

Selective perturbation of visual input during prehension movements

2. The effects of changing object size

Y. Paulignan¹, M. Jeannerod¹, C. MacKenzie², and R. Marteniuk^{2*}

¹ Vision et Motricité, INSERM U94, 16 Avenue du Doyen Lépine, F-69500 Bron, France

² Department of Kinesiology, University of Waterloo, Waterloo, Ontario, Canada

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Summary. 1. Subjects were instructed to reach and grasp cylindrical objects, using a precision grip. The objects were two concentric dowels made of translucent material placed at 35 cm from the subject. The inner (“small”) dowel was 10 cm high and 1.5 cm in diameter. The outer (“large”) dowel was 6 cm high and 6 cm in diameter. Prehension movements were monitored using a Selspot system. The displacement of a marker placed at the wrist level was used as an index for the transport of the hand at the location of the object. Markers placed at the tips of the thumb and the index finger were used for measuring the size of aperture of the finger grip.

2. Kinematics of transport and grasp components were computed from the filtered displacement signals. Movement time (MT), time to peak velocity (TPV) and time to peak deceleration (TPD) of the wrist, time to peak velocity of grip aperture (TGV), time to maximum grip aperture (TGA) were the main parameters used for comparing the movements in different conditions. Spatial paths of the wrist, thumb and index markers were reconstructed in two dimensions. Variability of the spatial paths over repeated trials was computed as the surface of the ellipses defined by X and Y standard deviations from the mean path.

3. Computer controlled illumination of one of the dowels was the signal for reaching toward that dowel. Blocks of trials were made to the small dowel and to the large dowel. Mean MT during blocked trials was 550 ms. The acceleration phase of the movements (measured by parameter TPV) represented 33% of MT. About half of MT (52%) was spent after TPD in a low velocity phase while the hand was approaching the object. This kinematic pattern was not influenced by whether movements were directed at small or large dowels.

4. Grip aperture progressively increased during transport of the hand. TGA corresponded to about 60% of MT, that is, maximum grip aperture was reached during the low velocity phase of transport. Following TGA, fingers closed around the object until contact was made. This pattern of

grip formation differed whether the movement was directed at the large or the small dowel: TGA occurred often earlier for the small dowel, and the size of the maximum grip aperture was larger for the large dowel. Variability of both the wrist and finger spatial paths was larger during the first half of MT, and tended to become very low as the hand approached the dowels.

5. Selective perturbations of dowel size were randomly produced at the onset of prehension movements. Perturbations involved increase in object size (the illumination was suddenly shifted from the small to the large dowel, S-L perturbation), or decrease in object size (from the large to the small dowel, L-S perturbations). During S-L perturbations MT was increased by 175 ms on average. As TPV and TPD did not differ from control unperturbed movements, increase in MT was entirely due to lengthening of the low velocity phase following TPD.

6. Grip formation was affected by the perturbation. Grip aperture first peaked to the size corresponding to the small dowel, then reincreased for accommodating the size of the large dowel. The time where grip aperture reincreased (as measured on the curve of grip velocity) occurred 329.8 ms on average after movement onset. Variability of wrist and finger spatial paths was increased with respect to controls, but it remained low during the final phase of the movement. L-S perturbations had similar effects, though attenuated with respect to S-L perturbations.

7. This relatively long time taken to initiate corrections in response to object size perturbations contrasts with the short time (about 100 ms) for initiating corrections during perturbations of object position. This difference suggests some degree of independence of the mechanisms generating finger movements during grip formation from those generating transport of the hand. In addition, the kinematic coupling of the two components (demonstrated here by lengthening of the low velocity phase of the transport during correction of finger grip size) suggests the existence of a different mechanism subserving temporal coordination of the two components.

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Offprint requests to: M. Jeannerod

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Introduction

The posture that is assumed by the hand before contact with an object represents the end result of a motor sequence which starts well ahead of the action of grasping itself. The fingers begin to shape during transport of the hand to the object location and contribute to a final spatial configuration termed opposition space by Arbib (1985; see also Iberall et al. 1986), where the relative positions of the hand and the object to be grasped are specified by object properties and task requirements.

Preshaping of the hand is a highly stable motor pattern. It first involves a progressive opening of the grip with straightening of the fingers, followed by a closure of the grip until its matches object size. The point in time where grip size is the largest is a clearly identifiable landmark which occurs during the deceleration phase of the transport of the hand, that is, well before the fingers come in contact with the object. The size of the maximum grip aperture correlates with the size of the object (Jeannerod 1981, 1984; see also Wing et al. 1986; Wallace and Weeks 1988, Marteniuk et al. 1990; Gentilucci et al. 1991). These movements of the fingers during grasping are largely predetermined by object-related visual input. In normal subjects, they are correctly achieved in situations where the hand remains invisible to the subject (Jeannerod 1984).

The existence of independent finger movements during transport of the hand at the spatial location of the object, however, implies that these two components of the action of prehension have to be linked or coordinated with each other, so that the time course of the finger movements matches that of the transport. This is critical for anticipatory closure of the finger grip to occur in tight synchrony with approach of the object by the fingertips. Early or late closure will both result in inaccurate grasps, with the consequence of bumping and eventually breaking fragile objects. The current model for the coordination between the components of prehension specifies that the mechanisms for achieving a correctly oriented and sized grip operate in parallel with other mechanisms for hand transport to object position in space. To help elucidate the nature of the motor coordination implied by this model, we designed a series of experiments where the visual input related to either grip formation (e.g., object size), or transport of the hand (object location) can be selectively perturbed during the movement. This paradigm of perturbing visual input in relation to movements has been widely used in the recent years for probing the mechanisms related to motor representation and preparation (Georgopoulos et al. 1981; Soechting and Lacquaniti 1983; Goodale et al. 1986; Pelisson et al. 1986).

Our initial prediction was that, if the two components of prehension operate independently, the reaction of the prehension system to these perturbations should be limited to the perturbed component, leaving the other component unaffected. In the first paper of this series, we reported the effects of changing object position. Indeed, this perturbation produced corrections of hand trajectory in space, such that movements were adequately redirected and rescaled. Movement time was increased by 100 ms on

average, and the first signs of correction (change in acceleration of the arm) were observed within about 100 ms from onset of the perturbation. However, in apparent contradiction to the model, the pattern of grip formation was also found to be consistently affected by the change in object position (Paulignan et al. 1990, 1991).

In the present paper, we present the complementary experiment where we studied the corrective responses to a sudden visual change in object size, without alteration of object position.

Methods

Recording technique

As in the previous experiment (Paulignan et al. 1991), prehension movements were recorded bidimensionally by a Selspot system camera equipped with a 50 mm lens, placed 3 m above the horizontal working plane. The camera monitored the displacements of 5 active markers (infrared emitting diodes, IREDS) placed on the right arm in the following positions: 1, on the lateral lower corner of the index finger nail; 2, on the medial lower corner of the thumb nail; 3, on the dorsal aspect of the hand immediately proximal to the metacarpophalangeal joint of the index finger; 4, on the skin immediately proximal to the styloid process of the radius at the wrist; and 5, on the skin above the cubital head at the elbow. The wrist IRED was used to measure the transport component of the prehension movements. The elbow, wrist and metacarpophalangeal IREDS were used for computing the wrist angle (not reported in this paper). Finally, the fingertip IREDS were used to measure the displacements of the index and thumb, respectively, and the size of the grip aperture (index-thumb distance). Dynamic accuracy tests indicated that spatial precision of the measures was 2 mm. Positions of the IREDS were sampled at 200 Hz and stored on a PDP 11/73 computer.

Subjects

Subjects were five right handed adults (3 females, 2 males) ranging in age between 25 and 35 years. Three of the subjects were naive with regard to the purpose of the experiment. The other two had also participated in the experiment reported in the previous paper.

Apparatus and procedure

During the experimental sessions, subjects were seated comfortably, without restraint, facing the working surface in a dimly lit room. The subject placed the right hand at the starting position in front of the body midline. The hand rested on its ulnar edge, with the tip of the index and the tip of the thumb in contact with each other, and the lower part of the thumb pressed against a start switch used for triggering perturbations (see below). The targets were two concentric dowels made of translucent material, placed at 20° to the right of subject's midline, at 35 cm from the hand. The inner dowel was 10 cm high and 1.5 cm in diameter; it will be referred to as the "small" dowel. The outer dowel was 6 cm high and 6 cm in diameter; it will be referred to as the "large" dowel. Computer controlled light emitting diodes (LEDs) embedded into the transparent material covering the working surface were used to transilluminate the dowels. One LED was placed below the small dowel, two LEDs were placed below the large one (Fig. 1).

