

INFLUENCE OF DIFFERENT TYPES OF GRASPING ON THE TRANSPORT COMPONENT OF PREHENSION MOVEMENTS

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Abstract—The main aim of the present study was to clarify whether different types of grasping may affect the transport component of prehension movements. To this purpose two experiments were carried out. In the first experiment the kinematics of arm movements (transport and manipulation components) were studied in eight normal subjects instructed to reach and grasp different objects located either 20 or 30 cm from their hand. The objects employed required two different types of grip: prehension with the whole hand and prehension with the index finger and the thumb (precision grip). In the second experiment subjects were instructed to point to the same objects employed in the first experiment. This experiment served as a control for the precision requirements related to the object size. The results showed that, once the precision requirements were taken into account, the transport component remained unmodified with the different types of grip. The time course of the manipulation component and its temporal relations with the transport component changed with the type of grasping. The maximal hand aperture was reached earlier in the precision grip than in the whole hand prehension and the temporal coupling with the transport component was weaker in the former condition than in the latter. The data are interpreted as further evidence in favour of independence between the transport and the manipulation “channels”.

INTRODUCTION

PREHENSION movements directed towards visual stimuli comprise three main different segmental components: transport, rotation and manipulation [2]. The first component (transport) brings the hand from its initial position to the target; the second component (rotation) orients the hand in a way congruent with the object orientation; the third component (manipulation) selects and controls the finger grip according to the stimulus size and shape.

The problem of the relationships between the various components of prehension and, in particular, that between transport and manipulation was addressed by JEANNEROD [11, 12] in a series of studies in which he varied the object size, shape and distance from the viewer. The profiles of arm tangential velocity were used to analyse the transport component. In agreement with other studies [1, 9, 18], Jeannerod found that the velocity profiles were

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approximately bell-shaped with an initial phase of acceleration followed by a deceleration phase. Mean and peak velocities increased with object distance. This increase was almost linear and tended to maintain the transport time as constant. The transport component did not change by varying the object size.

The manipulation component was found to consist of two phases. The first one (grip formation) was characterized by a finger extension reaching a maximum (maximal grip aperture) proportional to the object size. The second phase (actual grasping) was characterized by finger closure on the object. The manipulation component was not influenced by stimulus distance.

On the basis of these data, JEANNEROD [13] proposed that the visuomotor mechanisms responsible for prehension are structured in a modular way. The "transport channel" extracts from the visual world information on the spatial location of the objects and activates those muscles which are relevant to carry the hand to the object location. The "manipulation channel" extracts information concerning the size and shape of the object and transforms it in the activation of distal muscles relevant to grasping the object.

JEANNEROD [11, 12] also observed that manipulation and transport components were frequently synchronized. The time to maximal hand aperture occurred at 70% of the manipulation time and corresponded to a break-point in the deceleration phase of the velocity profile of the transport component. Jeannerod postulated that in addition to the input-output information flow related to the various prehension components, there is also a global representation of the action of prehension. The global representation, which in many aspects is similar to the ephorator proposed by BERNSTEIN [3], controls the integrated aspects of prehension and coordinates its components.

Subsequent studies [23] fully confirmed that the manipulation channel is not influenced by the stimulus location in space. In contrast, it is less clear whether and, if so, to what extent, the transport channel is influenced by the physical (intrinsic) properties of the object.

The problem of how the size of the stimuli may influence the transport component has been recently addressed by MARTENIUK *et al.* [16] in an experiment in which subjects were instructed to reach and grasp two objects identical in shape, but differing in size. The results showed that transport time and peak velocity were both affected by the size of the stimulus. The shape, however, of the velocity profiles remained unmodified. The authors concluded that, since the velocity profiles belonged to the same scalar family of curves, the transport component depended in both tasks upon the same motor programme [20]. This common motor programme was only modulated according to the task precision requirements. Similar conclusions were reached by WALLACE and WEEKS [23] in an experiment in which the accuracy of prehension was examined.

In the experiment of MARTENIUK *et al.* quoted above [16], the subjects grasped the objects using the same type of grip, object size being the independent variable. A problem that was not addressed was whether a change in the type of grip and hence a modification in manipulation programme would produce a change in the motor programme of the transport channel. Evidence that this may occur derives from a second experiment of the same authors in which the transport component was compared during prehension and hitting [16]. This experiment showed that the velocity profiles of the transport component were markedly different in hitting and grasping and that these profiles did not belong to the same scalar family of curves. The authors concluded that the transport programme is influenced by the manipulation.

This conclusion is not necessarily true. To be sure, hitting and grasping imply different

distal programmes, but this difference is not the only one between the two tasks. Another difference and, in our opinion, by far more important is that the other two tasks differ in the purpose of the arm movement. In the case of prehension, the transport component is a part of a goal-directed action where grasping represents the purpose of the movement, whereas in the case of hitting, the transport coincides with the action goal. Thus, the observed difference in the transport component very likely reflects the different purposive request of the two tasks rather than differences in their distal programmes.

The main purpose of the present study was to verify whether modifications in the programme of the distal channel produce changes in the transport component. To avoid the confusing factors described above, we changed the type of grasping but we kept the task purpose, object prehension, identical. Changes in type of grasping were obtained by asking the subjects to grasp objects either with their index finger and thumb (precision grip) or with the whole hand (whole hand prehension).

Two experiments are presented. Experiment 1 describes the results obtained with different types of grip. Experiment 2 is a control experiment in which the importance of the accuracy factor was independently assessed by requiring the subjects to point to the same objects used in Experiment 1. The results showed that, once the accuracy factor is taken into consideration, manipulation programming does not affect the transport component.

A further purpose of the present experiment was to study the temporal relations between transport and manipulation components. In particular, we were interested to find out whether the different types of grasping were temporally coupled with the same event in the transport velocity profiles. As mentioned above, this type of synchronization was suggested by JEANNEROD in his pioneering studies [11, 12]. The results of our study showed that maximal hand aperture is achieved much earlier in precision grip than in whole hand prehension and that there is no event in the transport velocity profiles with which one can correlate with certainty the timing of the distal movements.

EXPERIMENT 1

Methods

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

Procedure. The subjects sat on a comfortable chair with their chest fastened to its back. They were instructed to reach and grasp three-dimensional objects resting on a table. The instruction was to perform the task naturally, with the same velocity as during spontaneous movements. The right arm of the subjects rested on the table where the objects were located and, at the beginning of each reaching-grasping trial, the subjects were required to put their hand on a position marked on the table. This location was central with respect to the subject's body and was 15 cm distant from it. The hand was kept prone and the index finger and the thumb were held in pinch position. The trial began with a "go" command given verbally by one experimenter. The subject was required to move his arm, but not his body and reach for the object. The object had to be grasped but not removed from its position.

Stimuli. Two stimuli were used: a large cylinder (diameter 6 cm, height 5 cm) placed horizontally on the table with its principal axis parallel to the subject's frontal plane and a small sphere (diameter 0.5 cm) placed on the top of a small platform (height 5.5 cm) attached to the table. The cylinder was grasped by the subject using a "whole hand prehension" (see [19]). This prehension (WHP) is characterized by a flexion of all fingers around an object in such a way as to form a ring around it. The sphere was grasped using a "precision grip". Precision grip (PG), as used in this article, consists in the opposition of the index finger on the thumb [19].

