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RESEARCH ARTICLE

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Distance estimation in the visual and visuomotor systems

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Abstract Previous work has demonstrated that monocular vision affects the kinematics of skilled visually guided reaching movements in humans. In these experiments, prior to movement onset, subjects appeared to be underestimating the distance of objects (and as a consequence, their size) under monocular viewing relative to their reaches made under binocular control. The present series of experiments was conducted to assess whether this underestimation was a consequence of a purely visual distance underestimation under monocular viewing or whether it was due to some implicit inaccuracy in calibrating the reach by a visuomotor system normally under binocular control. In a purely perceptual task, a group of subjects made similar explicit distance estimations of the objects used in the prehension task under monocular and binocular viewing conditions, with no time constraints. A second group of subjects made these explicit distance estimations with only 500-ms views of the objects. No differences were found between monocular and binocular viewing in either of these explicit distance-estimation tasks. The limited-views subjects also performed a visually guided reaching task under monocular and binocular conditions and showed the previously demonstrated monocular underestimation (in that their monocular grasping movements showed lower peak velocities and smaller grip apertures). A distance underestimation of 4.1 cm in the monocular condition was computed by taking the *y* intercepts of the monocular and binocular peak velocity functions and dividing them by a common slope that minimised the sum of squares error. This distance underestimation was then used to predict the corresponding underestimation of size that should have been observed in the monocular reaches – a value closely approximating the observed value of 0.61 cm. Taken together, these results suggest that the monocular underestimation in the prehension task is not a consequence of a purely perceptual bias but rather it is visuomotor in nature – a monocular input to a system that normally calibrates motor output on the basis of binocular vision.

Key words Humans · Prehension · Monocular · Binocular · Limb movements · Distance estimation · Visual feedback · Visuomotor behaviour

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Introduction

Depth vision and the calibration of motor output

Although the study of depth vision in humans has a long history, the majority of work has concentrated on the role of different depth cues in judgements of relative depth or in the segregation of figure from ground (Freeman 1970; Bishop 1973, 1987; Poggio and Poggio 1984; Arditi 1986; Julesz 1986). Far fewer studies have examined the contribution of depth cues to judgements of absolute distance; that is, judgements of the actual distance from the observer to a stimulus of interest. The plethora of studies investigating judgements of relative depth and the segregation of figure from ground is due in part to the fact that most of this sort of research has been concerned with perceptual or cognitive judgements of depth, rather than the use of depth information for the visual control of motor output such as locomotion or arm movements.

Although some monocular cues, such as motion parallax and accommodation (Servos et al. 1992; Goodale and Servos 1996), could potentially be used for the computation of distance estimations in humans, it is likely that binocular cues, such as vergence, stereopsis and binocular vertical disparities provide the most accurate distance information (Foley and Held 1972; Foley 1980; Morrison and Whiteside 1984; Bishop 1989; Goodale and Servos 1996). Because humans are exquisitely adept at reaching out and grasping objects, it is likely that this type of behaviour relies on accurate distance estimations. When we initiate a grasping movement, not only do we reach toward the correct spatial location of the goal object, but the posture of our hand and fingers anticipates the size, shape and orientation of that object well before contact is made.

Neurological, developmental and anatomical evidence suggest that visually guided prehension consists of two relatively independent, but temporally coupled, components (for review, see Jeannerod 1988). One of these components is the reach itself, in which the hand is transported to the location of the target object. The other is the grasp, in which the posture of the hand and fingers is adjusted to reflect the size, shape and orientation of the object before contact is made. The peak velocity of the reach and several other transport parameters vary as a function of object distance. For the target distances we have used in our previous work, there is a linear scaling between target distance and reach variables such as movement duration and peak velocity. The peak velocity of the reach can be used as an index of the estimated target distance prior to movement onset (Servos et al. 1992; Goodale and Servos 1996). The grasp varies as a function of the size of the target object (Marteniuk et al. 1987; Jeannerod 1988; Jakobson and Goodale 1991; Servos et al. 1992; Servos and Goodale 1994). The calibration of the size of the maximum grip aperture during the reach (which occurs before object contact) also depends on estimations of distance (Jakobson and Goodale 1991; Servos et al. 1992; Servos and Goodale 1994), particularly with unfamiliar objects for which object distance must be combined with the size of the subtended retinal image to compute the target object’s size.

The effects of replacing binocular vision with monocular vision

In previous work, we have shown that the depth and distance cues provided by binocular vision appear to affect the kinematics of not only the transport component but also the grasp component of skilled visually guided reaching movements in humans (Servos et al. 1992; Servos and Goodale 1994). In these experiments, subjects reached out and picked up objects placed at various distances from them either under full binocular vision or under monocular viewing conditions. Their view of the object and the surrounding table top was unrestricted and most of the normal distance cues were available, including static cues such as perspective, elevation, relative position with respect to the table edge, accommodation and motion parallax. Despite the rich array of distance and size cues, however, covering one eye affected the kinematics of the subjects’ reaching and grasping movements. Their reaching and grasping movements showed longer movement times, lower peak velocities, proportionately longer deceleration phases and smaller grip apertures than movements made under binocular viewing. These differences were not simply due to strategy effects (i.e. an anticipation of reduced visual information during monocular reaches) but rather to the nature of the monocular array itself, an array lacking binocular depth cues (for an elaboration see Servos et al. 1992; Servos and Goodale 1994).

Evidence from analysis of both the reach and the grasp components of prehension is consistent with the notion that, when subjects viewed the object monocularly, they consistently underestimated its distance and thus its size as well. First, the peak velocities of reaches in the monocular condition were lower relative to the binocular condition even though subjects were still scaling for target distance. The long period of deceleration evident in the monocular reaches could have reflected, in part, the need to adjust a trajectory that was programmed on the basis of an underestimation of object distance. Second, when subjects reached, under the monocular condition, they tended to generate smaller grip apertures, even though they still scaled their grips for object size. Such behaviour is consistent with the idea that they were underestimating object distance, since the retinal image of the object combined with an underestimation of object distance would generate a corresponding underestimation of object size.

Is the underestimation visual or visuomotor in nature?

There is a large body of evidence suggesting that it is reasonable to treat the use of vision for perceptual report as a rather different thing from the use of vision for visuomotor control. For example, dissociations between perceptual report and visuomotor control have been observed in normal subjects in a number of different paradigms where the location of a visual target has been manipulated (Bridgeman et al. 1979; Goodale et al. 1986; for review see Goodale and Servos 1996). Moreover, there is neuropsychological evidence suggesting that the neural substrates for visual perception and associated cognitive judgements may be quite independent of those underlying the visual control of skilled movements of the hand and limb (Goodale et al. 1991, 1994; Milner and Goodale 1995). The ventral stream projecting to the inferotemporal region of cerebral cortex has been characterised as the pre-eminent object recognition system in the primate, while the dorsal stream, which projects to the posterior parietal cortex, is known to process spatial information that is used for the control of skilled visually guided action (Ungerleider and Mishkin 1982; Goodale and Milner 1992).