The illumination of a dowel was the signal for the subject to start the movement. The subject was requested to reach, grasp and lift the dowel accurately and rapidly, using the distal pads of the thumb and index finger. A few trials were used for instructing the subject. In the first part of the experiment, two counterbalanced blocks of trials

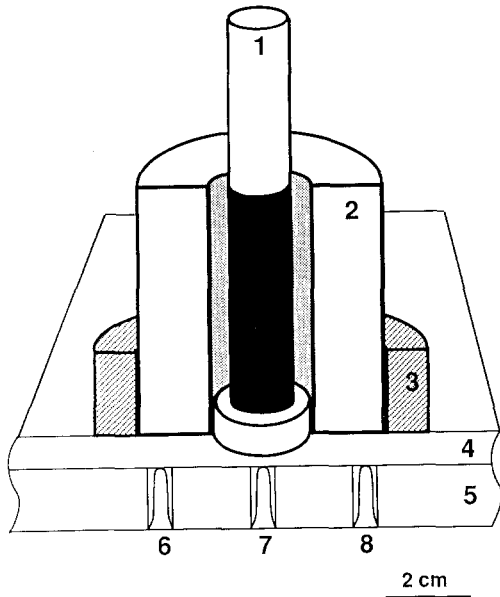


Fig. 1. Target objects used in the experiment. 1: Small dowel; 2: Large dowel. The Small dowel can be lifted independently from the Large one. The large dowel can be removed from the opaque support (3); 4: transparent working surface; 5: Light emitting diodes (LEDs). The middle LED (7) illuminates the small dowel, the other two LEDs (6 and 8) illuminate the large dowel

were run by illuminating either the small or the large dowel 10 consecutive times (Small and Large *blocked* trials, respectively). In the second part, a single block of 100 trials was run. Each single trial during this run started with illumination of either the small or the large dowel. In 80% of the trials, no perturbation occurred (Small and Large *control* trials). In 20% of the trials, the light was unexpectedly shifted from the dowel illuminated first to the other one (i.e., 10 trials from Small to Large and 10 trials from Large to Small, S-L and L-S *perturbed* trials, respectively). The shift was produced by the release of the start switch when the hand left its resting position. Since the room was dimly lighted, the appearance was that of an instantaneous change in dowel size. Corrective movements performed during perturbed trials involved a small upward (in the L-S trials) or downward (in the S-L trials) component. This component, the maximum amplitude of which was about 4 cm (see Fig. 1), was neglected in the present experiment.

Data processing

Data were processed as reported previously (Paulignan et al. 1991). A second-order Butterworth dual pass filter (cutoff frequency, 8 Hz, see Franks et al. 1990) was used for data processing. X and Y trajectories of each IRED were computed after filtering. Tangential velocities (e.g., for the wrist IRED) were also computed after filtering. Acceleration data were derived by differentiating the tangential velocity data. Movement time was measured as the interval between the onset of the thumb IRED movement, and the time when the fingers came in contact with the object (as seen from computation of the grip size).

Spatiotemporal variability of the wrist, thumb, and index trajectories was quantified after time normalization of the data. First, with respect to the spatial path, the standard deviations of the mean X and Y positions of each IRED were calculated for each of the 100 normalized time frames. In addition, to obtain a global estimate of variability (index of variability) for each IRED in each condition, the surface areas of the ellipses defined by the standard deviations in X and Y dimensions were computed (in cm²), and the values of these

surfaces in each condition were cumulated (Georgopoulos et al. 1981).

Results

Blocked trials

Movement time. Since subjects were instructed to move accurately and rapidly, large interindividual variations in movement time (MT) occurred. Mean MT ranged from 390 ms in one subject to 650 ms in another one. The grand mean was around 550 ms. No significant differences in MT were found (using an unpaired t test) between movements directed at small or at large dowels (Table 1).

Transport component

Kinematic analysis. The wrist IRED was used for analysing kinematically the transport component of the movements. As in the experiment reported in the previous paper, wrist movements had a single peak, bell-shaped, velocity profile (Fig. 2). The peak value of resultant velocity (parameter APV) was 1203 mm/s for Small trials and 1128 mm/s for Large ones. The acceleration phase of the movement (between movement onset and the time of the velocity peak, parameter TPV) represented 33% of MT. The deceleration phase was marked by a sharp deceleration, which peaked at about 290 ms following movement onset (parameter TPD). Thus, about 52% of movement time was spent during the low velocity phase following peak deceleration.

Inspection of Table 1 reveals that none of the parameters used for describing wrist kinematics (TPV, APV, TPD) was influenced by the size of the dowel. Because TPV was similar in both Small and Large trials, it was

Table 1. Kinematic characteristics of prehension during Small (S) and Large (L) blocked trials (Intersubject mean and SD)

Transport	MT	TPV	APV	TPD
S	548.7 (108)	183.4 (32)	1203.3 (158)	283.6 (40)
L	555.7 (104)	189.3 (39)	1128.6 (124)	295.5 (32)
Grasp	TGV	TGA	AGA	
S	195.4 (58)	319.3 (54)	92.2 (11)	
L	188.4 (43)	385.2 (106)	124.9 (7)	

MT: Movement Time (ms), TPV: Time to Peak Velocity (mm/s), APV: Amplitude of Peak Velocity (mm), TPD: Time to Peak Deceleration (ms), TGV: Time to maximum Grip Velocity (ms), TGA: Time to maximum Grip Aperture (ms), AGA: Amplitude of maximum Grip Aperture (mm)

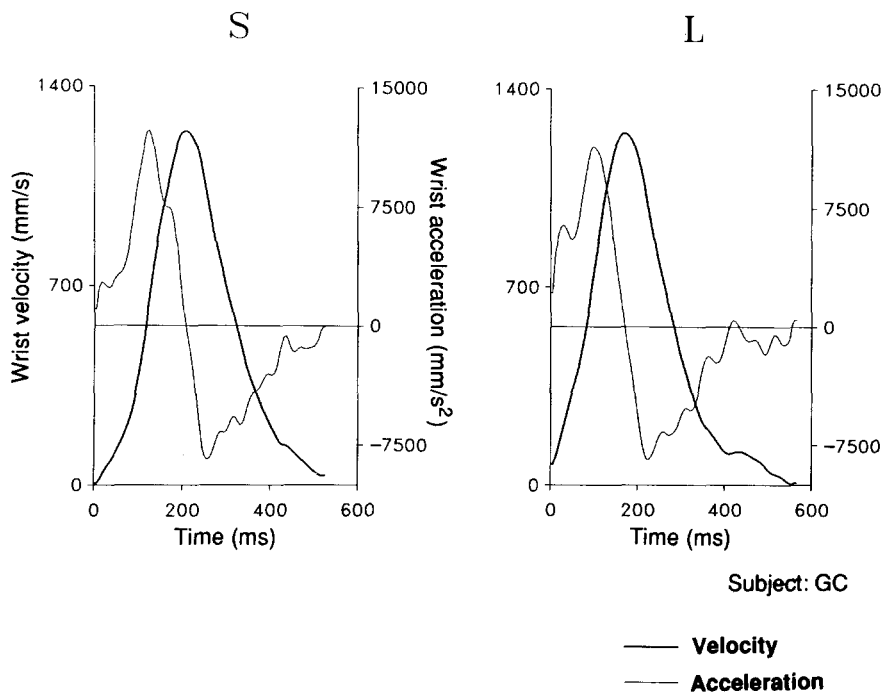


Fig. 2. Kinematic profile of the wrist displacement during blocked trials. Velocity and acceleration curves are shown as a function of time in two representative trials directed at the Small dowel (*S*, left) and the Large dowel (*L*, right) respectively

considered unnecessary to tabulate the values of time to peak acceleration (parameter TPA) in this experiment.

Spatial path and variability of the wrist trajectory. As shown by the averaged trajectories from one subject in Fig. 3a and b, transport components during blocked trials had a rectilinear spatial path. The variability of the spatial paths over repetitions of the same movement is indicated by vertical and horizontal bars placed on the trajectory at the location corresponding to each of the 100 frames. The horizontal bar represents variability in the X dimension, and the vertical bar, in the Y dimension. The mean index of variability, which cumulates the measures over the 100 frames, was 291 cm² for the Small trials, and 273 cm² for the Large ones. Variability, however, was not evenly distributed over the trajectory. It increased from the starting position up to a point representing about half of target distance, and then decreased until contact with the object. Distribution of variability in movement time is shown in Fig. 3c, d. The time at which variability was the largest corresponded roughly to 35% of MT, that is, it was close to the time of the velocity peak.

The temporal frames corresponding to maximum velocity (TPV) and to maximum deceleration (TPD) have been marked on the wrist paths of Fig. 3. This confirms graphically the asymmetry of wrist movement kinematics, where more than 50% of movement duration was spent in the low velocity phase within the last one fourth of target distance.