The objects were placed either at 20 cm or at 30 cm from the hand starting position on the sagittal axis passing through the body midline. The stimulus-distance combinations produced four experimental conditions: WHP 20 cm, WHP 30 cm, PG 20 cm and PG 30 cm. Each condition was tested in blocks of 10 experimental trials preceded by 30 practice trials. Order of blocks was counterbalanced across the subjects.

Movement recording. The prehension movements were recorded and analysed using the ELITE system [6] which consists of two TV cameras (sampling rate 50 Hz) and a processor. The cameras were distant 3 m from the working space where the apparatus was placed. The cameras were distant about 3 m each from other and

were inclined in the vertical axis of about 30° . The working space was a parallelepiped 60 cm long, 60 cm high and 30 cm deep. The length and the height of the parallelepiped coincided approximately with the subject's sagittal and vertical axis, respectively.

The cameras were connected to the processor which computed the position in space 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 reconstructed with an accuracy of $1/2500$ over the field of view and sent to a host computer (PDP 11/53). The host computer performed the following operations: (a) three-dimensional reconstruction of the positions of the markers; (b) data filtering by using a FIR linear filter [5]; and (c) computation of the kinematic parameters: trajectory, movement, velocity, acceleration and angle.

The transport component was studied by analysing the kinematics of the point corresponding to the centroid of the marker placed on the subject's wrist (Fig. 1, marker 7). The manipulation component was studied by analysing

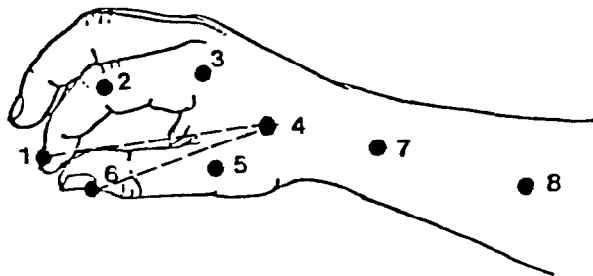


Fig. 1. Experiment 1. Positions of the markers recorded with the ELITE system in the subject's hand and forearm. Position of marker 1: distal phalange of index finger; position of marker 2: first interphalangeal joint of index; position of marker 3: metacarpophalangeal joint of index; position of marker 4: carpometacarpal joint; position of marker 5: metacarpophalangeal joint of thumb; position of marker 6: distal phalanges of thumb; position of marker 7: radial part of wrist; position of marker 8: radial part of forearm. (Distance of marker 7 from marker 8, 10 cm.) Dashed lines delimit the angle used to study manipulation component.

the kinematics of the angle formed by markers 1–4–6. Marker 1 was placed on the distal phalanx of the index finger, marker 4 on the first carpometacarpal joint and marker 6 on the distal phalanx of the thumb. The following parameters of the transport component were analysed: trajectory, movement, tangential velocity profile and acceleration profile. Since the spatial error of the ELITE system, measured on a stationary stimulus, is of 0.4 mm, transport movements were considered to start and stop in those frames in which the marker displacement was respectively greater and lesser than 0.4 mm.

The manipulation component was studied by analysing the temporal variations of the angle formed by the thumb and index finger. Since the angular error, as measured on a stationary angle, was of 0.4° , the manipulation movements were considered to start and stop in those frames in which the angular displacement was respectively greater and less than 0.4° .

Results

Transport component

Examples of typical arm trajectories recorded during whole hand prehension (WHP) and during precision grip (PG) are presented in Fig. 2. In A, stimuli were located at 20 cm from the subject's hand, whereas in B they were located at 30 cm. The trajectories shown in this figure are in the sagittal plane. Displacements on the transverse plane were negligible.

The kinematic parameters of the transport component studied in the present experiment are shown in Table 1. The values represent the average values of all subjects. For each parameter an analysis of variance (ANOVA) was performed taking as main factors distance (20 and 30 cm) and type of grasping (WHP and PG).

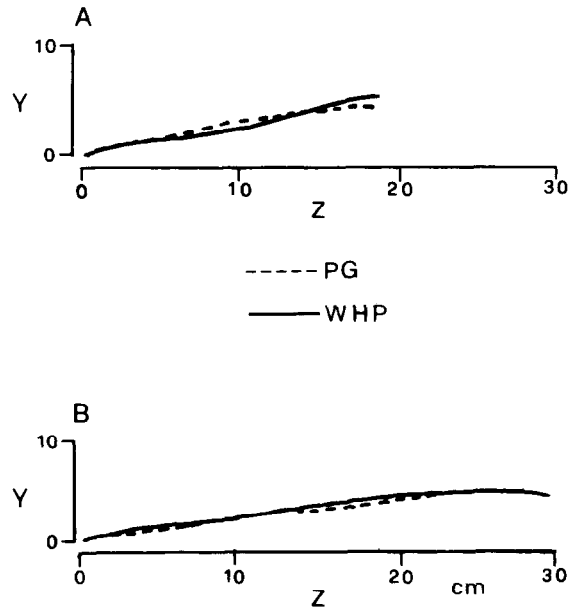


Fig. 2. Experiment 1. Representative examples of trajectories of the transport component on the sagittal plane in the four basic conditions (subject 1). Panel A shows the trajectories when the stimuli were located at a distance of 20 cm; in B the stimuli were located at the distance of 30 cm. The continuous lines represent trajectories during whole hand prehension, and dashed lines during precision grip. Axis z = sagittal axis; axis y = vertical axis.

Table 1. Experiment 1: Kinematic parameters of transport component

	WHP20	WHP30	PG20	PG30
Transport time (msec)	580.0	654.0	595.0	683.0
Mean velocity (cm/sec)	38.8	47.9	32.9	43.0
Peak velocity (cm/sec)	74.4	95.5	64.6	90.1
Time to peak velocity (T1) (msec)	240.0	264.0	244.0	254.0
Time after peak velocity (T2) (msec)	343.0	390.0	347.0	427.0
(%T2)	(58.1)	(59.6)	(58.9)	(62.7)
Peak acceleration (A1) (cm/sec ²)	478.0	558.0	400.0	513.0
Peak deceleration (A2) (cm/sec ²)	375.0	400.0	305.0	372.0
Time to peak deceleration (msec)	372.0	412.0	380.0	409.0
(%)	(66.0)	(64.0)	(64.0)	(60.0)

Transport time. There was a clear effect of distance on transport time, regardless of type of grasping. The average transport time was 585 msec when the the distance was 20 cm and 669 msec when the distance was 30 cm [$F(1, 7) = 42.787$, $P < 0.001$]. Transport time was also longer for PG (639 msec) than for WHP (617 msec). Although it is likely that this difference is real (see velocity data), type of grasping was not significant [$F(1, 7) = 0.20$].