More recent work with visual form agnosics has replicated our previous work demonstrating that the kinematics of neurologically intact humans’ visually guided reaching movements are adversely affected when they are made under conditions of monocular vision (Marotta et al. 1997). The lack of efficiency of reaches made under monocular vision in normal subjects was even more exacerbated in the visual form agnosics. This finding presents the possibility that the dorsal and ventral streams of visual processing treat monocular and binocular visual information differently. It is possible that the dorsal stream has difficulty making use of monocular information for the control of prehension because it is essentially a system that has developed in concert with the binocular distance cues for egocentric computations.

Given the various dissociations reviewed, it seems quite possible that the type of distance information needed for the initial programming of a reaching movement is different from that needed when a purely perceptual judgement is required. As discussed earlier, nearly all of the studies investigating depth judgements have relied on some sort of explicit report or cognitive judgement (i.e. they have depended on the subject's conscious perception of distance). Subjects have not been asked to produce a motor output, such as a reaching movement towards a goal object – where the distance estimation is *implicit* in the act itself rather than explicitly required.

The present study was conducted to examine whether the monocular effect observed in previous studies was a consequence of a purely visual distance underestimation under monocular viewing or whether this effect was due to some implicit inaccuracy in calibrating the reach by a visuomotor system that is normally under binocular control.

The first experiment assessed whether there were differences between a monocular and binocular condition in estimating distance using perceptual report. As in our previous prehension work, the size and distance of the target objects were varied. Moreover, a viewing environment was selected that afforded a rich array of monocular and binocular depth and distance cues, an array similar to that available in everyday life and identical to that used in the prehension task. We reasoned that, if the apparent distance underestimation observed in the monocular condition of the prehension task (Servos et al. 1992; Servos and Goodale 1994) was a consequence of a purely perceptual error in the estimation of distance, then we should observe an underestimation of distance relative to binocular viewing.

In the second experiment, subjects performed a distance estimation task using perceptual report. However, in this task, target viewing times were comparable with the amount of time that subjects had available prior to movement onset in the previously described prehension task (Servos et al. 1992; Servos and Goodale 1994). This limited-views task was used to test for the possibility that the monocular underestimations in the prehension task were due to diminished perceptual information during the period prior to movement onset. The subjects who performed the limited-views task also performed the prehension task. It was predicted that a pattern of results similar to the previously described studies would be observed in which reaches made under monocular viewing had lower peak velocities and displayed smaller grip apertures relative to when the reaches were made under binocular viewing. If the same subjects did *not* produce monocular distance underestimations in the perceptual limited-views task, then this would provide support for the idea that underestimation of target distance in the monocular condition of the prehension task was not due to a purely visual effect but to an inherent inaccuracy in calibrating reaches made by a visuomotor system under monocular control. Moreover, by analysing the monocular and binocular functions relating peak velocity to target distance, one could calculate the distance underestimation of the monocular reaches. This value could then be used to predict (on geometric grounds) the corresponding underestimation of target size that one should expect in the monocular reaches. By analysing the monocular and binocular functions relating maximum grip aperture to target size, the size underestimation of the monocular reaches could thus be calculated and compared with that predicted on the basis of the geometry of the viewing situation.

Experiment 1

As outlined in the Introduction, we have shown previously that the spatiotemporal organisation of prehensile movements is quite different when such reaches are made under monocular vision than when they are made under binocular vision. Moreover, it appears that subjects under the monocular condition are underestimating the distance of the target objects. What is not clear is whether this underestimation is a consequence of non-veridical estimations in the perceptual domain or in the visuomotor transformations underlying the prehension movements. Under reduced cue settings, subjects quite frequently underestimate far target distances (Crannell and Peters 1970; Komoda and Ono 1974; Morrison and Whiteside 1984) and overestimate target distances presented within grasping space (Foley and Held 1972; Komoda and Ono 1974; Foley 1977; Morrison and Whiteside 1984). These estimations are typically entirely perceptual (that is no motor response is required) or consist of explicit manual responses (that is, subjects merely indicate with their hand a given target's location – typically without visual feedback) (Crannell and Peters 1970; Foley and Held 1972; Foley 1977).

Experiment 1 was devised to investigate whether or not subjects under a monocular viewing condition would produce less accurate perceptual estimations of target distance than when they made the same judgements in a binocular condition. The same experimental conditions as those described in Servos et al. (1992) were used; however, subjects were not required to actually reach out and pick up the objects. Rather, subjects produced explicit distance estimates either verbally or with their index finger without time constraints. Based on the evidence from previous studies involving explicit judgements of distance, it was predicted that no differences would arise between the two viewing conditions – given that neither time restrictions nor reduced cue settings were used. Moreover, it was predicted that there would be no differences between the two response conditions (verbal or pointing), because the pointing response would involve an explicit estimation of distance much more similar to the verbal response than to the sort of implicit distance estimation underlying prehension.

Methods

Subjects

Twelve University of Western Ontario graduate and undergraduate students with normal or corrected-to-normal vision participated in the study for pay (six males and six females; mean age 24.9 years). All subjects were strong right handers, as determined by a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). Nine subjects were right-eye dominant; the remaining three subjects were left-eye dominant. All subjects had stereoscopic vision in the normal range with assessed ‘crossed’ disparity stereoacuities of 40” of arc or better as determined by the Randot Stereotest (Stereo Optical Co., Chicago, Ill.).

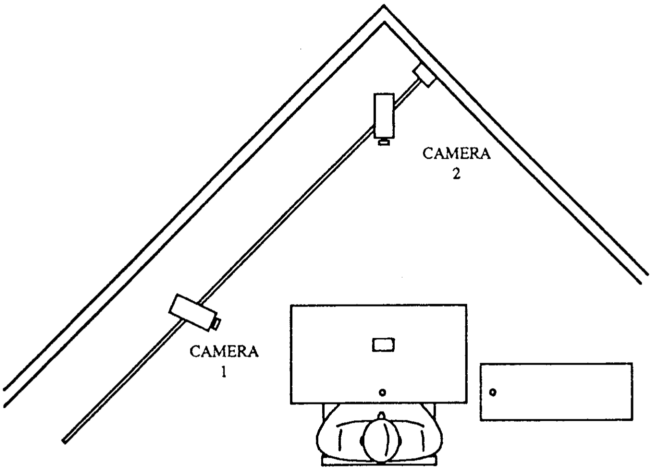

Fig. 1 Overhead view of the experimental arrangement of experiment 1

Apparatus

The set-up was identical to that described by Servos et al. (1992) except that an additional table surface (painted flat black) was positioned adjacent to the right of the table used in the prehension task (Fig. 1). This table, which was the same height as the original table, measured 86 cm in depth (its depth plane was oriented at a 90° angle with respect to the original table) and 31.5 cm in width. A circular button (1-cm diameter) was located along the midline of the second table, at a location 15 cm in from the edge of the table closest to the subject. This button was directly in line with the start button of the original table. Three red, oblong wooden blocks with the following top surface dimensions were used: 2×5 cm, 3×7.5 cm, and 5×12.5 cm. All of the objects were 2-cm high.

