Temporal coupling between transport and grasp components during prehension movements: effects of visual perturbation

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The temporal coupling between the transport and grasp components of prehension movements was investigated through two experiments. In Experiment 1, six normal subjects were required to reach and grasp each of three spheres located at three different distances (Blocked trials). In Experiment 2, a visual perturbation paradigm was used in which the location of the object to be reached and grasped could change at the beginning of arm movement (Perturbed trials). The same subjects participated in both experiments. Kinematics of wrist trajectory (transport component) and of distance between thumb and index finger (grasp component) were analyzed. The results of Experiment 1 showed that the two components could be temporally coupled during their time course. In Experiment 2, the visual perturbation affected both the components, but different times were required by each component to reorganize the movement towards the new target. These different times caused the decoupling of those events that appeared synchronized in Experiment 1. Finally, evidence was found to suggest that planning of grip formation takes into account not only the perceived characteristics of the object, but also the time planned by the transport component to reach the object.

INTRODUCTION

Prehension movements directed to visual stimuli require the coordination of three different motor components: hand transport, wrist rotation and grasp. The first component (transport) controls the arm displacement in order to bring the hand from its initial position to the target; the second component (rotation) controls arm rotation in order to orient the hand to correspond to the object orientation; the third component (grasp) selects and controls the fingers' configurations according to the stimulus size and shape[1].

Kinematic studies[10–12] have hypothesized the existence of distinct systems (visuo-motor channels), working independently and specialized to program only transport or grasp using different visual object attributes. The visuo-motor channel for the transport component extracts extrinsic object properties (e.g. spatial location) and integrates them in corresponding motor

pathways. The visuo-motor channel for grasp codes intrinsic properties of the object (e.g. size and shape) in order to program appropriate finger movements.

The concept of visuo-motor channels has received independent support from neurophysiology. Single neuron recordings from inferior area 6 have demonstrated that in this area there are two sets of neurons coding respectively transport and grasp components[6,7,18]. Neurons related to the transport component respond to the specific spatial location of the object (3D-receptive field) and appear to 'command' arm movements towards specific space sectors. Neurons related to the grasp component fire during particular types of grasping and frequently respond to visual objects, provided that the object size is congruent with the type of grasping controlled by the neuron.

Although the programming of the two components, at an early stage, is likely to be independently executed[6,7,18], an important question remains unresolved: that is, how grasp and transport movements are temporally coordinated. Previous kinematic studies showed that the two components start and stop simultaneously[5,11,22–24]. This temporal correspondence remained unchanged also for movements of different amplitudes in which transport time increased with dis-

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tance[5]. Since the grasp component has no access to visual information about target location[10] a mechanism must be hypothesized that assures this temporal correspondence between the two components.

This problem was solved, suggesting the existence of a synchronizing center similar to the ecphorator proposed by Bernstein[2]. This center, generating a double clustering of signals couples kinematic events of the two components. The first signal burst synchronizes the beginning of transport movement with that of the finger opening; the second signal burst synchronizes the low velocity phase (that corresponds to a secondary acceleration of the arm) with finger closure[11].

The existence of a temporal coupling between kinematic features of the two components was investigated by Jeannerod and coworkers[14,15]. In their experiment they used a visual perturbation paradigm in which the target shifted from the central position to the right or the left at the onset of arm movement. Although they found that maximal finger aperture occurred after peak transport velocity, correlation coefficients between the two parameters were significant only for some subjects. This result suggests that a temporal coupling between these two events is very unlikely.

In another study[5] we found that the time to peak deceleration of the transport component was weakly correlated with time to maximal finger aperture, although the significant correlations between these two parameters occurred more frequently in our study than in the experiment of Paulignan et al.[14,15]. However, the problem remains unresolved. To test for the existence of a temporal coupling between the two components it is necessary to investigate the possible temporal relationships of other kinematic events besides transport peak velocity or peak deceleration and maximal finger aperture.

The result emphasized by Paulignan et al.[14,15] was that transport kinematic modification started very early after visual perturbation. Examining acceleration profiles, they found that the beginning of transport motor reorganization occurred at about 100 ms after visual perturbation. Although the grasp component was also affected by visual perturbation, no data were reported about the motor reorganization of this component. It was only reported that the grip formation was interrupted when the transport component was reoriented towards the new stimulus. The analysis of the time course of grasp motor reorganization is important in order to establish whether the reorganization of the two components occurred in the same time and whether the onset of the two movements directed towards the new object were temporally coordinated.

The present study was designed to verify whether

kinematic events of transport and grasp components exist that are temporally coupled. Two experiments were carried out. In Experiment 1 (Blocked trials) the subjects were required to reach and grasp an object located at three different distances. The aim of this experiment was to test for the existence of a temporal coupling between kinematic events of transport and grasp components that remained unmodified when movement amplitude changed. The results showed that some events of the two components appeared temporally coupled. This finding was tested in Experiment 2 (Control and Perturbed trials) in which we used a visual perturbation paradigm similar to that employed by Paulignan et al.[14,15]. The only difference was that visual perturbation affected movement amplitude instead of movement direction. We studied the time course of motor reorganization of transport and grasp components after visual perturbation in order to verify whether possible different times required to reorganize transport and grasp could cause the decoupling of those events that were found temporally coordinated in Experiment 1. The results showed that these events were temporally decoupled by the visual perturbation. However, evidence was found that the time course of the grasp component is planned according to the time required to reach the object to be grasped.

EXPERIMENT 1 (BLOCKED TRIALS)

In Experiment 1 we analyzed the kinematics of transport and grasp components during prehension movements executed in the normal condition and directed to targets located at three different distances. The aim was to verify whether kinematic events of the two components could be temporally coupled.

