Exp Brain Res (1998) 120:31–40

RESEARCH ARTICLE

U. Castiello · K. Bennett · H. Chambers

Reach to grasp: the response to a simultaneous perturbation of object position and size

Received: 3 March 1997 / Accepted: 4 October 1997

Abstract This study assessed the reach to grasp movement and its adaptive response to a simultaneous perturbation of object location and size. The aim was to clarify the means by which integration between the neural pathways modulating transport and manipulation is achieved. Participants ($n = 11$) were required to reach 30 cm to grasp a central illuminated cylinder of either small (0.7 cm) or large (8 cm) diameter. For a small percentage of trials (20/100) a visual perturbation was introduced unexpectedly at the onset of the reaching action. This consisted of a shift of illumination from the central cylinder to a cylinder of differing diameter (large in session A; small in session B) that was positioned 20° to the left ($n = 10$ trials) or to the right ($n = 10$) of the central cylinder. The subject was required to grasp the newly illuminated cylinder. Movement duration for these "double" (position and size) perturbed trials was much longer than those of control trials to the central cylinder (session A: by an average of 250 ms; session B: 180 ms), and the increased values were much greater than those reported previously in "single" perturbation studies where either size or location of the object was perturbed. Initial signs of a response to the "double" perturbation were seen almost simultaneously in the transport parameter of peak arm deceleration and in the manipulation parameter of maximum grip aperture, but these changes were not evident until more than 400 ms after movement onset, a response onset much later than that found in "single" perturbation studies. It is proposed that the visual change resultant from the double perturbation activates integration centres that at first gate the flow of information to the parallel channels of transport and manipulation. Following processing of this information, these centres act to instigate a synchronised and coordinated response in both components. These results add support to the existence of neural centres dedicated to the integration of parallel neural pathways, and which exercise flexibility in the degree to which these components are "coupled" functionally.

Key words Reach to grasp · Perturbation · Kinematics · Motor control · Human

Introduction

The everyday action of reaching to grasp an object is commonly described in terms of a proximodistal distinction. The reaching and positioning actions, effected by upper arm and forearm musculature, are subserved by central nervous system visuomotor mechanisms that are largely independent of mechanisms subserving the hand and digit opening and closing upon the object for its grasp. With this description the two neural channels, transport and manipulation, are said to be activated simultaneously and in parallel ("channel" hypothesis of Jeannerod 1981, 1984), being coupled functionally for the goal-directed action by a higher-order coordinative structure (Jeannerod 1994; Paulignan et al. 1991a, b; Hoff and Arbib 1993). The "transport" channel is said to extract information about the spatial location of the object for transformation into motor patterns that bring the hand appropriately towards the object. The "manipulation" channel extracts information about the intrinsic properties of the object (such as size and shape) for the determination of a suitable grasping pattern.

Many behavioural studies of the kinematics of the human reach to grasp movement have tested the hypothesis that the two modules, transport and manipulation, are operationalised through separate neural channels. An approach common to many of these studies is that of attempting to choose experimental conditions that exert effects upon only one visuomotor channel. Thus, because arm transport serves the function of bringing the hand to the target object, its neural channel could be proposed

---

U. Castiello (✉) · H. Chambers
Department of Psychology, The University of Melbourne,
Parkville, Victoria 3052, Australia
e-mail: u.castiello@psych.unimelb.edu.au

K. Bennett
Faculty of Health Sciences, La Trobe University, Burdoora,
Victoria, 3083 Australia

to be more affected by changing the object's spatial location. Indeed, if the same object is presented at different locations, parameterisation of the manipulation component remains constant (Castiello 1996). In contrast, changing the intrinsic properties of the object, in an attempt to isolate the visuomotor channel subserving manipulation, affects both components. For example, velocity of the reaching arm is generally lower and the duration of its deceleration time longer for objects that are perceived to require greater precision (small, delicate, etc.) than for objects requiring less precision handling (for review see Weir 1994).

The means by which the two components are coupled functionally, if indeed they can be considered as separate visuomotor channels, remains unclear. The results from studies that have assessed how the two components are coordinated in time suggest, generally, that the coupling can be described as "loose". For example, significant correlations between temporal parameters of the transport component (e.g. maximum deceleration of the reaching arm) and parameters of the manipulation component (e.g. maximum hand aperture) are sometimes found across a wide range of experimental conditions and participant types. Overall it appears that the "neural talking", or the degree to which the channels communicate during operation, is flexible, with stronger coupling being evident in particular participant groups, such as the elderly (Bennett and Castiello 1994) or blind subjects (Castiello et al. 1993).

Studies that change the characteristics of the object between trials but present the same object prior to and during the action of reaching to grasp share the characteristic of giving participants full visual information prior to trial onset. This means that it is not possible to assume confidently that a given neural channel is not affected by an object change, as sufficient time is given prior to movement onset for compensatory adjustments. The use of perturbation paradigms has served to address the issue of how a pre-planned action is adjusted in response to an unexpected change in the intrinsic or extrinsic characteristics of the target object. By observing the impact of a perturbation that is intended to disturb only one channel, inferences about the degree of differential processing can be made. Thus, if a perturbation directed primarily at one component affects only the targeted rather than the non-targeted component greater confidence can be placed upon the assumption of channel independence. Conversely, if effects are observed in both channels when only one is targeted the implication is that information derived from the perturbation accesses both channels, simultaneously or in sequence, or that it activates neural centres common to or shared by both channels. It could also lend support to the rejection of "channel" theory, and acceptance of the notion that grasp and reach are coordinated in common integrative units (Jakobson and Goodale 1991; Haggard and Wing 1995; Desmurget et al. 1996).