Procedure

Subjects sat in front of the table used in the previously described prehension task with the additional table to their immediate right and with their hands in their laps. Head movements were not restricted. A given trial consisted of subjects sitting with their eyes closed, while one of the three blocks used in the study by Servos et al. (1992) was placed on the prehension table along the body midline at one of five possible distances relative to the start button (20, 25, 30, 35 and 40 cm). After a signal to open their eyes, subjects were required to estimate the distance between the leading edge of the object and the start button. Two methods were used to generate these estimates. One of these consisted of producing a verbal estimate of the distance in inches or centimetres (whatever units the individual subject felt most comfortable with). The other method consisted of having subjects reproduce the perceived distance of the block relative to the start button by placing their right index finger along the table surface to their right and making the estimation relative to the button on its surface. Measurements were taken from a ruler on the side of the table only visible to the experimenter. Subjects were encouraged to be as accurate as possible and to take as long as they needed to generate their estimations; subjects typically required 5 s. For each trial, subjects produced both types of estimations. The order of these responses was randomised.

Subjects completed two different blocks of this task. In one, vision was restricted to the sighting dominant eye (the non-dominant eye was covered with a patch), while in the other block full binocular viewing was available. Subjects completed a total of 60 trials in each viewing condition – four instances of each of the 15 possible combinations of object size and distance. Trial presentations were random except for the stipulation that no more than

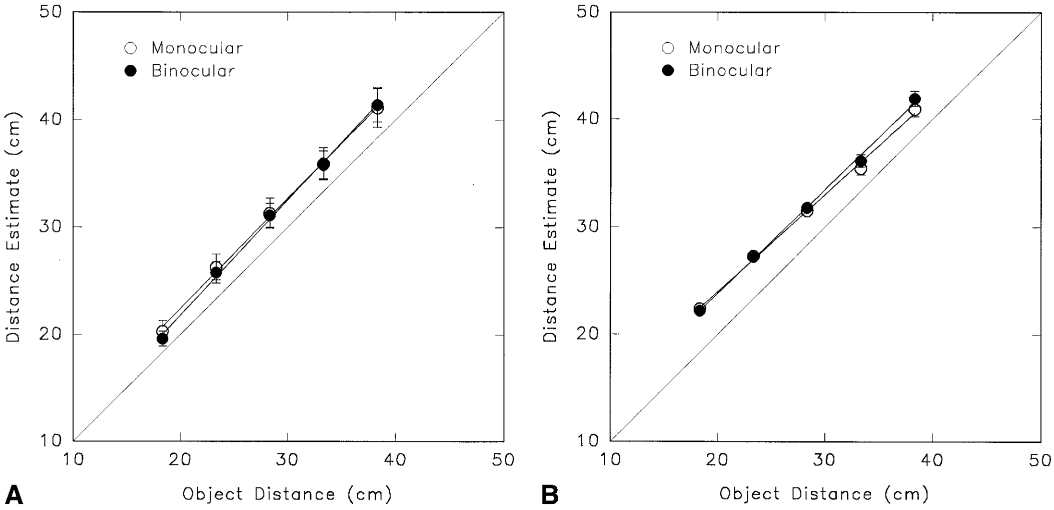

Fig. 2 Verbal and manual estimates of object distance with unlimited viewing time. **A** Verbal estimates. **B** Manual estimates. *Error bars* represent the standard error of the means across subjects

three consecutive, identical trials were allowed. Half of the subjects were given the binocular testing block first followed by the monocular block while the remaining subjects received the reverse order. The experimental trials were preceded by a handedness questionnaire, a test for eye dominance, and the stereoacuity test. Each testing session lasted approximately 90 min.

Results

Mean values of each of the dependent variables were calculated for each response mode × object size × object-distance combination in each viewing condition for each of the 12 subjects. The mean values were entered into separate 2×3×5×2 (viewing condition × object size × object distance × response mode) repeated-measures analyses of variance. All tests of significance were based on an alpha level of 0.05.

Not surprisingly, object distance had a very large effect on the estimates that subjects produced ($F_{4,44}$=262.87, P<0.00001). There were no significant main effects for any of the other factors (viewing $F_{1,11}$=0.02; response mode $F_{1,11}$=0.11). There were no significant interactions.

As Fig. 2 summarises, subjects produced reasonably accurate distance estimations across all of the conditions with a bias towards overestimation.[1] In both the monocular and binocular conditions of the verbal task, this was found to be approximately a 2.5-cm overestimation of target distance. A slightly higher overall overestimation of 3.3 cm was found for the monocular and binocular conditions of the manual task.

Discussion

When subjects were required to generate explicit distance estimations without time constraints, their performance was equally accurate under both monocular and binocular conditions. In addition, no differences were observed between the two response modes – subjects produced equally accurate verbal and manual estimations. This makes sense given that the manual task, like the verbal task, requires an explicit estimation of distance – subjects are not making visually guided reaching movements to a target (where an implicit distance estimation is made by the visuomotor system), rather they are simply using their finger as a pointer to indicate their estimation of distance. The lack of an effect of response mode is consistent with the work of Smeets and Brenner (1995, 1999). It also is supported by anecdotal data from subjects that have performed the manual task who claim to have often "thought" of what an appropriate distance would be and then lined up their index finger with that estimate. Subjects performing the visually guided prehension tasks described in the Introduction (see experiment 2) never reported making such verbal estimations prior to reaching for a target object.

Generally, subjects slightly overestimated object distance across both response and viewing conditions. This is consistent with work by Foley who found that subjects overestimated (either with verbal or pointing responses) the distance of point light sources in both monocular and binocular viewing conditions when these targets were presented within grasping space and when no time constraints were associated with the responses (Foley and Held 1972; Foley 1977).