METHODS

Subjects

Six right-handed male students (age 18–23) participated in the experiment. All of them were naive as to the purpose of the experiment.

Apparatus and procedure

The subjects sat on a comfortable chair with their chest fastened to its back. Their right hand rested on a platform (starting position) fixed to the plane of a table. The height of the platform was 6 cm. The location of the starting position was in the subject's midsagittal plane and was 20 cm distant from the body. The hand was kept prone and the index finger and the thumb were held

in pinch position. The subjects were instructed to reach and grasp three-dimensional objects resting on the table and to bring them back to the starting position. The instruction was to perform the task naturally, using the same velocity as during spontaneous movements.

Targets were three spheres (diameter 4 cm), made of translucent material, placed at 15.0 cm, 27.5 cm and 40.0 cm from the starting position along the subject's sagittal plane. Inside each sphere there were five LEDs connected to two metallic contacts on the exterior of the sphere. These contacts met with two other metallic plates fixed to the table and connected to a personal computer (Apple II). At the beginning of the trial, the illumination of a sphere indicated the target to be reached and grasped, and it was also the signal for the subject to start the movement. Three counterbalanced blocks of ten trials were run by illuminating a single sphere.

Movement recording and data analysis

Ten trials for each distance were recorded and analyzed using ELITE system[4]. This system consists of two TV cameras (sampling rate 50 Hz) and a processor. The TV cameras were 3 m distant from the working space where the apparatus was placed. The cameras were about 3 m distant from each other and were inclined about 30 degrees on the vertical axis. The working space was a parallelepiped long 60 cm, high 60 cm and deep 30 cm. The length and the height of the parallelepiped coincided approximately with the subject's sagittal and vertical axes, respectively.

The cameras were connected to the processor which computed the position of body points on which passive markers were placed. The markers were plastic spheres (diameter 0.5 cm) covered with reflecting material. The ELITE processor elaborated the video images in real time and recognized the shape of the markers. The coordinates of the marker centroids were sent to a host computer (PDP 11/53). The host computer performed in succession the following operations: (a) three-dimensional reconstruction of the position of the markers; (b) data filtering using a FIR linear filter[3]; (c) computation of the kinematic parameters: trajectory, velocity and acceleration.

The marker placed on the subject's wrist was used to analyze the kinematics (trajectory, velocity, acceleration) of the transport component. The grasp component was studied by analyzing the time course of the distance between the tips of thumb and index finger, on which two markers were placed. Moreover, the velocity and acceleration of the grasp component were analyzed using another marker placed on the first carpometacarpal joint and measuring the angle formed by this point

and the tips of the two fingers. Angular velocities were computed by differentiating filtered angles. Angular accelerations were derived by differentiating velocity data.

Since spatial error of the ELITE system, as measured on a stationary stimulus, is 0.4 mm, transport and grasp movements were considered to start and stop in those frames in which the marker displacement was greater and lesser than 0.4 mm, respectively. These frames were used to compute time data.

RESULTS

Transport component

Fig. 1 shows a representative example of trajectory during Blocked trials. In A, B and C, the hand trajectories to reach the target objects located respectively at 15.0 cm, 27.5 cm and 40.0 cm are represented. The trajectories are shown in the sagittal plane. The displacements along the transverse axis were negligible. The curves are approximately parabolic.

The maximal elevation of wrist increased with greater movement amplitudes (23.9 mm for the distance of 15.0 cm, 33.9 mm for the distance of 27.5 cm, 41.0 mm for the distance of 40.0 cm). Maximal elevation was
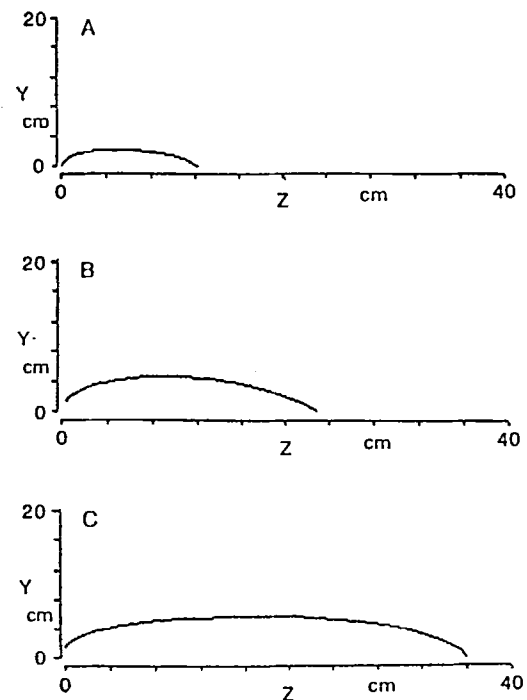

Fig. 1. Representative examples of transport component trajectories in Blocked trials. Three individual movements are represented in the sagittal plane (Subject DAL). Panel A shows the trajectory when the stimulus was located at 15.0 cm, in B when the stimulus was located at 27.5 cm, in C when the stimulus was located at 40.0 cm. Z = sagittal axis; Y = vertical axis.

reached at about 37.0% of the displacements along the sagittal axis.

Fig. 2 (upper and middle row) shows a representative example of velocity and acceleration profiles. In A, B and C the movements directed to stimuli located respectively 15.0 cm, 27.5 cm and 40.0 cm are represented. Note that the peak velocity and peak acceleration increased with the distance.

The kinematic parameters of the transport component studied in this experiment are shown in Table I.