Grasp component

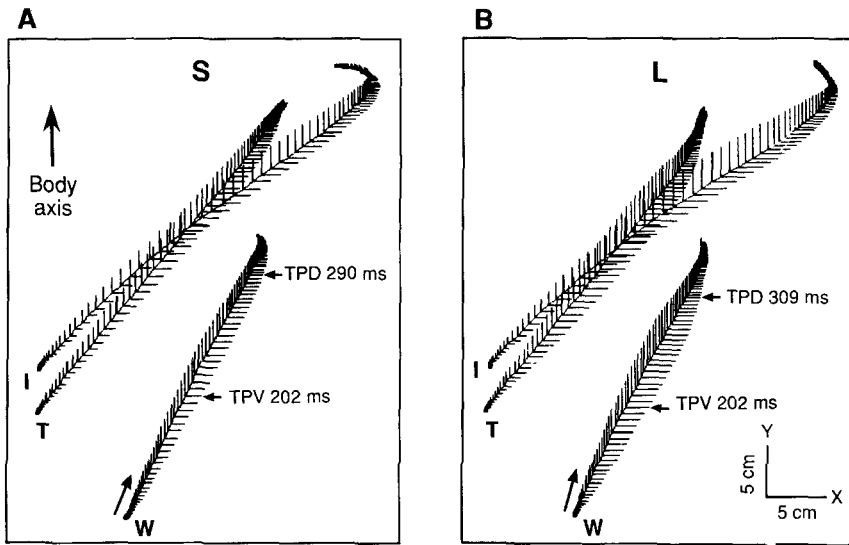
The grasp component was analysed by recording the distance between the tip of the index finger and the tip of the thumb. The index-thumb distance corresponds to grip

size, a measure which accounts for the combined movements of the two fingers.

Kinematic analysis. As in all previous studies of the grasp component during prehension, grip size was found to increase during transport of the hand, up to a maximum aperture, before enclosing the object. As shown by Table 1, the mean amplitude of this maximum grip aperture (parameter AGA) was related to dowel size: it was 92.2 mm for the Small trials, and 124.9 mm for the Large trials ($P < 0.0005$) (see Fig. 4 for two representative trials).

The time at which maximum grip aperture occurs (parameter TGA) is also an important parameter, because it is indicative of how the grasp component is coordinated in time with the transport component. TGA corresponded to 58% and to 69% of movement time for Small and Large trials, respectively (Table 1), that is, in both cases it occurred after deceleration of the wrist, during the low velocity phase near the object. The difference between Small and Large trials was highly significant ($P < 0.0005$).

The rate of change of grip aperture (represented graphically in Fig. 4 as the curve of the first derivative of grip size over time) was marked by an early peak followed by a deceleration. This deceleration was marked by an inflexion which corresponded to the plateau in grip aperture before grip closure. The time at which aperture change was the fastest (parameter TGV) was similar in Small and Large trials (Table 1). This is congruent with both the smaller AGA and the earlier occurrence of TGA in Small trials: grip size increased at the same rate in Small and in Large trials, but stopped to increase earlier in the Small trials. One subject (PG), however, adopted a different strategy. In this subject, TGA had the same value in Small and Large trials (330 ms), whereas TGV was shorter (by 46 ms) in Large trials than in Small ones. Thus, for this



Subject: CU

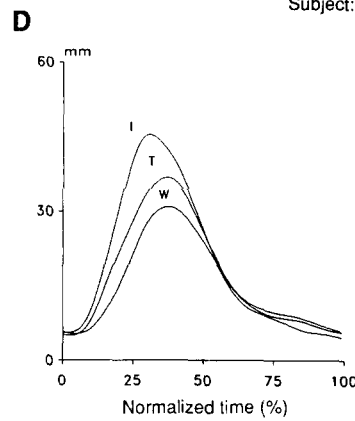
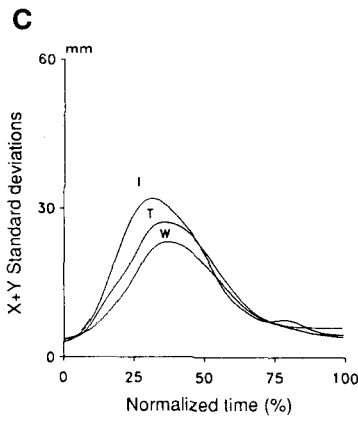
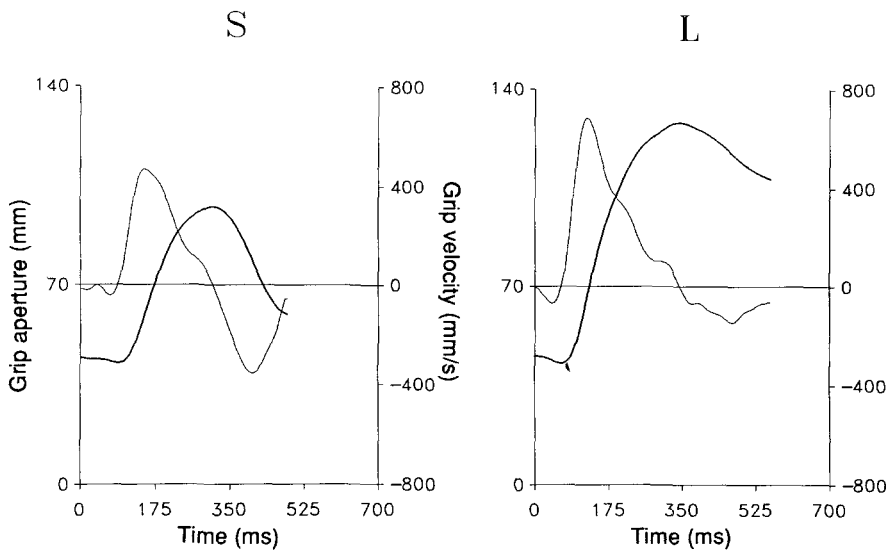


Fig. 3A-D. Spatial path and variability of prehension movements in the Blocked trials condition. In **A, B** are represented the normalized and averaged spatial paths of the wrist (W), the tip of the thumb (T) and the tip of the index finger (I), in 2 blocks of 10 trials directed at the small dowel (**A**) and the large dowel (**B**), respectively. Movements are shown in 2 dimensions (X, Y) as seen from above. The Y coordinate was aligned with body axis. The hand starting position is at the bottom part of the drawings. Numbers on the wrist spatial paths are the mean values of time to peak velocity (TPV) and time to peak deceleration (TPD). Horizontal and vertical bars on the averaged spatial paths represent the amplitude of one standard deviation in X and Y dimensions, respectively. Each pair of bars represents one of the 100 time frames of the normalized movements. **C, D** Amplitude of X and Y standard deviations (computed as the square root of $Sd X^2 + Sd Y^2$) as a function of time for wrist, thumb and index finger spatial paths. Due to normalization, time is represented in % of total movement time



Subject CU

— Grip aperture
 — Grip velocity

Fig. 4. Kinematic profile of grip formation during Blocked trials. Grip aperture (distance between tip of thumb and tip of index finger) and grip velocity are shown as a function of time in two representative trials directed at the Small dowel (**S, left**) and the Large dowel (**L, right**), respectively. Note larger aperture in the Large trial

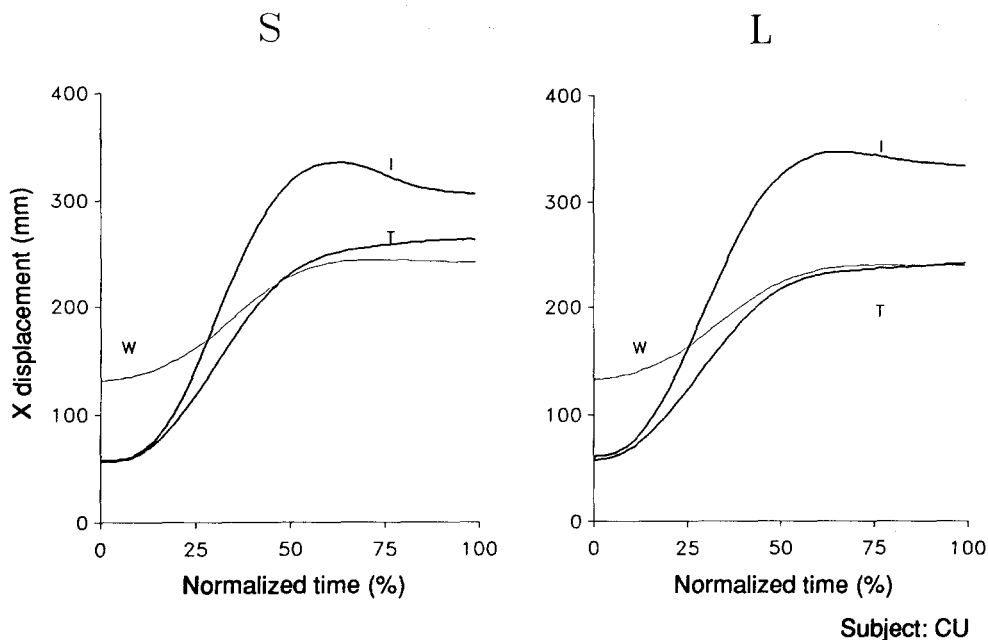


Fig. 5. Mean displacement in the X dimension of wrist (W), tip of the thumb (T) and tip of the index finger (I) as a function of normalized time in Blocked trials. S, trials directed at the Small dowel, L, at the Large dowel. Note relative invariance of thumb position with respect to wrist position

one subject, the rate of increase in grip size was faster in Large trials, hence allowing for a larger opening within the same amount of time.