The pattern of results in experiment 1 is not entirely consistent with the pattern observed in the prehension tasks (Servos et al. 1992; Servos and Goodale 1994). Subjects in the latter experiments appeared to be underestimating target distance in the monocular condition whereas under both viewing conditions in experiment 1, subjects produced slight overestimations of distance. This suggests that, relative to binocular vision, monocular vision is only at a disadvantage when relatively fast distance estimations are needed for skilled prehensile movements. When subjects make purely perceptual distance estimations and no time constraints are present, the monocular system is not at a disadvantage relative to the binocular system.

Experiment 2

Experiment 1 showed that when there are no time constraints on the distance estimations that subjects generate, there are no accuracy differences between monocular and binocular viewing conditions. Experiment 2 investigated whether the apparent monocular underestimation of distance in the prehension task (Servos et al. 1992; Servos and Goodale 1994) was a visuomotor effect per se or a visual effect. If it were a purely visual effect, it could be a consequence of the reduced amount of time available for estimating the distance of the target objects in the prehension task. Subjects in experiment 2 made perceptual distance estimations under monocular or binocular conditions with 500-ms views of the objects. This viewing time was selected because, in the original study reporting the effects of monocular vision on the kinematics of human prehension, subjects required approximately 500 ms to initiate their reaches in the monocular and binocular conditions (Servos et al. 1992). In addition, experiment 2 was an attempt to replicate the findings of the previous monocular–binocular prehension studies (Servos et al. 1992; Servos and Goodale 1994) in a set of subjects who have also been tested in a perceptual distance estimation task. If subjects display the decreases in the peak velocity of their reaches and in the size of their maximum grip apertures that have been previously observed, then the data could be

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[1] Because the objects actually straddled a given distance marker (i.e. 20, 30, or 40 cm), the leading edge of a particular object would be slightly closer to the subjects. Taking the three different sized objects into account results in a mean distance reduction of 1.66 cm. To reflect this, distance estimates have been plotted against actual distance for a given distance marker. For example, the value on the abscissa for the 20-cm marker would be 18.33 cm and so on.

analysed to determine the kinematic underestimations of distance and size in the monocular reaching movements. In other words, the monocular and binocular functions relating peak velocity to target distance could be used to calculate the distance underestimation of the monocular reaches. This in turn could be used to predict, on geometric grounds, the corresponding underestimation of target size that one should expect in the monocular reaches. By analysing the monocular and binocular functions relating maximum grip aperture to target size, the size underestimation of the monocular reaches could be calculated and then compared with the size underestimation predicted on the basis of the geometry of the viewing situation.

It was reasoned that if subjects in experiment 2 did not show the monocular underestimation of distance in the perceptual task, but *did* show a monocular underestimation of distance in the prehension task (a situation where all experimental conditions were the same except for the nature of the response), then this would provide strong evidence that the underestimation in the prehension task is a visuomotor effect and not a purely visual effect.

Method

Subjects

Twelve University of Western Ontario undergraduate and graduate students with normal or corrected-to-normal vision participated in the study for pay (six males and six females; mean age 24.4 years). None had participated in experiment 1. All subjects were strong right handers, as determined by a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). Eleven subjects were right-eye dominant (the remaining subject was left-eye dominant) and all had stereoscopic vision in the normal range with assessed ‘crossed’ stereoacuities of 40″ of arc or better, as determined by the Randot Stereotest (Stereo Optical Co.). Two of the subjects’ data were not analysable due to equipment failure.

Apparatus

Subjects sat at a table, 100-cm wide and 55-cm deep (Fig. 1). The surface of the table was painted flat black. A circular 1-cm diameter microswitch button located 15 cm from the subject indicated where subjects were to place their right hand during each trial of the verbal estimation task. This button was located directly at the body midline. This button was also the start position for each reaching movement in the prehension task. The side table used in experiment 1 was removed.

A circular fluorescent lamp was suspended approximately 80 cm above the table surface. This lamp, in which the condenser was pre-activated, could be illuminated by the experimenter from a remote switch which also triggered the start of data collection in the prehension task. Illumination was achieved within 100 ms.

The underside of each of the three wooden blocks used in experiment 1 contained an embedded magnet, which could be positioned so as to make contact with one of three magnetic switches located under the table surface at distances of 20, 30 or 40 cm from the microswitch, along the midline. For the prehension trials of experiment 2, when the subject picked up an object, the contact between these two magnets was broken, signalling the end of data collection for a given trial.

Light-emitting diodes (IREDs) were attached with small pieces of cloth tape to the head of the radius at the wrist, the distal portion of the right border of the thumbnail and the distal portion of the left border of the index fingernail. The tape permitted complete freedom of movement of the hand and fingers. In the prehension trials, the three IREDs were monitored by two high-resolution cameras positioned approximately 2 m from the subject. The instantaneous positions of the IREDs were digitised at a rate of 100 Hz into two-dimensional (2D) co-ordinates and then passed on to the data collection system of a WATSMART computer (Waterloo Spatial Motion Analysis and Recording Technique, manufactured by Northern Digital Inc., Waterloo, Ontario).

Procedure

Verbal estimation task. Subjects sat in front of the table with the index finger and thumb of their right hands on the start button before each trial. A given trial consisted of subjects sitting with their eyes closed while one of the three blocks was placed on the table along the body midline at one of the three possible distances relative to the start button (20, 30, and 40 cm). For a 5-s period before a given trial (i.e. as soon as the overhead fluorescent light was extinguished at the end of the previous trial), subjects sat in the dark with their eyes shut. Once a block had been placed in position by the experimenter, subjects were given a ready signal, which prompted them to open their eyes and to anticipate the illumination of the overhead light approximately 1–2 s later. The overhead fluorescent light was then illuminated for a 600-ms period (the actual period of illumination was approximately 500 ms because the light required a warm-up period of around 100 ms) and subjects were required to estimate the distance between the leading edge of the object and the start button. Subjects gave a verbal estimation of the distance in inches or centimetres – whatever units individual subjects felt most comfortable with. Subjects were encouraged to be as accurate as possible and to provide their estimations as soon as the light was extinguished. Subjects completed two different blocks of this task. In one condition, vision was restricted to the sighting dominant eye, while in the other condition full binocular viewing was available. A total of 36 trials were used in each viewing condition – four instances of each of the nine possible combinations of object size and distance. Trial presentations were random except for the stipulation that no more than three consecutive, identical trials were allowed.

The testing session consisted of a handedness questionnaire, a test for eye dominance, a stereoacuity test, the distance-estimation task, and the prehension task. Six subjects were tested first in the distance-estimation task and the remaining subjects were first tested in the prehension task. Half of the subjects in each of the experiments were first tested monocularly using their dominant eye (the non-dominant eye was patched) and the other half were first tested under binocular vision. Each testing session lasted approximately 2 h.