To target a perturbation at the transport component the spatial location of the object to be grasped is unexpectedly changed. Paulignan et al. (1991a; see also Castiello et al. 1991; Gentilucci et al. 1992) employed such a paradigm. The usual target to reach and grasp was the central cylinder of three placed directly in front of the participant on a table. Perturbation was achieved by unexpectedly shifting illumination (20% of trials) at reaching movement onset from this central to one of the laterally placed cylinders. As expected, the spatial and temporal parameterisation of the transport component reflected disruption to the planned action, with the earliest behavioural change manifest in the parameter of maximum arm acceleration, on average, 100 ms after movement initiation. Of particular interest, however, was the finding of changes to the manipulation component despite the fact that the intrinsic properties had not been altered. Shortly before the reaching arm began to veer towards the new target location (at an average of 275 ms) the hand reached a maximum aperture (at an average of 217 ms) that was of lower magnitude and earlier than the peak of non-perturbed trials. Following this peak the hand began to close slightly before reopening and re-closing for the final grasp. In other words, information derived from the perturbation had accessed both channels – a result which is in accordance with the findings of Haggard and Wing (1995) for a mechanical, as opposed to a perceptual, perturbation of the reaching action.

To target perturbation at the manipulation component, an intrinsic property can be changed prior to or during the action. For example, in experiments by Paulignan et al. (1991b; see also Castiello and Jeannerod 1991; Castiello et al. 1992, 1993) the size of the target object was perturbed. Participants were presented with two targets: a small-diameter cylinder inserted vertically into the centre of a slightly shorter large-diameter cylinder. Using light-emitting diodes implanted in the supporting table surface, either cylinder could be selectively illuminated. Perturbations (20% of trials) could be achieved by shifting this illumination at the onset of the reaching action, from the small to the large cylinder or vice versa. Once again, the results supported the concept of shared processing. Not only did the timing and magnitude of hand aperture reflect the introduction of perturbation, but changes to the transport component were evident during the deceleration phase of the movement. In particular, the time of reaching arm peak deceleration was earlier (Castiello et al. 1992, 1993) and deceleration time was longer for perturbed than for non-perturbed trials (Paulignan et al. 1991b).

Results from studies that have attempted to isolate the perturbation to one channel give confidence to the concept of neural communication between the two channels, and to the idea that this neural cross-talk may act in a sequential mode. A given channel appears to show earlier changes when it is targeted than when it is not the prime intended target. Thus, the response to a perturbation of the transport component is first manifest in the acceleration, or early, phase of the reach, followed by changes in the manipulation component. Conversely, the response of the transport component to a perturbation of the manipulation component is in the deceleration phase as the hand hones in upon the object. In processing terms such results suggest that the visual change information resulting from perturbation influences primarily the targeted channel but can be forwarded to influence the non-targeted channel. Such interchannel transmission can be proposed to operate through separate channels – one from the transport to the manipulation visuomotor channel, the other from the manipulation to the transport (see Haggard 1994) – or through a neural module, or synchronising centre, which can be accessed by both channels. This module can be conceptualised as being dedicated to the transmission, and possibly processing and filtering, of information that is relevant to both channels.

In the current study perturbation is targeted at both channels by changing both the position and the size of the object at the onset of the reaching movement. The aim is to clarify the means by which cross-talk between the visuomotor pathways is achieved. If interchannel transmission channels are independent the expectation would be for evidence of adjustments in both the acceleration and deceleration phases of both components, and implementation of the entire reach to grasp action within a duration similar to that observed when only one component is targeted (approximately 80–200 ms greater than the movement duration of non-perturbed trials). In other words, the transmission of information from, say, transport to manipulation channels would not be subject to interference from the transmission of information from manipulation to transport channels. In contrast, if information is transferred through a shared neural centre, the expectation would be for some evidence of processing overload as the two components compete for similar resources.

Materials and methods

Participants

Twelve university students (6 female, 6 male; aged 24–30 years) volunteered to participate, but data from one participant were discarded due to abnormally noisy signals. All participants showed right hand dominance (Edinburgh Inventory: Oldfield 1971) and were naive as to the experimental design or purpose. None reported visual or psychomotor dysfunction.

Apparatus

The working surface was a semicircular table the surface of which was implanted with concentric rows of light-emitting diodes (LEDs). The participant was seated on a height-adjustable chair so that the thorax pressed gently against the front edge of the table and the feet were supported. A pressure-sensitive starting switch was positioned 10 cm anterior to the mid-line of the participant's thorax. With the hypothenar eminence of the right hand placed upon this switch, the starting position was slight shoulder flexion and 70–80° of internal rotation, 90° of elbow flexion, semipronation of the forearm, 5–10° wrist extension and opposition between the pads of the index finger and thumb.

Reflective passive markers (0.25 cm diameter) were attached to the following points of the reaching limb: (a) wrist – radial aspect of the distal styloid process of the radius; (b) index finger – radial side of the nail; and (c) thumb – ulnar side of the nail. Movements were recorded with the ELITE system (Ferrigno and Pedotti 1985). This consisted of two infra-red cameras (sampling rate 100 Hz) inclined at an angle of 30° to the vertical, and placed 3 m in front of the table and 3 m apart. The calibrated working space was a parallelepiped (length 60 cm, breadth 30 cm, height 60 cm) from which the spatial error measured from stationary and moving stimuli was 0.4 mm. Coordinates of the markers were reconstructed with an accuracy of 1/3000 over the field of view and sent to a host computer (Pentium). The SD of the reconstruction error was 1/3000 for the vertical (Y) axis and 1.4/3000 for the two horizontal (X and Z) axes.

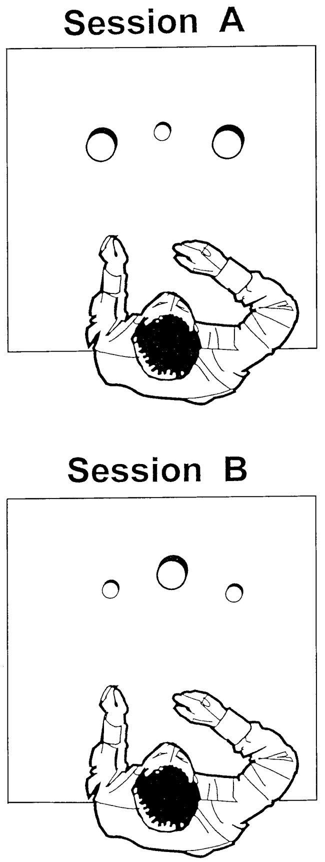

Fig. 1 The experimental setup showing a view of the participant from above and behind the working surface. In session A the stimulus array consisted of a small diameter cylinder 30 cm directly in front of the participant, and two large diameter cylinders, one 20° to the left and one 20° to the right of this central cylinder. In session B, the array consisted of a large diameter cylinder placed centrally, and small diameter cylinders placed laterally. (Note: this diagram is not drawn to scale)

