Factors affecting higher-order movement planning: a kinematic analysis of human prehension

L.S. Jakobson and M.A. Goodale

Department of Psychology, The University of Western Ontario, London, Ontario, N6A 5C2 Canada

Summary. Past studies of the kinematics of human prehension have shown that varying object size affects the maximum opening of the hand, while varying object distance affects the kinematic profile of the reaching limb. These data contributed to the formulation of a theory that the reaching and grasping components of human prehension reflect the output of two independent, though temporally coupled, motor programs (Jeannerod 1984). In the first experiment of the present study, subjects were required to reach out and grasp objects, with or without on-line, visual feedback. Object size and distance were covaried in a within-subjects design, and it was found that both grip formation and reach kinematics were affected by the manipulation of either variable. These data suggest that the control mechanisms underlying transport of the limb and grip formation are affected by similar task constraints. It was also observed that when visual feedback was unavailable after movement onset subjects showed an exaggerated opening of their hands, although grip size continued to be scaled for object size. The question remained as to whether the larger opening of the hand during no-feedback trials reflected the lack of opportunity to fine-tune the opening of the hand on-line, or the adoption of a strategy designed to increase tolerance for initial programming errors. To address this question, a second experiment was carried out in which we manipulated the predictability of visual feedback by presenting feedback and no-feedback trials in a random order. In contrast to the situation in which feedback and no-feedback trials were presented in separate blocks of trials (Exp. 1), in the randomly-ordered series of trials presented in Exp. 2, subjects always behaved as if they were reaching without vision, even on trials where visual feedback was continuously available. These findings suggest that subjects adopt different strategies on the basis of the predictability of visual feedback, although there is nothing to suggest that this takes place at a conscious, or voluntary, level. The results of both experiments are consistent with the notion of a

hierarchically-organized motor control center, responsible for optimizing performance under a variety of conditions through the coordination of different effector systems and the anticipation of operating constraints.

Introduction

The act of prehension involves three distinct components: spatial positioning of the arm (the reaching or transport component), anticipatory posturing of the hand (the grip formation component), and object manipulation. In this paper, we will focus primarily on the distinction which is often drawn between the control of the reaching arm and the control of the independent movements of the fingers involved in grip formation. A wealth of anatomical and physiological studies in monkeys have confirmed the predominant role of the crossed, corticospinal projections in fine control of the distal musculature (e.g., Lawrence and Hopkins 1972; Muir 1985; Muir and Lemon 1983; Passingham et al. 1978). The reaching or transport component, in contrast, can be adequately controlled by the hemisphere ipsilateral to the reaching limb (Brinkman and Kuypers 1973; Trevarthen 1965). These findings in monkeys are in agreement with observations from human patients in whom the two cerebral hemispheres have been surgically disconnected (Gazzaniga et al. 1967; Volpe et al. 1982). Furthermore, relatively late myelinization of the corticospinal tract in human infants (see Jeannerod 1988) may underlie the observation that reaching and precision grip have rather different developmental profiles (e.g., Von Hofsten 1979). Other evidence for a dissociation between the neural substrates for the grip and transport components of prehension comes from lesion studies. In monkeys, for example, the control of grip formation is disturbed by damage at the parieto-occipital junction (area 5), while

more extensive damage involving the superior parietal lobe (areas 5 and 7) produces clear deficits in both reaching and grasping (Denny-Brown et al. 1975; Faugier-Grimaud et al. 1985; Faugier-Grimaud et al. 1978; Haaxma and Kuypers 1975).

Jeannerod (1981, 1984, 1986) has provided further evidence for the relative independence of the reaching and grip formation components of human prehension by carrying out detailed analyses of movements in normal, healthy adults. With the use of highspeed film, Jeannerod (1981) found that maximum grip aperture en route to a given target object increased with increasing object size, and that unexpected changes in object size during a reaching movement led to corresponding changes in hand shaping. Despite these changes in grip formation, the shape of the resultant velocity profiles for the wrist movement remained unchanged by the experimental manipulations of object size, although peak velocity was increased for movements of greater amplitude.

Jeannerod (1981) concluded from these findings that the reaching and grip formation components of a prehension movement were generated by independent visuomotor channels. Nonetheless, it became clear that the two components of human prehension were not temporally independent. It was found, for example, that the onset of hand closure was highly correlated with the final approach to the target object (Jeannerod 1981, 1984). Jeannerod (1986) suggested that this finding might reflect the presence of a higher-order program governing the temporal coordination of two otherwise separate components. [It is interesting to note that in an earlier account of this finding (Jeannerod and Biguer 1982), he argued that "postulation of a hierarchy appears unnecessary" and that "temporal ordering would be produced automatically, as a passive consequence of peripheral inbuilt constraints such as conduction time or duration of isometric tension" p. 399.] Unfortunately, however, since the range of movement times in Jeannerod's (1981, 1984) experiments was quite limited, it is difficult to determine whether or not this apparent invariance in timing would extend over a broad range of movement durations. One aim of the present research, then, was to explore the robustness of the temporal coupling between reaching and grip formation by examining these motor outputs over a greater range of movement times in a much larger sample of subjects than Jeannerod had used (Experiment 1).

Although clearly the temporal coordination of different visuomotor outputs is important in complex movements (Goodale 1988), evidence has accumulated suggesting that the temporal linkage between the transport and grip formation components of prehension reflects just one aspect of a more fundamental interaction between the two components (Wing et al. 1986; Wallace and Weeks 1988). Wing et al. (1986) suggested that the thumb, while an element of the grasp, plays an important role in the visual guidance of the transport component. They further demonstrated that requiring subjects to reach quickly or without visual feedback resulted in corresponding increases in the maximum opening of the hand. Although this was interpreted in terms of a speed/

accuracy trade-off, Wallace and Weeks (1988) suggested that the maximum aperture between the finger and thumb during a reach was positively related to *movement time,* as opposed to movement speed. Nonetheless, the maximum opening of the hand was consistently achieved when approximately 60% of total movement time had elapsed, for both small and large objects.