Prehension task. Subjects were instructed at the beginning of each session to make quick, accurate, and natural reaches with their right hand, picking up each object with their thumb and index finger along the long axis of the object, which was always perpendicular to the body midline. They were instructed to pick up the block as soon as the overhead light was illuminated and the block became visible.

Prior to the start of a trial, subjects placed the tips of the index finger and thumb of their right hand on the start button. For approximately a 5-s period before the trial (i.e. as soon as the overhead fluorescent light was extinguished from a previous trial), subjects sat in the dark with their eyes closed. Once an object had been placed in position by the experimenter, subjects were given a ready signal which prompted them to open their eyes and to anticipate the illumination of the overhead light approximately 1–2 s later. The period of illumination lasted 500 ms.

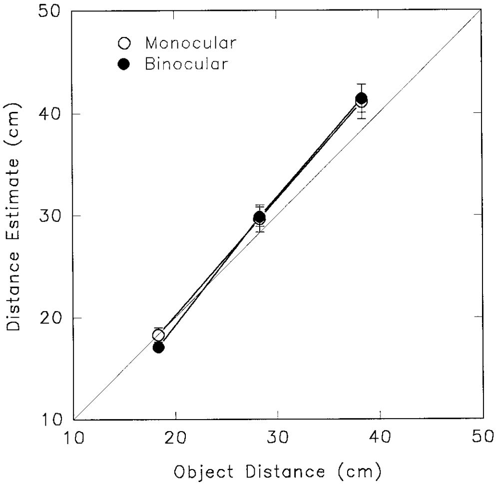

Fig. 3 Verbal estimates of object distance with 500-ms view. *Error bars* represent the standard error of the means across subjects

Each block of trials (monocular or binocular viewing) consisted of four instances of each of the nine possible distance × object size combinations. Trial presentations were random except for the stipulation that no more than three consecutive, identical trials were allowed. Each block was preceded by a series of five practice trials.

Accuracy of system

Calibration of the WATSMART system involved placing in the experimental workspace a rigid frame to which 24 IREDs were attached at known locations. The WATSMART calibration software calculated the 3D root mean square error of reconstruction for the locations of a minimum of 22 IREDs to be less than 2 mm. An independent assessment of the system's accuracy was also made, and sampling errors were also found to be less than 2 mm for all measurements (for details see Servos et al. 1992; Servos and Goodale 1994).

Data processing

The stored sets of 2D co-ordinates were converted into 3D coordinates off-line and filtered (a second-order Butterworth filter with a 7-Hz cut-off). The IREDS on the index finger and thumb provided information about the grip portion of the reach, while all other kinematic variables were based on information from the wrist IRED.

Dependent measures

Five kinematic measures were computed from the 3D co-ordinates corresponding to a given prehension movement. These 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) peak resultant velocity of the reach and (4) the time at which it occurred following movement onset; and (5) maximum grip aperture (the maximum vectored distance between the thumb and index finger IREDs). Measures 1–4 were based on data from the wrist IRED.

Results

Verbal estimation task

Mean values of each of the dependent variables were calculated for each size × distance combination in each viewing condition for each of the ten subjects. 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 on an alpha level of 0.05.

Not surprisingly, there was a very large effect of distance on this task ($F_{2,18}=131.72$, $P<0.00001$). There was a small effect of object size on the distance judgements, in that distances were more often underestimated with increasing object size ($F_{2,18}=3.52$, $P=0.051$). This was a consequence of having subjects make their judgements of distance with respect to the leading edge of the objects and the fact that the objects were centred at the three different target distances. The leading edge of, for example, the largest object would be 1.5 cm closer to the subject than the leading edge of the smallest object (see footnote 1).

Figure 3 makes it clear that there were no differences between the two viewing conditions ($F_{1,9}=0.06$, n.s.). Subjects under both conditions produced rather accurate distance estimations with a slight overall bias towards overestimation. Inspection of the two curves reveals that subjects under both viewing conditions slightly underestimated the closer objects and overestimated the objects at the farther distances. There were no significant interactions.

Prehension task

For each subject, mean values of each of the dependent variables were calculated across a minimum of three observations for each size × distance combination in each viewing condition. Equipment failure resulted in some loss of data but this constituted less than 1% 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 on an alpha level of 0.05.

General effects of object distance and size

Consistent with other work on visually guided prehension, object distance had a strong effect on the transport components of the reach such as peak velocity ($F_{2,18}=191.74$, $P<0.00001$) and movement duration ($F_{2,18}=162.82$, $P<0.00001$) (Fig. 4A; Jeannerod 1988; Jakobson and Goodale 1991; Servos et al. 1992; Servos and Goodale 1994). Thus, reaches to distant objects took longer and reached higher peak velocities than did reaches to closer objects.

The size of the objects clearly affected the maximum grip aperture generated by subjects ($F_{2,18}=347.66$,

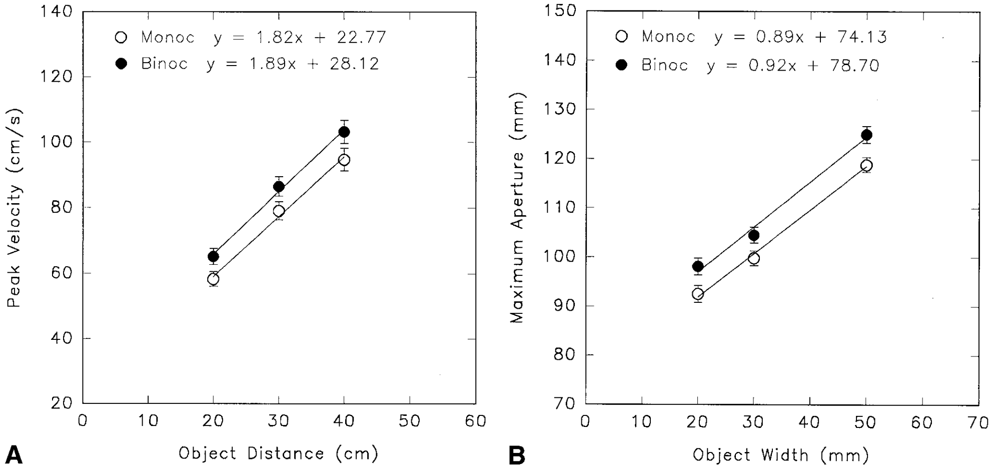

Fig. 4 **A** Peak velocity as a function of object distance and viewing condition. **B** Maximum grip aperture as a function of object size and viewing condition. *Error bars* represent the standard error of the means across subjects

