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Adapting to monocular vision: grasping with one eye

Abstract The aim of the present study was to determine whether normal subjects with one eye covered and patients in whom one eye had been enucleated generate more head movements than subjects using binocular vision during the performance of a visually guided grasping movement. In experiment 1, 14 right-handed normal subjects were tested binocularly and monocularly in a task in which they were required to reach out and grasp oblong blocks of different sizes at different distances. Although the typical binocular advantage in reaching and grasping was observed, the overall head movement scores did not differ between these testing conditions. In experiment 2, seven right-handed enucleated patients were compared to seven age and sex-matched control subjects (tested under binocular and monocular viewing conditions), on the same task as used in experiment 1. While no differences were found in the kinematics of reaches produced by the enucleated patients and the control subjects, the patients did produce larger and faster resultant head movements, composed mainly of lateral and vertical movements. This suggests that enucleated patients may be generating more head movements in order to better utilize retinal motion cues to aid in manual prehension.

Key words Prehension · Enucleation · Monocular and binocular · Visuomotor behaviour · Human

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Introduction

A recent examination (Servos et al. 1992) of the contribution of binocular vision to the control of reaching and grasping movements revealed that manual prehensile movements made under monocular viewing conditions differed substantially from those performed under binocular conditions. Those reaches made under monocular viewing exhibited longer movement times, longer latencies before beginning movement, lower peak velocities, proportionally longer deceleration phases and smaller grip apertures than movements made under binocular viewing. The Servos et al. (1992) study provides clear evidence that binocular vision makes a significant contribution to the accurate programming of manual prehensile movements in humans. Nevertheless, although monocular reaches were "less efficient" than binocular reaches, subjects were still able to perform the task remarkably well when using only one eye. Subjects must have been utilizing monocular depth cues, such as accommodation, retinal motion cues, or perhaps other pictorial cues, to control their reaching movements.

Dees (1966) found that, with proper training, a cyclical (side-to-side) head motion added significantly to the accuracy of distance and size estimation. This head motion allowed for better use of the powerful monocular depth cue motion parallax which produces a reliable, consistent, and unambiguous impression of relative depth in the absence of all other cues to depth and distance (Rogers and Graham 1979). Motion parallax depends on the perspective transformations of the retinal image and can be produced by movement of the observer or by the movement of an object itself (Rogers and Graham 1979). The effectiveness of motion parallax as a result of self-produced head movements has been examined in only a few motion perception studies. Typically, studies of motion parallax have relied on a stationary observer with a moving stimulus display. However, studies where motion parallax was derived from self-produced motion have found that subjects make more accurate judgements of depth when their heads are free to move (Ferris 1972; Biguer et al. 1984).

Humans are not the only organisms to utilize motion depth cues. Previous insect literature has revealed that locusts perform side-to-side "peering" head movements to obtain motion depth cues, and that the amplitude of these head movements increases with increasing object distance (Wallace 1959; Collett 1978). Rodents have also been observed making head movements prior to jumping a gap (Russell 1932; Legg and Lambert 1990). Previous research in our laboratory has revealed that Mongolian gerbils, under binocular and monocular viewing conditions, execute a series of vertical head movements prior to jumping a gap, the amplitude and velocity of which were strongly correlated with gap distance, as was the case in the above-mentioned locust research, and to each animal's accuracy. Specifically, gerbils were found to bob the head more often before jumping a gap when using monocular vision than when using binocular vision. Head bobbing incidence was also related to an animal's readiness to initiate a jump. Those animals that bobbed their heads the most had the least difficulty jumping the gap. This suggests that the gerbils were employing retinal motion, derived from self-generated head movements, to judge distance and that when animals were tested using monocular vision they generated more head bobs to better utilize retinal motion (Ellard et al. 1984, 1986; Goodale et al. 1989).

It is important to make a distinction between retinal motion cues, which are used to calibrate absolute distance, and motion parallax, which yields only relative depth judgements. While motion parallax can be generated by any relative movement of the observer and the world, it can be used to calibrate real distance only when the distance of one of the objects in the array is already known. It is possible, however, to generate an accurate estimate of distance from the movement of a point on the retina if one "knows" the magnitude of one's head movements (and/or the movements of the eyes in the orbit as one fixates that point). In short, the term "motion parallax" should perhaps be reserved for situations where relative depth is being computed, and the term "head-generated retinal motion" be used in situations where the computation of absolute distance is required. In the perception literature, however, there is often little distinction made between these two kinds of retinal motion computations. For this reason, throughout the paper, we will use the term "motion cues" rather than "motion parallax cues".

Steinbach and Ono (1991) compared the relative effectiveness of rotating or translating the head, either horizontally or vertically, on the perception of depth from the resulting motion cues for subjects under a monocular viewing condition. Although vertical head movements produce motion cues for depth, which has also been reported in the above-mentioned animal literature, side-to-side head movements yielded the most precise depth judgements, irrespective of whether the movements were translational or rotational.