One-way repeated measures analyses of variance (ANOVA) were performed on averaged data. The factor was target Distance. ANOVA showed that the transport time increased significantly as Distance increased ($F_{2,10} = 49.22$, $P < 0.001$). Also the values of peak velocity ($F_{2,10} = 207.62$, $P < 0.001$) and those of peak acceleration ($F_{2,10} = 40.12$, $P < 0.001$) were significantly greater when the movement amplitude increased. Although the increase of time to peak acceleration was minimal as Distance increased (see
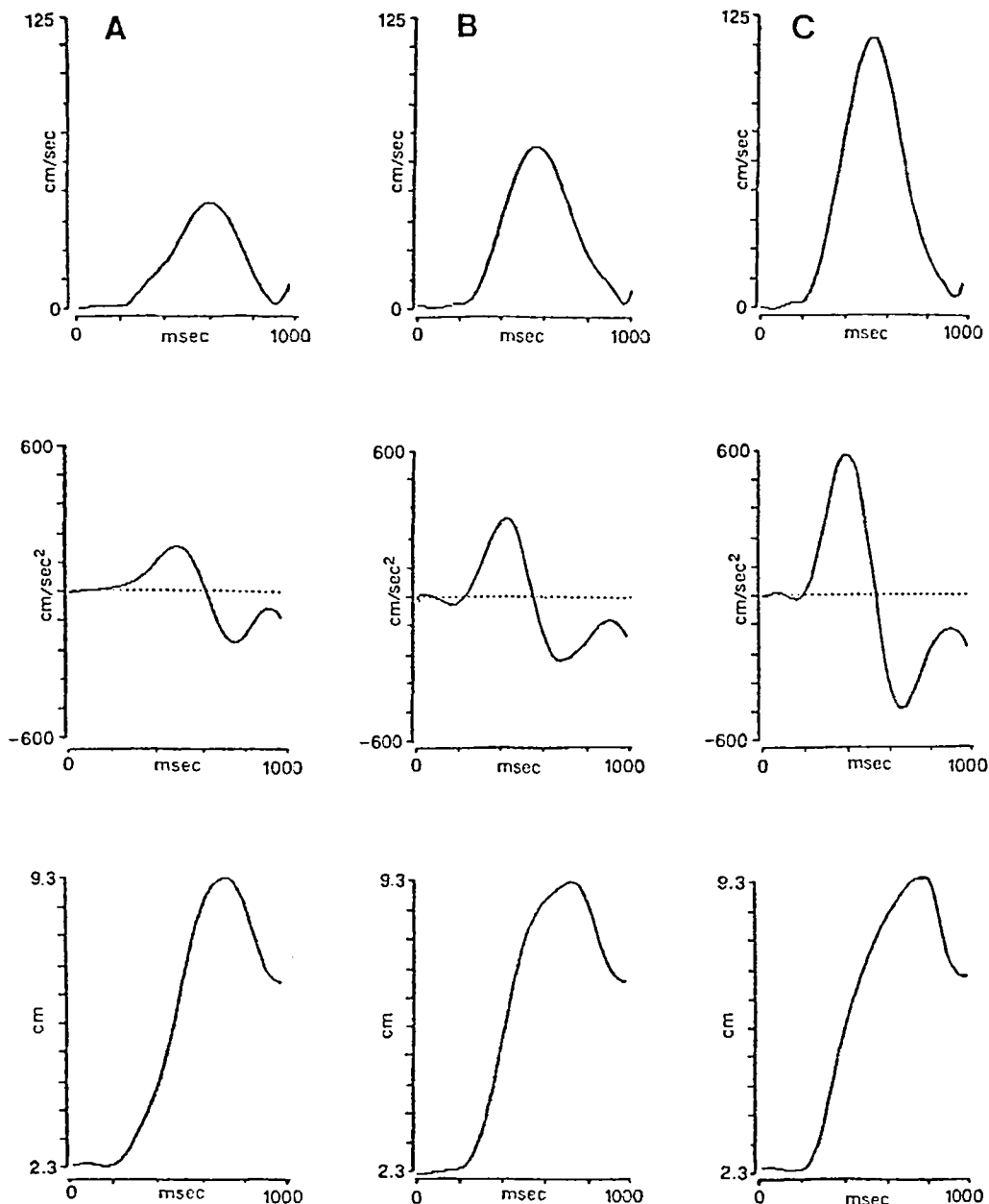

Fig. 2. Representative examples of kinematic patterns of prehension movements in Blocked trials. Three individual movements (same movements as in Fig. 1) directed respectively to stimuli located at 15.0 cm (A), 27.5 cm (B), 40.0 cm (C) are represented. The velocity curves (upper row) and the acceleration curves (middle row) are related to kinematics of transport component. Note that deceleration does not reach zero. This was due to the acceleration of the return movement (negative values). The time courses of distance between thumb and index finger (grasp component) are represented in lower row. The zero value on the time axis corresponds to the beginning of ELITE system recording.

TABLE I

Intersubject means (S.D.s in parentheses) of prehension kinematic parameters during Blocked trials