Table 1 Summary table of effect of viewing condition on various kinematic variables (standard error of mean values across subjects indicated in parentheses)

Kinematic variable	Viewing condition		
	Monocular	Binocular	F statistic
Movement onset (ms)	478 (10.9)	466 (9.6)	$F_{1,9}$=0.3, n.s.
Movement duration (ms)	986 (27.1)	863 (23.2)	$F_{1,9}$=13.18, P<0.005
Peak velocity (mm/s)	773 (22.7)	850 (23.8)	$F_{1,9}$=5.98, P<0.03
Time spent decelerating[a] (ms)	598 (20.1)	491 (15.6)	$F_{1,9}$=15.62, P<0.003
Normalized time spent[b] decelerating (%)	60.0 (0.5)	56.4 (0.6)	$F_{1,9}$=7.59, P<0.02
Maximum grip aperture (mm)	104 (1.4)	109 (1.5)	$F_{1,9}$=5.39, P<0.05

[a] Calculated by subtracting the time to peak velocity from movement duration

[b] Calculated by subtracting the time to peak velocity from movement duration and dividing this difference by the movement duration (expressed as a percentage)

P<0.00001). Subjects scaled the size of their grips with increasing object size (Fig. 4B; Jeannerod 1988; Jakobson and Goodale 1991; Servos et al. 1992; Servos and Goodale 1994).

The effects of viewing condition on the transport component

As summarised in Table 1, the basic effects of monocular vision on the kinematics of prehension observed in previous work were replicated (Servos et al. 1992; Servos and Goodale 1994). Under monocular vision, subjects took longer to complete their reaches. This was a consequence of subjects in the monocular condition producing lower peak velocities and spending more time decelerating relative to their binocular reaches. Indeed, when reaching under monocular viewing conditions, subjects spent proportionately more time in the deceleration phase of the reach (60% of their movement time) than under normal binocular viewing (56%).

It should be noted that although there was a main effect of viewing on kinematic variables that are normally affected by target distance (e.g. movement duration and peak velocity), consistent with the idea that subjects were underestimating object distance in the monocular condition, there was still a strong correlation between these measures and object distance in the monocular condition (Fig. 4A). In other words, removing binocular information did not abolish the usual linear relationship between distance and such measures as movement duration, peak velocity, that others have reported (Jeannerod 1988; Jakobson and Goodale 1991; Servos et al. 1992; Servos and Goodale 1994).

The effects of viewing condition on the grasp component

Consistent with our previous work (Servos et al. 1992; Servos and Goodale 1994), subjects appeared to be generating smaller maximum grip apertures under the monocular condition (relative to the binocular condition) although they still scaled their grasp for object size (Table 1 and Fig. 4B).

Predicting the monocular size underestimation on the basis of a distance underestimation

The peak velocity and maximum grip aperture data have been interpreted to reflect a monocular underestimation of distance in the prehension task. A more direct test of this idea would be to use the peak velocity data and maximum aperture data in a regression analysis to provide an actual measure of the monocular distance and consequent size underestimation. These values could then be compared with the change in size of an object that would be expected based on a change in its distance using the geometric principle of size-distance scaling.

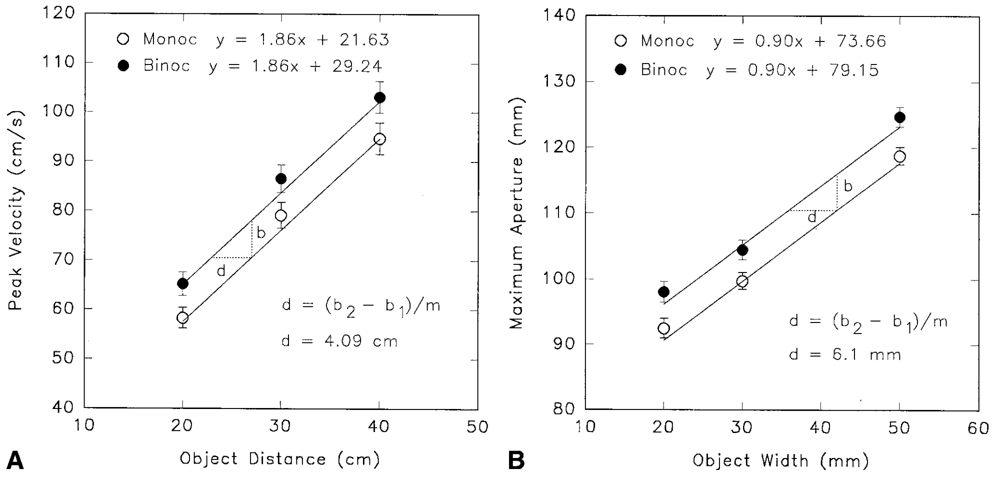

Fig. 5 Common slopes calculated for: (**A**) peak velocity as a function of object distance and viewing condition and (**B**) maximum grip aperture as a function of object size and viewing condition. *Error bars* represent the standard error of the means across subjects

Before such linear regression calculations can be made, the data need to satisfy several criteria. First, the four data sets used for the analysis (peak velocity and maximum grip aperture data sets in the monocular and binocular conditions) need to be linear in nature. Second, for a given variable (i.e. peak velocity or maximum aperture), the monocular and binocular data need to be shifted and/or scaled copies of each other. Examination of Fig. 4 makes it clear that not only are the data sets linear in nature but the monocular data are more or less a shifted version of the binocular data (see below for an elaboration). One final assumption about the analysis is that the binocular visuomotor distance and size estimations are considered veridical, whereas the monocular visuomotor estimations are in some way aberrant. This seems reasonable given that one would have expected the subjects under the monocular condition to have actually generated larger grip apertures relative to their binocular reaches, in order to program in a larger margin of error, as has been observed in other experiments, in which the quality of visual information has been degraded (Wing et al. 1986; Jakobson and Goodale 1991). Moreover, the binocular data both in the present study and in other studies that have examined the effects of monocular and binocular vision on prehension (Servos et al. 1992; Servos and Goodale 1994) do not seem to differ from other prehension paradigms that presented subjects with initial binocular views of the hand and target object but then manipulated the presence of visual feedback during the reach (Jakobson and Goodale 1991; Servos et al. 1992; for an elaboration see Goodale and Servos 1996).