While the results of Wallace and Weeks (1988) supported the proposal that the transport and grip formation components are linked in some way, these researchers (like Jeannerod 1981) found that varying object size affected only the manipulation component, and not the transport component. This latter observation seems puzzling given that object characteristics, including object size and fragility, have been found by other investigators to affect the kinematic profile of wrist movements in prehension tasks (Marteniuk et al. 1987). This apparent discrepancy may have arisen due to the fact that Wallace and Weeks always presented their test objects at a standard distance from the subject. In Experiment 1 of the present study, we covaried object size and distance simultaneously in a within-subject design and determined the effects of these manipulations on the kinematics of both grip formation and reaching.

We were also interested in assessing how the removal of visual feedback affects prehension in normal subjects. Jeannerod (1984) has shown that maximum grip aperture continues to be scaled for object size when subjects cannot see their moving limb or the target object (see also LaMotte and Acuna 1978, for similar observations in the macaque), and that the temporal relationship between transport and grip formation is maintained under these conditions. These results suggested to him that movement patterning for grip formation and intersegmental coordination in human prehension relies on a feedback-independent central motor program, or some intermediate level of control, and that little (if any) modification of the grip takes place during its execution. Data from other experiments suggest that when visual feedback is not available the hand opens wider than it does under normal viewing conditions (Wing et al. 1986). This difference in performance in the two conditions does not necessarily pose a problem for Jeannerod's (1984) conjecture that most of the grasp is preprogrammed. It could simply mean that a *larger margin of error* is pre-programmed into the grip under conditions where visual feedback is not available. An equally plausible alternative, however, is that under restricted viewing conditions the closing of the hand begins later, because the subject cannot use on-line visual information to fine-tune the aperture of the grip. [Of course, even under restricted viewing conditions other sources of information (proprioceptive or kinesthetic feedback, or efference copy) about limb position are available to guide movement execution (cf. Goodale et al. 1986).] The question of how much the kinematics of the grasp are pre-programmed and how much response modification can be done on-line is a fundamental issue in motor control. Experiments 1 and 2 examined this question by manipulating the predictability of available visual feedback.

In summary, the present experiments were undertaken

(1) to provide a thorough, normative study of prehension in healthy adults (Experiment 1); (2) to determine whether the distal and proximal components of human prehension are controlled through independent programs which are simply run off in the same time domain, or whether there is evidence that an integrated program specifies the entire movement (Experiment 1); and (3) to examine the role played by visual feedback in grip formation (Experiments 1 and 2).

Experiment 1

Method

Subjects. The subjects were eight males and seven females (mean age = 25.3 years) employed or enrolled in courses at the University of Western Ontario. All subjects were strongly right handed, as determined by a modified version of the Kimura Hand Preference Inventory (Kimura 1986). Subjects were paid for their participation.

Apparatus. Each subject sat facing a table surface (1.00 m × 0.55 m) over which a fluorescent lamp was suspended at a height of approximately 80 cm. Three magnetized, oblong blocks (2 × 5 cm, 3 × 7.5 cm, and 5 × 12.5 cm), all 2 cm in height, served as target objects. On a given trial, one of these objects was placed in front of the subject (along the midline, sagittal axis), centered directly over one of three concealed, magnetic switches located 20, 30 and 40 cm beyond the hand's start position.

Infrared light-emitting diodes (IREDs) were attached with a non-restricting cloth bandage to opposing sides of the nails of the right index finger and thumb, and opposite the styloid process of the ulna of the right hand. The positions of these IREDs were monitored continuously by two high resolution cameras. The two-dimensional (2D) positions of these IREDs provided by each camera were digitized at a rate of 100 Hz and passed to the data collection system of a WATSMART computer (Waterloo Spatial Motion Analysis and Recording Technique, Northern Digital Inc., Waterloo, Ontario, Canada).

Calibration of the WATSMART system involves placing in the experimental workspace a rigid frame to which 24 IREDs are attached at known locations. As calculated by WATSMART calibration software, the 3D root mean square error of reconstruction for the locations of a minimum of 22 IREDs was always less than 2 mm. To provide an independent assessment of the system's accuracy, we used a procedure similar to that described by Haggard and Wing (1990). Three IREDs were embedded in a rigid surface to form the vertices of a right-angled triangle (measuring approximately 10 × 15 × 18 cm). This surface was positioned near the start key of the experimental apparatus, and (in a subsequent trial) approximately 30 cm beyond this position, in the x (forward-going) dimension. The 3D coordinates of the static IREDs were sampled for 2 s in each location, at a sampling frequency of 100 Hz. Comparisons of the average distance between any two given IREDs in both regions of the workspace were very consistent, with differences ranging from 0.93 mm–2.18 mm. The standard deviations of these measurements within each 2 s sampling period varied from 0.29–1.10 mm.

Procedure. Subjects were told to begin each trial with the tips of the thumb and index finger of the right hand touching one another and depressing the start key. Between trials, the room lights were extinguished and the subject sat with eyes closed. On the experimenter's instruction, the subject opened his/her eyes, shortly after which the table surface was illuminated with the overhead fluorescent lighting. The subject was instructed to reach out and pick up the target object as soon as it became visible, using the index finger and thumb to which the IREDs were attached. Data collection began when the table surface was illuminated and ended when the magnetic contact between the surface and the test object was broken (i.e., when the object was picked up).