Spatial path and variability of the finger trajectories. Spatial path of the tip of the thumb was rectilinear, and paralleled that of the wrist. This means that, as suggested by previous authors (e.g., Wing and Fraser 1983), the position of the thumb remained invariant with respect to the wrist during the movement. By contrast, the spatial path of the index finger showed a marked curvature which tended to surround the dowel. This difference in spatial path between the thumb and the index finger is shown both in Figs 3a and b and in Fig. 5. In the latter Figure, the path of the thumb in the X dimension can be seen to closely follow that of the wrist, which is not the case for that of the index.

The variability of the finger trajectories was larger than for the wrist (Fig. 3c, d); this shows that variability of finger movements did not merely reflect that of wrist movements. Variability amounted to 484/432 cm² for the thumb and 665/668 cm² for the index, in Small and Large trials, respectively. The variability of the finger trajectories was also larger at the time where velocity of the wrist was maximum, and tended to become very low before the fingers contacted the dowel. The low terminal variability indicates that the fingers tended to contact the object at the same points on each repetition of the movement, irrespective of the size of the object.

Control trials

Control trials corresponded to the cases (80%) where the same dowel (large or small) remained illuminated throughout the trial and where no perturbation occurred. Movement times during these trials were found to be shorter than during the corresponding blocked trials. Mean MT

was 505 ms, that is, about 50 ms less than in blocked trials (compare Small and Large control trials in Tables 2 and 3, respectively, with blocked trials in Table 1).

Although MT was shorter, the time values of kinematic landmarks for the wrist (parameters TPV and TPD), as well as the amplitude value of APV, were not different from those of blocked trials. This was the case for both Small and Large control trials. Thus, the shorter MT found for control trials was due to shortening the low velocity phase of the movement at the vicinity of the target.

The grasp component was also similar in control and blocked trials, except for the difference in time to grip aperture (TGA) between Small and Large trials. This

Table 2. Kinematic characteristics of prehension during Small control trials (S) and Small to Large perturbed trials (S-L) (Intersubject mean and SD)

Transport	MT	TPV	APV	TPD	
S	507.8 (82)	189.3 (29)	1203.7 (120)	286.8 (34)	
S→L	683.9 (91)	188.3 (26)	1159.8 (109)	292.9 (34)	
Grasp	TGV	TGA	AGA	TGA2	AGA2
S	194.9 (46)	308.6 (47)	95.4 (8.3)		
S→L	179.4 (41)	293.6 (33)	97.8 (13.9)	475.2 (86)	121.6 (10.4)

MT: Movement Time (ms), TPV: Time to Peak Velocity (mm/s), APV: Amplitude of Peak Velocity (mm), TPD: Time to Peak Deceleration (ms), TGV: Time to maximum Grip Velocity (ms), TGA: Time to maximum Grip Aperture (ms), AGA: Amplitude of maximum Grip Aperture (mm), TGA2: Time to Second peak in Grip Aperture (ms), AGA2: Amplitude of Second peak in Grip Aperture (mm)

Table 3. Kinematic characteristics of prehension during Large control trials (L) and Large to Small perturbed trials (L-S) (Intersubject mean and SD)

Transport	MT	TPV	APV	TPD
L	501.3 (71)	179.1 (28)	1191.2 (134)	280.4 (39)
L→S	598.8 (94)	185.2 (30)	1188.0 (136)	278.1 (39)
Grasp	TGV	TGA	AGA	TGA2
L	176.2 (34)	314.4 (43)	126.4 (8)	
L→S	179.2 (35)	322.8 (57)	121.3 (9)	392.1 (106)

MT: Movement Time (ms), TPV: Time to Peak Velocity (mm/s), APV: Amplitude of Peak Velocity (mm), TPD: Time to Peak Deceleration (ms), TGV: Time to maximum Grip Velocity (ms), TGA: Time to maximum Grip Aperture (ms), AGA: Amplitude of maximum Grip Aperture (mm), TGA2: Time to Second peak in Grip Aperture (ms), AGA2: Amplitude of Second peak in Grip Aperture (mm)

difference, which amounted to 65 ms in blocked trials, no longer existed in control trials. This result seems to be explained by the strategy adopted by the subjects of making faster movements in the situation where perturbations occurred. Indeed, the rate of opening of the grip, as measured by parameter TGV, was faster in Large control trials than in Small ones, which accounts for the fact that TGA occurred at the same time in both cases. The difference in TGV between Small and Large control trials was significant ($P < 0.025$).

Finally, the morphology of wrist and finger spatial paths in control trials did not differ from that of blocked trials. In Small trials, the index of variability was 197, 349, 468 cm² for wrist, thumb and index finger trajectories, respectively, and for Large trials, 230, 401, and 645 cm².

Perturbed trials

Movements during perturbed trials were compared with movements during control trials starting with illumination of the same dowel. Accordingly, movements during Small to Large perturbed trials will be compared with movements during Small control trials, and movements during Large to Small perturbed trials, to Large control trials.

Perturbation from the Small to the Large dowels

Movement time. The mean MT in Small to Large (S-L) perturbed trials was increased by about 175 ms with respect to the Small control trials (Table 2). In individual subjects, this increase ranged from 74 ms in subject CU, up to 255 ms in subject YR.

Transport component

Kinematic analysis. No significant changes were found in the time values of the wrist kinematic landmarks during S-L perturbed trials, with respect to the Small control trials. As shown by Table 2, parameters TPV and TPD were within the same range in both cases. The amplitude of the velocity peak (APV) was lower in perturbed trials by 44 mm/s ($P > 0.05$).

This result shows that the wrist kinematics were little affected by the perturbation, at least during the first 300 ms or so following movement onset. The MT increase in perturbed trials was therefore likely to be due to lengthening the low velocity phase following peak deceleration. Indeed, the acceleration phase of the movement (reflected by parameter TPV), which in control trials represented 37.2% of MT, represented only 27.5% in perturbed trials. The low velocity phase was prolonged and was marked by small changes in velocity which, in some subjects, created the impression of secondary sub-movements. Figure 6 shows a comparison between kinematic profiles of a movement during a Small control trial (Fig. 6, S) and a Small to Large perturbed trial (Fig. 6, S-L).

Spatial path and variability of wrist movement. The S-L perturbation had little effect on the spatial path of the wrist, except that the movement was slowed down at the vicinity of the object. Fig. 7 clearly shows that a higher proportion of temporal frames were concentrated near the object (compare the spatial positions of parameters TPV and TPD in Small control trials, Fig. 7a and in S-L perturbed trials, Fig. 7b).

Variability of wrist trajectories over repeated movements was increased during S-L perturbed trials with respect to Small control trials. The index of variability in perturbed trials was 499 cm², as compared to 197 cm² for Small control trials ($P < 0.05$).

Grasp component

Kinematic analysis. In all subjects, the profile of change in grip size during the movement in S-L perturbed trials was marked by a discontinuity. In three subjects, grip size first increased up to a first peak, then decreased and finally reincreased up to a second peak before decreasing until contact with the dowel. Kinematic analysis revealed that the first peak in fact corresponded to the maximum grip aperture observed in Small control trials. The time value of this first peak was not significantly different from that of parameter TGA in Small controls. Finally, the amplitude of the first peak of grip amplitude was the same as AGA in Small trials (Table 2). The second peak in grip size occurred later in time (475 ms after movement onset), and its amplitude corresponded to the size of grip observed in Large control trials (compare the value of AGA₂ in Table 2 with that of AGA for Large trials in Table 3). In the other two subjects, the distinction between two peaks was less easily made, and the grip aperture profile was only marked by an inflexion. The example shown in Fig. 8 (S-L) belongs to the latter category.

