out by van der Willigen et al. (1998) have shown that owls have stereo vision which is functionally equivalent to that of humans. By means of ingenious experiments with owls, van der Willigen et al. (2002) recently discovered that translational side-to-side head movements in the horizontal plane are stimulus-evoked. With an amplitude of 2–6 cm, these movements are considerably larger than those in the vertical and/or depth plane. These authors found that owls trained to distinguish between objects and holes using binocular disparity alone (stereopsis) could immediately apply this discrimination to novel stimuli where the depth categories could be determined only on the basis of differences in motion information produced by head movements.

2.3. Head motion in rodents and rabbits

The lateral placement of the eyes of rodents permits very little if any overlap of the visual fields of the two eyes. In rabbits, the binocular overlap is approximately 10°. Thus, binocular vision is possible only to a very limited extent (Artal et al., 1998). In addition, like insects, rodents lack the possibility of accommodation, that is, of focusing the eye at different distances. However, rodents have panoramic vision and are far-sighted; they can perceive more distant objects considerably better than nearby ones. Rodents can be readily observed executing head movements immediately before jumping (Collett and Harkness, 1982). For instance a diurnal tree squirrel in a takeoff position on a branch shifts its head from side to side along the pitch axis or up and down along the yaw axis; the number of head movements can vary (own observations). It is possible that the translational components of these self-generated movements are used in estimating the jump distance. Likewise, rabbits can be observed bobbing up and down while viewing a distant object (own observations). However, in many cases the investigations which would be required in order for concrete statements to be made are lacking, such as an analysis of head movements and takeoff velocity.

Concrete experimental indications of the visual significance of distinct head movements involving translational components have been found in the case of gerbils. Mongolian gerbils (*Meriones unguiculatus*) were trained to jump across gaps of different widths (10–36 cm) to land on a platform; the jump distance was varied randomly in 2 cm steps (Goodale et al., 1990; see also Ellard et al., 1984, 1986). To determine the jump distance, the animals used the retinal image size (the angle subtended by the object on the retina) and retinal image motion of a stationary target object. In order to make the latter possible, they executed characteristic translational head movements in the vertical plane. If unable to make use of retinal image size because of the presence of unfamiliar objects or objects of different sizes, they increased the number of head movements, evidently in order to intensify the image motion. It was found that the number of head movements was directly dependent upon the distance to the landing platform. The course of the movements associated with the different distances to be jumped indicated that the absolute distance was measured by means of motion parallax.

In a study of hooded rats, Legg and Lambert (1990) investigated the significance with respect to distance estimation of retinal motion cues arising from vertical translational head movements executed immediately before a jump to a platform. The first experiment indicated a relationship between head movements and the visual background. It was found that in the case of a structured background the rats executed a significantly larger number of head movements before jumping than in the case of an unstructured background. In the second experiment, these authors found that stroboscopic illumination had a disruptive effect on the jumps. However, the rats executed precise jumps to the platform when only the edge of the platform was visible. Evidently, like the Mongolian gerbils, the rats used absolute rather than relative motion parallax for distance measurement.

2.4. Head motion in larger mammals

To what extent the often very distinct head movements of other mammals are associated with depth perception by means of retinal motion cues is largely uninvestigated. A few investigations examine mammalian vision, especially that of domestic species. There is, however, no study that has systematically investigated the ability to determine motor output as a function of distance information. In the case of horses, which exhibit incipient translational head movements along the yaw axis, studies of the optics of the eye indicate that the typical up and down movements of the head evidently serve to adjust the eyes to nearby and distant regions, so as to scan either the ground or the horizon with an acute area of the visual field (Harman et al., 1999). The head movements of dogs and some cats, which can also contain translational movement components along the yaw axis and the pitch axis, could be used to assist in depth perception (Miller and Murphy, 1995). As shown in behavioural studies, dogs have a binocular overlap of approximately 30–60°, much less than that of humans (Sherman and Wilson, 1975). An experiment by Miller and Murphy (1995) shows that dogs not only exhibit binocular depth perception, although only at close range, but in conjunction with head movements also exhibit monocular depth perception.