In one block of trials, the subject had a continuous view of the reaching limb and of the target object. In another block of trials, the fluorescent light was extinguished when the subject, in initiating his/her reach, released the start key. Since the decay time for the fluorescent lighting was less than 80 ms, and since average movement duration was 477 ms, approximately 85% of the subject's arm movement was completed in the dark in this condition, on average. The order of testing was counterbalanced across subjects.

In both viewing conditions subjects reached to each target in each of the three locations four times, for a total of 36 trials. Each block of 36 trials followed a different random order, with the stipulation that no more than three consecutive reaches were to the same location or target object. Trials in which the object was dropped were repeated at the end of the current block of trials. (These trials accounted for a very small proportion of experimental trials: objects were dropped on 1% of all trials when visual feedback was available, and on 2% of all trials when reaches were completed in the dark). Only data from trials in which the target object was successfully retrieved were included in the analysis. Each block was preceded by a five-trial practice series.

Data management. Movements of each of the IREDs during each trial were reconstructed in three-dimensions and filtered off-line with a 7 Hz cut-off using a second-order Butterworth filter. To generate a detailed kinematic description of the reaching component of human prehension, a number of measures were extracted from the filtered data from the wrist IRED. To describe grip formation, filtered data from the fingertip IREDs were analyzed.

The wrist's movement onset time was determined by scanning each file to find the point at which the mean resultant velocity over three consecutive frames (30 ms) exceeded a velocity of 5.0 mm/s. This criterion was adopted because, due to the high resolution of the WATSMART system, even slight movements of the wrist are evident when the hand is at rest in the starting position. Unlike the wrist, the fingertips rested directly on the start key at the beginning of each trial. For this reason, movement onset for the fingertips was measured as the time taken to release the mechanical start key. (These two measures of movement onset are, clearly, highly correlated.)

Other dependent measures extracted from the filtered data from the wrist IRED included: peak negative acceleration in the X (forward/backward) dimension (cf. Jeannerod, 1984), peak resultant velocity, peak height in the arm's trajectory (measured in the Z dimension), and the time at which each of these markers occurred after the wrist began to move. Duration of movement was calculated by subtracting the wrist's movement onset time from the time at which the object was lifted.

Dependent measures used to describe grip formation included the maximum vectored distance (in mm) achieved between the two IREDs on the fingertips (maximum grip aperture) during the course of a reaching movement, and the time (in ms) at which this occurred after the release of the start key.

Results

For each subject, mean values of each dependent measure were calculated for each object/distance combination under each viewing condition. Each mean value was based on a minimum of three observations; some data was lost due to technical problems, and an error in the protocol meant that only three observations of the medium-sized target were made at the 20 cm distance for three subjects in the visual feedback condition, and for three subjects in the no visual feedback condition. (In

most cases, however, means for a particular condition were calculated on the basis of all four trials.) The mean values for each dependent measure were entered into separate $2 \times 3 \times 3$ (Viewing Condition × Object Size × Object Distance) factorial analyses of variance, using Geisser-Greenhouse adjustments to the degrees of freedom (Kirk 1982). An alpha level of 0.05 was adopted for all tests of significance. Post-hoc contrasts were carried out using the Newman-Keuls testing procedure.

Effects of the manipulations of object size and distance. The manipulations of object size and distance had predictable effects on the grip formation and transport components, respectively. Specifically, there were direct relationships between the size of the object and the maximum opening of the hand en route to the target, and between the size of the object and the time taken to open the hand maximally (Fig. 1A). Furthermore, movements of the wrist to distant objects had a longer latency, accelerated to peak velocity more quickly, attained a higher peak velocity, and lasted longer than movements to near objects (Fig. 1B). The maximum height above the table surface to which the wrist was raised was also greater for more distant objects. (Means and tests of significance are summarized in Table 1.)

In addition to these results, a number of kinematic parameters were affected by the experimental manipula-

tions in ways that one would not predict based on a strict interpretation of the proposal that the transport and grip formation components operate through independent visuomotor channels. Thus, as *object size* increased there were corresponding increases in the peak velocity and duration of the wrist movements (Fig. 1D). In addition, the wrist was raised higher above the table surface during reaches to larger objects, despite the fact that the three objects were all the same height, differing only in length and width. Moreover, with increases in *object distance* the maximum opening of the hand increased (Fig. 1C). (This effect was particularly strong for the smaller objects, Object Size × Distance: $F_{(3.45, 48.24)} = 3.34, p < 0.05$.) It also took subjects longer to achieve maximum grip aperture when reaching to more distant objects. (Means and tests of significance are summarized in Table 1.)