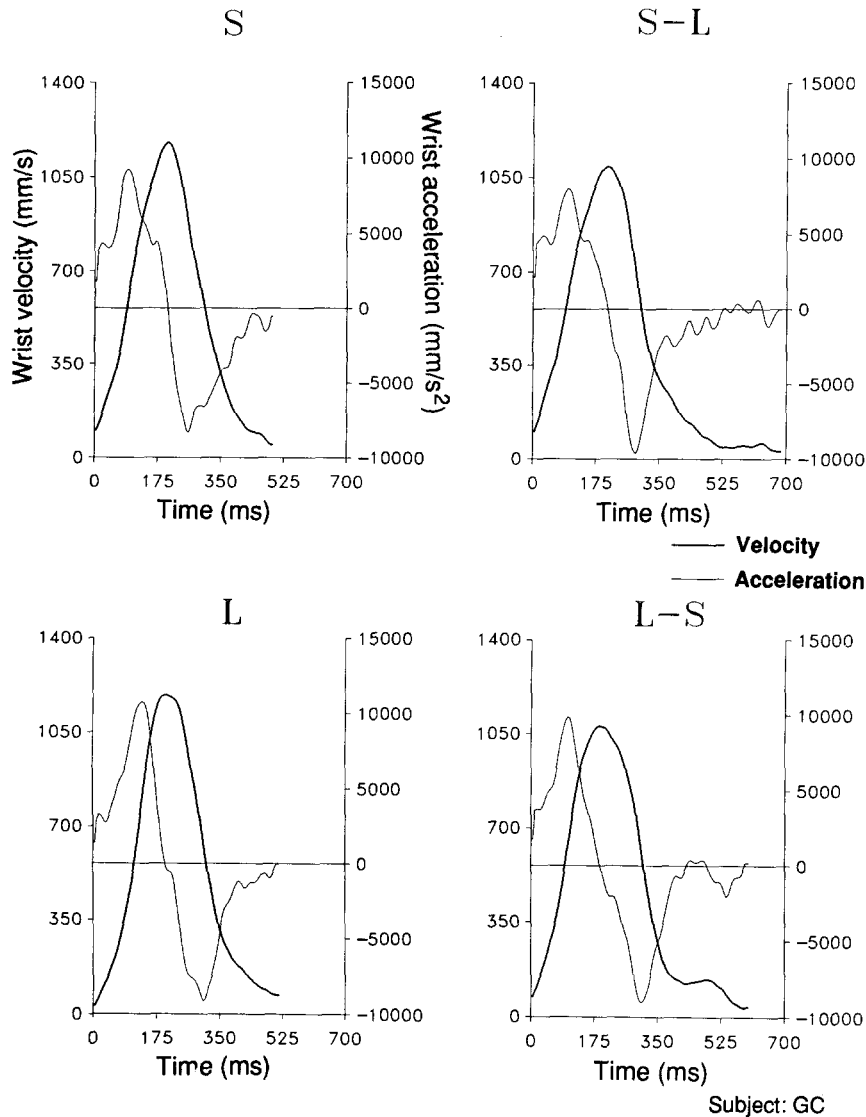


Fig. 6. Kinematic profiles of the wrist displacement during control and perturbed trials. Four representative trials are shown. S: Small control trial; S-L: Small to Large perturbed trial; L: Large control trial; L-S: Large to Small perturbed trial. Note longer movement time and longer duration of low velocity phase following peak deceleration in perturbed trials. Legend as in Fig. 2

Subject: GC

The double-peak pattern in grip size, however, was clearly visible in all subjects on the curve of grip “velocity” (e.g., Fig. 8 S-L). On this curve, the time occurrence of the first velocity peak had the same value as for Small control trials (parameter TGV). This first velocity peak was followed by a second one corresponding to the reopening of the grip. The time of the valley between the two velocity peaks where grip size velocity was the lowest thus represented the earliest consistent sign of corrective finger movements aimed at grasping the large dowel. This important landmark was located at a mean time value of 329.8 ms following movement onset.

Spatial path and variability of finger trajectories. Due to the fact that changes in grip size occurred late, the spatial path of the fingers was little modified by the perturbation. However, in order to accommodate for the larger size of the object, both fingers contributed. First, the curvature of the index finger path during enclosure was less marked

than in control trials. Second, the thumb tended to over-extend in order also to increase grip size. This point is demonstrated by Figs. 7 and 9. Figure 7b shows the averaged finger paths during S-L perturbed trials. Figure 9b shows the lack of index finger flexion and the thumb extension following the perturbation.

Variability of finger trajectories over repeated trials was increased with respect to control trials. The mean index of variability was 916 and 1337 cm² for thumb and index finger, respectively. These values were significantly greater than the corresponding values in the control trials (thumb, $P < 0.05$, index, $P < 0.025$). Variability was more pronounced during the early part of the movement, near the time where velocity of the wrist was the highest. However, in spite of the perturbation, variability remained low during the low velocity phase of the movement near the object. This finding confirms the tendency for the fingers to come in contact with the object at the same points (Fig. 7b, d).

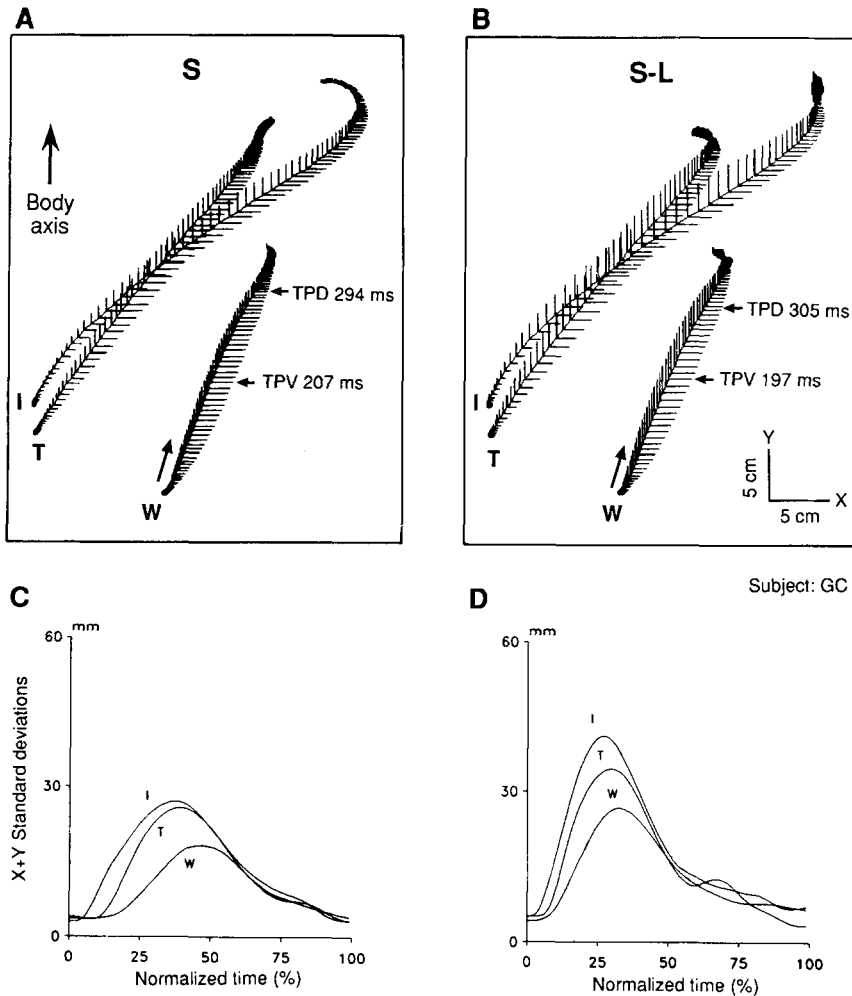


Fig. 7A–D. Spatial path and variability of prehension movements in the Small control condition (A, C) and in the Small to Large perturbed condition (B, D). Note in this subject contributions of both thumb and index to corrective increase in grip aperture (B). Also note increased variability in perturbed trials (D). Same legend as in Fig. 3

Perturbation from the Large to the Small dowels.

Corrections in response to the L-S perturbation were apparently generated more easily than corrections to S-L perturbations. Movement time was increased by about 85 ms with respect to large control trials ($P > 0.0005$).

Transport component

No differences were found in time of occurrence of the kinematic landmarks. Parameters TPV, TPA and TPD had the same values as in Large control trials (Table 3). The increase in MT (less marked than for the S-L perturbation) was therefore due to a lengthening of the low velocity phase at the end of the movement (Compare Fig. 6, L with Fig. 6, L-S). The spatial path of the wrist was similar to that of control trials. Its variability was not significantly increased (*t*-test): the mean index of variability was 245 cm².

Grasp component

The grasp component in L-S trials was unaffected with respect to control trials until late in movement time.

Parameters TGV, TGA and AGA had values very similar to those in Large control trials (Table 3). The curve of grip size as a function of time showed only one peak, as confirmed by the curve of grip velocity (Fig. 8, L-S). The main change with respect to control trials was the prolongation of the enclosure phase of the grip size until it reached the size of the small dowel (Fig. 8, L-S).