One question that arises then is: When subjects are required to grasp an object under monocular viewing conditions, as in the study by Servos et al. (1992), do they generate head movements to create motion cues that could compensate for the lack of binocular information? The first experiment of the current study was designed to answer this question. In this experiment, head movements were measured in normal subjects as they reached out and grasped objects under monocular or binocular viewing conditions. The second experiment was conducted in parallel with the first and examined head movements in individuals who had lost an eye (enucleated patients). It is possible that these patients might have learned to use head movements to generate motion cues that would assist them in calibrating the distance (and size) of objects that they might wish to grasp. Previous enucleation research suggests that some form of adaptation must take place, since enucleated patients with good vision in their remaining eye typically report no permanent visual difficulty following enucleation and return to normal activities within 1 year, often making the adjustment in less than 1 month (Allara et al. 1986; Schwartz et al. 1987).

Gonzalez et al. (1989) tested monocular children enucleated before the age of 2 years in a depth discrimination task using a version of the Howard Dolman test that left retinal motion (motion parallax) as the only available cue. They found that both enucleated and normal binocular children with one eye covered moved their heads very little, resulting in relatively poor precision. However, both groups improved their performance significantly after being instructed to move their head. Gonzalez et al. concluded that it would be useful for enucleated individuals to move their head when discriminating depth. Steinbach and Ono (1991) also came to this conclusion when they found that horizontal head movements produced quite precise depth judgement in normal subjects under a monocular condition. They suggested that enucleated patients be taught the value of horizontal head movements when trying to resolve small depth differences.

Thus, previous research has highlighted the strength and effectiveness of the use of motion cues by enucleated patients. Although Gonzalez et al. (1989) reported that enucleated children did not spontaneously move their head during depth discrimination tasks, it is possible that during reaching tasks adult enucleated patients may move their head to employ motion information. The action of reaching towards a visual goal involves a combination of movements. In normal conditions, a subject will first orient his gaze, then his head, and finally his arm in the proper direction (Biguer et al. 1982, 1984). Moreover, movements of the head and torso are also required to deal with the forces generated by movements of the limb and to extend the range of the limb. Enucleated patients may exaggerate these natural head (and torso) movements during a reach in order to better utilize motion cues to assist in estimating depth.

In summary, experiment 1 of our current study was an attempt to determine whether normal subjects generate more head movements during a visually guided grasping movement when they are wearing an eye patch than when they are using binocular vision. An increased

amount of head movements under monocular viewing could indicate that subjects are trying to better utilize retinal motion depth cues to aid in the control of grasping. Experiment 2 compared adaptations made by enucleated patients to those of age and sex-matched control subjects performing the same reaching tasks under both monocular and binocular viewing conditions.

Materials and methods

Both experiments were carried out at the University of Western Ontario in compliance with the Social Sciences and Humanities Research Council Guidelines (1981).

Experiment 1

Subjects

Fourteen adult subjects (7 males, 7 females, mean age 28.3 years) with normal or corrected-to-normal vision participated in experiment 1, for which they were paid. All subjects were strongly right-handed, as determined using a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). All subjects had stereoscopic vision in the normal range with assessed stereoacuity of $40''$ of arc or better as determined by the Randot Stereotest (Stereo Optical, Chicago).

Apparatus

Subjects sat at a table (100 cm wide and 61 cm deep) with a matte grey surface. A circular, 1-cm-diameter microswitch button located 15 cm from the subject functioned as the start position for each reaching movement. This start button was located directly in front of the subject along the sagittal plane of the body. A circular fluorescent lamp was suspended approximately 80 cm above the table's surface. This lamp was illuminated by the experimenter from a remote switch that also triggered the start of data collection.

Three red, oblong wooden blocks (2 cm thick) with surface areas of 2×5 cm, 3×7.5 cm, and 5×12.5 cm were used. The objects were positioned with their long axis perpendicular to the body midline. The underside of each of the objects contained an embedded magnet which, when placed in position, closed one of three magnetic switches located under the table surface at distances of 20, 30 or 40 cm from the microswitch along the subject's midline. When subjects picked up the object, contact between the two magnets was broken, signalling the end of collection for a given trial.

Three 4-mm-diameter infrared light-emitting diodes (IREDs) were attached with small pieces of cloth adhesive tape to the head of the radius at the right wrist, the ulnar portion of the right border of the thumbnail, and above the radial edge of the first knuckle on the index finger. The tape allowed complete freedom of movement of the hand and fingers.