The manipulations of object size and distance also affected the *relative timing* (expressed as a percent of total movement time) of a number of parameters. Thus, both the peak velocity and the peak negative acceleration (in the x dimension) of the wrist occurred proportionately sooner in time when the subject was reaching toward either a more distant object *or* a larger object. In other words, the deceleration phase of the reach was proportionately longer under these conditions. Similarly, despite the fact that the wrist was lifted higher off the table surface when reaching to more distant objects (see
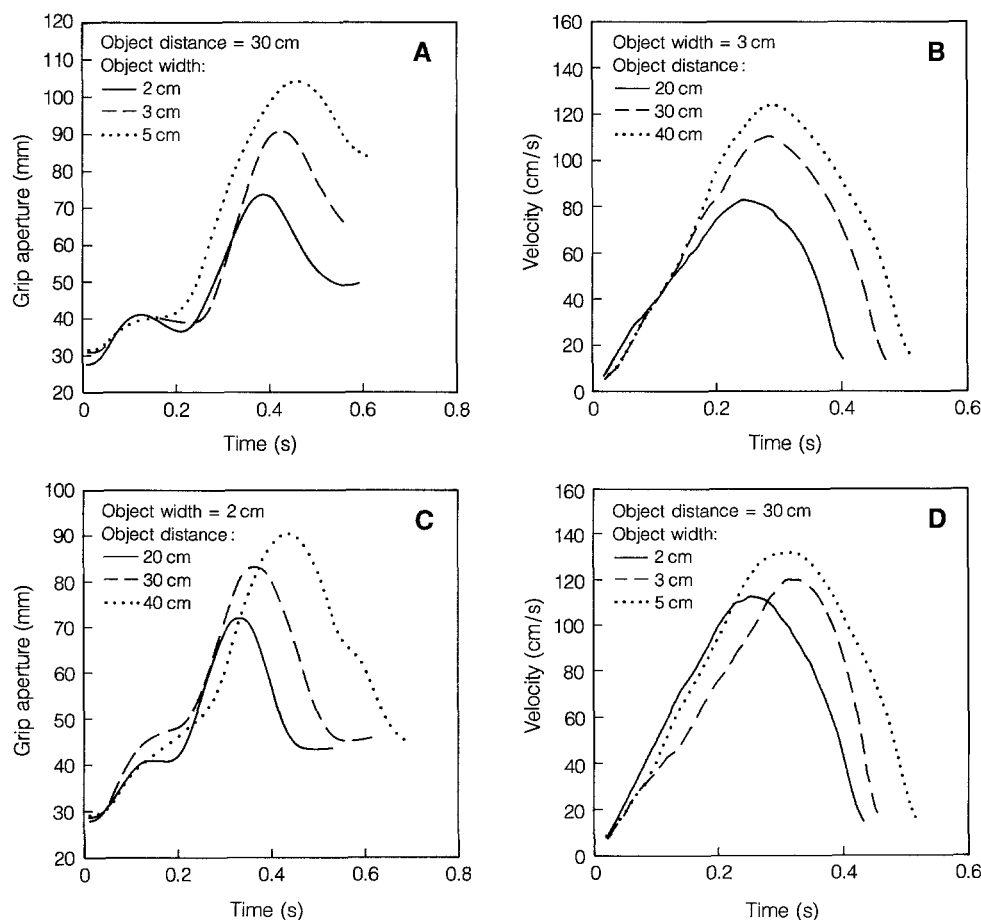

Fig. 1A–D. Representative traces from one subject demonstrating: A scaling of maximum grip aperture for object size; B scaling of acceleration, peak velocity, and duration for object distance; C scaling of maximum grip aperture for object distance; and D scaling of peak velocity and duration for object size. (Movement onset times are not depicted)

Table 1. Effects of manipulating object size and distance on measures characterizing grip formation and transport of the arm. (Standard error of mean values indicated in parentheses)

	2 cm	3 cm	5 cm	F statistic
Object width				
Maximum grip aperture (mm)	93 (1.9)	98 (1.8)	112 (1.7)	$F_{(1.34, 18.72)} = 274.52,\ p < 0.001$
Time to max. grip aperture (ms)	305 (12.1)	305 (12.6)	328 (13.3)	$F_{(1.77, 24.81)} = 9.75,\ p < 0.005$
Peak velocity (mm/s)	1152 (38.0)	1169 (38.2)	1177 (38.2)	$F_{(1.32, 18.48)} = 9.45,\ p < 0.005$
Duration (ms)	477 (17.1)	475 (16.8)	499 (17.6)	$F_{(1.60, 22.46)} = 22.87,\ p < 0.001$
Maximum height (mm)	56 (2.1)	57 (2.2)	60 (2.1)	$F_{(1.46, 20.44)} = 35.7,\ p < 0.001$

	20 cm	30 cm	40 cm	F statistic
Object distance				
Movement onset (ms)	476 (8.4)	473 (7.5)	488 (8.5)	$F_{(1.74, 24.36)} = 3.93,\ p < 0.05$
Time to peak velocity (ms)	197 (4.2)	220 (4.5)	241 (4.9)	$F_{(1.26, 17.60)} = 99.77,\ p < 0.001$
Peak velocity (mm/s)	895 (24.7)	1197 (30.0)	1407 (36.9)	$F_{(1.06, 14.89)} = 221.79,\ p < 0.001$
Duration (ms)	414 (13.7)	487 (16.0)	550 (18.4)	$F_{(1.17, 16.45)} = 114.53,\ p < 0.001$
Maximum height (mm)	46 (1.4)	57 (1.8)	69 (2.3)	$F_{(1.11, 15.51)} = 108.68,\ p < 0.001$
Maximum grip aperture (mm)	99 (2.0)	101 (2.0)	104 (2.0)	$F_{(1.28, 17.97)} = 9.46,\ p < 0.005$
Time to max. grip aperture (ms)	264 (10.1)	304 (11.1)	371 (14.0)	$F_{(1.13, 15.79)} = 65.24,\ p < 0.001$

Table 2. Effects of manipulating object size and distance on the relative timing of a number of kinematic markers, expressed as a percent of total movement time. (Standard error of mean values indicated in parentheses)

	2 cm	3 cm	5 cm	F statistic
Object width				
% time to peak vel.	48.2 (0.9)	48.1 (0.9)	46.7 (0.9)	$F_{(1.94, 27.19)} = 8.4,\ p < 0.005$
% time to peak neg. acceleration in X	75.0 (1.3)	74.7 (1.6)	72.8 (1.3)	$F_{(1.58, 2.11)} = 8.61,\ p < 0.005$

	20 cm	30 cm	40 cm	F statistic
Object distance				
% time to peak vel.	49.8 (1.0)	47.3 (0.9)	45.9 (0.8)	$F_{(1.19, 16.60)} = 7.47,\ p < 0.05$
% time to peak neg. acceleration in X	76.5 (1.6)	73.1 (1.2)	73.0 (1.3)	$F_{(1.57, 21.94)} = 6.90,\ p < 0.01$
% time to max. hgt. in wrist trajectory	52.9 (0.9)	46.9 (0.7)	44.9 (0.7)	$F_{(1.18, 16.54)} = 61.64,\ p < 0.001$
% time to maximum aperture	66.5 (0.9)	66.4 (0.7)	71.2 (0.7)	$F_{(1.29, 18.07)} = 8.32,\ p < 0.01$

above), subjects spent proportionately less time raising their limb (and proportionately more time lowering it) as movement amplitude increased. In contrast, and somewhat unexpectedly, the distance manipulation also affected the relative timing of hand closure, such that maximum grip aperture was achieved proportionately later in movements to more distant objects. (See Table 2.)