	Target at 15.0 cm	Target at 27.5 cm	Target at 40.0 cm
Transport time (ms)	700.0	765.3	873.0
	(23.5)	(48.2)	(46.8)
Transport peak velocity (cm/s)	46.7	76.0	101.6
	(6.0)	(10.0)	(8.8)
Transport peak acceleration (cm/s^2)	279.5	411.1	503.1
	(64.0)	(80.0)	(67.3)
Time to transport peak acceleration (ms)	210.3	211.0	229.0
	(46.9)	(45.0)	(41.0)
Time to transport peak acceleration (ms)	460.3	476.0	537.0
	(57.0)	(47.1)	(50.9)
Percentage of time to peak deceleration	65.1	62.4	61.5
	(6.5)	(5.7)	(5.0)
Grasping time (ms)	696.3	763.3	837.0
	(55.3)	(51.0)	(127.2)
Maximal finger aperture (mm)	88.9	86.3	84.3
	(5.9)	(6.9)	(6.3)
Time to maximal finger aperture (ms)	497.0	569.3	711.7
	(32.1)	(26.7)	(45.6)
Percentage of time to maximal finger aperture	70.6	74.5	77.4
	(4.3)	(3.7)	(3.2)
Finger closure time (ms)	205.0	196.7	194.7
	(31.0)	(39.9)	(28.6)
Hand distance from target at the beginning of finger closure (mm)	25.6	25.1	25.8
	(11.1)	(5.2)	(7.1)
Hand velocity at the beginning of finger closure (cm/s)	25.8	28.6	28.0
	(6.8)	(5.6)	(6.5)

Table I), it reached the statistical significance ($F_{2,10}$ = 4.18, $P < 0.05$). Time to peak deceleration increased significantly with Distance ($F_{2,10}$ = 16.05, $P < 0.001$). Also, the percentage of time to peak deceleration was affected significantly by Distance ($F_{2,10}$ = 4.71, $P < 0.05$). However, it decreased with Distance (see Table I).

Grasp component

The subjects chose spontaneously to grasp the objects using finger prehension[18]. The time course of distance between the tips of the thumb and index finger is shown in Fig. 2 (lower row). Note the typical pattern of aperture/closure of fingers as described previously[11,12]. Note also the coincidence between the beginning of the grasp component and the transport component.

The kinematic parameters of the grasp component are shown in Table I. Grasping time corresponded closely with transport time (see Table I; first and seventh row) and, as transport time, significantly increased with Distance ($F_{2,10}$ = 14.24, $P < 0.001$). As expected[5,10-12,24], because the three spheres were of the

same size, the maximal finger aperture (see Table I) remained constant with Distance ($F_{2,10}$ = 1.07).

The percentage of time to maximal finger aperture was significantly affected by Distance ($F_{2,10}$ = 12.72, $P < 0.005$). Since this parameter increased as Distance increased (see Table I), we further verified that finger closure time was the same for the three distances ($F_{2,10}$ = 0.48). Moreover, hand distance from target at the beginning of finger closure did not vary with Distance ($F_{2,10}$ = 0.02).

The coefficients of variation of finger closure time and hand distance from target at the beginning of finger closure were calculated as ratio between standard deviation and mean. The intersubject coefficients of variation for target distances of 15.0, 27.5 and 40.0 cm were respectively 18.0%, 22.5%, 18.7% for finger closure time and 34.2%, 29.5%, 25.9% for hand distance from target at the beginning of finger closure.

The maximal finger aperture occurred after peak deceleration (see Table I). However, the time interval between maximal finger aperture and peak deceleration increased with the distance. On average it was 36.7 ms

for the distance of 15.0 cm, 93.3 ms for the distance of 27.5 cm and 174.7 ms for the distance of 40.0 cm. That is, a fixed delay between the two events was not found. Moreover since the percentage of time to peak deceleration and the percentage of time to maximal finger aperture were inversely scaled with distance, a temporal coupling between the two events is unlikely.

The time interval between peak deceleration and maximal finger aperture increased with distance, and also when hand velocity was higher. Thus it was possible that finger closure started, during deceleration phase, when hand velocity reached a threshold value. Hand velocity at the beginning of finger closure (see Table I) remained constant with Distance ($F_{2,10} = 1.45$).

EXPERIMENT 2 (CONTROL AND PERTURBED TRIALS)

The results of Experiment 1 showed that the kinematic events of transport and grasp components that can be temporally coupled are: (1) the beginning and (2) the end of the two components; (3) the beginning of finger closure and the occurrence of a fixed threshold value of hand velocity, following peak deceleration.

In Experiment 2, the effects produced by visual perturbation on transport and grasp components were studied. This experiment was carried out mainly to verify whether the visual perturbation caused the decoupling of those kinematic events that were found coupled in Experiment 1.

METHODS

Subjects

The same subjects used in Experiment 1 participated in this experiment.

Apparatus and procedure

The apparatus and the stimuli were the same as in Experiment 1. The procedure was the following. The trial started by illuminating the nearest sphere. In 20% of cases (Perturbed trials) the light shifted to one of the two far spheres at the onset of the arm movement. The onset of the movement was signaled by a microswitch located under the starting position platform and connected to the personal computer. The subjects were required to reach and grasp the newly illuminated sphere. In the other trials the first sphere remained illuminated (Control trials). In this experiment 100 trials were run.

Movement recording and data analysis

Twenty Perturbed trials (ten of Perturbed at 27.5 cm and ten of Perturbed at 40.0 cm) and ten Control trials were recorded and analyzed using the ELITE system. The recording and data analysis were the same as in Experiment 1.

RESULTS

Transport component

Fig. 3 shows a representative example of transport trajectory in the sagittal plane during one Control trial (A) and during two Perturbed trials in which the target shifted from 15.0 cm to 27.5 cm (B) and from 15.0 cm to 40.0 cm (C). Note the change of direction along the vertical axis during Perturbed trials.

Fig. 4 (upper and middle row) shows a representative example of velocity and acceleration profiles during the same trials presented in Fig. 3. Velocity and acceleration profiles show that the entire movement was composed of two submovements. The beginning of the second submovement is indicated by the pointers in the velocity and acceleration profiles.