Three more IREDs were mounted on a head-piece that had been painted flat black and was attached to a Velcro band placed around the subject's head. The head-piece consisted of a T-bar mounted on a cork base, with an IRED angled at 45° at the end of each arm of the T-bar, 10 cm apart. The head-piece extended two of the IREDs 7.5 cm from the subject's forehead. The third IRED was positioned on the cork base of the head-piece, so that it extended 4 cm from the subject's forehead.

The IREDs were monitored by two high-resolution infrared-sensitive cameras positioned approximately 2 m from the subject. The positions of the IREDs were digitized at a rate of 100 Hz into two-dimensional coordinates and then passed on to the data collection system of a WATSMART computer (Waterloo Spatial Motion Analysis and Recording Technique; Northern Digital, Waterloo, Ontario, Canada).

Procedure

At the beginning of the test session, subjects were given the handedness questionnaire and tested for eye dominance (viewing prefence) and stereoacuity (Randot Stereotests). Subjects were then seated at the testing table and instructed to pick up the target object with the thumb and index finger of their right hand across the narrow part of the block as soon as they could see it after the overhead light was illuminated. They were instructed to reach as quickly, accurately and "naturally" as possible.

At the beginning of each trial, subjects placed the tips of the index finger and thumb of their right hand on the start button. Between trials, the room lights were extinguished and subjects were instructed to keep their eyes closed during this time. Once a block had been placed in a given position by the experimenter, subjects were given a verbal signal to open their eyes and the overhead light was turned on, which started the collection of the trial.

Subjects were administered testing blocks of 45 experimental trials, each consisting of five instances of each of the nine possible distance × object size combinations. Trial presentation was random and each testing block was preceded by a series of five practice trials. Each subject performed one block of trials using binocular vision and one block under monocular presentation to their dominant eye. These trials were counterbalanced between subjects. Any experimental trial in which the subject dropped an object was repeated at the end of a given block. The testing session lasted for approximately 60 min.

Accuracy of system

Calibration of the WATSMART system involved placing in the experimental work-space a rigid frame to which were attached 24 IREDs at specific locations. The WATSMART calibration software calculates the three-dimensional root mean square error of reconstruction for the locations of a minimum of 22 IREDs to be less than 2 mm. To calibrate the orientation of the axes to be used during the experiments, a rigid board, imbedded with three IREDs forming the vertices of a right-angled triangle with sides measuring approximately 10, 15, and 18 cm was placed on the table directly in front of the microswitch such that one of the triangle's axes was aligned parallel with the subject's midline, and a 0.5 s sample was stored on the file of each subject.

Data processing

Stored sets of two-dimensional (2-D) coordinates were converted into three-dimensional (3-D) coordinates off-line and filtered (with a low pass second-order Butterworth filter with a 7-Hz cut-off). The IREDs on the index finger and thumb provided information about the kinematics of the grasp, while the wrist IRED provided information about the reach. The centre IRED mounted on the head-piece provided information about the head movements made by the subject during the entire reach.

Dependent measures

The kinematic measures computed from the 3-D coordinates corresponding to a given prehension movement were the same as those used by Servos et al. (1992) and all of them have been shown to vary as a function of viewing condition. These measures were: (1) time to movement onset for the reach (the first frame from a series of ten consecutive frames in which the resultant velocity exceeded 5.0 cm/s); (2) movement duration of the reach (calculated by subtracting the movement onset time from the time at which an object was lifted, breaking the magnetic switch); (3) maximum grip aperture (the maximum vectored distance between the thumb and index finger IREDs), (4) peak resultant velocity of the reach; (5) the time following movement onset at which this peak velocity occurred; (6) peak acceleration of the reach in the Z (forward/backward) dimension; (7) the time following movement

onset at which peak acceleration occurred; (8) peak deceleration of the reach in the Z dimension and (9) the time following movement onset at which this peak deceleration occurred. Measurements 4–9 were based upon data from the wrist IRED.

The kinematic measures for the head movements were: (1) peak resultant displacement of the head movement; (2) the time during the reach at which this peak displacement occurred; (3) the X (horizontal), Y (vertical), and Z (forward/backward) components that make up the peak resultant displacement; (4) the time during the reach at which these components occurred; (5) the peak resultant velocity of the head movement; (6) the time at which peak velocity occurred; (7) the X, Y, and Z components that make up the peak resultant velocity; (8) the time at which these components occurred. All of the measurements for the head were based on the middle head IRED. In addition, all three IREDs were used to calculate the amount of head rotation that occurred during the production of head movements.

Experiment 2

Subjects

Subjects consisted of seven adult, enucleated patients (six males, one female, mean age 32.4 years; four right eye enucleations, three left eye enucleations, enucleations performed 17 months to 35 years prior to testing, mean time since enucleation 18.9 years) and seven age- and sex-matched control subjects (mean age 33 years). All subjects participated for financial compensation, were strongly right-handed and had normal or corrected-to-normal visual acuity.