Each reported change in the relative timing of a particular kinematic marker may in itself seem trivial. Indeed, a close inspection of Table 2 confirms that the
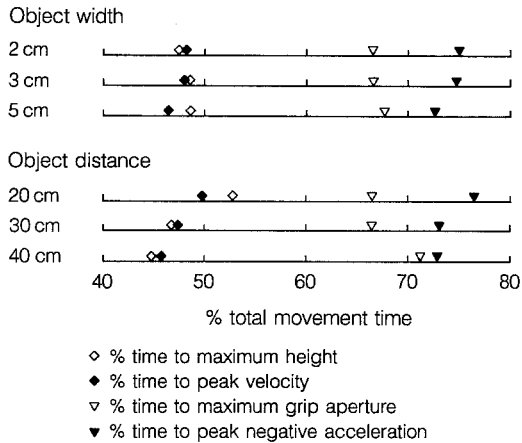
Object width

2 cm

3 cm

5 cm

Object distance

20 cm

30 cm

40 cm

40   50   60   70   80

% total movement time

◇ % time to maximum height
◆ % time to peak velocity
▽ % time to maximum grip aperture
▼ % time to peak negative acceleration

Fig. 2. Changes in the relative timing (expressed as a percent of total movement time) of a number of kinematic markers as a function of object size and distance

Fig. 3. Mean values of the maximum aperture (in mm) between the index finger and thumb of the right hand under full and restricted viewing conditions. Note that in both conditions maximum grip aperture is scaled for the size of the object. (Error bars represent the standard error of mean values)

percent change from one condition to the next (though statistically significant) is invariably quite small, ranging from 1.5 to 8.0%. Nonetheless, if one looks at the temporal pattern for a number of kinematic markers simultaneously (Fig. 2), one sees that the relationships between particular kinematic markers change substantially as a function of task demands.

Effects of removing visual feedback. The most striking effect of removing visual feedback was that there was an overall increase in maximum grip aperture during reaching movements when subjects could not see their moving limb, relative to when they could ($F_{(1,14)} = 16.67$, $p = 0.001$). The average maximum grip aperture in the no visual feedback condition was 8 mm greater than that measured when the subjects could see their moving limbs [mean values (SE) were 105 (1.7) mm and 97 (1.6) mm for no visual feedback and visual feedback trials, respectively]. Despite this, maximum grip aperture continued to be scaled for object size even in the absence of visual feedback (Object Size, $F_{(1.34,18.72)} = 274.52$, $p < 0.001$; Viewing Condition × Object Size, $F_{(1.35, 18.84)} = 0.91$, n.s.). (See Fig. 3.) In addition, while movement onset times increased slightly with increasing target distance under full viewing conditions, movement onset times were not significantly different for each of the three distances when reaches had to be completed in the dark (Viewing Condition × Object Distance $F_{(1.97, 27.51)} = 3.41$, $p < 0.05$), and were equivalent to the longest latencies when subjects had unrestricted viewing of their limbs (see Fig. 4).

Removing visual feedback also affected the relative timing of a number of kinematic markers. Specifically, both maximum grip aperture ($F_{(1,14)} = 7.28, p < 0.05$) and the maximum height in the trajectory of the wrist ($F_{(1,14)} = 14.81, p < 0.005$) were achieved proportionately sooner in time when the subject could not see his/her reaching limb than when the entire movement was visible.
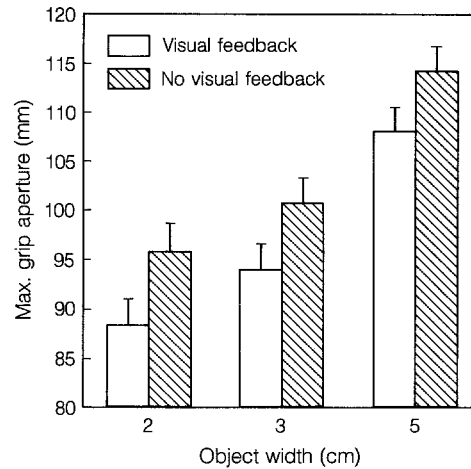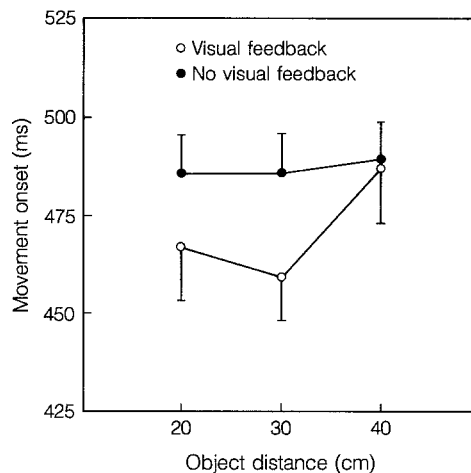
Fig. 4. Effect of removing visual feedback on movement onset times (in ms) for reaches of different amplitudes. (Error bars represent the standard error of mean values)

Discussion

In agreement with earlier reports in the literature describing aiming movements (Marteniuk et al. 1987; Prablanc et al. 1979), increasing the amplitude of the required movement in the present study led to corresponding increases in both the peak velocity and the duration of the transport component of prehension. This occurred despite the fact that the range of movement amplitudes studied was highly comparable to that used in Jeannerod's (1984) study of prehension. This finding contradicts Jeannerod's (1984) suggestion that prehension movements are generated in such a way as to achieve invariant movement durations. Also in contradiction with earlier findings from some laboratories, we observed that our distance manipulation affected the timing and formation of the grasp, and that our size manipulation

produced reliable changes in the kinematic profile of the wrist (cf. Jeannerod 1981; Wallace and Weeks 1988). Thus, these data suggest that object characteristics such as size and distance do not have independent effects on the grasp and reach, respectively. Changes in either variable will affect both of these components of prehension.