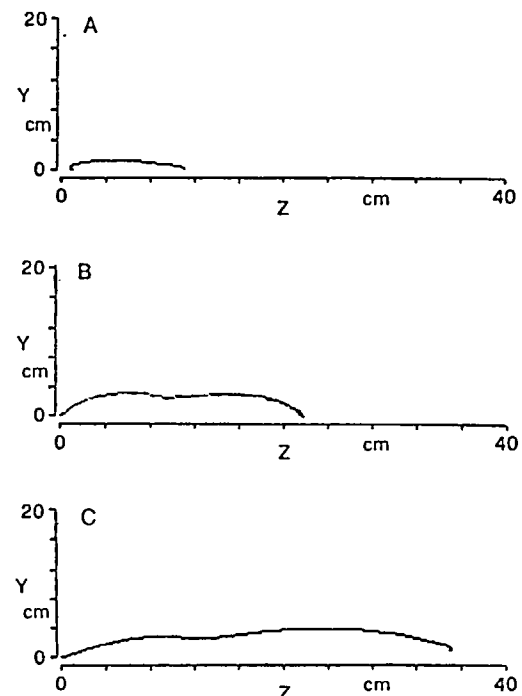In Tables II and III, the values of the kinematic

Fig. 3. Representative examples of transport trajectories in Control trials and Perturbed trials. Three individual movements (Subject DAL) are represented in the sagittal plane. In A a Control trial is represented. In B and C two Perturbed trials in which the target shifted from 15 cm to 27.5 cm (B) and from 15 cm to 40.0 (C) are represented. Other conventions as in Fig. 1.
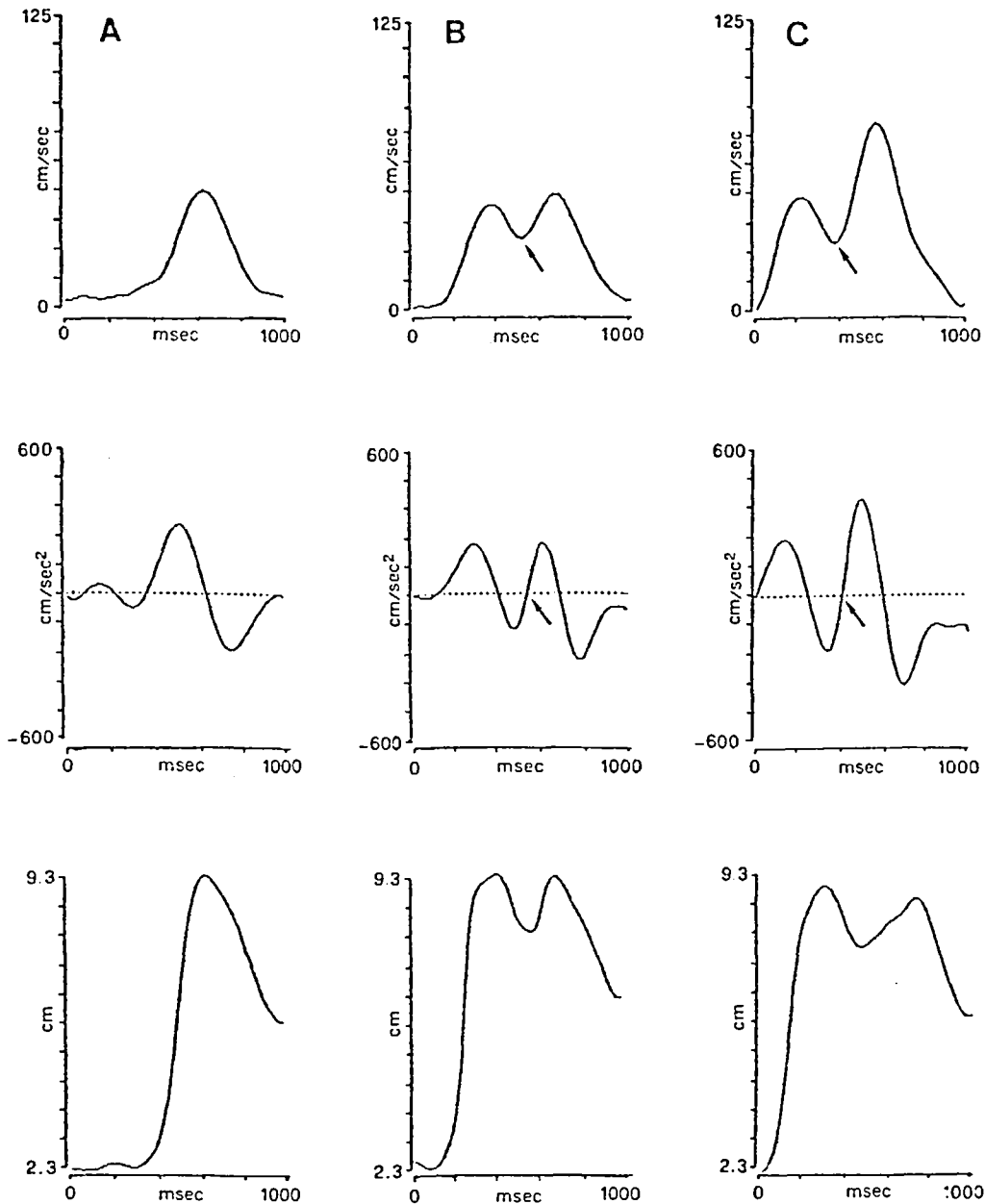
Fig. 4. Representative examples of prehension movements in Control and Perturbed trials (same movements as in Fig. 3). In A a Control trial is represented. Two Perturbed trials in which the target shifted from 15.0 cm to 27.5 cm and from 15.0 cm to 40.0 cm are represented respectively in B and C. In upper and middle rows velocity and acceleration profiles of transport component are represented. Arrows indicate the onset of the movement directed to the new target. In lower row the time courses of distance between thumb and index finger (grasp component) are represented.