The target stimuli were three translucent Perspex cylinders placed vertically upon the table surface above the implanted LEDs. One, the central cylinder, was placed 30 cm directly in front of the starting switch. The other cylinders were placed 20° to the right and left of the mid-sagittal plane, 30 cm from the switch. Each cylinder could be selectively illuminated in pink/red hues by computer activation of the underlying LEDs. In the case of the small cylinder one underlying LED was activated; in the case of the large cylinder three LEDs were activated. Two types of cylinders were employed. The small cylinder was of diameter 0.7 cm, height 10 cm and weight 9 g. The large cylinder was of diameter 8 cm, height 8 cm and weight 202 g. For perturbed trials (see later) these differences in diameter, height and weight would all contribute to the necessity of recruiting a different grasp from that initially employed at movement onset.

Two target object configurations were presented (Fig. 1). In one (session A), a small cylinder was placed centrally and large cylinders were placed laterally to the left and right. In the other (session B), a large cylinder was placed centrally and small cylinders were placed in the two lateral positions. Perceptual perturbation of both object size and position could be achieved by deactivating the LED(s) under the central cylinder, to extinguish illumination, while activating simultaneously the LED(s) under a lateral cylinder so that it became illuminated. For a low percentage of trials (see Procedure), release of the starting switch activated the computer control of this shift in illumination.

Procedure

To avoid fatigue and lack of concentration/attention, each participant performed two experimental sessions (A and B) conducted at the same time of day on separate days over a 1-week period. The order of sessions was counterbalanced across participants. The anatomical landmarks for the markers were dotted with indelible ink to ensure that the same points were recorded across sessions.

At the beginning of each session, the experimental requirements were explained. The participant was informed that shortly after positioning the hand upon the starting switch a tone would be heard to indicate that a cylinder would become illuminated soon after. The instruction was to begin the movement as soon as a cylinder became illuminated, and then reach for, grasp and lift the illuminated cylinder a small distance off the table. The participant was advised to perform the movement without undue emphasis on speed or on the demonstration of high performance. No instructions were given as to the type of grasp to adopt for each size of cylinder. Prior to blocked trials each participant was informed that only one cylinder would be illuminated for a series of trials. Prior to control/perturbed trials the participant was informed that for most trials the central cylinder would be illuminated but that for some trials illumination could change unexpectedly, and that, in this case, the requirement was to grasp the cylinder that became illuminated.

From each of the two sessions, 130 trials were recorded. At the beginning of each trial the participant placed the hand on the starting switch and the experimenter initiated a computer-generated tone (880 Hz; duration 250 ms). To reduce expectancy and rhythmical effects, the duration between this tone and subsequent illumination of a cylinder was randomly set at 500, 1000, 1500 or 2000 ms. Data acquisition began with illumination of the cylinder and continued until after the cylinder had been lifted. The experimenter was given computer screen feedback of the three-dimensional position of each marker; if one marker was “missing” (indicating that the cameras were not detecting the signal) during task performance the trial was manually discarded. Following each trial, the cylinder was replaced in its original position by the experimenter. Experimentation continued until the required number of successful trials was collected.

Prior to each recording session the participants were given 10 practice trials, including one example of a perturbation. During this practice session, all participants naturally adopted a precision grip (PG, opposition between the index finger and thumb) to grasp the small cylinder and whole hand prehension (WHP, all fingers opposing the thumb) to grasp the large cylinder.

During both sessions four sets of trial types were presented. All three cylinders were placed on the table to ensure consistency of visual display. The sets were as follows: (a) blocked central cylinder, (b) blocked lateral right cylinder, (c) blocked lateral left cylinder, and (d) control/perturbed trials. The order of set presentation was counterbalanced across participants. For each blocked set (a, b, c), ten trials were performed to the same cylinder, in session A the central cylinder being of small diameter and both lateral cylinders being of large diameter, and in session B the central cylinder being of large diameter and both lateral cylinders being of small diameter. For the control/perturbed set (d) 100 trials were conducted, 80 of these being control trials to the central cylinder and 20 being perturbed trials, ten to the left and ten to the right cylinder. The perturbed trials were randomly interspersed with the control trials. In session A the perturbation was thus from a small central cylinder to one of the lateral large cylinders. In session B the perturbation was from a large central cylinder to one of the small lateral cylinders.

Data processing and analysis

The ELIGRASP (B|T|S| 1994) software package was used to assess the data. This gave a three-dimensional reconstruction of the marker positions. The data were then filtered using a finite impulse response (FIR) linear filter-transition band of 1 Hz (sharpening variable = 2; D’Amico and Ferrigno 1990, 1992). The transport component was assessed by analysing the trajectory, velocity and acceleration profiles of the wrist marker. The manipulation component was assessed by analysing the trajectory of each of the hand markers, and the distance between these two markers. Movement initiation time, so called because no emphasis was placed on a rapid response, was taken from release of the starting switch. The end of the movement was taken as the time when the fingers closed on the cylinder and there was no further change in the distance between the index finger and thumb. The period following this, during which the cylinder was lifted, was not assessed.

The dependent variables were (a) initiation time, (b) movement duration, (c) transport component parameters – times to peak velocity, peak acceleration, peak deceleration of the wrist marker, and the amplitudes of these peaks (amplitude peak velocity, amplitude peak acceleration and amplitude peak deceleration, respectively) – and (d) manipulation component parameters – time to maximum grip aperture and amplitude of maximum finger aperture. Each temporal value of the transport and manipulation component was also calculated as a percentage of movement duration (relative values).