Despite the fact that manipulations of object size and distance affect both components of prehension, the net effect of all this is to regulate the timing of hand closure with some precision such that it always begins at approximately the same relative point in time, when approximately two-thirds of the total movement time has elapsed. For the most part, these observations are in good agreement with work from other laboratories and suggest that Jeannerod's (1981, 1984) original conclusion is largely correct; there is a strong temporal coupling between the reach and the grasp. Yet, one should not ignore the fact that there may be small, but significant, changes in the relative timing of a number of kinematic markers, depending on task demands. It should be emphasized, however, that identical central algorithms could still produce rather different temporal relationships between kinematic markers, when such algorithms are calibrated for different distances or object sizes. Indeed, the small differences we observed may reflect not so much differences in programming within the central nervous system as differences in synergies between different muscle groups and other mechanical constraints.

The fact that manipulating object distance and size affects both the proximal and distal components of prehension suggests that at some level programs generating these components are integrated. While studies of brain-damaged individuals will shed light on how and where this integration takes place, the present examination of the performance of normals when visual feedback was unavailable also provides us with insight into the mechanisms through which prehension is achieved. The results of Experiment 1 indicate that maximum grip aperture was scaled for object size, and that this scaling was maintained even in the absence of visual feedback (cf. Jeannerod 1981, 1984), although the hand opened more under these conditions (cf. Wing et al. 1986). More importantly, Experiment 1 showed that movement onset times were shorter, particularly for the nearest objects, when subjects knew they would be able to use vision on-line to guide their movements. Furthermore, both maximum grip aperture and the maximum height in the trajectory of the wrist were achieved proportionately sooner in time when the subject could not see his/her reaching limb than when the entire movement was visible. These findings contradict Jeannerod's (1984, p. 236) proposal that visual feedback does not influence "movement patterning and intersegmental coordination" in prehension movements. They suggest, rather, that visual information, when present, may be used *both* to program the coordinated movement, and to improve the precision of the grasp and of the trajectory of the reaching movement, on-line.

Previous work on *aiming* movements has suggested that even when vision is present, it is not always used to full advantage. For example, Zelaznik, Hawkins, and

Kisselburgh (1983) and Elliott and Allard (1985) have shown that when visual feedback is *unpredictably* available subjects preprogram their reaches. That is, when feedback and no-feedback trials were presented in a random fashion, subjects did not use vision on the feedback trials to improve their pointing accuracy. In Experiment 1, the feedback and no-feedback trials were run in separate blocks, so subjects always knew whether or not they would be able to see their moving limb. Experiment 2 was designed to see whether the visual control of grip formation is affected in the same way that aiming movements are by manipulating the predictability of visual feedback. We had subjects go through a random series of feedback and no-feedback trials. The rationale was that, if subjects do adopt a preprogramming strategy when they suspect that they may not be able to modify their reach on-line, they should open their hand widely on every trial in a randomly ordered series of feedback and no-feedback trials, since they will be unable to predict whether or not they will be able to see their hand.

Experiment 2

Method

Subjects. To allow for a direct comparison of individual performance across the two experiments, eight of the original group of 15 subjects recruited for Experiment 1 (six males, two females) were retested. A reanalysis of the data from Experiment 1 for only these eight subjects revealed that, with one exception, the findings described above regarding the effects of removing visual feedback were still statistically significant with this restricted sample size. The one exception was that, while there was a strong trend in the data for the removal of visual feedback to be associated with a decrease in the proportion of movement time spent attaining the maximum height in the wrist's trajectory, this effect did not quite reach statistical significance, $(F_{(1,7)} = 4.71, p = 0.067)$.

Apparatus and procedure. The apparatus was identical to that used in Experiment 1. The same three objects were used, but because the effects of primary interest for the present analysis did not interact with the distance to the object (or were present at the 30 cm distance), the target object was always placed 30 cm in front of the subject's start position. Trials in which visual information was continuously available, or was removed after the release of the start key, were randomly interspersed, with the stipulation that no more than three consecutive reaches were carried out in the same viewing condition. Five reaches were directed toward each object in each viewing condition, for a total of 30 experimental trials. Trial initiation, instructions to the subjects, and data management were the same as outlined for Experiment 1. Once again, trials in which the object was knocked over or missed were repeated at the end of the series and only trials in which the object was successfully retrieved were included in the analysis.