Linear regressions were performed on the peak velocity profiles (Fig. 4A) and the maximum aperture mean plots (Fig. 4B) for both the monocular and binocular data. With respect to the velocity data, the following linear fits were derived:

$y_{\mathrm{Monoc}}=1.82x+22.77$

$y_{\mathrm{Binoc}}=1.89x+28.12$

With respect to the aperture data, the following linear fits were derived:

$y_{\mathrm{Monoc}}=0.89x+74.13$

$y_{\mathrm{Binoc}}=0.92x+78.70$

The regression coefficients for each of the four data sets were 0.99 or greater. For both the velocity and aperture data sets, the monocular and binocular slopes were highly similar. Separate *t*-tests were calculated for each of the data sets to test whether the monocular and binocular slopes differed from each other. The monocular and binocular slopes were not different for the velocity and aperture data sets (respectively, $P>0.49$ and $P>0.65$). Common slopes that minimised the sum of squares error were then calculated for each of the subjects' velocity and aperture data sets (Fig. 5) – the regression coefficients for each of the data sets were 0.98 or greater. For the velocity data:

$y_{\mathrm{Monoc}}=1.86x+21.63$

$y_{\mathrm{Binoc}}=1.86x+29.24$

For the aperture data:

$y_{\mathrm{Monoc}}=0.90x+73.66$

$y_{\mathrm{Binoc}}=0.90x+79.15$

The distance underestimation under the monocular condition was computed by taking the y intercepts of the monocular and binocular functions and dividing them by their common slope (Fig. 5A). This was calculated to be 4.09 cm. With this average underestimation of 4.09 cm in the monocular condition, we can then calculate what the expected change in size of the target objects would be.

Geometric prediction of size/distance underestimation

Figure 6 depicts the relationship between the distance of the target objects and their retinal image size. For these calculations, a 3.33-cm wide object (corresponding to the average width of the three objects used in the experiment) at a distance of 28.33 cm (the average distance used in the experiment) was used. The retinal image size of this 3.33-cm ob-

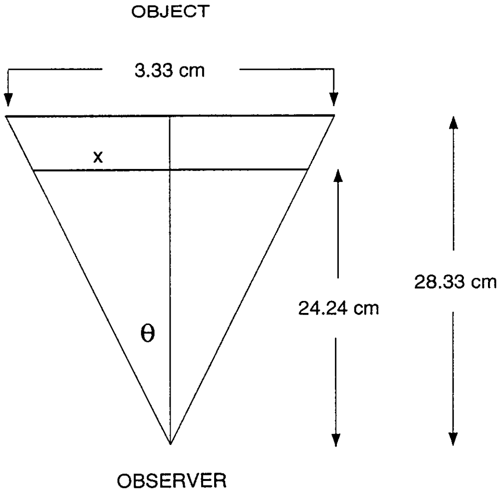

Fig. 6 Diagram of size-distance scaling. Given an average object distance of 28.33 cm and an average object size of 3.33 cm, the predicted size of an object underestimated by a distance of 4.09 cm would be 2.85 cm. See text for details

ject at a 28.33-cm viewing distance equals 6.73° of visual angle given: tan(Θ/2)=[(3.33/2)/28.33 cm]. So, given an underestimation of 4.09 cm, the 28.33-cm distance would be reduced to 24.24 cm. Given, too, that the retinal image size of the object would remain constant at 6.73° under monocular viewing, the monocular visuomotor system must therefore assume that an object that appears closer than it actually is (24.24 cm instead of 28.33 cm) has an actual size that is smaller by 0.48 cm, i.e. 3.33 cm (actual size of object)–2.85 cm (inferred size of object by monocular visuomotor system).

On geometric grounds, one would expect the monocular visuomotor system to underestimate the size of the target objects by an average of 0.48 cm relative to the binocular visuomotor system. If we use the experimentally observed mean maximum grip apertures generated under the monocular condition and substitute them into the linear equation for the binocular maximum aperture data (Fig. 5B), we find a corresponding size reduction of 0.61 cm – a value that approximates the 0.48-cm value calculated on the basis of geometric size-distance scaling. The 0.13-cm difference between these two values falls within the standard error bars of the monocular and binocular functions calculated for maximum grip aperture in Fig. 5B.

Discussion

Like subjects in the perceptual task of experiment 1, subjects in experiment 2 were as accurate in verbally estimating object distance in the monocular condition as they were in the binocular condition. As in experiment 1, subjects in the verbal task of experiment 2 appeared to be slightly overestimating object distance, although examination of Fig. 3 suggests that for the closest object distance, subjects were very slightly underestimating target distance.

It is not clear whether the overall overestimation of distance in the untimed condition (experiment 1), the farther distances in the limited-views task of experiment 2 or the slight underestimation of distance for the closest distance in the limited-views task of experiment 2 reflect genuine differences in the way that distance is computed under these two conditions. Regardless, the main point is that there were no differences between the monocular and binocular conditions in either experiment 1 or the verbal estimation task of experiment 2.

The results of the prehension task of experiment 2 replicates previous work demonstrating that restricting vision to only one eye affects the normal pattern of reaching and grasping movements (Servos et al. 1992; Servos and Goodale 1994). The monocular reaches achieved a lower peak velocity and lasted longer than reaches made with binocular vision. In addition, under monocular viewing conditions, subjects spent proportionately more time decelerating and achieved smaller grip apertures than they did under binocular viewing.

A monocular visuomotor underestimation of distance

Evidence from both the reach and grasp components of prehension is consistent with the notion that subjects under the monocular viewing condition of experiment 2 were underestimating the distance of the target object and, thus, also its size. First, the overall peak velocity of reaches was lower under the monocular viewing condition than the binocular condition, even though subjects were still scaling for object distance. As suggested in the Introduction, the long period of deceleration observed in the monocular reaches could have reflected in part the need to adjust a trajectory that was programmed on the basis of an underestimation of object distance. Second, subjects in the monocular condition tended to generate smaller grip apertures although they still scaled their grips for object size. That subjects were generating smaller grip apertures under the monocular condition is consistent with the idea that they were underestimating object distance, since the retinal image of the object combined with an underestimation of object distance would generate a corresponding underestimation of object size.

The visuomotor parameter of maximum grip aperture can be used to provide an index of size constancy (Marteniuk et al. 1987; Jeannerod 1988; Jakobson and Goodale 1991). Reaches directed at an object of a given size should result in a constant maximum grip aperture regardless of whether the object is close or far away. In other words, an adequate size constancy mechanism will take into account object distance when processing retinal image size. Thus, no interactions between object size and object distance should be expected for the maximum grip aperture variable if the visuomotor system exhibits size constancy. Under binocular viewing, this is the case. Under monocular viewing, even though subjects exhibited a systematic underestimation of object size, they still showed some degree of size constancy because there were no interactions between object size and object distance for the maximum grip aperture variable. If size constancy had been completely abolished under monocular viewing, subjects would have generated larger grip apertures for the objects when they were closer than when they were farther away (i.e. if maximum grip aperture had simply been driven by retinal image size and not true object size).