Mean values (absolute and relative) of each measure for each participant were entered into analyses of variance (ANOVAs; 0.05 alpha level of significance). Post hoc contrasts were conducted using the Newman-Keuls procedure. For each session three repeated measures ANOVAs were conducted with the independent variable being ‘Trial Type’. In one analysis (three levels) the comparison was between central control (ten trials randomly selected from 80), perturbed right and perturbed left trials. Thus in the case of session A, trials to the small central cylinder were compared with perturbed trials to the large lateral cylinders. In the case of session B, trials to the large central cylinder were compared with perturbed trials to the small lateral cylinders. This analysis was conducted to assess the effect of the double perturbation upon movement kinematics. A second analysis (two levels) compared central blocked trials with central control trials to determine whether the participant’s knowledge of the possibility of perturbation affected performance. A third analysis (two levels) compared blocked right with blocked left trials to assess the difference between trials performed to an ipsilateral target and those performed to a contralateral target.

Perturbed trials were characterised by a double step movement, evident for both transport and manipulation parameters (see Results), whereby the first movement was halted and a secondary movement initiated. For the dependent variables measured from the secondary movements (times and amplitudes of peak wrist velocity, acceleration and deceleration, and of peak grip aperture) a comparison was performed only between perturbed right and perturbed left trials given that control trials did not show such a patterning. The onset of the second movement was determined from the velocity and grip aperture profiles, being taken arbitrarily as the minimal value between the first and second peaks that preceded a clear rise to peak.

Results

For all parameters and in both sessions A and B, no differences were detected between central control and central blocked trials, indicating that the expectation of perturbation did not affect the results. A comparison between the first ten control trials and the last ten control trials of each session showed no differences, suggesting that fatigue effects were absent. The following sections present the results separately for sessions A and B.

Session A (small central cylinder; large lateral cylinders)

Comparison between control and perturbed trials

Means, standard deviations and results from the statistical analyses are presented in Table 1.

Table 1 Means (and standard deviations) of kinematic parameters together with significant ANOVA results: session A. (For temporal parameters, ANOVA results are for relative values unless indicated)

		Control Central small	Perturbed		*F* value and significance
			To large left	To large right	
Movement duration	(ms)	748 (139)	993 (112)	999 (107)	$F_{(2,20)}$=12.27, P<0.0001
Transport component					
Time to peak acceleration	(ms & %)	154 (44) 20 (4)	160 (36) 16 (3)	163 (47) 16 (3)	$F_{(2,20)}$=8.26, P<0.05
Time to peak velocity	(ms & %)	326 (81) 43 (3)	329 (80) 33 (6)	303 (42) 30 (2)	$F_{(2,20)}$=29.89, P<0.0001
Time to peak deceleration	(ms & %)	461 (99) 61 (5)	432 (86) 43 (7)	416 (45) 42 (3)	$F_{(2,20)}$=41.95, P<0.0001
Amplitude of peak acceleration	(mm/s^2)	4657 (1976)	4445 (1949)	4900 (2269)	n.s.
Amplitude of peak velocity	(mm/s)	783 (202)	725 (196)	750 (208)	n.s.
Amplitude of peak deceleration	(mm/s^2)	3282 (1226)	4251 (1513)	5458 (1772)	$F_{(2,20)}$=14.89, P<0.0001
Secondary movement					
Time to 2nd peak acceleration	(ms & %)		549 (73) 53 (5)	571 (66) 57 (6)	$F_{(1,10)}$=4.8, P<0.05
Time to 2nd peak velocity	(ms & %)		648 (61) 65 (3)	681 (59) 68 (2)	$F_{(1,10)}$=4.94, P<0.05
Time to 2nd peak deceleration	(mm/s^2)		764 (91)	766 (76)	n.s.
Amplitude of 2nd peak velocity	(mm/s)		500 (67)	566 (80)	n.s.
Amplitude of 2nd peak acceleration	(mm/s)*		3375 (1870)	4623 (1394)	$F_{(1,10)}$=5.26, P<0.05
Amplitude of 2nd peak of deceleration	(mm/s^2)		2682 (1235)	3414 (801)	$F_{(1,10)}$=5.68, P<0.05
Manipulation component					
Time to peak grip aperture	(ms & %)	427 (102) 57 (11)	452 (174) 45 (14)	474 (131) 48 (14)	$F_{(2,20)}$=3.76, P<0.05
Amplitude of peak grip aperture	(mm)	60 (17)	96 (29)	98 (20)	$F_{(2,20)}$=38.41 P<0.0001
Secondary movement					
Time to 2nd peak grip aperture	(ms & %)		760 (62) 78 (6)	853 (98) 82 (5)	$F_{(1,10)}$=8.05, P<0.05 (abs)
Amplitude of 2nd peak grip aperture	(mm)		103 (12)	108 (8)	

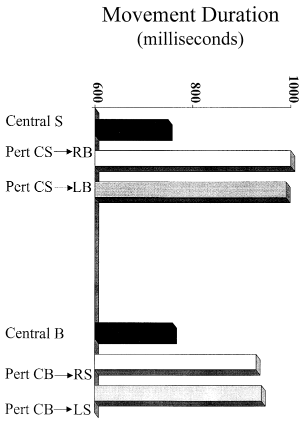

Fig. 2 Average values for the parameter of movement duration for perturbed and control trials in session A (*above*) and session B (*below*). *Central* control trials to central cylinder, *Pert* perturbed trials, *C* central, *S* small cylinder, *B* large cylinder, *R* right, *L* left. The *arrow* indicates the direction of the perturbation, e.g. *CS → RB* refers to trials where illumination shifted from the small central cylinder to the right large cylinder. Note the significantly longer movement durations for perturbed trials

On average, movement duration was 248 ms longer for perturbed than for control trials (996 vs 748 ms; Fig. 2). Kinematics of the reaching action showed differences in relative terms, with the first peaks of wrist acceleration, velocity and deceleration all being earlier for perturbed than for control trials (acceleration: 16% vs 20%; velocity: 31.5% vs 43%; deceleration: 42.5% vs 61%). The absolute values of these parameters showed no significant differences. The amplitude of the first peak of deceleration was greater for perturbed than for control trials (4855 vs 3282 mm/s^2). In absolute temporal terms, this peak occurred at an average of 424 ms (Fig. 3).

