Mini-review

Interrelation of kinetic and stereoscopic depth: behavior and physiology in vertebrates☆

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Abstract

The target article gathers compelling behavioral evidence that motion parallax provides depth information in a variety of animal species. A more general evaluation of kinetic depth cues subserving depth perception would call attention to recent studies in monkeys, demonstrating the interrelation of kinetic and stereoscopic depth cues both on a behavioral and physiological level. Furthermore, it is argued that binocularity in birds has a clear function in stereopsis.
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1. Introduction

Kral provides an interesting summary on the role of head movements in a variety of animal species. Especially informative is the section about head motion in insects, the author's area of expertise. As indicated by the title, observer-induced motion cues subserving depth perception are emphasized, and the dominant part of the article deals with motion parallax.

Motion parallax (translational motion), however, is only one kinetic depth cue that can be exploited when the animal (or its head) moves. A superordinate concept for depth perception from relative 2-D motion would be structure-from-motion (SFM), which refers to the reconstruction of an object's 3-D shape from the relative 2-D motion of its parts. It is a pity that studies about non-human primates are not included in the review; the recent investigation of depth from kinetic cues both on a psychophysical and a neural level have been especially fruitful in monkeys. In the current article, therefore, some additional remarks about kinetic depth should be added.

Besides monocular kinetic cues, binocular stereoscopic cues are equally effective in depth perception. There is clear evidence that mammals and birds use horizontal disparity to compute 3-D information. However, while reading Kral's review, the reader gets the impression that the function of binocularity for depth perception in bird seems to be unclear. Some authors even deny that binocularity in birds is used to extract stereoscopic depth information and speculate, without any behavioral testing, that the "true" function of binocularity is related to optical flow field analysis (Martin and Katzir, 1999). Such speculations are hardly justified as behavioral, anatomical, and physiological studies provide convincing evidence indicating doubtlessly that one dominant

function of binocularity (at least in diurnal and nocturnal birds of prey) is stereoscopic depth vision. This article will summarize evidence to support this notion.

2. Kinetic and stereoscopic depth are interrelated

The perception of surface structure from stereopsis and from kinetic depth exhibits similar psychophysical characteristics and obeys common constraints (reviewed in Kham and Blake, 2000). The recognition of 3-D shape from motion can be as compelling and as accurate as that created by stereopsis (Rogers and Graham, 1982), making it sometimes impossible to distinguish depth based on kinetic depth from stereoscopic depth (Nawrot and Blake, 1993). In addition, both cues elicit depth capture, which refers to the intriguing phenomenon that the 3-D shape/depth of stationary objects is altered by virtue of its proximity to depth surfaces specified by stereopsis (stereo capture) or by structure-from-motion (kinetic depth capture; Ramachandran and Cavanagh, 1985; Kham and Blake, 2000). Psychophysical studies together with neurophysiological evidence suggest that kinetic depth and stereoscopic depth may share similar neural mechanisms (reviewed in Freeman, 1998).

3. Structure-from-motion—behavior in vertebrates

Behavioral studies demonstrate that owls and monkeys exploit kinetic cues for depth/3-D vision. Van der Willigen and co-authors (2002) provided elaborate and convincing evidence that motion parallax in owls is used for depth perception. In this study with operant conditioned barn owls, motion parallax induced by the owl's own head movements was shown to provide similar depth and structure information as stereoscopic cues. Apart from this study, evidence for the use of motion parallax in walking or flying pigeons is speculative. Kral discussed an unpublished study by Troje and Kelly, which is definitely worth mentioning, but it only provides theoretical reasoning why certain movement patterns could provide depth information through motion parallax. It would be important to show a direct impact of such information on the bird's perceptual ability.

In rhesus monkeys, Cao and Schiller (2002) recently examined depth perception through stereoscopic and kinetic depth cues. Object-induced motion parallax (translational movements by object motion) rather than the more complex, but functionally similar observer-induced motion parallax (translational movements of the observer) was investigated. The monkeys exploited depth information conveyed by both motion parallax and stereopsis. Mirroring results in humans, stereopsis was found to be slightly more effective for depth discrimination than motion parallax. Siegel and Andersen (1988), showed that monkeys can detect 3-D structure from motion in the same way as human subjects. Monkeys were trained to detect an 'illusory' rotating cylinder that appears when a certain dot-motion pattern was shown on a two-dimensional screen. This computer-generated dot-motion pattern was equivalent to the dot pattern generated by projecting points on a transparent rotating cylinder onto a plane orthogonal to the monkeys' line of sight. Although the resulting dot patterns on the two-dimensional screen move in opposite directions, dots moving in one direction appear to be in front of, or behind, those moving in the opposite direction. Monkeys were trained to detect the direction of the dots that appeared to them to be in front. By computer-controlled variation of the degree of correlation of dot motion (from unstructured to structured motion), the monkeys' detection of the 'illusory' rotating cylinder declined in a predictable way. The same result was obtained with three human observers.