The spatial paths of the fingers were virtually identical to those of Large control trials, except for the prolongation of grip closure. Both fingers participated in this process. As shown in Figs 9, L-S and 10b, closure was achieved by an increase in index finger flexion, as well as by a flexion of the thumb. Variability of finger trajectories over repeated trials was not increased with respect to control trials. The mean index of variability was 402 and 600 cm² for thumb and index finger, respectively. These values were not significantly different from those of the control trials (unpaired *t*-test). Finally, due to the low variability during the final phase of the movement, the fingers consistently appeared to contact the object at the same points on each repetition.

Discussion

The main problem that we addressed in this paper was the degree of independence of grasping with respect to the

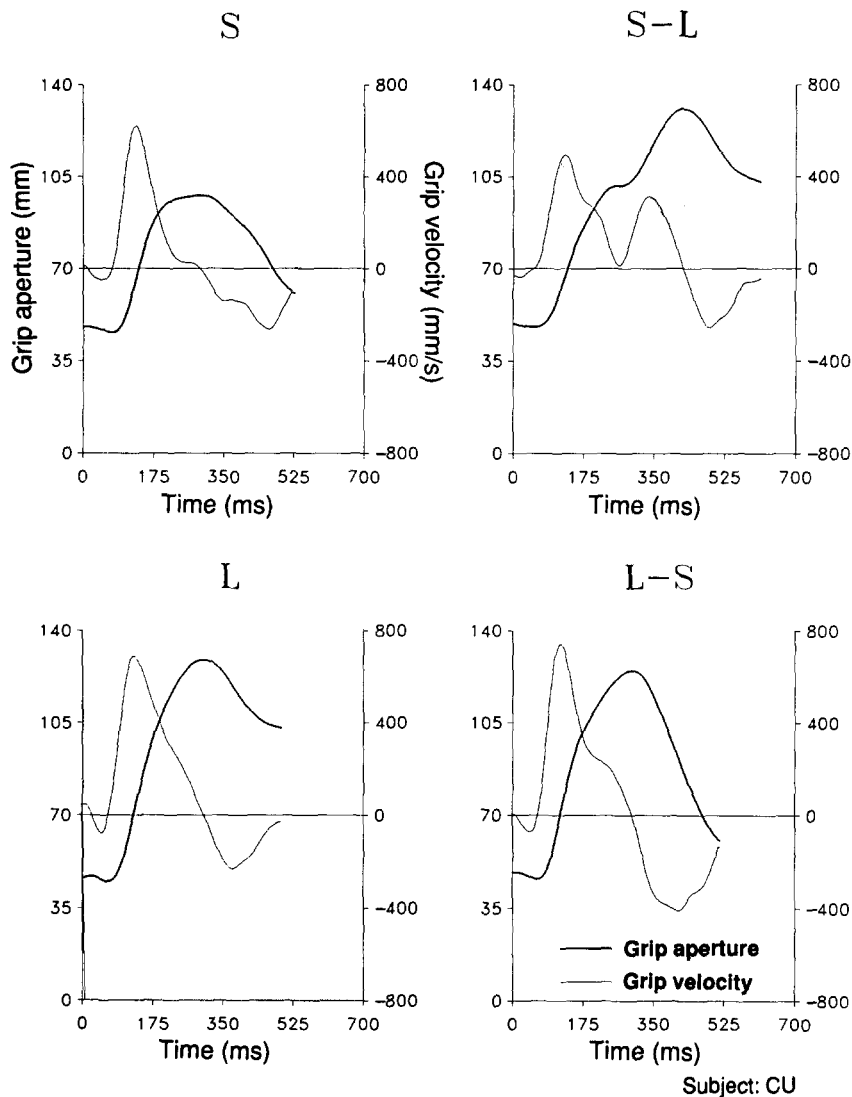


Fig. 8. Kinematic profile of grip formation during control and perturbed trials. Four representative trials are shown. S, Small control trial; S-L, Small to Large perturbed trial; L, Large control trial; L-S, Large to Small perturbed trial. Same legend as in Fig. 4

Subject: CU

other components of prehension, such as the transport of the hand at the location of the target object. The answer to this question is not a simple one, as there are arguments both in favor and in disfavor of independent, or parallel, organization of these components.

Arguments in favor of independent visuomotor subsystems

A first argument in favor of a relative independence of the two components is the fact that in the present unperturbed condition, the pattern of grip formation covaried with object size, whereas the transport component remained uninfluenced (at least within the limited range of object sizes that we used in this experiment). The main effect of object size on grip formation was the well-known increase in maximum grip aperture with object size (Jeannerod 1981, 1984; Wallace and Weeks 1987; Marteniuk et al. 1990). Marteniuk et al. (1990) found that for each increase of 1 cm in object size, the maximum grip aperture increased by 0.77 cm. According to this result, the difference

in diameter between our two dowels (4.5 cm) would predict a difference in maximum grip aperture of 3.5 cm. The difference of 3.2 cm that we found (Table 1) is very close to that prediction. The subjects used two different strategies for achieving this pattern. In the blocked trials, the grip size increased at the same rate for both small and large objects, with the consequence that maximum grip aperture was reached earlier in movement time for a small object than for a large object (see Marteniuk et al. 1990). By contrast, in Control trials, the rate of increase was faster for a large than for a small object, with the consequence that grip size peaked nearly at the same time for both large and small objects. This second pattern corresponds to that described earlier by Jeannerod (1981). For each given strategy, however, these object size related changes in grip formation occurred without affecting movement time or transport kinematics. It seems that the only determinant for using either one of the two strategies was movement duration, so that the subjects tended to equate the time to maximum grip aperture for large and small objects when the movement became faster. Finally, the fact that these changes in grip formation were found to occur without

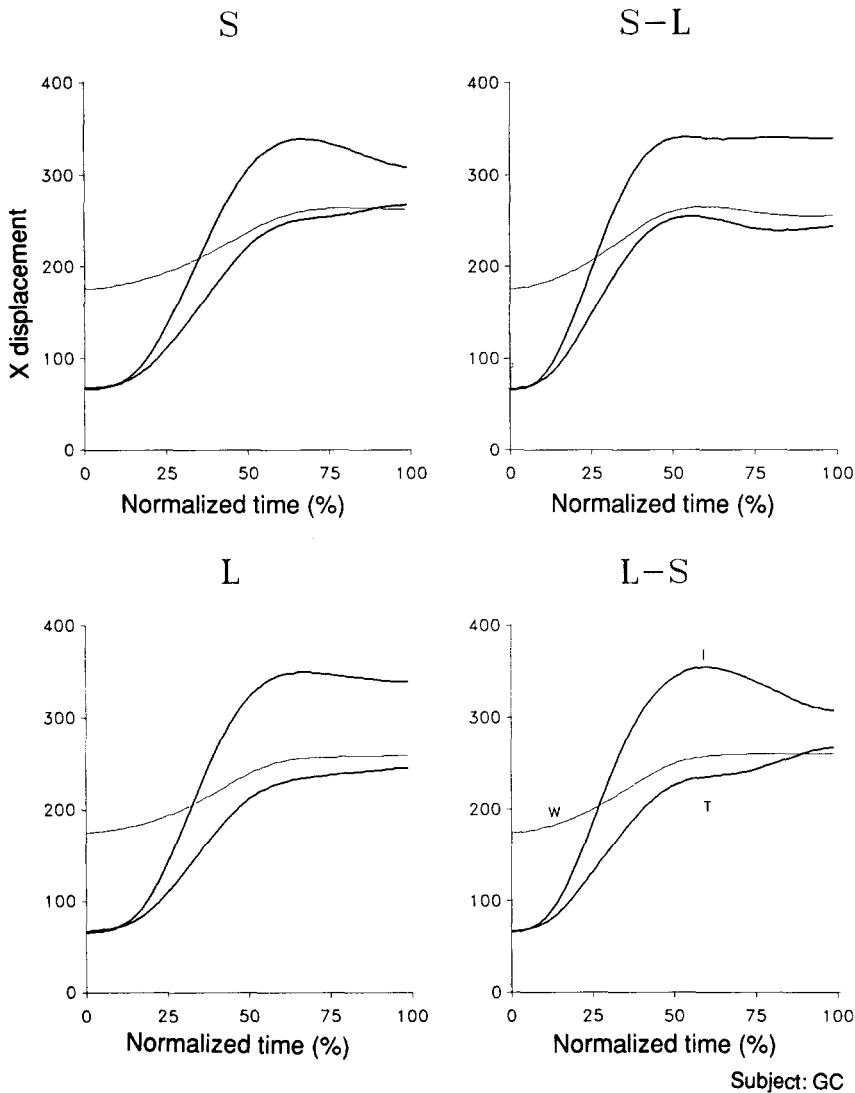


Fig. 9. Mean displacement in the X dimension of the wrist (W), tip of the thumb (T) and tip of the index (I) in Control and Perturbed trials. S, Small trial; S-L, Small to Large perturbed trial; L, Large control trial; L-S, Large to Small perturbed trial. Note in this subject the large contribution of the thumb to the corrections in grip aperture. Legend as in Fig. 5

affecting transport kinematics is also suggestive of an independence of the visuomotor control systems for finger movements and for arm movements. Previous authors (Wing et al. 1986; Von Hofsten and Ronnqvist 1988; Wallace and Weeks 1988; Marteniuk et al. 1990), however, had found faster movements for larger objects.