Deceleration time, the time from peak arm velocity to the end of the movement, was absolutely and relatively longer for perturbed than for control trials (659 vs 385 ms; 65.5% vs 52%). Kinematics of the hand opening/closing action showed differences, but again only in relative terms, with the first peak of grip aperture occurring at an average of 46.5% for perturbed trials but at 57% for control trials. In absolute terms this parameter occurred at an average of 463 ms for perturbed trials (Fig. 3). The amplitude of this aperture was significantly greater for perturbed (97 mm) than for control trials (60 mm).

All participants showed secondary movements for perturbed trials. This was evidenced by second peaks of acceleration (at 55% of movement duration), velocity (66.5%) and deceleration (76%), and a second peak on the grip aperture profile that was of 105.5 mm, and at an average of 80% of movement duration (Fig. 4).

Movement duration and the relative times of the first movement's kinematic parameters did not differ according to the direction of perturbation to the large cylinder. However, there were some differences, particularly with regard to later phases of the perturbed transport action. Deceleration time of the reaching arm was relatively longer, and the amplitude of the first peak of deceleration

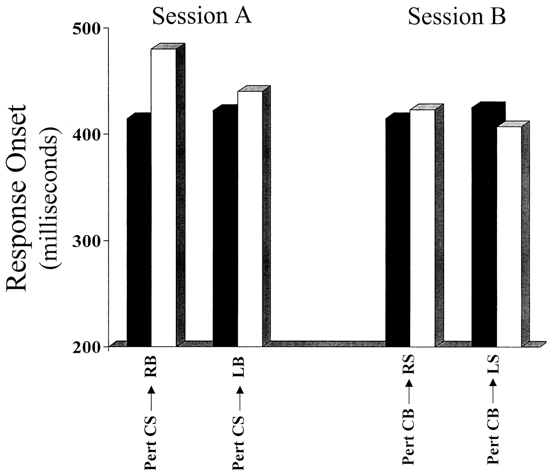

Fig. 3 Average times at which a response to perturbation was first observed in the transport (*black rods*) and manipulation (*white rods*) components. *Pert* perturbed trials, *C* central, *S* small cylinder, *B* large, *R* right, *L* left. The *arrow* indicates the direction of the perturbation, e.g. *CS → RB* refers to trials where illumination shifted from the small central cylinder to the right large cylinder. Note that responses to perturbation do not occur until more than 400 ms after reaching onset. For both types of perturbation the change was noted in peak arm deceleration (transport component) and in the aperture between the thumb and index finger

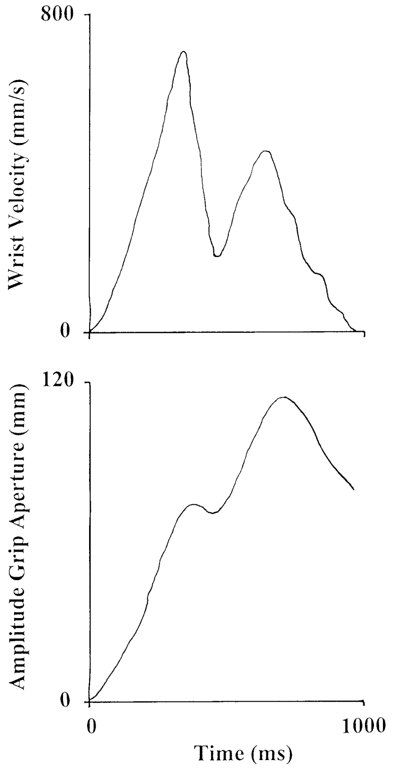

Fig. 4 An example of submovements in both the transport (velocity profile) and manipulation (aperture profile) components with the perturbation from small central cylinder to large right lateral cylinder (participant 6)

greater, for right (68% and 5458 mm/s^2 respectively) than for left (63% and 4251 mm/s^2) perturbations ($P_s < 0.05$). The amplitudes of the second peaks of acceleration and deceleration were also greater for right (4623 mm/s^2 and 3414 mm/s^2, respectively) than for left (3375 mm/s^2 and 2682 mm/s^2) perturbations, and the second peaks of arm acceleration and velocity were earlier for right (53% and 65%, respectively) than for left (57% and 68%) perturbations. Parameters of the manipulation component showed no differences according to direction.

Coordination between the two components

Analyses were performed to determine the degree to which the two components were correlated in time. For control trials to the small cylinder four participants (P7, P8, P10, P11) showed significant correlation between the peaks of arm deceleration and peak grip aperture. The left section of Table 2 (session A) shows the results for the perturbed trials (collapsed according to direction of perturbation). For the first movement, four of the 11 participants showed significant correlation between the time of the first peak of reaching arm deceleration and the time of the first peak in grip aperture. Interestingly, when analysing the same parameters for the submovement, a greater number of participants (nine) showed significant correlation, and the mean relative timings of these two parameters were quite similar (second peak deceleration = 76%; second peak grip aperture = 80% of movement duration).

Correlation between the onset times of the transport (onset of second velocity peak) and manipulation (onset of second hand opening) submovements were also found for nine of 11 subjects, and the timing of these onsets were similar with velocity onset occurring at an average of 486 ms, 48.5% of movement duration, and grip opening beginning at an average of 492 ms, 49.5% of movement duration.

In summary, and considering all parameter pairs in this correlational analysis, all but one participant (P2) showed significant correlation between the two components of perturbed trials.

Comparison between right and left blocked trials

Movement duration was longer for left than for right blocked trials (756 vs 682 ms, respectively; $F_{1,10} = 24.91$, $P < 0.001$). In absolute terms, the times of peak arm velocity and deceleration were later for actions directed to the left than for those directed to the right (velocity: 337 vs 292 ms, $F_{1,10} = 30.15$, $P < 0.0001$; deceleration: 461 vs 413 ms, $F_{1,10} = 11.33$, $P < 0.01$). No differences were found for the relative values. For the manipulation component, the amplitude of maximum hand opening was lower when reaching for the left as opposed to the right cylinder (104 vs 114 mm; $F_{1,10} = 29.74$, $P < 0.0001$).