Velocity. Both distance [$F(1, 7) = 112.625$, $P < 0.001$] and type of grasping [$F(1, 7) = 31.947$, $P < 0.001$] affected the transport mean velocity. The mean velocity was 45.4 cm/sec when the distance was 30 cm and 35.8 cm/sec when the distance was 20 cm. The mean velocity was also higher for WHP (43.3 cm/sec) than for PG (37.9 cm/sec).

Like mean velocity, peak velocity was also influenced by distance [$F(1, 7) = 163.873$, $P < 0.001$] and type of grasping, [$F(1, 7) = 22.211$, $P < 0.001$]. The peak velocity was higher when the distance increased (69.5 cm/sec for 20 cm vs 92.8 cm/sec for 30 cm) and for WHP (84.9 cm/sec) than for PG (77.4 cm/sec).

Examples of velocity profiles during WHP and PG at 20 cm and at 30 cm are shown in Fig. 3. In agreement with previous data [1, 9, 18], the profiles were approximately bell-

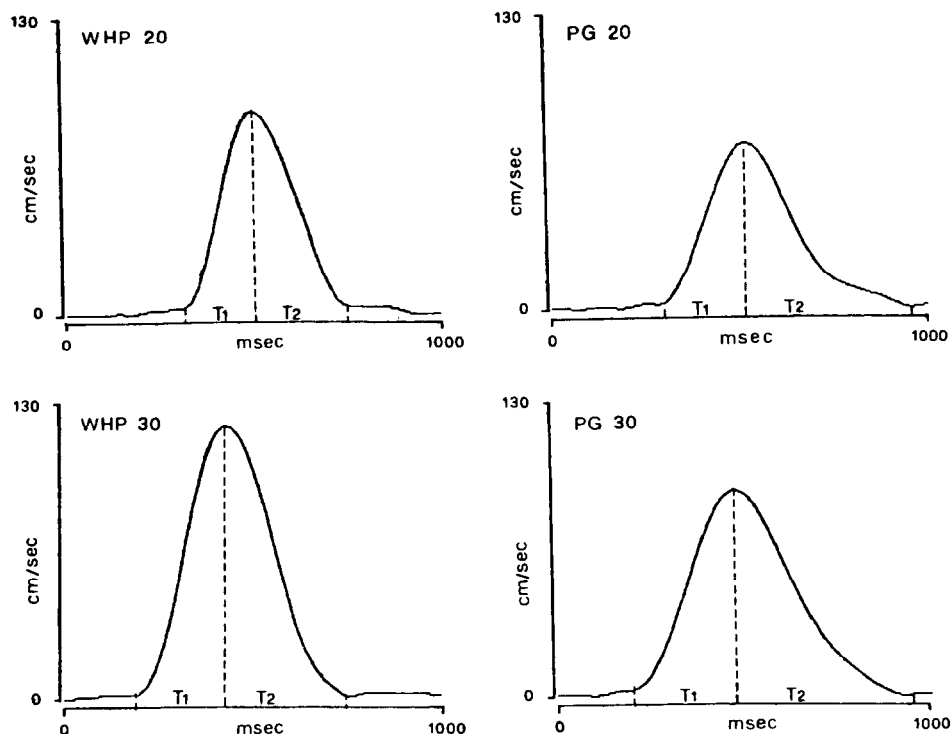


Fig. 3. Experiment 1. Representative examples of tangential velocity profiles of the transport component in the four basic conditions (same trials as in Fig. 2). T1 represents the time to peak velocity, T2 the time after peak velocity.

shaped. Shapes of velocity profiles similar to those represented in the figure were found in the majority of the trials (80%). In the remaining, a break-point could be observed in the deceleration phase (the analysis was made verifying in acceleration curves the presence of a plateau or of a secondary peak in the deceleration phase). These break-points were present in 21% of WHP 20 cm condition trials, in 27% of WHP 30 cm trials, in 12% of PG 20 cm trials and in 15% of PG 30 cm trials.

The values of the time to peak velocity (T1) and those of the time after peak velocity (T2)

were submitted to an ANOVA. T1 was significantly longer when the distance was 30 cm than 20 cm (260 msec vs 242 msec) [$F(1, 7) = 5.586$, $P < 0.05$], whereas it did not change with type of grasping. In contrast, T2 varied both with distance [$F(1, 7) = 50.048$, $P < 0.001$], and type of grasping [$F(1, 7) = 5.611$, $P < 0.005$]. T2 was longer for distances of 30 cm than for distances of 20 cm (408 msec vs 345 msec) and for PG than for the WHP condition (388 msec vs 366 msec).

In order to assess whether the different velocity profiles found in the four basic conditions belonged to the same scalar family of curves (see the Introduction), the velocity profiles were normalized with respect to time from the onset to the end of the movement. The normalized values of T2 for each subject are shown in Table 2. Note that at a distance of 20 cm T2 was

Table 2. Experiment 1: Percentage of time after peak velocity (%T2)

Subject	WHP20	WHP30	PG20	PG30
1	61.2	62.3	59.8	65.2
2	57.8	60.9	60.4	61.6
3	57.8	61.3	57.7	60.7
4	55.5	58.4	55.5	60.3
5	60.8	60.6	62.7	59.8
6	63.5	65.0	63.4	69.6
7	49.0	52.5	56.1	57.5
8	59.0	56.2	56.1	66.9
Mean	58.1	59.6	58.9	62.7

very similar for WHP and PG, whereas at a distance of 30 cm it was longer for PG than for WHP. An ANOVA showed that both distance [$F(1, 7) = 16.25$, $P < 0.001$] and type of grasping [$F(1, 7) = 7.548$, $P < 0.05$] were significant. The interaction between the two factors did not reach significance [$F(1, 7) = 1.32$].

Acceleration. The values of peak acceleration (A1) and peak deceleration (A2) were analysed separately (see Table 1). A1 results were significantly influenced by distance [$F(1, 5) = 9.9$, $P < 0.05$] and type of grasping [$F(1, 5) = 15.5$, $P < 0.05$]. Peak acceleration was greater for 30 cm than for 20 cm (536 cm/sec² vs 439 cm/sec²) and in the WHP condition than in the PG condition (518 cm/sec² vs 457 cm/sec²). In contrast, only type of grasping influenced significantly the peak deceleration [$F(1, 5) = 21.9$, $P < 0.001$]. This was higher for the WHP condition (387 cm/sec²) than for the PG condition (339 cm/sec²).

Examples of acceleration profiles in the four basic conditions are shown in Fig. 4. Note their similarity until the peak deceleration. The time to peak decelerations was submitted to an ANOVA. The results showed that the values of this parameter were significantly greater for movements of 30 cm (411 msec) than for movements of 20 cm (376 msec) [$F(1, 7) = 12.0$, $P < 0.01$]. Type of grasping was not significant [$F(1, 7) = 0.066$].