Results

The variable of greatest interest in the present experiment was maximum grip aperture. When visual feedback was unpredictably available, subjects continued to scale the maximum opening of their hand for the size of the object to be grasped (Object Size, $F_{(1.43, 10.02)} = 102.15$, $p < 0.001$). In contrast to the results of Experiment 1,
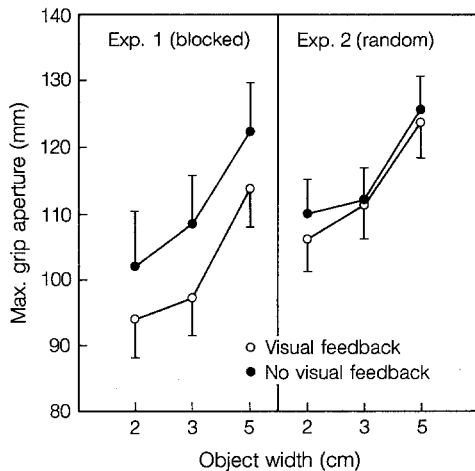
Fig. 5. A comparison of the mean maximum apertures (in mm) between the index finger and thumb of the right hand when subjects could (blocked series, Exp. 1) or could not (random series, Exp. 2) predict whether visual feedback would be available during the movement. (Error bars represent the standard error of mean values)

however, the extent to which the hand opened was equivalent for feedback and no-feedback trials (Viewing Condition, $F_{(1,7)} = 3.02$, n.s.). In comparing the data of these eight subjects from Experiments 1 and 2, it was clear that when visual feedback was unpredictably available (Experiment 2), subjects performed in a manner very similar to when visual feedback was predictably *not* available (in the no-feedback trials of Experiment 1). In contrast, when subjects did know ahead of time that they would be able to use vision to guide their movements (in the feedback trials of Experiment 1) they opened their hands much less, overall, when reaching to target objects (see Fig. 5).

Although when these eight subjects were tested in Experiment 1 movement onset times were longer when visual feedback was not available than when it was, there was no difference between the onset times of feedback and no-feedback trials in Experiment 2, when trials were presented in a random series ($F_{(1,7)} = 0.47$, n.s.). In fact, a comparison of the results of these eight subjects in Experiments 1 and 2 revealed that movement onset times for targets at the 30 cm distance were highly comparable when visual feedback was predictably *not* available (in the no-feedback trials Experiment 1) and when it was unpredictably available (in Experiment 2). In either case,

onset times were longer than when visual feedback was predictably available, in the feedback trials of Experiment 1 (see Table 3).

In the blocked series (Experiment 1), both maximum grip aperture and the maximum height in the trajectory of the wrist tended to be achieved proportionately sooner when the subject could not see his/her reaching limb than when the entire movement was visible. In the random series (Experiment 2), the relative timing of these two kinematic markers on all trials (whether visual feedback was available or not) was more similar to that on trials in which subjects knew they would be unable to see their reaching limb in Experiment 1. (See Table 3.)

Discussion

It appears that when visual feedback is not predictably available subjects adopt the same strategy that they use when they know they will not be able to see their moving limb. First, they are slower to initiate their movements, a finding which would be consistent with the notion that longer onset times are indicative of more preprogramming (Klapp 1975). Second, they build a larger margin of error in their grasp by opening their hand more widely. Finally, the reach is programmed in such a way that the maximum opening of the hand and the maximum height in the trajectory of the wrist occur proportionately sooner in time. Thus, the data from this second experiment qualify the conclusion drawn in the discussion of Experiment 1, that the availability of visual feedback influences movement programming and intersegmental coordination in prehension movements. These data suggest, rather, that for vision to be used for on-line control of movements, such information must be *predictably* available from trial to trial. In other words, the predictability of visual information influences the degree to which a prehension movement is preprogrammed.

How is grip formation controlled when subjects cannot see their reaching limb, or when they cannot predict whether vision will be available to guide their movements? It is unlikely that the entire movement is preprogrammed in these situations. The present data suggest only that the maximum opening of the hand and the timing of the hand's closure and descent onto the object may be preprogrammed. It seems likely that what happens during the final approach is modifiable not only on the basis of visual feedback if it is available, but also

Table 3. A comparison of mean values on a number of kinematic measures for reaches directed to target objects located 30 cm from the hand's start position, when subjects could (blocked series, Exp. 1) or could not (random series, Exp. 2) predict whether visual feedback would be available during the movement. (Standard error of mean values indicated in parentheses)

	Order of trials	Feedback condition	
		Vision	No vision
Movement onset (ms)	blocked (Exp 1)	444 (6.1)	472 (5.7)
	random (Exp 2)	473 (9.3)	471 (10.2)
% time to maximum aperture	blocked (Exp 1)	71.3 (0.9)	67.6 (0.8)
	random (Exp 2)	64.5 (1.3)	63.3 (1.2)
% time to maximum height	blocked (Exp 1)	48.9 (0.9)	46.5 (0.9)
	random (Exp 2)	46.3 (0.7)	45.3 (0.8)

through the integration of visual information available before the movement begins with non-visual sources of information (proprioceptive/kinesthetic feedback, efference copy) about limb position as the movement is being executed. In fact, Jeannerod, Michel and Prablanc (1984) studied a patient with hemianesthesia and found that when proprioceptive/kinesthetic information is unavailable the success of a prehensive movement is *critically* dependent upon the availability of visual feedback, a finding which suggests that this information *is* normally used to guide the closing the hand upon the object when the reaching limb cannot be seen.

Conclusions

The data from these two experiments have shown that the control mechanisms underlying transport of the limb and grip formation are affected by similar task constraints including visually-based estimates of object size and distance, and by the subject's expectations regarding the availability of visual feedback. These results are consistent with other observations suggesting that a variety of intrinsic and extrinsic task constraints, such as instructions to the subject and perceived object fragility, can affect different effector components of a coordinated action (Fisk and Goodale 1990; Marteniuk and MacKenzie 1990). One interpretation of these observations is that the apparent relationship between the transport and grip components of prehension involves more than temporal coupling and that a higher-order control system is responsible for their integration. Additional support for this hypothesis comes from recent observations of patients with optic ataxia who show deficits in the visual control of both reaching and grasping (Jakobson et al. in press; Perenin and Vighetto 1983, 1988).