Table 2 Results of correlational analysis of perturbed trials. Values are the standardised Pearson-product moment correlation coefficients (*P* participant number, *n* number of trials with 2nd grip aperture peak, *TPD* time to peak arm deceleration, *TGA* time to peak grip aperture, *1* first movement, *2* submovement, *OV* onset of 2nd velocity peak, *OO* onset of 2nd hand opening)

P	Session A				Session B			
	TPD1–TGA1	*n*	OV2–OG2	TPD2–TGA2	TPD1–TGA1	*n*	OV2–OG2	TPD2–TGA2
1	0.63	20	0.74	–	–	17	0.77	–
2	–	20	–	–	–	0	–	–
3	–	20	0.93	0.76	0.85	19	0.92	0.85
4	0.77	20	0.82	0.88	0.84	8	–	–
5	0.82	20	–	0.92	–	6	0.81	0.67
6	–	20	0.92	0.79	–	13	0.7	0.58
7	–	20	0.78	0.82	–	7	–	–
8	–	20	0.92	0.95	–	7	–	0.91
9	0.94	20	0.88	0.96	0.75	18	0.85	0.74
10	–	20	0.9	–	0.82	16	0.95	0.63
11	–	20	0.91	–	–	2	–	–

Table 3 Means (and standard deviations) of kinematic parameters together with significant ANOVA results: session B. (For temporal parameters, ANOVA results are for relative values unless indicated)

		Control Central large	Perturbed		*F* value and significance
			To large left	To small right	
Movement duration	(ms)	758 (118)	945 (114)	932 (138)	$F_{(2,20)}=31.23$, $P<0.0001$
Transport component					
Time to peak acceleration	(ms & %)	180 (75) 23 (6)	168 (57) 17 (4)	155 (40) 16 (4)	$F_{(2,20)}=15.40$, $P<0.0001$
Time to peak velocity	(ms & %)	349 (84) 45 (5)	318 (69) 32 (4)	304 (58) 33 (3)	$F_{(2,20)}=74.82$, $P<0.0001$
Time to peak deceleration	(ms & %)	492 (118) 64 (7)	438 (142) 42 (3)	408 (92) 45 (4)	$F_{(2,20)}=97.72$, $P<0.0001$
Amplitude of peak acceleration	(mm/s^2)	4994 (2157)	4752 (1860)	4838 (2282)	n.s.
Amplitude of peak velocity	(mm/s)	804 (170)	728 (186)	718 (222)	n.s.
Amplitude of peak deceleration	(mm/s^2)	3492 (1263)	4473 (1886)	5085 (1730)	$\mathrm{F}_{(2,20)}=9.75$, $P<0.0001$
Secondary movement					
Time to 2nd peak acceleration	(ms & %)		509 (59) 52 (3)	550 (78) 57 (5)	$F_{(1,10)}=4.76$, $P<0.05$
Time to 2nd peak velocity	(ms & %)		581 (70) 61 (3)	624 (70) 67 (3)	$F_{(1,10)}=32.82$, $P<0.0001$
Time to 2nd peak deceleration	(mm/s^2)		672 (47)	721 (90)	n.s.
Amplitude of 2nd peak velocity	(mm/s)		3900 (1668)	3842 (1545)	n.s.
Amplitude of 2nd peak acceleration	(mm/s^2)		537 (71)	440 (81)	n.s.
Amplitude of 2nd peak of deceleration	(mm/s^2)		2784 (1033)	3020 (1201)	n.s.
Manipulation component					
Time to peak grip aperture	(ms & %)	497 (79) 23 (6)	410 (59) 17 (4)	416 (64) 16 (6)	$F_{(2,20)}=15.40$, $P<0.0001$
Amplitude of peak grip aperture	(mm)	97 (29)	71 (23)	78 (20)	$F_{(2,20)}=27.71$, $P<0.0001$
Secondary movement					
Time to 2nd peak grip aperture	(ms & %)		686 (95) 71 (6)	706 (106) 74 (9)	n.s.
Amplitude of 2nd peak grip aperture	(mm)		57 (19)	64 (9)	n.s.

Session B (large central cylinder; small lateral cylinders)

Comparison between control and perturbed trials

Means, standard deviations and results from the statistical analyses are presented in Table 3.

As was found for session A, movement duration was longer (by around 180 ms) for perturbed than for control trials (938.5 vs 758 ms; Fig. 2). Again, kinematics of the reaching action showed differences in relative but not absolute terms. The peaks of arm acceleration, velocity and deceleration were all relatively earlier for perturbed than for control trials (acceleration: 16.5% vs 23%; velocity: 31% vs 46%; deceleration: 43% vs 65%). The amplitude of the first peak of deceleration (occurring at an average of 423 ms; Fig. 3) was greater for perturbed (4937 mm/s^2) than for control trials (3492 mm/s^2) and deceleration time was once again longer for the former than the latter trials (65% vs 49%). For the manipulation component, the peak of grip aperture (occurring at an average absolute value of 413 ms; Fig. 3) was relatively earlier and of lower amplitude for perturbed than for control trials (44% vs 65% and 74.5 mm vs 97 mm, respectively).

Secondary movements were again evident for perturbed trials. The second peaks of acceleration, velocity and deceleration of the transport component (evident for all trials of all participants) occurred, on average, at 54.5%, 64% and 73% of movement duration, respectively. For some perturbed trials (49%), a second peak was also evident on the grip aperture profile. The number of trials demonstrating this second peak is shown in Table 2 (right section; session B). The second peak showed an average amplitude of 60.5 mm (around 14 mm less than the first peak grip aperture) and occurred at 72.5% of movement duration.

As for session A, movement duration and the relative times of early kinematic parameters did not differ according to the direction of perturbation to the small cylinder, but some differences were evident in the later movement stages. Reaching deceleration time was relatively longer, and the amplitude of the first peak of deceleration greater, for right (67% and 5085 mm/s^2 respectively) than for left (63% and 4473 mm/s^2) perturbations ($P_s < 0.05$). The temporal parameters of peak acceleration and peak velocity of the second movement's transport component were later for perturbed right than for perturbed left trials (acceleration: 57% vs 52%, respectively; peak velocity: 67% vs 61%) and peak deceleration showed a non-significant trend in the same direction (70% vs 76%). Parameters of the manipulation component showed no differences according to direction.