Manipulation component

The angle formed by the thumb and index finger was used to measure the manipulation component. In agreement with previous data [11, 12], two phases were distinguished (see Fig. 5). The first phase consisted of a finger extension (grip formation), the

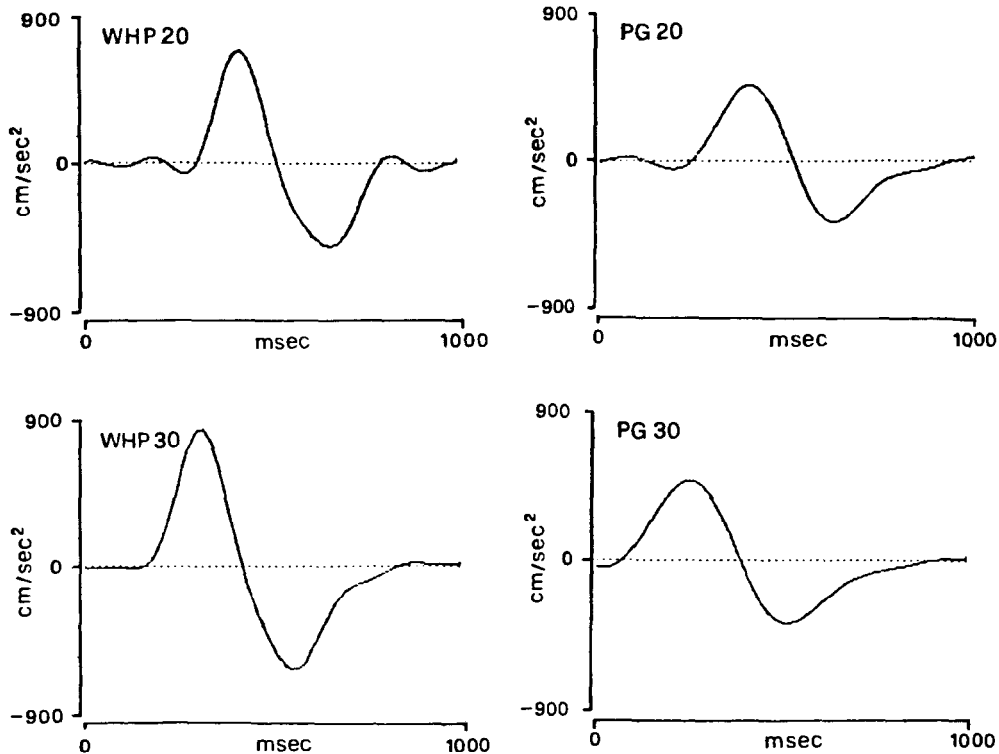


Fig. 4. Experiment 1. Representative examples of acceleration profiles of the transport component in the four basic conditions (same trials as in Figs 2 and 3). Note that deceleration after the peak tended to decrease more slowly during precision grip than during whole hand prehension.

second, successive phase, consisted of a finger flexion (actual grasping). Figure 5 shows that the hand maximal aperture increased with the object size. It was of 47° for large objects (35° at the end of grasping) and of 17° for small objects (10° at the end of grasping). The grip formation and the hand transport started simultaneously.

The kinematic parameters of the manipulation component are shown in Table 3. Each parameter was submitted to an ANOVA with distance and type of grasping as main sources of variability.

Grasping time. Grasping time measures the time from onset of finger movement until its end on the grasped object. Regardless of distance and type of grasping, grasping time closely corresponded to transport time (compare Table 1 and Table 3). As transport time, grasping time was affected by distance [$F(1, 7) = 35.670$, $P < 0.001$] and, to a lesser extent, by type of grasping. Type of grasping, however, was not significant [$F(1, 7) = 0.38$].

Maximal hand aperture. This parameter was calculated at the ratio between the maximal finger aperture and the finger aperture at the end of grasping (object size). Only type of

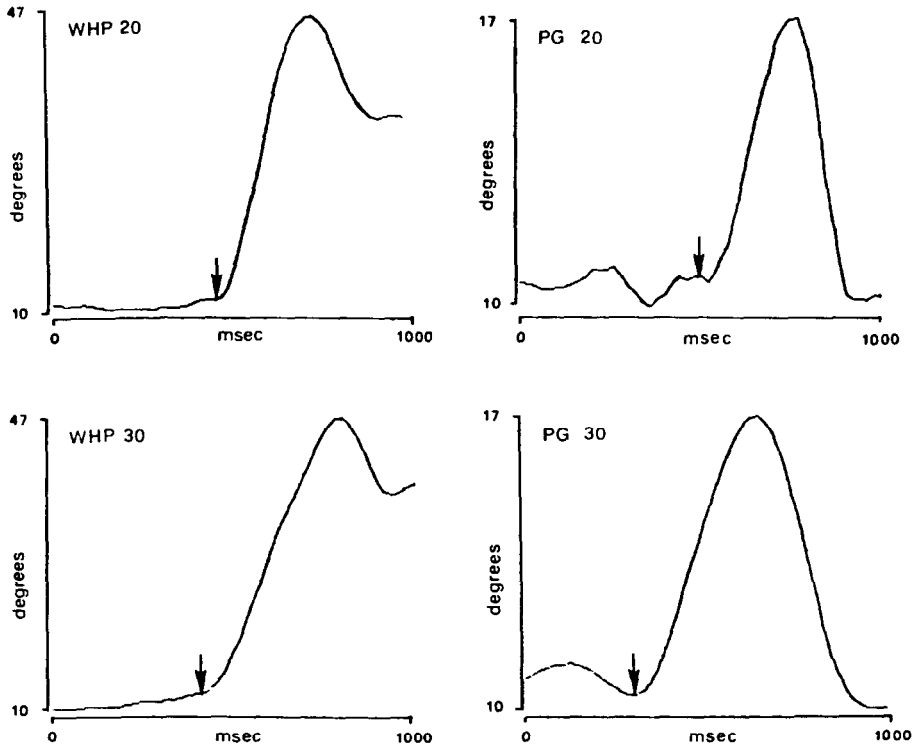


Fig. 5. Experiment 1. Representative examples of temporal variations of the grip aperture in the four basic conditions. The ordinate shows the angle formed by the thumb and the index finger. Note that in the ordinate the scales are different for precision grip and the whole hand prehension. Arrows indicate the onset of the transport movement.

Table 3. Experiment 1: Kinematic parameters of manipulation component

	WHP20	WHP30	PG20	PG30
Manipulation time (msec)	571.0	650.0	592.0	655.0
Maximal hand aperture	1.28	1.25	2.40	2.64
Time to maximal hand aperture (msec)	413.0	497.0	350.0	395.0
(%)	(72.0)	(76.0)	(59.0)	(58.0)

grasping was significant [$F(1, 7) = 38.447$, $P < 0.001$]. The values were 1.26 for the WHP condition and 2.52 for the PG condition.

Time to maximal hand aperture. Both distance [$F(1, 7) = 24.020$, $P < 0.001$] and type of grasping [$F(1, 7) = 5.582$, $P < 0.05$] were significant. The time to maximal aperture increased with distance (446 msec and 382 msec for 30 and 20 cm, respectively) and was longer for the WHP (455 msec) than for the PG condition (373 msec).

The percentage of grasping time necessary to reach the maximal hand aperture varied only

according to the type of grasping [$F(1, 7) = 9.263$, $P < 0.05$]. The maximal aperture was reached earlier in the PG condition (58%) than in the WHP condition (74%).