parameters during Control and Perturbed trials are shown. Transport times of Perturbed trials and the corresponding values of Blocked trials were submitted to two-way ANOVA. The factors were Experiment (Blocked vs. Perturbed trials) and Distance (27.5 cm vs. 40.0 cm). The only significant source of variance was the Distance ($F_{1,5}$ = 90.3, P < 0.001). Transport times of the trials at 40.0 cm (899.5 ms) were greater than those of trials at 27.5 cm (777.8 ms). Transport times of Control trials and the corresponding values of

Blocked trials were subjected to one-way ANOVA, which revealed a main effect of Experiment factor ($F_{1,5}$ = 11.15, P < 0.02). Transport times of Control trials were significantly shorter than those of the corresponding Blocked trials. Since in Perturbed trials the visual perturbation should have caused an increase of the movement time, the subjects very likely used the strategy of increasing speed during Experiment 2 in an attempt to compensate for this effect.

In order to measure the beginning of the second

TABLE II

Intersubject means (S.D.s in parentheses) of prehension kinematic parameters during Control and Perturbed trials

	Control 15 cm	Perturbed 27.5 cm	Perturbed 40.0 cm
Transport time (ms)	603.0	790.3	926.0
	(82.5)	(65.3)	(74.4)
Transport peak acceleration (cm/s^2)	363.1	386.0[1]	386.7[1]
	(104.8)	(80.4)	(100.5)
Time to transport peak acceleration (ms)	186.3	146.0[1]	158.0[1]
	(58.0)	(55.7)	(53.2)
Time to transport peak deceleration (ms)	412.0	618.0[2]	680.0[2]
	(55.3)	(18.6)	(17.3)
Grasping time (ms)	626.3	798.3	953.7
	(107.1)	(107.0)	(108.1)
Time to peak angular acceleration of finger aperture (ms)	146.0	153.0[1]	152.0[1]
	(37.4)	(46.8)	(35.4)
Peak angular acceleration of finger aperture (deg#/s^2)	1506.7	1864.2[1]	1618.2[1]
	(679.1)	(465.7)	(677.4)
Time to maximal finger aperture (ms)	425.3	391.7[1]	411.3[1]
	(67.2)	(42.6)	(48.3)
Maximal finger aperture (mm)	90.9	90.6[1]	89.1[1]
	(6.7)	(8.7)	(9.6)
Finger closure time (ms)	173.7	192.7[2]	180.7[2]
	(48.6)	(57.3)	(45.4)
Hand distance from target at the beginning of finger closure (mm)	24.3	31.8[2]	30.1[2]
	(7.9)	(8.1)	(7.4)
Hand velocity at the beginning of finger closure (cm/s)	36.0	45.0[2]	41.2[2]
	(13.7)	(11.2)	(16.3)

[1] Values of the 1st submovement.
[2] Values of the 2nd submovement.
Decimal degrees.

submovement, we used the acceleration profiles and calculated the time from the onset of arm movement to hand reacceleration (arrow in Fig. 4). The beginning of the second submovement in Perturbed trials was submitted to an ANOVA in which the factor was Distance

TABLE III

Intersubject means (S.D.s in parentheses) of prehension kinematic parameters during Perturbed trials

	Perturbed 27.5 cm	Perturbed 40.0 cm
Time to beginning of transport second submovement (measured by acceleration profiles) (ms)	368.0 (17.4)	372.0 (27.4)
Time to the beginning of the second grip (measured by grip profiles) (ms)	495.0 (29.0)	538.0 (51.0)
Maximal finger aperture of the second grip (mm)	87.9 (6.4)	89.0 (8.3)
Time to maximal finger aperture of the second grip (ms)	603.0 (22.6)	759.7 (55.2)

(27.5 cm vs. 40.0 cm). The result of the ANOVA revealed that the beginning of the second submovement did not differ significantly between the trials Perturbed at 27.5 cm and those Perturbed at 40.0 cm ($F_{1,5} = 0.09$). On the average it was 370 ms.

Considering the results of a previous experiment[14,15] in which, using acceleration profiles, a modification in transport component was found about 100 ms after visual perturbation, we compared the times to peak acceleration of the first submovement of Perturbed trials with those of Control trials. The values of this parameter were submitted to one-way ANOVA taking as factor Distance (15.0 cm, 27.5 cm, and 40.0 cm). The Distance effect was significant ($F_{2,10} = 20.11, P < 0.001$). A post-hoc test (Newman–Keuls) showed that peak acceleration occurred earlier in both Perturbed trials than in Control trials. No difference was found between the two Perturbations. This result confirms that during Perturbed trials transport component was modified after about 150 ms.

This result suggested the possibility that when peak acceleration was reached, the visual information of

second target position could have been used to program a movement towards the new target. Since the value of peak acceleration increases with more distant targets (see Blocked trials), it should be greater in the trials perturbed at 40.0 cm than in those perturbed at 27.5 cm. One-way ANOVA (Distance as factor) showed that the values of peak acceleration did not change significantly between the trials perturbed at 27.5 and the trials perturbed at 40.0 cm ($F_{1,5} = 0.001$). We concluded that the subjects, when peak acceleration was reached, were interrupting the first submovement.

Grasp component

Fig. 4 (lower row) shows an example of the time course of grip during a Control trial (A) and during two Perturbed trials in which the target shifted from 15.0 cm to 27.5 cm (B) and from 15.0 cm to 40.0 cm (C). Note the double pattern of finger aperture/closure in response to visual perturbation.