4. Neural integration of motion and stereopsis in monkeys

Several electrophysiological investigations indicate that neurons in areas along the 'dorsal visual stream' of the mammalian cortex (like middle temporal area, MT, and medial superior temporal area, MST) process both kinetic and stereoscopic depth cues (Bradley et al., 1998; DeAngelis et al., 1998; Sugihara et al., 2002; Grunewald et al., 2002). In an elegant study, Bradley et al. (1998) trained rhesus monkeys to view an 'illusory' rotating cylinder that was created by two-dimensional projections of a trans-

parent, revolving cylinder. These stimuli appear to be three-dimensional, but the surface order (front as opposed to back) as well as the rotation direction which is perceived tends to reverse spontaneously. These reversals occur because the stimulus is ambiguous. While the monkeys viewed such images, recordings were made from neurons in MT. Neurons in MT show a preferred motion direction to which they heavily discharge, while the opposite, not-preferred motion direction suppresses the neuron's activity. Interestingly, the neurons reflected the rotation direction of the 'illusory' cylinder currently perceived by the monkey, even though the physical dot motion was identical for both motion direction conditions. These reports suggest the involvement of MT in the processing of SFM.

Neurons in area MT are not only selective to motion, but also to stereoscopic depth (Bradley et al., 1995; DeAngelis et al., 1998). In the above mentioned study by Bradley et al. (1998), therefore, many randomly interleaved trials were added in which the dots of the revolving 'illusory' cylinder contained stereoscopic disparity information. In these cases the cylinders are not ambiguous, but the motion direction of the cylinder's front is clearly defined by stereopsis. These trials were designed to control that the monkeys performed reliable on the trials with the bi-stabile kinetic depth stimuli. In addition, MT neurons were recorded to cylinder rotations defined by stereopsis. Many neurons responded strongly when the stereoscopically defined cylinder's front moved in the neurons' preferred motion direction. These data demonstrate that monkey MT responses directly reflect the perceived depth of moving surfaces, whether the surface is defined by kinetic depth or stereoscopic depth.

5. The function of avian binocular vision in depth perception

Stereoscopic depth perception has been demonstrated in a diurnal raptor, the falcon (Fox et al., 1977), and in a nocturnal raptor, the barn owl (van der Willigen et al., 1998). Behaviorally trained barn owls are able to see depth in computer-generated random-dot stereograms and possess global stereopsis comparable to that of humans (van der Willigen et al., 1998, 2002; Nieder and Wagner, 2001). The visual Wulst, the telencephalic termination zone of the thalamofu-

gal pathway in nocturnal (owls) and diurnal raptors (e.g. falcons), receives binocular information (Karten et al., 1973; Pettigrew, 1978; Bagnoli and Francesconi, 1984). In addition, Wulst neurons integrate binocular information (Pettigrew and Konishi, 1976), a prerequisite for stereopsis. A neural correlate for stereoscopic depth perception has been found in the visual forebrain of behaving owls. A large proportion of neurons in the visual Wulst discharged as a function of horizontal disparity in random-dot stereograms (Nieder and Wagner, 2000). The response characteristics of such disparity-sensitive neurons mirror precisely those found in the visual cortex of cats and non-human primates (Nieder and Wagner, 2000, 2001). Besides monkeys, the barn owl is the only model organism where the neural basis of stereopsis has been investigated in behaving animals. Stereopsis is doubtlessly one dominant functions of binocularity in birds.

6. Beyond depth: stereopsis and form perception

It is important to point out that depth perception is only one function of stereopsis. Another dominant function is form perception. Binocular horizontal disparity in random-dot stereograms also gives rise to sharp illusory contours at the depth-induced edges. Thus, stereopsis may not only be used for depth perception, but also for form perception in the absence of luminance-contrast contours. It is probably not a coincidence that barn owls also perceive illusory contour (generated by abutting gratings) and that Wulst neurons encode such illusory contours (Nieder and Wagner, 1999). Recent electrophysiological studies in monkeys revealed that neurons in early visual cortical areas (V2, and to a lesser extend V1) encode contours defined by stereoscopic depth (von der Heydt et al., 2000; Heider et al., 2002). Thus, binocularity and the resulting exploitation of stereoscopic depth is likely to support cue-independent perception of object borders in addition to depth perception.

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