2.5. *Monocular versus binocular inputs*

The findings for vertebrates indicate that monocular visual inputs based on motion parallax provide sufficient information for depth perception. In the case of invertebrates, with the exception of mantispids, the results may suggest that the visual system or the visuomotor system or both require binocular inputs. With regard to the visual system, binocular inputs could be important for target localisation, that is, the correct estimation not only of the distance but also the direction of the target. The latter may be possible only in the case of similar, maximal stimulation of the two eyes. This hypothesis is supported by findings in water stick insects (Cloarec, 1986) and bulldog ants (Eriksson, 1985), where binocular processing of motion parallax signals has been postulated. However, it could also be that in insects the visuomotor system determines motor outputs only on the basis of binocular vision.

2.6. *Possible mechanisms for determining absolute distance by means of motion parallax*

It follows from the studies reviewed here that insects use both absolute and relative motion parallax for depth perception (Sobel, 1990; Kral and Poteser, 1997), while rodents make use of absolute motion parallax (Goodale et al., 1990; Legg and Lambert, 1990). In other words, motion parallax reveals not only relative but also absolute distance information. In contrast, birds seem able to use only relative motion parallax (Casperson, 1999; van der Willigen et al., 2002; Troje and Kelly, in preparation). However, in all cases self-generated translational head movements are a necessary prerequisite. The head movements themselves must be taken into account during the processing of visual information in the case of absolute distance determination, but not in the case of relative distance determination. The following are possible mechanisms which would allow motion parallax generated by head movements to be used for the determination of absolute distances: (1) the velocity of the head movement is kept constant, with the result that the distance to the target object is inversely proportional to the image velocity; (2) the velocity of the head movement varies while the amplitude of the head movement is kept constant, allowing the distance to the target object to be computed from the relationship between the head amplitude and the amplitude of the image motion; (3) the amplitude of the head movement is adjusted in such a way that the amplitude of the image motion is kept constant, as close as possible to the threshold; a linear increase in the amplitude of head movement with distance is pre-programmed, and the object distance is determined on the basis of the amplitude of the head movement; (4) the velocity of the head movement is adjusted in such a way that the velocity of the image motion is kept constant, as close as possible to the threshold, and a linear increase of the velocity of head movement with distance is pre-programmed; and (5) both the amplitude and velocity vary; this variability is taken into account and the distance to the target object is determined from the relationship between the velocity (or amplitude) of head movement and the velocity (or amplitude) of the image motion.

From the structure of the head movements observed in these studies, it seems likely that of the above-mentioned alternatives, those based on a relatively simple principle (1 and 2) are most probably the methods used, with the velocity or amplitude of the head movement being kept constant. In the case of mantids it can be concluded with a high degree of certainty that distance information is provided by image velocity (Fig. 6), which points to the first possibility mentioned above (Kral, 1998a, b, 1999; Poteser et al., 1998; Srinivasan et al., 1999). The evidence for water birds (Casperson, 1999), gerbils (Goodale et al., 1990) and rats (Legg and Lambert, 1990) also suggests the same conclusion, but with a lower degree of