Since transport time and grasping time coincided, these last findings excluded that the maximal hand aperture could correspond to a single particular event of the transport component. The possibility, however, remained that the maximal hand aperture might correlate with some transport events, as, for example the peak deceleration which after time normalization was fairly constant in the four conditions (see Table 1, last row, percentage values). In order to test this possibility, we calculated the correlation coefficients between peak deceleration and time to maximal hand aperture at 20 and 30 cm. The correlations calculated over all trials and separately for each subject, are shown in Table 4. A significant correlation was found in seven out of eight subjects for WHP and in five out of eight subjects for PG. Thus, in both cases there appears to be a certain degree of temporal coupling between transport and manipulation components.

Table 4. Experiment 1: Correlation coefficients between time to peak deceleration and time to maximal hand aperture

Subject		WHP	PG
1		0.69*	0.27ns
	Slope	1.45	0.45
2		0.70*	0.61*
	Slope	1.09	0.67
3		0.30ns	0.54†
	Slope	0.72	1.04
4		0.75*	0.72*
	Slope	0.98	0.71
5		0.71*	0.75*
	Slope	0.95	0.93
6		0.65*	-0.06ns
	Slope	0.74	0.09
7		0.92*	0.64*
	Slope	0.92	0.86
8		0.79*	0.43ns
	Slope	1.20	0.66

* $P < 0.01$.

† $P < 0.05$.

ns, not significant.

EXPERIMENT 2

An important result of Experiment 1 was the demonstration that several parameters of the transport component changed with type of grip. Since, by necessity, objects of different size were used in PG and in WHP, the transport modifications could have resulted either from different distal programming or from the different precision requirements of the two tasks. To decide between these two possibilities, a control experiment was carried out in which subjects were required to point, instead of grasping, the same stimuli used in Experiment 1.

Methods

Subjects. Eight new subjects participated in this experiment. They were all right-handed, university students (age 18–27). They were naive as to the purpose of the experiment.

Procedure and stimuli. Subjects were instructed to point to the two three-dimensional objects used in the previous experiment. The objects were placed at 20 or at 30 cm, as in Experiment 1. The stimulus–distance combinations produced four experimental conditions: large stimulus at 20 cm (LP20), large stimulus at 30 cm (LP30), small stimulus at 20 cm (SP20) and small stimulus at 30 cm (SP30). The experimental procedure was almost identical to that of Experiment 1. The only difference was that, at the start of the trials, the thumb was not in contact with the index finger.

Movement recording. The ELITE system was used to record and analyse the movements. Only one marker (marker 7) was used. This is the marker which was employed to study the kinematics of the transport component in Experiment 1. For analogy with Experiment 1, the time from the beginning of the pointing movement to its end will be referred to as the transport time.

Results

The kinematic parameters studied in the present experiment are shown in Table 5. The values represent the average values of all subjects. For each parameter an analysis of variance (ANOVA) was performed taking as main factors distance (20 and 30 cm) and stimulus size (large and small).

Table 5. Experiment 2: Kinematic parameters of pointing movements

	LP20	LP30	SP20	SP30
Transport time (msec)	536.9	573.3	578.0	637.6
Mean velocity (cm/sec)	49.8	64.5	43.8	55.6
Peak velocity (cm/sec)	64.1	89.8	60.5	83.5
Time to peak velocity (T1) (msec)	236.6	225.9	232.9	242.8
Time after peak velocity (T2) (msec)	300.3	347.4	345.1	394.7
(%T2)	(54.6)	(58.7)	(58.3)	(60.7)
Peak acceleration (A1) (cm/sec ²)	447.8	609.1	402.2	533.1
Peak deceleration (A2) (cm/sec ²)	405.8	511.5	342.3	412.5
Time to peak deceleration (msec)	373.4	360.7	363.1	379.0
(%)	(69.3)	(68.9)	(65.8)	(62.6)

Transport time. Both distance [$F(1, 7) = 89.657$, $P < 0.001$] and stimulus size [$F(1, 7) = 8.998$, $P < 0.05$] affected transport time. The average transport time was 557 msec when the distance was 20 cm and 605 msec when the distance was 30 cm. Transport time was longer for small stimuli (608 msec) than for large stimuli (555 msec).

Velocity. As for transport time, both distance and stimulus size significantly modified mean velocity [distance: $F(1, 7) = 44.271$, $P < 0.001$; stimulus size: $F(1, 7) = 8.796$, $P < 0.05$] and peak velocity [distance: $F(1, 7) = 197.788$, $P < 0.001$; stimulus size: $F(1, 7) = 10.783$, $P < 0.05$]. Mean velocity increased with distance (46.8 cm/sec vs 60.0 cm/sec) and decreased with stimulus size (57.1 cm/sec vs 49.7 cm/sec). The same effect was found for peak velocity. The peak velocity was 62.3 cm/sec for the distance of 20 cm and 86.6 cm/sec for the distance of 30 cm. It was 76.9 cm/sec for large stimuli and 72.0 cm/sec for small stimuli.

Examples of velocity profiles during pointing to large and small objects at 20 and 30 cm are shown in Fig. 6. The majority of trials (97.2%) had shapes similar to those represented in the figure. In the remaining, a break-point was observed in the deceleration phase.

The values of the time to peak velocity (T1) and those of the time after peak velocity (T2) were submitted to an ANOVA. T1 remained constant with the distance (234.7 msec vs 234.3 msec) and increased 7 msec during pointing to small stimuli (237.8 msec vs 231.2 msec) [$F(1, 7) = 13.941$, $P < 0.01$]. T2 varied both with distance [$F(1, 7) = 27.282$, $P < 0.001$] and stimulus size [$F(1, 7) = 7.202$, $P < 0.05$]. T2 was longer for distances of 30 cm