Coordination between the two components

For control trials to the large cylinder, eight participants (excluding P2, P4 and P9) showed significant correlation between the peaks of arm deceleration and grip aperture. The right section of Table 2 shows the results for the perturbed trials. For the first movement, and as also found for session A, four of the 11 participants showed significant correlation between the time of peak reaching arm deceleration and the time of the first maximum grip aperture. As also found for session A perturbed trials, the number of participants with significant correlation between peak deceleration and peak grip aperture was greater for the submovement (6/11).

Six subjects showed correlation between the onset of the second velocity peak and the onset of the second hand opening; however, unlike the findings for session A, the onset times were not similar, with velocity onset at an average of 477 ms (51% of movement duration) and second grip opening at an average of 458 ms (59.5%). This may reflect measurement difficulties in determining the onset time of the second grip opening (going from a large to a small object there is a continuum in the grip aperture profile as the hand closes).

In summary, and considering all parameter pairs in this correlational analysis, all but three participants (P2, P7 and P11) showed significant correlation between the two components in perturbed trials.

Comparison between right and left blocked trials

As found for session A, movement duration was longer for blocked trials to the left than for those to the right (774 vs 690 ms; $F_{1,10} = 36.24$, $P < 0.0001$). Differences were again found with the absolute but not the relative temporal values of the transport component. The times of peak arm velocity and deceleration were later for actions directed to the left than for those directed to the right (velocity: 345 vs 293 ms, $F_{1,10} = 26.77$, $P < 0.0001$; deceleration: 483 vs 421 ms, $F_{1,10} = 31.67$, $P < 0.0001$). For the manipulation component, maximum grip aperture was later for left than for right blocked trials (460 vs 423 ms; $F_{1,10} = 36.24$, $P < 0.01$), and of lower amplitude for the former trial types (51 vs 63 mm; $F_{1,10} = 17.34$, $P < 0.002$).

Discussion

In this study, participants were presented with a central target that they were required to reach towards and grasp. For 20% of trials, and at the onset of movement to the initially processed stimulus, the location and size of the target to grasp was altered, requiring that the participant modify the initially recruited motor pattern. This type of "double" perturbation is used in an attempt to target both transport and manipulation visuomotor channels, in contrast to the single-channel focus in previous perturbation studies. The aim is to clarify the means by which cross-talk between the simultaneously activated channels is achieved under conditions that place demands upon the on-line execution of both channels.

The main results of this study are (1) that movement duration of perturbed trials is much longer than that of control trials, (2) that the response to perturbation is in both the transport and manipulation components, and almost synchronous, and (3) that this response is late (400–460 ms after the introduction of the perturbation).

Discussion of these results will focus on various models of the neural mechanisms underlying the organisation of reach and grasp movements. One model is that the channel for transport operates independently of that for manipulation (Jeannerod 1981). The results do not support this model. Movement duration is well above that which might be expected if two channels reacted independently to the perturbation. Further the response to perturbation is not simply a combination of responses to "single" perturbations; for example, with both adjustments to the acceleration phase of the action, reminiscent of the response to a perturbation of object location (Paulignan et al. 1991a; Castiello et al. 1991; Gentilucci et al. 1992), and adjustments to the deceleration phase, reminiscent of the response to a perturbation of object size (Paulignan et al. 1991b; Castiello and Jeannerod 1991; Castiello et al. 1992, 1993).

Another model is that the transport channel communicates with that of manipulation in a sequential mode. This could explain the "additive" increase in movement duration – processing occurring first in one and then in the other channel. In fact, using the results from studies that have found increases of movement duration under perturbation conditions (although this is not always the case: see Desmurget et al. 1996), the increase in movement duration of around 250 ms for perturbed trials of the current study is remarkably similar to the value obtained by adding a "location perturbation" movement duration increase value (of around 100 ms; Paulignan et al. 1991a; Castiello et al. 1991; Gentilucci et al. 1992) to a "size perturbation" increase value (80–170 ms; Paulignan et al. 1991b; Castiello and Jeannerod 1991; Castiello et al. 1992, 1993). This effect occurs despite differences in the experimental paradigms such as the extent of directional change. However, the late concurrent response in both components argues against a sequential mode of processing.

The results favour a model that incorporates common processing. One way of viewing this is that communication between the channels is achieved by a processing centre common to both channels. An alternative view is that the processing of grasp and transport is coordinated in an integrated centre rather than via two channels that communicate. In this latter model, the two functions may be recruited to varying degrees, at various times and with a varying degree of cross-coordination according to specifications dictated by the integrating centre. The current study does not allow support for one over the other of these common processing centre options.

The late response to perturbation, together with the very long movement duration, could suggest overloading of the common processing centre. However, the absence of obvious errors in movement performance, the evidence for a distinction between contralateral and ipsilateral movements even for perturbed trials (Prablanc et al. 1979; Fisk and Goodale 1985), and the synchronous nature of the response more suggest a controlled response to perturbation. In particular, this control appears to consist of gating, information processing and timing/coordination functions.

The evidence for a gating function is provided by the similarity of kinematic parameterisation between perturbed and non-perturbed trials. Neither grasp nor reach "react" until more than 400 ms following the change to the stimulus, suggestive of a strategy that allocates an interim period for signal reorganisation. The lack of the very early responses that have been reported in "single" perturbation paradigms, also suggests that this gating mechanism operates at a very early processing stage. To date, however, evidence for the existence of gating mechanisms in the visual cortex, such as post-synaptic gating, is formalistic (for review see Van Essen et al. 1994). The reasons for such gating may include processing to bind the two changed object features (i.e. size and location). With respect to size, this would entail the need to refocus attention upon the attributes of a newly presented object and process these elementary features into a meaningful entity to be grasped. With respect to location, a new spatial locus would need to be processed for contribution to the planning of the reaching action. The sum of the time taken to perform these processes could explain the late correction.