A second, and more elaborate, argument as to this point stems from the comparison between the corrections observed in response to the different types of perturbations. In the experiment reported earlier, where the perturbation affected the spatial position of the object, changes in wrist acceleration could already be detected within about 100 ms following the perturbation (Paulignan et al. 1990, 1991). This early correction sharply contrasts with the effects of perturbations in object size studied in the present experiment. Our results demonstrate that the earliest change produced in prehension movements by these perturbations did not occur before about 330 ms, when the closure of the grip was interrupted and the sign of grip velocity began to revert. No sign of correction could be detected before this time on the velocity profile of the wrist. In accordance with Jeannerod

(1981), who reported a similar result from a preliminary experiment, the latest considered wrist landmark (time to peak deceleration, TPD) was unchanged with respect to control unperturbed trials. This difference between the two types of corrections is a somewhat counterintuitive finding, since the inertial properties (e.g., the musculoskeletal mass) of the systems respectively involved in correcting for position or size perturbations would lead to the expectation that fingers should react at least as fast as the arm. The fact that this did not occur means that the limiting factor for the speed of corrections to size perturbations must be looked for at the central stage of visuomotor processing, rather than at the execution level.

The parallelist hypothesis would thus be a likely one for explaining the timing differences in responses to position and size perturbations. In neurophysiological terms, it could be speculated that the slower response to size perturbations relates to the higher degree of complexity of the visuomotor pathways for controlling distal movements. This pathway involves processing the visual attributes of objects which relate to object identification and recognition. Such processing, which seems to involve

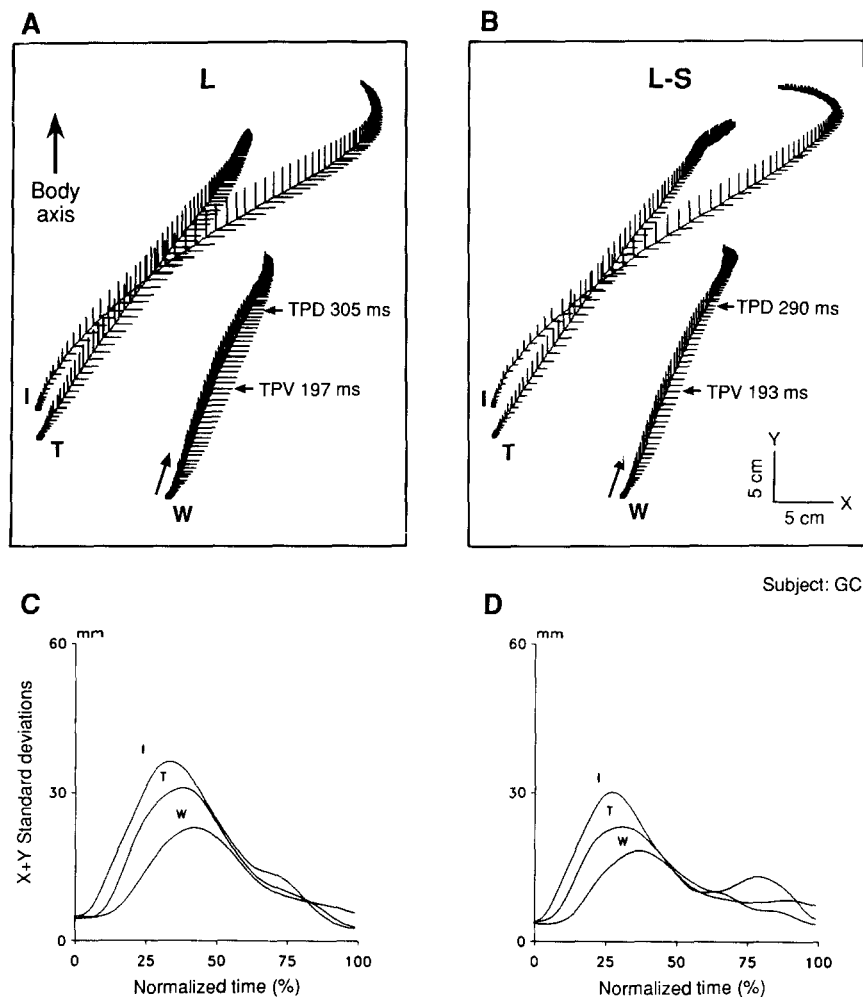


Fig. 10A–D. Spatial path and variability of prehension movements in the Large control condition (A, C) and in the Large to Small perturbed condition (B, D). Same legend as in Fig. 3

cortical mechanisms (e.g., Jeannerod 1986), would likely be time consuming and would be compatible with the observed correction delay of 330 ms. By contrast, the pathway for processing spatial localization and controlling proximal movements would be simpler and have a shorter time constant. In this regard, a tectospinal pathway with only a few synapses has been proposed by Alstermark et al. (1990, in the cat) for explaining the short correction delays during perturbation of target position.

A hypothesis for coordination of the two components

Other results obtained in these perturbation experiments, however, are in apparent disfavor of independent visuomotor subsystems and could lead to a different interpretation of the organization of prehension. In the previous paper dealing with perturbation of object position we showed that the two components became kinematically coupled during the corrective responses. The alteration of the wrist trajectory for reorienting the movement was immediately followed (within about 50 ms) by a brief interruption of grip aperture, unrequired by the situation since object shape and size remained unchanged (Paulignan et al. 1990, 1991). This finding was recently

replicated by Haggard and Wing (1991). In their situation, the subject's arm was suddenly pulled back by a mechanical device during approach to the object. This perturbation triggered a rapid correction of the transport component, such that the arm was reaccelerated in order to reach for object position. In about 70% of perturbed trials, the perturbation applied to the arm also provoked a reversal of grip aperture which occurred some 70 ms later than the change in transport.

In the present experiments involving perturbation of object size, the correction was also not limited to the affected component, since it was made at the expense of movement duration or, more specifically, at the expense of the low velocity phase of the transport component. These results, which show that components of prehension are mutually influenced, do not necessarily speak against independence of the two components. Instead, they suggest the existence of a coordination mechanism.

The general hypothesis that we would like to propose for explaining this coordination is that, in addition to the separate parametrization of transport and grasp, there would exist another mechanism for encoding the resultant goal of the complete action. Separate parametrization implies, for each of the involved visuomotor channels, selection of the proper muscles and calibration of the

motor commands applied to these muscles. Encoding the resultant goal implies controlling the timing of these commands and the kinematics of the resulting movements in order to precisely coordinate arrest of the reach and closure of the fingers at contact with the object. This idea of a central coding of the "desired" position of an effector system has already been proposed by several authors for the control of various kinds of movements (e.g., speech movements, MacNeilage 1970; Abbs and Gracco 1984; arm movements, Bizzi et al. 1984; finger movements, Cole and Abbs 1987).

Some speculation can be offered on the nature of the coordination mechanism and on the way it could operate for synchronizing transport and grasp. The resultant goal would be encoded as a temporal structure, comparable to a music score where both the action of the instruments and their relative timing are represented. At each step of the movement this temporal structure would be used as a reference to which incoming signals arising from execution would be compared. The corresponding motor commands would be modulated for minimizing the mismatch of the segmental movements with respect to the reference. When a perturbation would occur during execution of the movement, a new parametrization of the output would be produced at the level of the affected visuomotor channel. The mechanism of comparison between incoming movement-related signals and the (updated) reference would operate for preserving temporal coordination between components (see Prablanc et al. 1979; Jeannerod 1990; for a computer model using the same principle, see Bullock and Grossberg 1988). The rate at which the reorganization and corrections can be generated following perturbations would depend on the amount and the rate of visual processing needed for detecting and analysing changes occurring in object attributes. Our experimental results suggest that the rate of processing differs according to whether the channels dealing with object spatial or iconic attributes are affected by the perturbation, i.e., it is longer for processing a change in iconic attributes.