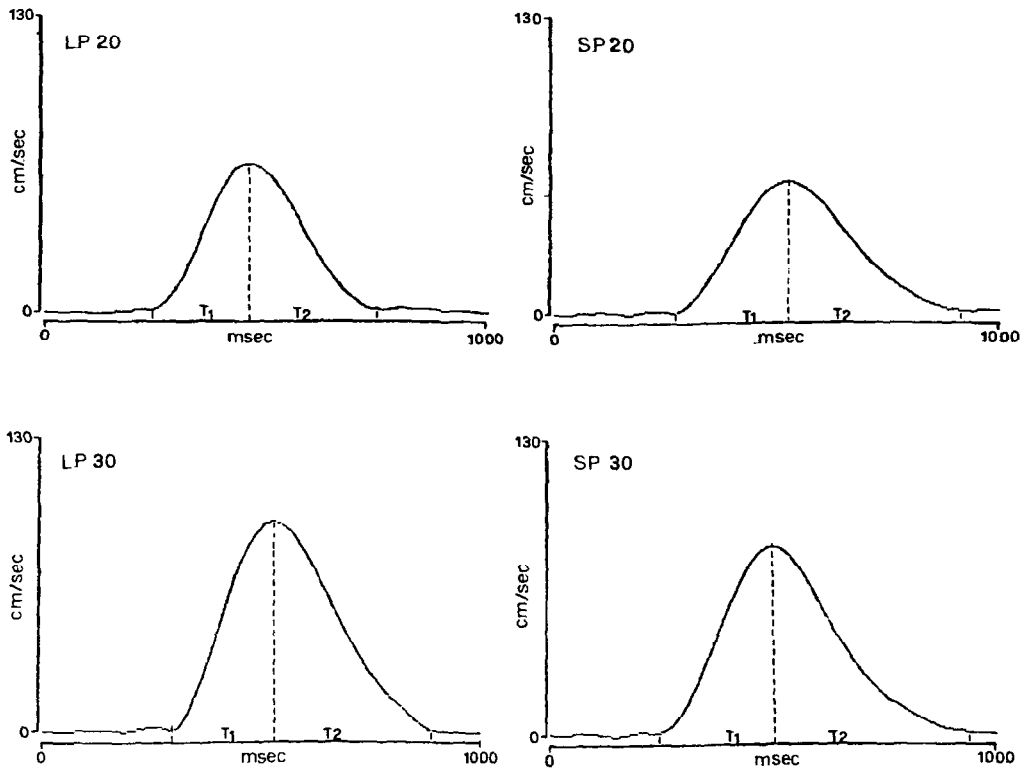


Fig. 6. Experiment 2. Representative examples of tangential velocity profiles of the transport component in the four basic conditions (subject 1). T1 represents the time to peak velocity, T2 the time after peak velocity.

than for distances of 20 cm (371.1 msec vs 322.7 msec) and for small stimuli than for large stimuli (369.9 msec vs 323.9 msec).

The normalized values of T2 for each subject are shown in Table 6. The most important result was that at both 20 and 30 cm the normalized value of T2 was longer for small stimuli than for large stimuli. T2 was also longer for longer distances. An ANOVA showed that both distance [$F(1, 7) = 28.501$, $P < 0.01$] and stimulus size [$F(1, 7) = 8.097$, $P < 0.05$] significantly influenced the normalized values of T2. The interaction between the two factors did not reach significance [$F(1, 7) = 1.063$].

Acceleration. The values of peak acceleration were significantly influenced by distance [$F(1, 7) = 63.013$, $P < 0.001$] and stimulus size [$F(1, 7) = 13.586$, $P < 0.01$]. Peak acceleration was 425.0 cm/sec² for distances of 20 cm and 571.1 cm/sec² for distances of 30 cm. It was greater for large stimuli (528.4 cm/sec²) than for small stimuli (467.7 cm/sec²). Peak deceleration increased significantly with distance (462.0 cm/sec² vs 374.0 cm/sec²) [$F(1, 7) = 83.647$, $P < 0.001$] and for large stimuli in respect to small stimuli (458.7 cm/sec² vs 377.4 cm/sec²) [$F(1, 7) = 7.065$, $P < 0.05$].

Examples of acceleration profiles in the four basic conditions are shown in Fig. 7. As for the prehension movements, the curves until peak deceleration were very similar. Time to peak deceleration was not affected neither by distance [$F(1, 7) = 0.039$] nor by stimulus size [$F(1, 7) = 0.130$].

Table 6. Experiment 2: Percentage of time after peak velocity (%T2)

Subject	LP20	LP30	SP20	SP30
1	59.6	63.5	68.0	67.6
2	56.2	66.6	59.6	65.0
3	59.0	60.0	60.4	61.2
4	66.5	68.9	65.8	66.1
5	51.0	57.5	57.8	64.2
6	49.3	49.0	50.6	56.3
7	41.7	47.9	47.0	48.1
8	53.5	56.1	57.2	57.0
Mean	54.6	58.7	58.3	60.7

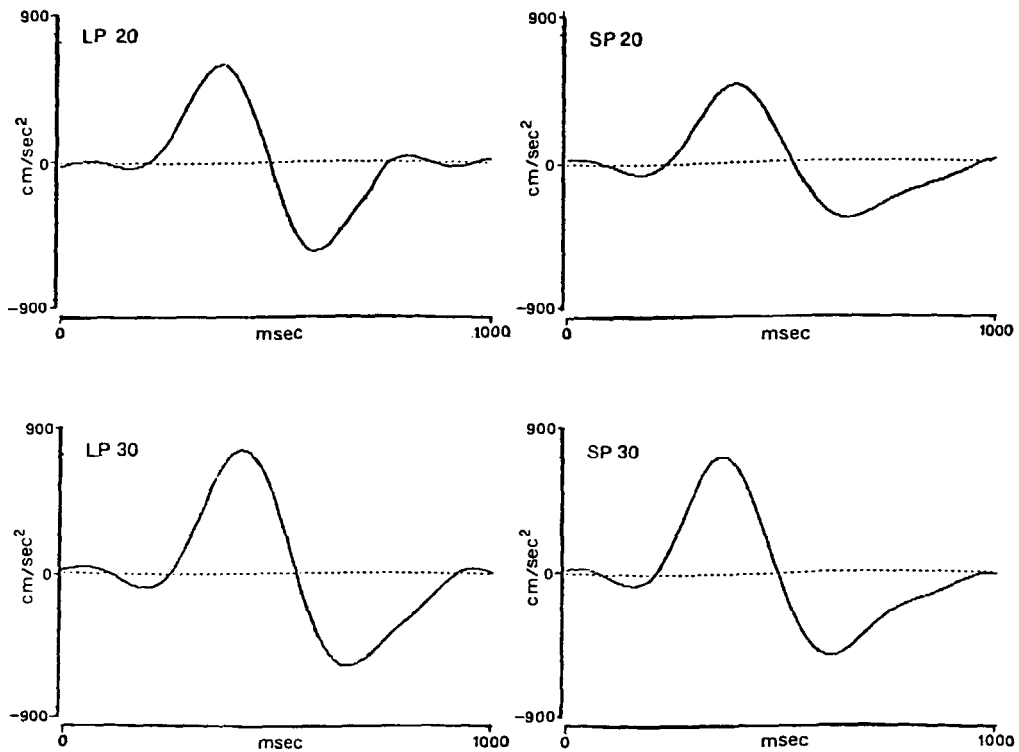


Fig. 7. Experiment 2. Representative examples of acceleration profiles of the transport component in the four basic conditions (same trials as in Fig. 6). Note that deceleration after peak deceleration tended to decrease more slowly during pointing movements towards small stimuli than towards large stimuli.

DISCUSSION

Transport component

According to the "channel" hypothesis of prehension, transport and manipulation are subserved by two functionally independent channels. The "transport channel" extracts

information about the spatial location of the object and transforms it in movements appropriate for bringing the hand to the object. The “manipulation channel” extracts information concerning the size of the object and transforms it into the distal movement pattern necessary to grasp the object.