The similarity of the timings of response onset in the grasp and reach actions provides evidence for timing and coordination functions. Further, the majority of participants (9/12) show some form of significant correlation between temporal parameters of the transport and manipulation components of the perturbed trials. Such a high incidence of overt coordination contrasts with the results from previous perturbation studies. For example, Paulignan et al. (1991a, b) found that the correlation between the time of maximal finger aperture and the time of peak reaching velocity in size or position perturbed trials was significant only for a few participants. In another study, Gentilucci et al. (1991) correlated the time of maximal finger aperture with the time of maximum peak deceleration and reported a larger number of significant correlations than found in the Paulignan et al. studies (1991a, b). However, this number was still insufficient for claiming the existence of a consistent pattern of temporal coordination. The results of the current study imply that integrative centres act to modulate the degree to which the components are coordinated in time ("coupled") according to output requirements.

In conclusion, simultaneous perturbation of both object position and size at the onset of a reach to grasp action results in a prolonged movement duration, and a late but synchronised and coordinated response in both the transport and manipulation components. It is proposed that integration between these parallel functional neural networks is achieved by mechanisms that actively control the passage of information to and between the channels. It is only speculation that can be applied to the proposal of a neural basis for this integration function. Brain-imaging studies of grasping actions point to the existence of distributed networks involving several cortical and subcortical regions (Grafton et al. 1991, 1992, 1996). These include the parietal cortex and thalamus, areas proposed by Goldman-Rakic (1988) as being possible candidates for integrating the form of an object with its position in space.

Acknowledgements This work was supported by grants to U.C. and K.B. from the Australian Research Council, and the Australian National Health and Medical Research Council. Suryani Lim and Mary-Lyn Draper are thanked for their assistance with programming and data analysis.

References

Bennett KMB, Castiello U (1994) Reach to grasp: changes with age. J Gerontol Psych Sci 49:1–7

Castiello U (1996) Grasping a fruit: selection for action. J Exp Psychol Hum Percept Perform 22:582–603

Castiello U, Jeannerod M (1991) Measuring time to awareness. Neuroreport 2:797–800

Castiello U, Paulignan Y, Jeannerod M (1991) Temporal dissociation of motor responses and subjective awareness. Brain 114:2639–2655

Castiello U, Bennett KMB, Paulignan Y (1992) Does the type of prehension influence the kinematics of reaching? Behav Brain Res 50:7–15

Castiello U, Bennett KMB, Stelmach GE (1993) Reach to grasp: the natural response to a perturbation of object size. Exp Brain Res 94:165–178

Castiello U, Bennett KMB, Mucignat C (1993) The reach to grasp movement of blind subjects. Exp Brain Res 96:152–162

D'Amico M, Ferrigno G (1990) Technique for the evaluation of derivatives from noisy biomechanical displacement data using a model-based bandwidth-selection procedure. IEEE Trans Biomed Eng 28:407–415

D'Amico M, Ferrigno G (1992) Comparison between the more recent techniques for smoothing and derivative assessment in biomechanics. IEEE Trans Biomed Eng 30:193–204

Desmurget M, Prablanc C, Arzi M, Rossetti Y, Paulignan Y, Urquizar C (1996) Integrated control of hand transport and orientation during prehension movements. Exp Brain Res 110:265–278

Ferrigno G, Pedotti A (1985) ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing. IEEE Trans Biomed Eng 32:943–950

Fisk JD, Goodale MA (1985) The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. Exp Brain Res 60:159–178

Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umilta C, Rizzolatti G (1991) Influence of different types of grasping on the transport component of prehension movements. Neuropsychologia 29:361–378

Gentilucci M, Chieffi S, Scarpa M, Castiello U (1992) Temporal coupling between transport and grasp components during prehension movements: effects of visual perturbation. Behav Brain Res 47:71–82

Goldman-Rakic PS (1988) Topography of cognition: parallel distributed networks in primate association cortex. Annu Rev Neurosci 11:137–156

Grafton ST, Woods RP, Mazziotta JC, Phelps ME (1991) Somatotopic mapping of the primary motor cortex in man: activation studies with cerebral blood flow and PET. J Neurophysiol 66:735–743

Grafton ST, Mazziotta JC, Woods RP, Phelps ME (1992) Human functional anatomy of visually guided finger movements. Brain 115:565–587

Grafton ST, Fagg AH, Woods RP, Arbib MA (1996) Functional anatomy of pointing and grasping in humans. Cereb Cortex 6:226–237

Haggard P (1994) Perturbation studies of coordinated prehension. In: Bennett KMB, Castiello U (eds) Insights into the reach to grasp movement. (Advances in psychology). North-Holland, Amsterdam, pp 59–84

Haggard P, Wing A (1995) Coordinated responses following mechanical perturbation of the arm during prehension. Exp Brain Res 102:483–494

Hoff B, Arbib MA (1993) Models of trajectory formation and temporal interaction of reach and grasp. J Mot Behav 25:175–192

Jakobson LS, Goodale MA (1991) Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res 86:199–208

Jeannerod M (1981) Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (eds) Attention and performance IX. Erlbaum, Hillsdale, NJ, pp 153–169

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

Jeannerod M (1994) Object oriented action. In: Bennett KMB, Castiello U (eds) Insights into the reach to grasp movement. (Advances in psychology). North-Holland, Amsterdam, pp 3–15

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh Inventory. Neuropsychologia 9:97–113

Paulignan Y, Jeannerod M, MacKenzie C, Marteniuk R (1991a) Selective perturbation of visual input during prehension movements. 2. The effects of changing object size. Exp Brain Res 87:407–420

Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M (1991b) Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. Exp Brain Res 83:502–512

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

Van Essen DC, Anderson CH, Olshausen BA (1994) Dynamic routing strategies in sensory, motor, and cognitive processing. In: Koch C, Davis JL (eds) Large-scale neuronal theories of the brain. Computational neuroscience. MIT Press, Cambridge, Mass, pp 271–299

Weir PL (1994) Object properties and task effects on prehension. In: Bennett KMB, Castiello U (eds) Insights into the reach to grasp movement. (Advances in psychology) North-Holland, Amsterdam, pp 129–150