In Tables II and III, the values of the kinematic parameters of the grasp component are reported. The values of the maximal finger aperture in Blocked trials and those of Control and Perturbed (second grip) trials were submitted to two-way ANOVA. The factors were Distance (15 cm, 27.5 cm, and 40 cm) and Experiment (Blocked vs Control and Perturbed trials). Both Distance ($F_{2,10} = 1.22$) and Experiment ($F_{1,5} = 0.89$) were not significant.

The beginning of the second grip occurred, on the average, at about 516 ms after perturbation. It occurred, therefore, very late with respect to the onset of the second transport submovement (370 ms). One-way ANOVA (Distance as factor) showed that the beginning of the second grip (see Table III) occurred significantly later in the trials Perturbed at 40.0 cm than in those Perturbed at 27.5 cm ($F_{1,5} = 7.97$, $P < 0.05$).

As for transport component, we looked for whether modifications of the grasp component occurred before the beginning of the second grip. We used the acceleration profiles of the angle formed by the marker placed in the first carpometacarpal joint and the markers placed on the tips of the thumb and index finger. One-way ANOVA (Distance as factor) revealed that the times to peak angular acceleration of the first grip ($F_{2,10} = 0.22$) and the values of peak angular acceleration ($F_{2,10} = 2.66$) in Control and in Perturbed trials were not significantly different (see Table II). The time to maximal finger aperture (first grip) of Perturbed trials tended to be shorter than the time to maximal finger aperture of Control trials ($F_{2,10} = 3.58$, $P < 0.066$).

These results indicate that a change in grasp component occurred very likely during or after the maximal

finger aperture of the first grip. Without doubt, the kinematic modifications of grasp component occurred later than those of transport component.

The finger closure time was submitted to one-way ANOVA taking Distance as factor. The finger closure time was not significantly different in Perturbed trials and Control trials ($F_{2,10} = 0.52$). Also, for hand distance from the target at the beginning of finger closure, no statistical effect of Distance was found ($F_{2,10} = 1.68$). The intersubject coefficients of variation in Control and Perturbed trials were respectively 21.7%, 19.0%, 21.0% for finger closure time, and 33.0%, 31.3%, 35.8% for hand distance from target at the beginning of finger closure. Hand velocity at the beginning of finger closure was constant in Perturbed and in Control trials ($F_{2,10} = 1.98$).

These last three parameters were submitted to two-way ANOVA in which the factors were Distance (15.0 cm, 27.5 cm and 40.0 cm) and Experiment (Blocked vs. Control and Perturbed trials). Only the hand velocity at the beginning of finger closure was significantly different between the two Experiments ($F_{1,5} = 8.40$, $P < 0.05$). The hand velocity at the beginning of finger closure was higher in Perturbed and Control trials than in Blocked trials (40.7 cm/s vs. 27.4 cm/s).

The time interval between maximal finger aperture of the second grip and peak deceleration of the second submovement (see Table II and III) was -15 ms in the trials Perturbed at 27.5 cm and 79.7 ms in the trials Perturbed at 40.0 cm.

DISCUSSION

The aim of the present experiment was to investigate how transport and grasp components of prehension movements are temporally coordinated. We verified whether there were some kinematic events of the two components that were temporally coupled. We carried out two experiments. In Experiment 1 (Blocked trials) this issue was addressed by studying the temporal relationships between the two components when movements of different amplitudes were executed. The results of this experiment confirmed that transport and grasp components start and stop at the same time[5,11,22-24]. Moreover since fingers started to close after peak deceleration when hand velocity reached a fixed threshold value independently of the distance, this additional coupling between the two components can be hypothesized. These results were tested again in Experiment 2 (Control and Perturbed trials). In this experiment, we used a visual perturbation paradigm in which the loca-

tion of the object to be reached and grasped changed at the onset of arm movement. We hypothesized that if a temporal coupling between events of the two components is necessary for the execution of each component, then it should not be altered by visual perturbation. On the contrary, if the two components can be executed independently, then the visual perturbation might cause a dissociation between those kinematic events that appeared coupled in Experiment 1.

The visual perturbation affected both transport and grasp components. Although this result was expected for transport, at first sight it was surprising for grasp because the visual perturbation consisted of changing object location (object extrinsic properties), whereas intrinsic properties of the new object (size and shape) remained unaltered. The reorganization of grasp observed in Experiment 2, could be consistent with the existence of a temporal coupling between the onset of the two components. As a consequence of this coupling, grasp was forced to restart, although visual computation of object intrinsic properties did not require a different grip aperture. However, this interpretation does not take into account that in Perturbed trials the two objects were presented in succession so that they might require two separate motor plans. Since the two plans were in succession, it is not surprising that the first grip was interrupted and a second grip was reprogrammed. Therefore the observation of a double pattern of finger aperture/closure is not sufficient to demonstrate the hypothesis of a temporal coupling between the beginning of the two components.

A way to solve the problem concerning the existence of a temporal coordination between the onsets of the two components has been to study how the temporal reorganization of the two components occurred in time, and whether a temporal correspondence between the beginning of the two components could be observed.

The beginning of transport second submovement occurred after about 370 ms. This result was obtained by analyzing acceleration profiles which allow a more accurate measure of movement changes. At first sight, this result appears to contradict the data of previous experiments in which prehension movements[14,15] and pointing movements that used double-step paradigm[8,20,21] were studied. In those experiments a change of trajectory was found after about 200 ms. This discrepancy can be explained if one takes into account that in their experiments the second target position required a change of movement direction, whereas in our study it required a change of movement amplitude. Our measure could be overestimated since in the last phase of the first submovement, the second submovement acceleration could be masked by the first submovement

deceleration. Another possible explanation is that, when the visual perturbation requires a change of movement direction, a shorter trajectory, and thus a shorter movement time, is obtained by modifying the direction as soon as possible. On the contrary, when the visual perturbation requires a change of movement amplitude, the trajectory is not lengthened by delaying the time to the onset of the second submovement. Thus, the necessity to quickly modify the movement to shorten the trajectory is less for amplitude changes than for changes of movement direction.