In the original formulation of the channel hypothesis, JEANNEROD [12] posited that the transport channel was not influenced by changes in the object size. Literally taken, this is a rather strong statement that runs against some serious conceptual and empirical difficulties. First, there is a vast literature (see [14]) showing that movement time depends on target size (Fitt’s law [7]). Although this literature concerns essentially pointing movements, it is difficult to imagine that the precision requirements that slow movements in pointing would not be effective in reaching-to-grasp movements. Secondly, JEANNEROD himself and his coworkers in a subsequent experiment, in which subjects were required to reach and grasp objects identical in shape, but differing in size, found that transport time and peak velocity were both affected by stimulus size [16]. However, they found that after normalization in time the shape of the velocity profiles remained unmodified. On the basis of the notion ([4, 17, 20, 21] for a review see [14]) that, when the temporal relations between acceleration and deceleration phases remain constant the motor programme is structurally the same, the authors concluded that the transport component resulted from the same central motor programme, irrespective of object size.

In the present experiment we addressed the issue of the independence of transport channel from size by asking the subjects to grasp and to point to objects of different size. The results showed that transport time, mean velocity and peak velocity were greater for large stimuli than for small stimuli, and that peak acceleration varied in accordance with velocity. The same pattern of results was obtained for pointing and for prehension movements. Furthermore, our data showed that even after normalization the stimulus size affected the velocity profiles both in pointing and in reaching-to-grasp movements. The deceleration phase was longer with small stimuli.

These findings confirm the observation of MACKENZIE *et al.* [15] who showed in a pointing task that arm trajectories changed their shape when targets of different size were used, and that this effect was due to modifications in the deceleration phase of the trajectory. In contrast, they are in disagreement with the data of MARTENIUK *et al.* [16]. This discrepancy is probably due to the fact that the stimuli they used varied in size much less than those employed in our experiment.

An interesting finding of our experiment was that in both pointing and reaching-to-grasp the time to peak deceleration remained the same, regardless of stimulus size. The increase in transport time with small stimuli was due exclusively to the final part of the trajectory. This appears to indicate that transport of the arm towards the target is temporally constituted by two phases, and that the duration of the second phase is influenced by stimulus size.

According to ARBIB [2], one characteristic of prehension movements is that they have a ballistic and a feedback-based phase. The ballistic phase is a product of a feedforward system that defines the initial state of the limb and the goal, and then determines a movement towards the appropriate target location. The feedback phase is used at the end of this movement to achieve an accurate contact with the object. An alternative possibility is that the second phase is controlled, as is the first one, by a feedforward system which takes into account the object size and accordingly sets its duration. The increase in duration of the second phase with small stimuli would have the function to give additional time to control accurate hand “homing” by visual feedback.

Taken together, these data indicate that the channel which controls proximal movements in reaching-to-grasp and in pointing, has information about stimulus size and accordingly modifies peak velocity and acceleration of the first phase and sets the duration of the second phase. It appears, therefore, that Jeannerod's proposal of two independent channels, one responsible for the computation of the stimulus location and arm transport, and the other responsible for the computation of stimulus intrinsic properties and the organization of manipulation, is not supported by empirical evidence.

The originality of Jeannerod's hypothesis consisted in the notion that the same stimulus is independently and in parallel processed for governing related but different, in their computational requirements, motor acts and that two types of processing are subserved by different neural structures. The finding that, contrary to the original formulation, size of the object is processed not only by the distal but also by the proximal channel, does not contradict the theory because it disproves neither the independence nor the parallelism of the two channels. In fact, it is difficult to conceive how the transport channel could act without extracting information about object size. For the mere fact that it occupies space, an object must have a size, and to locate it entails necessarily information about its dimensions. The alternatives are either the computation of a point corresponding to the centre of the stimulus location, or the transport of the arm towards a space position whose size has no relation with the size of the stimulus. Both these alternatives appear logically weak and physiologically implausible.

Whereas the processing of size by both channels is neutral for the theory, the channel "impermeability" to the programmes implemented in the other channel is crucial. Thus, if different distal programmes would alter the kinematic parameters of transport, the theory would be falsified. The testing, however, of the transport channel "impermeability" is less simple than it may appear at first glance. Apparently, the easiest and the most direct way is to ask subjects to grasp objects that have the same size with different types of grip, and to measure the kinematic parameters of transport. From our studies of monkeys, however, it is clear that the choice of grasping is strictly determined by object size, and that different types of grasping are subserved by different populations of neurons [19]. To ask a subject to grasp a small object with whole hand prehension, or a large object with the index and thumb represents an improper way of analysing grasping mechanisms. To make an example, the grasping of a small object with the whole hand leads to a "decomposition" of the action into two parts: hitting the object with the palm, and subsequently performing a tactile-driven precision grip of the object. This type of action is not based, as the natural grasping is, on extraction of stimulus features and selection of the appropriate effectors. It is a combination of different motor acts. For this reason, and because different types of grip are subserved by different types of neurons [19], this experiment cannot provide any useful information concerning the relation between manipulation and transport channels.

In order to avoid these difficulties, in the present experiment we analysed the kinematic parameters of the transport component during two different types of grip directed towards objects of different size. Since, as discussed above, object size modified the transport trajectory, in order to control for this variable, we studied transport during pointing, as well as during grasping. Note that in pointing, the distal programme remains unmodified for small and large objects.

Our results showed that different distal programmes did not modify the transport parameters more than one would expect from the concomitant change in stimulus size. In pointing, where the distal programme remained unchanged, the peak velocity increased from

72 to 77 cm/sec when the stimulus increased in size; in grasping it increased from 77 to 85 cm/sec with change in grip. Similarly, the peak acceleration increased from 467 to 528 cm/sec² in pointing and from 457 to 518 cm/sec² in grasping, the highest acceleration being observed with the largest stimuli. An identical pattern of results was observed when the data were examined after normalization in time. In both pointing and grasping, there was a lengthening of the final part of the transport with small stimuli. However, there was no indication whatsoever that different distal programmes added any effect to that due to different precision requirements related to object size.

Finally, the strongest and more direct proof in favour of the "impermeability" of the transport channel to distal channel computations came from the analysis of the initial part of the transport curve. Object processing and effector selection by the distal channel occur in the early phase of reaching. This is shown by the fact that the hand starts to open with the beginning of the reaching movement and reaches its specific grasping shape rather early in respect to the total reaching time (58% in the case of PG). Thus, one should expect that, if distal programmes somehow affect the transport programme, this should be reflected in the early phase of transport. No evidence in this sense was found. Both at 20 and 30 cm the time to peak deceleration was identical with PG and with WHP. This indicates that the processing of the external stimulus and the selection of the distal effectors did not affect, in any observable way, the transport channel.

Manipulation component and its relationship with transport component

In agreement with previous studies [8, 11, 12, 13, 22, 23, 24], the analysis of the manipulation component showed that shaping of the hand was determined by the physical characteristics of the stimulus. The maximal hand aperture was greater for large objects than for small objects, whereas the ratio between maximal hand aperture and stimulus dimension was greater for small stimuli than for the large ones. Distance of the stimulus did not influence the maximal hand aperture.

The most interesting finding related to manipulation concerned the time course of this component. The data showed that, while the normalized maximal aperture time did not depend on distance, this manipulation parameter varied dramatically with the type of grasping. In particular, the maximal aperture occurred much earlier in PG (58% of the manipulation time) than in WHP (74%).