Procedure

The apparatus and procedure were identical to those used in experiment 1, except that enucleated patients were presented with only one block of trials.

Results

Experiment 1

For each of the 14 subjects, mean values of each of the dependent variables were calculated across five observations for each size and distance combination in both viewing conditions (equipment failure resulted in some loss of data, but this constituted less than 2% of the trials). The mean values were entered into separate 2×3×3 (viewing condition × object size × object distance) repeated-measures analyses of variance. All tests of significance were based upon an alpha level of 0.05. Post hoc Newman-Keuls analyses were then performed where necessary.

Reach kinematics

In agreement with Servos et al. (1992), the typical binocular advantage in reaching and grasping was observed; that is, reaches made under monocular vision exhibited longer movement times and produced longer deceleration periods than reaches made under binocular vision (see Fig. 1).

Grasp kinematics will not be reported here since, in the current study, the index finger IRED was placed above the left edge of the first knuckle rather than on the distal portion of the left border of the index fingernail as
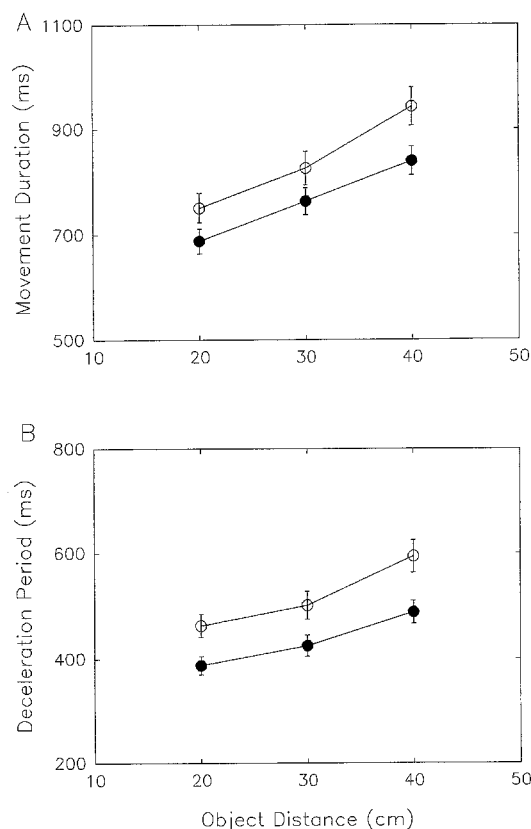

Fig. 1 **A** Movement duration and **B** deceleration period as a function of object distance and viewing condition (*error bars* SEMs, *open circles* monocular viewing condition, *filled circles* binocular viewing condition)

per Servos et al. (1992). Although this was necessary in order for all of the IREDs to be within the cameras' field of view, in retrospect this may have been a mistake since the movement of the most distal portion of the finger was not being measured. As a consequence, the measurements obtained were not directly comparable to those reported by Servos et al. (1992) and indeed did not reflect the full range of movement of the finger.

Head movements

Subjects' resultant head movements did not differ significantly in peak displacement or velocity between the testing conditions (see Table 1). However, as seen in Fig. 2, when the subjects' resultant head movements were separated into their component parts, subjects under the monocular viewing condition were found to make larger and faster forward (Z component) head movements towards the goal object, but smaller horizontal (X component) head movements, than they did under binocular viewing.

Experiment 2

Mean values of the dependent variables were calculated for each viewing condition, in the same manner as in experiment 1. (Equipment failure resulted in some loss of

Table 1 Summary of the main effects of viewing condition on various kinematic variables related to head movements averaged over all other conditions for experiment 1 (*displ.* displacement)

Kinematic variable	Viewing condition		
	Monocular	Binocular	*F* value
	Mean (SEM)	Mean (SEM)	
Peak head displ. (mm)	30.6 (1.6)	34.2 (1.8)	2.04 n.s.
Time to peak head displ. (ms)	1223.4 (24.5)	1159.2 (18.8)	7.54*
Peak head velocity (mm/s)	96.4 (3.5)	105.3 (4.1)	2.61 n.s.
Time to peak head velocity (ms)	886.4 (17.3)	849.0 (15.7)	4.97*
Peak *X* head displ. (mm)	18.0 (1.0)	23.8 (1.4)	9.13**
Time to peak *X* head displ. (ms)	1221.1 (24.7)	1178.7 (19.2)	2.17 n.s.
Peak *X* head velocity (mm/s)	49.3 (1.7)	61.9 (2.5)	8.30*
Time to peak *X* head velocity (ms)	880.1 (15.1)	840.5 (13.8)	5.22*
Peak *Z* head displ. (mm)	13.0 (1.4)	9.5 (1.2)	4.57*
Time to peak *Z* head displ. (ms)	882.90 (41.3)	711.1 (38.3)	29.40***
Peak *Z* head velocity (mm/s)	61.7 (2.9)	53.5 (3.1)	5.91*
Time to peak *Z* head velocity (ms)	938.5 (22.5)	840.5 (24.8)	11.15**
Peak *Y* head displ. (mm)	11.5 (1.0)	12.5 (1.0)	0.51 n.s.
Time to peak *Y* head displ. (ms)	981.0 (25.4)	920.0 (27.2)	6.17*
Peak *Y* head velocity (mm/s)	56.0 (2.7)	58.8 (3.0)	0.49 n.s.
Time to peak *Y* head velocity (ms)	793.0 (13.5)	778.1 (12.9)	1.38 n.s.