Previous suggestions, partly based on experimental results, have been made for the temporal structure used as a reference for maintaining coordination between transport and grasp. One of these suggestions was that movement duration would keep constant for prehension over a wide range of conditions. In this case the temporal structure would be preserved, only the amount of contraction to the arm muscles would be changed for projecting the arm at different distances; or only the amount of grip opening would be changed for objects of different sizes. Data showing invariance of movement duration for different amplitudes have been reported during prehension by Jeannerod (1984) and during writing by Viviani and Terzuolo (1980). In the experiments reported in the present paper, the time to maximum grip aperture (TGA) was also maintained constant for different objects sizes (at least in the control trials, see Tables 2 and 3), thus indicating that not only movement duration, but also the all temporal structure of coordination can be preserved while parametrization of the segmental movements is changed.

Temporal invariance in the strict sense, however, cannot be considered as a universal way of maintaining

coordination. First, this mechanism could not hold for all the conditions of prehension, which can differ widely from case to case. Second, under certain conditions, changes in object size can affect movement duration (Marteniuk et al. 1990) and timing of the grip (Marteniuk et al. 1990, and present results, blocked trials). These data are thus more compatible with a relative invariance of kinematic landmarks within a changing movement duration (kinematic scaling). Among these kinematic landmarks, one, the onset of the low velocity phase of the movement (our parameter TPD), seems to be preserved in nearly all the investigated conditions. Indeed, the duration of the low velocity phase represents a constant proportion of total movement time. In the present experiment, the mean proportion of movement time spent in the low velocity phase was between 43% and 48% in blocked and control trials (see also Jeannerod 1981, 1984; Wallace and Weeks 1988, Von Hofsten and Rönqvist 1988). Remarkably, the onset of this low velocity phase (TPD) corresponds to the time (TGA) where the fingers begin to enclose the object. This is also the time where variability of the wrist and finger spatial paths is at its lowest. Temporal coordination between TPD and TGA might also explain the coupling between transport and grasp that we observed during the corrections of both types of perturbations. In perturbation of object position, the deceleration which stopped the first wrist movement in the wrong direction was consistently associated with finger closure. In the present experiment where finger closure was prolonged because of changes in object size, the deceleration of the wrist was also prolonged.

The hypothetical mechanism outlined above for coordination between transport and grasp postulates the existence of a central representation of the action of prehension, which permanently monitors movement-related signals and compares them with the ongoing efferent commands. There are several possible neural structures that could fulfill this function of an on-line comparator. One of these structures could be the C3-C4 propriospinal neurons described by the Lundberg group (see Alstermark et al. 1990). These neurons are under the influence of upper level, including cortical, structures, they are likely to receive proprioceptive signals generated by several segments of the same limb and they control the activity of the corresponding motoneuron pools. One prediction arising from this suggestion is that peripherally deafferented subjects should lose the temporal coordination between transport and grasp and, in addition, would be unable to correct their prehension movements in response to perturbations of either object position or size. Although this prediction, to our present knowledge, has never been tested directly, there are indirect arguments against such a pure spinal mechanism. Prehension movements were examined by Jeannerod et al. (1984) in one patient with a complete anaesthesia (including loss of position sense) of one hand and forearm, due to a lesion of parietal cortex. While in this patient kinesthetic input was spared at the spinal level, her prehension movements were deeply disorganized, and coordination between components was lost. This result indicates that mechanisms for temporal coordination between motor components during prehension

should lie upstream with respect to spinal cord, possibly at the cortical level.

A number of experimental arguments in humans and animals point to the posterior parietal cortex as a possible site for this mechanism. Lesions of posterior parietal cortex produce a profound disorganization of prehension. First, the accuracy of reaching toward the object is impaired, the kinematics of the transport component are altered, with increase in movement duration due to lengthening of the deceleration phase, decrease in peak velocity, and occurrence of several secondary velocity peaks during deceleration. Second, grip formation is impaired, with exaggerated grip opening, incomplete or absent grip closure, inaccurate posturing of the fingers (Faugier-Grimaud et al. 1978 in monkey; Jeannerod 1986 and Perenin and Vighetto 1988 in humans). This massive impairment in object-oriented action suggests that posterior parietal cortex might be involved in building the representation of the desired final configuration of opposition space during prehension. Indeed, this region of cerebral cortex contains neurons, the activity of which is selective in the configuration and/or the orientation of the object for intended manipulation (Taira et al. 1990). These neurons are likely to play a role in matching the pattern of hand movement with the spatial characteristics of the object to be manipulated.

References

- Abbs JH, Gracco VL (1984) Control of complex motor gestures: orofacial muscle responses to load perturbations of lip during speech. *J Neurophysiol* 51: 705–723
- Alstermark B, Gorska T, Lundberg A, Petterson LG (1990) Integration in descending motor pathways controlling the forelimb in the cat. 16. Visually guided switching of target-reaching. *Exp Brain Res* 80: 1–11
- Arbib MA (1985) Schemas for the temporal organization of behavior. *Hum Neurobiol* 4: 63–72
- Bizzi E, Accornero N, Chapple W, Hogan N (1984) Posture control and trajectory formation during arm movement. *J Neurosci* 4: 2738–2744
- Bullock D, Grossberg S (1988) Neural dynamics of planned arm movements. Emergent invariants and speed-accuracy properties during trajectory formation. *Psychol Rev* 95: 49–90
- Cole KJ, Abbs JH (1987) Kinematic and electromyographic responses to perturbation of a rapid grasp. *J Neurophysiol* 57: 1498–1510
- Faugier-Grimaud S, Frenois C, Stein DG (1978) Effects of posterior parietal lesions on visually guided behavior in monkeys. *Neuropsychologia* 16: 151–168
- Franks IM, Sanderson DJ, van Donkelaar P (1990) A comparison of directly recorded and derived acceleration data in movement control research. *Hum Mov Sci* 9: 573–582
- Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umiltà C, Rizzolatti G (1991) Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia* 29: 361–378
- Georgopoulos AP, Kalaska JF, Massey JT (1981) Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty and change in target location. *J Neurophysiol* 46: 725–743
- Goodale MA, Pélisson 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
- Haggard P, Wing AM (1991) Remote responses to perturbation in human prehension. *Neurosci Lett* (in press)
- Hofsten C Von, Rönnqvist L (1988) Preparation for grasping an object: a developmental study. *J Exp Psychol [Hum Percept]* 14: 610–621
- Iberall T, Bingham G, Arbib MA (1986) Opposition space as a structuring concept for the analysis of skilled hand movements. In: Heuer H, Fromm C (eds) *Generation and modulation of action pattern* (Exp Brain Res Series 15). Springer, Berlin Heidelberg New York, pp 158–173
- Jeannerod M, Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (eds) *Attention and Performance IX*. Erlbaum, Hillsdale, 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 (1990) The interaction of visual and proprioceptive cues in controlling reaching movements. In: Humphrey DR, Freund HJ (eds) *Motor Control: concepts and issues*. Wiley, New York, pp 277–291
- 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
- Mac Neilage PF (1970) Motor control of serial ordering of speech. *Psychol Rev* 77: 182–196
- Marteniuk RG, Leavitt JL, MacKenzie CL, Athenes S (1990) Functional relationships between grasp and transport components in a prehension task. *Hum Mov Sci* 9: 149–176
- Paulignan Y, MacKenzie CL, Marteniuk R, Jeannerod M (1990) The coupling of arm and finger movements during prehension. *Exp Brain Res* 79: 431–436
- Paulignan Y, MacKenzie CL, Marteniuk R, Jeannerod M (1991) Selective perturbation of visual input during prehension movements. I. The effects of changing object position. *Exp Brain Res* 83: 502–512
- Pélisson D, Prablanc C, Goodale MA, Jeannerod M (1986) Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Exp Brain Res* 62: 303–311
- Perenin MT, 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, Jeannerod M, Komilis E (1979) Optimal response of eye and hand motor systems in pointing at a visual target. II. Static and dynamic visual cues in the control of hand movement. *Biol Cybern* 35: 183–187
- Soechting JF, Lacquaniti F (1983) Modification of trajectory of a pointing movement in response to a change in target location. *J Neurophysiol* 49: 548–564
- Taira M, Mine S, Georgopoulos AP, Murata A, Sakata H (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movements. *Exp Brain Res* 83: 29–36
- Viviani P, Terzuolo C (1980) Space-time invariance in learned motor skills. In: Stelmach GE, Requin J (eds) *Tutorials in motor behavior*. North-Holland, Amsterdam, pp 525–533
- Wallace SA, Weeks DL (1988) Temporal constraints in the control of prehensive movements. *J Mot Behav* 20: 81–105
- Wing AM, Fraser C (1983) The contribution of the thumb to reaching movements. *Q J Exp Psychol* 35A: 297–309
- Wing AM, Turton A, Fraser C (1986) Grasp size and accuracy of approach in reaching. *J Mot Behav* 18: 245–260