It has been suggested by JEANNEROD [11, 12] that the beginning of hand closure (which occurs immediately after maximal hand aperture) starts after the peak velocity of the transport movement and coincides with a break-point in the velocity profile. The occurrence of this break-point was observed at about 70% of the transport time and did not vary with object size. Our data confirm the observation that hand closure initiates during the deceleration phase. However, as mentioned above, the precise moment of the closure varied as a function of type of grasping and did not have any specific counterpart in the velocity profiles of the transport component.

The observation by JEANNEROD [11, 12] of a precise event on the velocity curve for the onset of hand closure was very appealing because it gave a hint on how the coordination of the proximal and the distal movements could occur. A synchronizing centre, similar to the ephorator proposed by BERNSTEIN [3], was postulated. It was proposed that this centre generates a double clustering of signals. The first signal burst would synchronize the fast phase of the transport component with the extension of the fingers, whereas the second burst would synchronize the low velocity phase with the finger closure. Unfortunately, the idea

that there is a centre which determines a fixed time at which the arm reaccelerates and the hand starts to close appears to be not supported by the findings. First, the onset of hand closure varies according to the type of grasping. Secondly, no reacceleration synchronous with hand closure onset was observed.

In spite of these negative findings, a further attempt was made to see whether a relation existed between hand closure onset and transport kinematics. This was done by correlating the hand closure onset with the time of occurrence of transport peak deceleration. As discussed above, this peak is one of the most stable transport events, being neither influenced by type of grasping nor (after normalization) by distance. The results showed several significant individual correlations, especially frequent in WHP. However, other individual correlations indicated a lack of relationship between the two variables. The correlation results, although suggestive of a relation between occurrence of peak deceleration and hand closure onset, appear to be insufficient to conclude that a synchronizing centre controls both grasping and transport.

In conclusion, our data confirm the existence of independent visuomotor channels for transport and manipulation in prehension movements. The transport component is influenced by spatial position of the object, by distance from the observer and by precision requirements due to object size. The distal channel extracts the physical (intrinsic) features of the objects and, accordingly, determines the type of grasping. Grasping is not influenced by the spatial position of the objects.

It is interesting to note that the input-output channels postulated by JEANNEROD [11–13] and ARBIB [2] on the basis of behavioural experiments, have recently received independent neurophysiological support. Single neuron recordings from inferior area 6 have demonstrated that in this area there are two sets of neurons coding, respectively, the transport and the manipulation components of prehension [10, 19]. The neurons related to transport respond to the specific spatial location of the object (3D-receptive fields) and appear to “command” arm movements towards this specific space sector. The neurons related to manipulation become active during particular types of grasping movements, frequently respond to visual objects, provided that object size is congruent with the type of grasping controlled by the neuron. Although quantitative data are necessary in order to establish a more precise correlation between behavioural and physiological data, the presence of neurons, that, at first glance, act as predicted by behavioural studies, indicates the fruitfulness of a modular model of motor control.

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REFERENCES

1. ABEND, W., BIZZI, E. and MORASSO, P. Human arm trajectory formation. *Brain* **105**, 331–348, 1982.
2. ARBIB, M. A. Perceptual structures and distributed motor control. In *Handbook of Physiology*, Section 1, Vol. 2, V. B. BROOKS (Editor), Part 2, pp. 1449–1480. William & Wilkins, Baltimore, 1981.
3. BERNSTEIN, N. *The Coordination and Regulation of Movements*. Pergamon Press, Oxford, 1967.
4. CARTER, M. C. and SHAPIRO, D. C. Control of sequential movements: evidence for generalized motor programs. *J. Neurophysiol.* **52**, 787–796, 1984.
5. D'AMICO, M. and FERRIGNO, G. Technique for the evaluation of derivatives from noisy biomechanical displacements data by a model-based bandwidth-selection procedure. *IEEE Trans. Biomed. Eng. BME* **28**, 407–415, 1990.

6. FERRIGNO, G. and PEDOTTI, A. ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing. *IEEE Trans. Biomed. Eng. BME* **32**, 943–950, 1985.
7. FITTS, P. M. The information capacity of the human motor system in controlling the amplitude of movement. *J. exp. Psychol.* **47**, 381–391, 1954.
8. FRASER, C. and WING, A. M. A case study of reaching by a user of a manually-operated artificial hand. *Pros. Orth. Int.* **5**, 151–156, 1981.
9. HOGAN, N. An organizing principle for a class of voluntary movements. *J. Neurosci.* **4**, 2745–2754, 1984.
10. GENTILUCCI, M., FOGASSI, L., LUPPINO, G., MATELLI, M., CAMARDA, R. and RIZZOLATTI, G. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and control of proximal movements. *Exp. Brain Res.* **71**, 475–490, 1988.
11. JEANNEROD, M. Intersegmental coordination during reaching at natural visual objects. In *Attention and Performance*, J. LONG and A. BADDELEY (Editors), pp. 153–168. Erlbaum, Hillsdale, New Jersey, 1981.
12. JEANNEROD, M. The timing of natural prehension movements. *J. Mot. Behav.* **16**, 235–254, 1984.
13. JEANNEROD, M. The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behav. Brain Res.* **19**, 99–116, 1986.
14. JEANNEROD, M. *The Neural and Behavioural Organization of Goal-Directed Movements*. Clarendon Press, Oxford, 1988.
15. MACKENZIE, C. L., MARTENIUK, R. G., DUGAS, C., LISKE, D. and EICKMEIR, B. Three dimensional movement trajectories in Fitts' law: Implications for control. *Q. J. exp. Psychol.* **39**, 629–647, 1987.
16. MARTENIUK, R. G., MACKENZIE, C. L., JEANNEROD, M., ATHENES, S. and DUGAS, C. Constrains on human arm movements trajectories. *Can. J. Psychol.* **41**, 365–378, 1987.
17. MEYER, D. E., SMITH, J. E. K. and WRIGHT, C. E. Models for the speed and accuracy of aimed movements. *Psychol. Rev.* **89**, 449–482, 1982.
18. MORASSO, P. Spatial control of arm movements. *Exp. Brain Res.* **42**, 232–237, 1981.
19. RIZZOLATTI, G., CAMARDA, R., FOGASSI, G., GENTILUCCI, M., LUPPINO, G. and MATELLI, M. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp. Brain Res.* **71**, 491–507, 1988.
20. SCHMIDT, R. A. *Motor learning and control: a behavioral emphasis* (2nd edn). Human Kinetics, Champaign, IL 1988.
21. VIVIANI, V. and TERZUOLO, C. Space-time invariance in learned motor skill. In *Tutorial in Motor Behavior*, G. E. STELMACH and J. REQUIN (Editors), pp. 525–533. North-Holland Publishing Company, Amsterdam, 1981.
22. VON HOFSTEN, C. and RONQUIST, L. Preparation for grasping an object: a development study. *J. exp. Psychol.* **4**, 610–621, 1988.
23. WALLACE, S. A. and WEEKS, D. L. Temporal constrains in the control of prehensile movements. *J. Mot. Behav.* **20**, 81–105, 1988.
24. WING, A. M. and FRASER, C. The contribution of the thumb to reaching movements. *Q. J. exp. Psychol.* **35A**, 297–309, 1983.