* *P*<0.05; ** *P*<0.01;
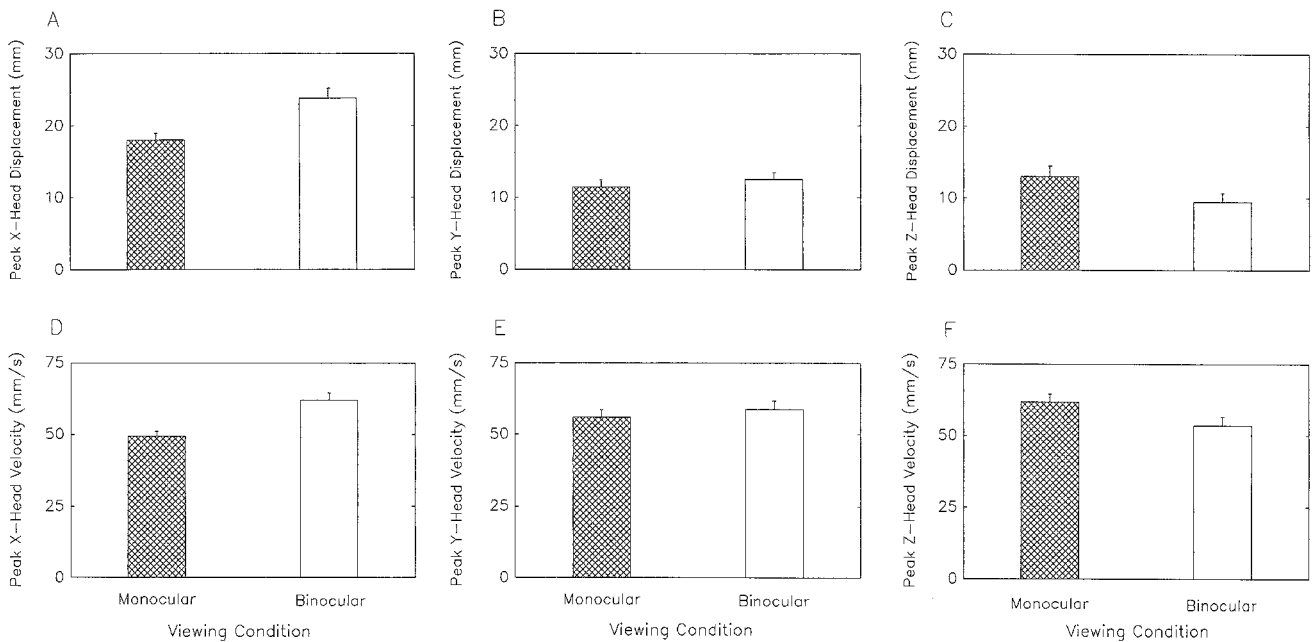***P*<0.001, *n.s.* not significant

Fig. 2A–F The effects of viewing condition on head movements for control subjects tested under monocular and binocular viewing conditions. **A** Peak *X* head displacement, **B** peak *Y* head displacement, **C** peak *Z* head displacement, **D** peak *X* head velocity, **E** peak *Y* head velocity, **F** peak *Z* head velocity (*hatched column* monocular viewing condition, *empty column* binocular viewing condition

data, but this constituted less than 2% of the trials.) The mean values were entered into separate 3×3×3 (viewing condition × object size × object distance) repeated measures analyses of variance. Post hoc Newman-Keuls analyses were then performed.

Reach kinematics

The enucleated patients' manual prehensile movements did not differ significantly from those of their age- and sex-matched control subjects (see Table 2).

Head movements

While no significant differences were found in the reach kinematics between the enucleated patients and the control subjects, the patients did produce larger and faster resultant head movements (see Table 3). These head movements were mainly composed of *X*-plane and *Y*-plane movements (see Fig. 3). The mean rotation of patients' head movements in the horizontal plane was found to be only 3.23° (SD=2.21°) and thus contributed little to the lateral movements that were observed.

Most kinematic measures of head movements were correlated with distance for the patients and their control subjects. As seen in Fig. 4, the increase in peak X-plane head displacement that occurred with distance was largest for the enucleated patients.