As discussed elsewhere (Goodale and Servos 1996), the initial visual array, be it monocular or binocular, determines a good deal about the subsequent kinematics of the reaching movement. During the 400 ms to 500 ms before a reach is initiated (i.e. the pre-movement programming phase), object location and distance are calculated and form the basis of many of the kinematic variables as the reach unfolds. Once the reach is underway, there are clearly opportunities to modify the reach and grasp (as we have shown in Servos and Goodale 1994), but, at least early in the reach, the nature of the kinematics seems to be largely a consequence of the initial programming prior to movement onset (Jeannerod 1988; Jakobson and Goodale 1991; Servos and Goodale 1994; Goodale and Servos 1996). For example, Servos and Goodale (1994) showed that switching from a binocular to a monocular view (or the converse) immediately after subjects have initiated their reaches does not affect kinematic markers such as the peak velocity of the reach or the maximum grip aperture. What does affect these two variables is the type of vision (i.e. monocular or binocular) that subjects receive *prior* to their reaching movements. Indeed, Jakobson and Goodale (1991) found that the peak velocity of reaches made in a condition in which binocular vision was available throughout the reach was the same as that for a condition in which subjects received an initial binocular view followed by no vision as soon as they had initiated their reach. These studies provide support for the notion that the setting of many of the kinematic parameters in prehension takes place during the initial view of the object. Thus, the two key variables that provide evidence for the idea that subjects are underestimating target distance under monocular viewing appear to be determined by the initial nature of the visual array (i.e. whether it is monocular or binocular) *prior* to movement onset. They can therefore provide an index of the initial distance estimation prior to movement onset.

The purpose of the present study was to determine whether the apparent underestimation of distance and size in the visually guided prehension task under monocular viewing was a consequence of a perceptual or visuomotor underestimation of distance prior to movement onset. Identical viewing environments were used in each of the experiments. In experiment 1, subjects generated distance estimates either verbally or by reproducing target distance by pointing with their index finger. Performance was found to be comparable in the monocular and binocular conditions, although in both conditions subjects did slightly overestimate object distance. No differences were found between the two response modes. One would not expect any differences between these two response modes because each of them requires an explicit estimate of target distance. As will be discussed, explicit judgements of this sort, even when made using a manual response, may well depend on visual processing that is quite separate from that controlling visually guided grasping movements. Experiment 1 demonstrates that when non-speeded perceptual tasks are used, subjects are not impaired in their ability to estimate distance when vision is restricted to one eye. In addition, it demonstrates that the difficulty evident under the monocular condition of the visuomotor task in experiment 2 cannot simply be reduced to a problem in reproducing distance with an effector system because, in the perceptual task, under monocular viewing, subjects had no difficulty in manually reproducing the various distances. In the verbal estimation task of experiment 2, when only short presentations of the visual scene were given to subjects (to approximate the short period of time that subjects would have had in the prehension task before initiating their reaching movements), subjects, again, did not produce less accurate monocular distance estimates relative to their binocular estimates. Experiment 2 demonstrates that the biases that arise under monocular viewing in the prehension task only come about when a relatively fast, skilled *visuomotor* response is required. Thus, what sets the prehension task of experiment 2 apart from experiment 1 and the verbal estimation task of experiment 2 is the type of distance estimation that is required. In the latter two tasks, purely perceptual estimates were required whereas in the former task the distance estimate was implicit in the reaching movement itself.

Depth processing in the dorsal and ventral streams

Mounting electrophysiological and neuropsychological evidence suggests that the dorsal and ventral processing streams have rather different functions (Goodale and Milner 1992; Milner and Goodale 1995). Goodale and Milner (1992) have proposed that the dorsal stream of projections to the posterior parietal lobule, in close conjunction with areas in premotor and prefrontal cortex, are involved in the control of skilled action, such as manual prehension. In contrast, the ventral stream of projections is primarily concerned with more perceptual functions, such as visual learning and object recognition (Goodale and Milner 1992; Milner and Goodale 1993, 1995).

The work of Goodale and Milner suggests that the computations involved in transforming visual information into motor output are probably performed quite independently of visual perception. This opens up the possibility that the computations setting the parameters for the reach trajectory and grip aperture of a prehensile movement may not be accessible to perceptual or cognitive judgements about the object. One might expect a distance cue such as familiar size and the pictorial depth cues to be processed primarily by the ventral system, whereas one might expect most of the distance cues (retinal image size and horizontal retinal disparity in conjunction with vergence and vertical retinal disparities) to be processed by mechanisms residing in the dorsal system. Indeed, there is evidence that visual agnosic patients with relatively intact dorsal streams but compromised ventral streams display quite normal reaching and grasping movements under binocular vision, whereas their reaches under monocular vision are quite impaired (Marotta et al. 1997). Thus, such patients display, just like normal subjects, the typical velocity–distance scaling and grip aperture-object size scaling in their binocular reaching and grasping movements. Under binocular viewing then, their reaching movements display size constancy. However, under monocular viewing, their reaches display much less size constancy in that the grasp and transport components of prehension become decoupled – consistent with the idea that they are scaling their grip to retinal image size and *not* to the actual size of the object.

The current study, in addition to the work reviewed here, makes it likely that two broad representations of visual space exist: one for perception and one for action. These two broad classes of representation may map onto different cortical structures as suggested by the work of Goodale and Milner (1992); visual space perception is likely mediated by the ventral stream of processing, whereas the visuomotor representation of space is subserved by the dorsal system.

It appears then, that as long as some depth cues are present, the monocular system is not compromised in purely *perceptual* distance estimate tasks. However, when skilled reaching and grasping movements are required, the visuomotor transformations that underlie such movements appear to rely on binocular depth cues which, of course, are not available in the monocular array. It might well be the case that the dorsal stream has difficulty processing pictorial depth information (i.e. monocular depth cues) because it is specialised for the processing of binocular depth cues for the control of skilled reaching movements. Monocular depth information is important for the object recognition functions of the ventral stream. For example, we learn to see flat 2D representations, such as pictures, as surrogates for 3D objects in the real world. Such perceptual learning is not likely a critical function of the dorsal stream.

Like the visual agnosic patients who show poor monocular prehension relative to their binocular reaches, presumably because the dorsal processing system is ill-equipped to deal with monocular depth cues, the current study demonstrates a similar dissociation in normal subjects. Moreover, it demonstrates that the "deficit" under monocular reaching is not due to a purely visual deficit in distance estimation but to a visuomotor effect of having to rely on monocular information for skilled visually guided reaching. It is suggested that even in normal subjects, the dorsal stream is unable to effectively use monocular information for the control of skilled reaching and grasping movements.

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