The notion that reaching and grip formation are controlled by a higher-order mechanism begs the question as to how apparent dissociations between these two components might arise. There are at least two plausible explanations for this. One is that, since it is difficult to compare spatial errors in reaching with postural errors in grip formation, the magnitude of an apparent deficit in one component in relation to the other may have been overemphasized in previous reports. A second plausible alternative is that the higher-order control mechanism could remain intact following brain damage while damage at a lower level of control could interfere with one component but not the other.

References

Brinkman J, Kuypers HGJM (1973) Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey. Brain 96:653–674

Denny-Brown D, Yanagisawa N, Kirk EJ (1975) The localization of hemispheric mechanisms of visually directed reaching and grasping. In: Zulch KJ, Creutzfeldt O, Galbraith GC, (eds.) Cerebral localization. Springer, Berlin Heidelberg New York

Elliott D, Allard F (1985) The utilization of visual feedback information during rapid pointing movements. Q J Exp Psychol [A] 37A:407–425

Faugier-Grimaud S, Frenois C, Stein DG (1978) Effects of posterior parietal lesions on visually guided behaviour in monkeys. Neuropsychologia, 16:151–168

Faugier-Grimaud S, Frenois C, Peronnet F (1985) Effects of posterior parietal lesions on visually guided movements in monkeys: Exp Brain Res 59:125–138

Fisk JD, Goodale MA (1990). The effect of instructions to subjects on the programming of visually directed reaching movements. J Mot Behav 21:5–19

Gazzaniga MS, Bogen JE, Sperry RW (1967) Dyspraxia following division of the cerebral commissures. Arch Neurol 16:606–612

Goodale MA (1988) Hemispheric differences in motor control. Behav Brain Res 30:203–214

Goodale MA, Pelisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. Nature 320:748–750

Haaxma R, Kuypers HGJM (1975) Intrahemispheric cortical connexions and visual guidance of hand and finger movements in the rhesus monkey. Brain 98:239–260

Haggard P, Wing AM (1990) Assessing and reporting the accuracy of position measurements made with optical tracking systems. J Mot Behav 22:315–321

Jakobson LS, Archibald YM, Carey DP, Goodale MA (in press) A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. Neuropsychologia (in press)

Jeannerod M (1981) Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (eds), *Attention and performance IX*. Hillsdale, Erlbaum pp 153–168

Jeannerod M (1984) The timing of natural prehension movements. J Mot Behav 16:235–254

Jeannerod M (1986) The formation of finger grip during prehension: a cortically mediated visuomotor pattern. Behav Brain Res 19:99–116

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Clarendon Press Oxford

Jeannerod M, Biguer B (1982) Visuomotor mechanisms in reaching within extrapersonal space. In: Ingle DJ, Goodale MA, Mansfield RJW (eds), Analysis of visual behavior. The MIT Press, Cambridge, MA pp 387–409

Jeannerod M, Michel F, Prablanc C (1984) The control of hand movements in a case of hemianaesthesia following a parietal lesion. Brain 107:899–920

Kimura D (1986) Neuropsychological test procedures. DK Consultants, London, Ontario

Kirk RE (1982) Experimental design: procedures for the behavioral sciences. Brooks/Cole, Belmont, California

Klapp ST (1975) Feedback versus motor programming in the control of aimed movements. J Exp Psychol 104:147–153

LaMotte RH, Acuna C (1978) Deficits in accuracy of reaching after removal of posterior parietal cortex in monkeys. Brain Research 139:309–326

Lawrence DG, Hopkins DA (1972) Developmental aspects of pyramidal control in the rhesus monkey. Brain Research 40:117–118

Marteniuk RG, MacKenzie CL, Jeannerod M, Athenes S, Dugas C (1987) Constraints on human arm movement trajectories. Canad Psychol 41:365–378

Marteniuk RG, MacKenzie CL (1990) Invariance and variability in human prehension: Implications for theory development. In: Goodale MA (ed), Vision and action: the control of grasping. Ablex Norwood, NJ, pp 49–64

Muir RB (1985) Small hand muscles in precision grip: a corticospinal prerogative? Exp Brain Res [Suppl] 10:155–174

Muir RB, Lemon RN (1983) Corticospinal neurons with a special role in precision grip. Brain Res 261:312–316

Passingham R, Perry H, Wilkinson F (1978) Failure to develop a

precision grip in monkeys with unilateral neocortical lesions made in infancy. Brain Res 145:410–414

Perenin M-T, Vighetto A (1983) Optic ataxia: a specific disorder in visuomotor coordination. In: Hein A, Jeannerod M, (eds), Spatially oriented behavior. Springer, Berlin Heidelberg New York, pp 305–326

Perenin M-T, Vighetto A (1988) Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. Brain 111:643–674

Prablanc C, Echallier JF, Komilis E, Jeannerod M (1979) Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. Biol Cybern 35:113–124

Trevarthen CB (1965) Functional interactions between the cerebral hemispheres in the monkey. In: Ettlinger EG (ed) Functions of the corpus callosum. Ciba Foundation, London, pp 24–40

Volpe BT, Sidtis JJ, Holtzman JD, Wilson DH, Gazzaniga MS (1982) Cortical mechanisms involved in praxis: observations following partial and complete section of the corpus callosum in man. Neurology 32:645–650

Von Hofsten C (1979) Development of visually directed reaching: the approach phase. J Hum Mov Stud 5:160–178

Wallace SA, Weeks DL (1988) Temporal constraints in the control of prehensile movement. J Mot Behav 20:81–105

Wing AM, Turton A, Fraser C (1986) Grasp size and accuracy of approach in reaching. J Mot Behav 18:245–260

Zelaznik HN, Hawkins B, Kisselburgh L (1983) Rapid visual feedback processing in single-aiming movements. J Mot Behav 15:217–236