Table 2 Summary of the main effects of viewing condition on various kinematic variables averaged over all other condition for experiment 2 (*vel.* velocity, *acc.* acceleration, *dec.* deceleration)

Kinematic variable	Viewing condition		
	Enucleated patients	Controls, monocular	Controls, binocular
	Mean (SEM)	Mean (SEM)	Mean (SEM)
Movement onset (ms)	469.8 (11.0)	543.8 (13.8)	475.5 (10.2) n.s
Movement duration (ms)	908.9 (19.1)	910.7 (38.0)	794.4 (29.2) n.s.
Deceleration period (ms)	565.5 (15.3)	569.9 (27.9)	466.8 (23.1) n.s.
Peak vel. of reach (mm/s)	731.6 (25.9)	768.4 (27.4)	836.4 (28.6) n.s.
Time to peak velocity (ms)	343.5 (6.6)	340.8 (13.9)	331.6 (10.3) n.s.
Peak acceleration (cm/s^2)	441.2 (16.2)	427.5 (13.9)	462.7 (17.1) n.s.
Time to peak acc. (ms)	174.8 (7.4)	170.2 (10.6)	172.6 (9.4) n.s.
Peak deceleration (cm/s^2)	327.1 (12.1)	385.2 (17.6)	453.0 (20.9) n.s.
Time to peak dec. (ms)	520.1 (10.5)	493.3 (12.1)	492.2 (10.9) n.s.

Table 3 Summary of the main effects of viewing condition on various kinematic variables related to head movements averaged over all other conditions for experiment 2

Kinematic variable	Viewing condition		
	Enucleated patients	Controls, monocular	Controls, binocular
	Mean (SEM)	Mean (SEM)	Mean (SEM)
Peak head displ. (mm)	58.7 (4.4)[*1,*2]	28.5 (2.5)[*1]	31.6 (2.3)[*2]
Time to peak head displ. (ms)	1315.8 (23.5)	1349.7 (42.0)	1217.5 (32.9) n.s.
Peak head vel. (mm/s)	133.6 (6.4)[*1,*2]	83.7 (4.9)[*1]	93.1 (4.9)[*2]
Time to peak head vel. (ms)	887.6 (23.3)	1012.2 (31.6)	897.4 (27.2) n.s.
Peak X head displ. (mm)	44.1 (3.0)[δ1, α2]	13.5 (1.0)[δ1]	19.4 (1.4)[α2]
Time to peak X head displ. (ms)	1339.1 (23.1)	1294.7 (39.1)	1185.7 (29.9) n.s.
Peak X head vel. (mm/s)	85.6 (4.0)[α1,*2]	43.1 (1.7)[α1]	56.1 (2.7)[*2]
Time to peak X head vel. (ms)	927.7 (20.3)	981.3 (31.8)	872.7 (29.3) n.s.
Peak Z head displ. (mm)	12.0 (2.5)	16.9 (2.8)	15.0 (2.3) n.s.
Time to peak Z head displ. (ms)	692.0 (64.3)	1046.7 (66.7)	900.1 (63.3) n.s.
Peak Z head vel. (mm/s)	67.5 (4.6)	62.0 (5.4)	57.0 (4.8) n.s.
Time to peak Z head vel. (ms)	969.2 (36.1)	1049.2 (31.5)	934.4 (31.5) n.s.
Peak Y head displ. (mm)	21.90 (2.2)[*1,β2]	7.4 (0.5)[*1]	7.4 (0.7)[β2]
Time to peak Y head displ. (ms)	1058.5 (23.5)	1017.3 (38.0)	817.4 (39.9) n.s.
Peak Y head vel. (mm/s)	66.9 (4.2)[α1, α2]	34.5 (1.5)[α1]	39.0 (2.0)[α2]
Time to peak Y head vel. (ms)	764.2 (13.9)	801.2 (30.1)	740.8 (26.5) n.s.