Using acceleration profiles, the first modification of the transport component was found to be in coincidence with peak acceleration of the first submovement. This result was in agreement with that of previous work[13-15]. This early modification of transport component can be interpreted in two ways: first as being due to a braking movement, second as being due to an attempt to reach the second target once the visual information of the new target position has been used. If the second hypothesis was true, the peak acceleration of Perturbed trials at 40.0 cm should have been greater than that of Perturbed trials at 27.5 cm since in Blocked trials the peak acceleration increased with distance. Our results excluded this hypothesis. In fact the values of peak acceleration did not change during Perturbed trials at 27.5 cm and at 40.0 cm. Thus, we suggest that this early modification of transport was due to a braking movement.

Although both grasp and transport components were influenced by visual perturbation, the time course of motor reorganization of grasp was very different from that of transport. The second grip started, on the average, after about 516 ms, whereas the transport second submovement started after about 370 ms. Moreover the first kinematic modification during the first grip was found to coincide with maximal finger aperture, and was later than that found for the transport component (390 ms vs. 150 ms).

The finding that the first modification of grasp occurred 240 ms after that of transport disagrees with the results of an experiment of Haggard and Wing[9]. In their experiment, both transport and grasp components were affected by mechanical perturbations of the arm and a fixed delay of 70 ms was found between modifications of transport and grasp. The authors concluded that grasp component received information about the development of transport, and they interpreted this result as a proof of a coordination between the two components. However, the different delays between transport and grasp modifications found in our Perturbed trials and those observed by Haggard and Wing do not support the hypothesis of the temporal coupling between the interruptions of the two movements. The delay of 70 ms

probably represents the minimum time necessary for grasp to initiate a response to the perturbation that affected the transport. In other words, although a cross-talking between transport and grasp exists, a temporal coupling between the two components is unlikely.

On the whole, our results do not support the hypothesis of a synchrony between the beginning of the two components. Moreover since the beginning of the second grip occurred in trials perturbed at 27.5 cm earlier than in those at 40.0 cm, whereas the onset of the transport second submovement remained constant in both Perturbed trials, it is difficult to accept the idea of a temporal coordination between the two events.

Why did grasp changes start after transport changes? The delay between the onset of transport second submovement and the onset of the second grip could depend on different requirements of object visual analysis to organize the two movements. The proximal movements (transport component) can be controlled in the first phase of movement with peripheral vision[16]. Moreover, it was found that the accuracy and the duration of pointing movements using peripheral vision are approximately the same as those using foveal vision, although the latency of arm movement increased about 25 ms for movements executed with peripheral vision[17]. Thus, transport component does not necessarily require the stimulus foveation in order to organize the appropriate arm movement, at least in the first phase of the movement. On the contrary we suggest that grasp component could require more detailed visual information of the object, by stimulus foveation, to precisely plan the finger grip. This interpretation of our results is supported by data of Sivak and MacKenzie[19] who found that foveal vision is necessary to plan and execute precisely grip component. A second interpretation, that does not exclude the first one, is that grasp might require information about transport time to reorganize its time course (see below).

The results concerning the temporal relations between kinematic events of the two components during their time courses appear not to support the hypothesis of a temporal coupling between the two components. Our results confirm that maximal grip aperture occurred after transport peak velocity[10,11,14,15] and suggested, at first sight, its temporal coordination with transport peak deceleration. However, in Experiment 1 its temporal relation, in absolute value and in percentage, with transport peak deceleration was so variable with distance as to exclude completely a temporal coupling between the two events.

Another possibility was the existence of a constant threshold value of hand velocity coupled with the beginning of finger closure. However it was not con-

firmed when we compared Blocked trials with Perturbed trials. This result suggests that a fixed threshold of arm velocity that triggers finger closure onset is unlikely. However, it is possible that different thresholds of velocity are coupled with finger closure onset when the experimental condition varies. If this hypothesis is true, it must be postulated that the execution of finger aperture is strictly correlated with arm velocity, in order to reach the same maximal finger aperture at a fixed value of hand velocity. If so, an interruption of transport would have to quickly influence the grasp component. This result was not observed in Perturbed trials. The delay between grasp and transport modifications was 240 ms, whereas the minimum delay was found to be 70 ms[9].

Since it has been possible, using a visual perturbation paradigm, to decouple transport and grasp components, one could hypothesize that also the grasp component uses information about spatial position of the object in order to plan its time course. Our results showed that distance of hand from object, at the beginning of finger closure, was practically constant in Blocked and in Perturbed trials. However since transport time changed with distance, this hypothesis requires that the grasp component also has information about hand velocity or transport time in order to reach, in different times, the same maximal finger aperture at a fixed distance from the object.

A more economic explanation of our results is that grasp component organizes its time course on the basis of the time planned by the transport component. In fact, finger closure time remained constant with distance and with different experimental conditions. The interpretation that transport time can be used to plan grasp, is supported by work of Wallace and Weeks[23]. In their experiment, in which distance and transport time were combined factorially to produce conditions with different transport mean velocity, kinematic parameters of grasp were dependent on the transport time rather than transport velocity or distance.

In conclusion, the results of this study indicate that, by using a visual perturbation paradigm, it is possible to decouple temporally transport and grasp components of prehension movements. However a temporal dependence between the two components remains after perturbation. In fact our results suggest that grasp component organizes its time course having information about the time required to reach the object.

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