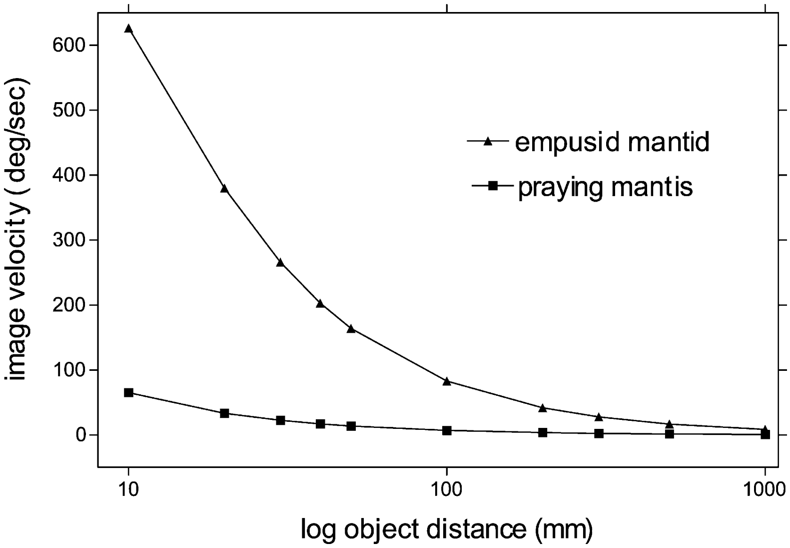

Fig. 6. Illustration of retinal image velocity as a function of object distance. An empusid mantid, *E. fasciata*, is compared with a praying mantis, *M. religiosa*. The greater amplitude and velocity of the peering movements of the empusid mantid enhance its ability to discriminate between different distances and enable it to measure distances over a significantly greater range than can the praying mantis. [Modified from Kral and Devetak (1999), reproduced with permission from Kluwer Academic Publishers.]

certainty. In owls, the head movements providing the decisive visual components for distance measurement to stationary objects seem to indicate that calculation of the amplitude or velocity of the head movement and the retinal image motion is involved (van der Willigen et al., 2002). In locusts, it was found that they could discriminate between different target distances even when the amount of image velocity (or the displacement) was identical (Sobel, 1990). This is contrary to the peering behaviour of mantids. Thus, in locusts the peering velocity (or displacement) can vary during peering directed toward a target. Whether the locust combines both head motion and image motion or simply does only compute its head motion (one of the last three strategies) remains the question.

How in insects neural processing of motion parallax may work is unclear. Non-directional motion cells identified in the optic lobe may be possible candidates for motion-parallax neurones (Kral, 1998a, b). However, neurones that are directly involved in a movement-detecting mechanism that measure image velocity or image displacement created by head translation and compares this information with the velocity or displacement of the head remain to be investigated (Srinivasan et al., 1999). In cats, neurones computing the velocity of retinal image motion have been found in the striate cortex, whereby recent electrophysiological recordings gave results which clearly demonstrate that motion and binocular disparity are encoded jointly by single neuron. Thus, such a complex neuron is sensitive to both binocular and monocular input (Anzai et al., 2001). Interestingly, these cortical areas are also candidates for interactions with head-motion-related signals (Cornilleau-Pérès and Gielen, 1996). The presence of primary depth cue equivalence in the owl’s visual system supports the hypothesis that neural systems evolved to detect differences in either disparity or motion parallax information are likely to share similar processing mechanisms (van der Willigen et al., 2002).

2.7. *Adaptive significance of distinct head motions*

These studies also give rise to questions concerning the adaptive significance and evolutionary development of the head motions. The conjecture arises that because of their survival value, head motions aiding in depth perception have evolved from locomotor movements. This would enable the organism to control the system precisely so that, if necessary, distance measurements could be made as inconspicuously as possible. In all probability, one of the primary reasons for the initial use of motion parallax was to break the camouflage of stationary potential predators or items of prey or, to take the example of shorebirds, where it is not a question of camouflage, to solve the problem posed by refraction at the air/water interface. This hypothesis relating to camouflage was plausibly postulated by Julesz (1971), for instance, in connection with the binocular mechanism. An animal which is camouflaged in terms of colour and texture can be detected by means of motion parallax if the animal appears as a distinct surface with a depth plane different from that of its surroundings. The camouflage-breaking hypothesis can account for the fact that peering can be used to detect a stationary target which possesses the same texture as a more distant static background; the target can be detected during peering since its image moves more rapidly than that of the more distant background. Evidently the use of motion parallax continued to evolve in the direction of absolute depth perception; in the case of some animals, such as praying mantids and rats, with decisive effect. This probably occurred, for example, in response to the urgent necessity for safe, optimal locomotion or optimal attack.

2.8. Outlook

The studies reviewed here illustrate the potential of a behavioural–analytical approach in investigating the role of head movements in depth perception. As can be seen from these studies, the use of motion parallax for depth perception is widespread throughout the animal kingdom. However, many questions concerning the underlying mechanisms involved remain unanswered. In order to arrive at more precise conclusions, carefully designed experiments are required that are based on the behavioural repertoire and quantifiable motor outputs of the species concerned. It is hoped that this paper may help to stimulate the design of such experiments.

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