* $P<0.05$, α $P<0.01$, β $P<0.025$, δ $P<0.005$, *n.s.* not significant (numbering of symbols indicates conditions under comparison)
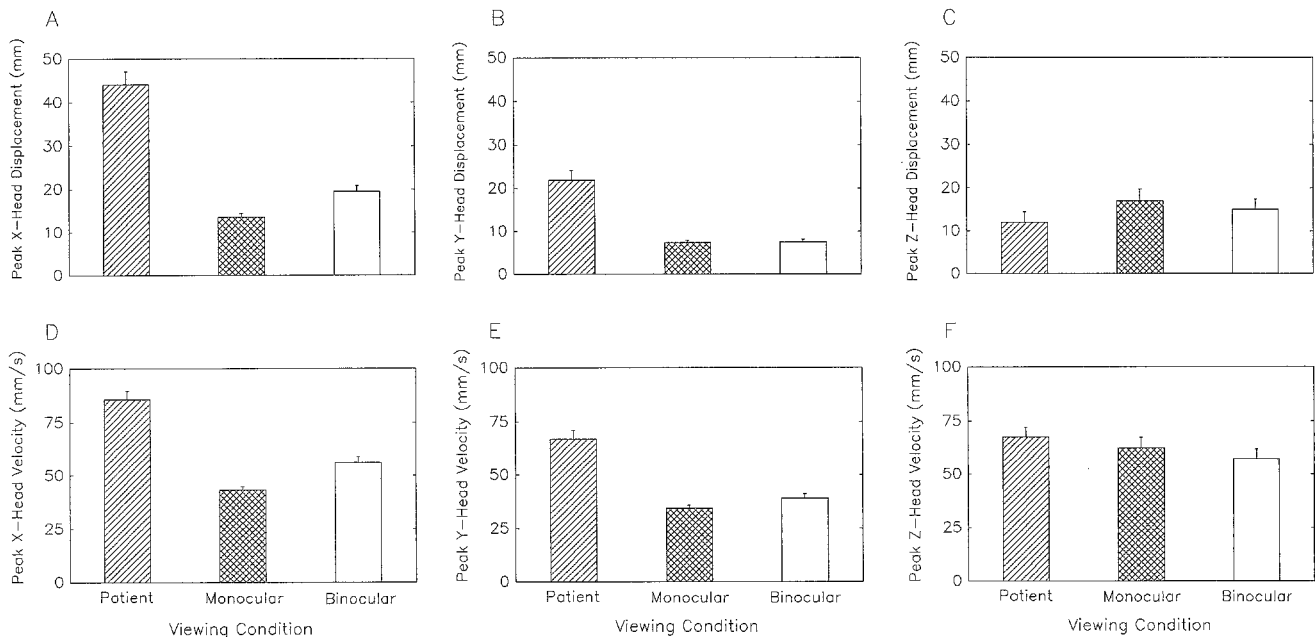

Fig. 3A–F The effects of viewing condition on head movements for the enucleated patients and for the control subjects in monocular and binocular viewing conditions. **A** Peak X head displacement, **B** peak Y head displacement, **C** peak Z head displacement, **D** peak X head velocity, **E** peak Y head velocity, **F** peak Z head velocity (*diagonally striped column* enucleated patients, *hatched column* mononuclear viewing condition: controls, *empty column* binocular viewing conditions: controls)
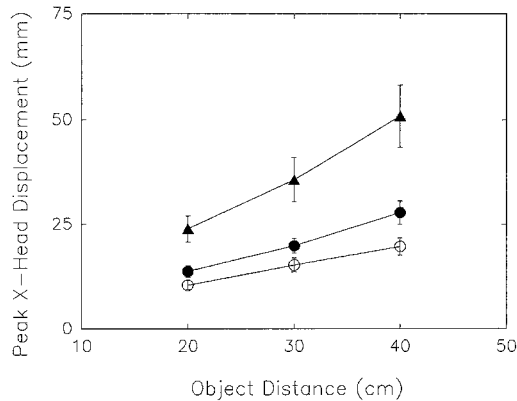
Fig. 4 Peak *X* head displacement as a function of object distance and viewing condition (*error bars* SEMs, *filled triangles* enucleated patients, *open circles* controls monocular viewing condition, *filled circles* controls binocular viewing condition

Discussion

As in the Servos et al. (1992) study, restricting vision to only one eye had dramatic effects on the normal pattern of reaching movements. Even though monocular cues were still available, performance was clearly disturbed by the removal of binocular information. Yet subjects were still able to perform the task under monocular viewing.

The question still remains: do subjects compensate for the loss of binocular cues by generating more head movements and thus increasing the availability of retinal motion cues? In the present experiment, there was little evidence that normal subjects were using this strategy since their overall head movements under the two viewing conditions did not differ. This result seems to support the findings of Gonzalez et al. (1989), who found that enucleated children and binocular children with one eye covered moved their heads very little during a depth discrimination task, resulting in relatively poor precision. Nonetheless, when the resultant head movements made by the subjects in our experiment were broken into their component parts it became clear that the pattern of head movements shown by the subjects did change as a function of viewing condition. When they were wearing an eye patch, subjects made larger and faster head movements in the forward plane towards the goal object. While these forward head movements would have generated "looming" motion cues which are potentially useful as a source of information of egocentric distance and "time-to-contact", any positional or velocity information generated by the changing retinal image would be less than half as large, and thus possibly not as helpful, as that generated by comparable displacements in the *X* or *Y* plane (Lappin 1991; Simpson 1993; Humphrey and Simpson, personal communication 1994). Yet there was no evidence that subjects increased the magnitude (or velocity) of these kinds of movements under monocular viewing, even though this would have been the best strategy. The fact that they failed to do this may have been due to the novelty of the monocular viewing condition for these subjects. When using monocular vision, sub-

jects may not have had sufficient time to learn that producing greater lateral head movements would provide the most useful retinal motion cues, and, instead, they may have tried to compensate for the lack of binocular cues by making greater forward head movements in order to bring themselves closer to the objects.

While the kinematic measurements of enucleated patients' manual prehensile movements did not differ significantly from those of the age- and sex-matched control subjects, there did seem to be a trend towards lower peak velocities for patients during their reaches. Although enucleated patients' movement durations and deceleration periods were similar to control subjects when the control subjects were reaching under the monocular conditions, their movements were generally longer than those of the control subjects when these subjects were reaching with full binocular vision. Yet there was no indication that enucleated patients were any slower off the mark than the control subjects, even when the controls were using binocular vision.

While there were no significant differences between the enucleated patients and the control subjects in the kinematics of their reaches, patients did generate larger and faster head movements. This indicates that, in contrast to the findings of Gonzalez et al. (1989), enucleated patients may have exaggerated the natural head movements involved during a reach in order to better utilize motion information in computing the distance (and thus the size) of objects. This finding does coincide with the suggestions of Gonzalez et al. (1989) and Steinbach and Ono (1991) that enucleated patients should be taught to produce horizontal head movements in order to better utilize motion parallax when having to make judgements of depth. Also, once the head movements were broken down into their component parts, it was clear that enucleated patients generated larger and faster lateral and vertical head movements, which Steinbach and Ono (1989) have indicated are effective movements for the production of motion parallax, than did the control subjects.

As revealed earlier, past insect and animal research has revealed the use of motion cues when judging depth. While locusts were found to perform side-to-side "peering" head movements (Wallace 1959; Collett 1978), rodents produce vertical "head bobs" to better utilize motion cues when judging depth (Legg and Lambert 1990). When Mongolian gerbils were tested under monocular viewing conditions, they generated more head bobs than when using binocular vision (Ellard et al. 1984, 1986; Goodale et al. 1989). As the current study indicates, enculeated patients appeared to be generating "gerbil-like" vertical head movements that may assist in their judgment of the objects' depth. Steinbach and Ono (1991) specifically found that side-to-side and rotational head movements produce the most precise depth judgements. In the current study, enucleated patients' resultant head movements were mainly composed of lateral movements in the *X*-plane (with a small rotational component), which strengthens the argument that enucleated patients are generating larger head movements to generate useful motion cues. The peak velocities of the lateral and verti-

cal head movements also indicate that enucleated patients have learned that these types of movements are effective in producing motion cues and they therefore are actively generating them. In the present study, as in the above mentioned insect and animal research, the amplitude and velocities of subjects' head movements increased with increasing distance, with enucleated patients seemingly increasing their lateral head movements in association with increasing distance more than the control subjects. Ellard et al. (1984) attributed this increase in animal and insect head movements and velocities to an attempt at maintaining some minimal amount of retinal image translation to allow for accurate depth judgements as distance of the target object increased.

As described earlier, enucleated patients took no longer to initiate a grasping movement than the control subjects reaching under binocular viewing. This finding can be compared to the relationship found by Ellard et al. (1984) between head bobbing incidence in Mongolian gerbils and the animals' readiness to initiate a jump. Gerbils that produced a large number of head bobs under binocular testing did not hesitate to jump over the gap as much as other animals when they were shifted to monocular viewing and therefore were able to perform the task more efficiently (Ellard et al. 1984). Perhaps then, by producing larger head movements, the patients, like the gerbils making a large number of head movements, were more confident about initiating a reach. Once the reach was initiated, however, the patients were more careful about their approach to the target, where a misjudgment in depth would produce a reaching error. If a larger pool of enucleated patients could be located and tested, the findings might serve to strengthen this conclusion.

In summary, this study represents the first examination of manual prehension in enucleated patients and clearly reveals that while control subjects under the monocular viewing condition generate large forward head movements, enucleated patients have learned that horizontal head movements are the most effective form of head motion for the production of motion depth cues which can aid in manual prehension. This has been further strengthened by additional research in our laboratory involving recently enucleated patients. These patients, compared with those in the present study who have lived with only one eye for a year or more, showed a pattern of head movements that was more similar to that of the control subjects; in other words, they made more forward than lateral or vertical head movements (Marotta et al., in press). Taken together, these results suggest that some adaptation must take place as the patients learn to cope with having one eye.

The finding that enucleated patients adapt over time to their visual situation by generating larger head movements in the X and Y planes supports the conclusions of Gonzalez et al. (1989) and Steinbach and Ono (1991) that a training program for recently enucleated patients should be initiated to teach the value of lateral and vertical head movements when performing depth judgements, especially when executing motor tasks.

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