RESEARCH ARTICLE

Jinsung Wang · George E. Stelmach

Spatial and temporal control of trunk-assisted prehensile actions

Abstract The present study utilized a trunk-assisted prehension task to examine the hypothesis that there is spatial regularity between the grasp and transport components. To test this hypothesis, we varied movement amplitude, reach speed, and object size. When examining the opening and closure phases of aperture formation, it was found that the distance to peak aperture increased systematically with hand-path trajectory length, while the distance from peak aperture to the object remained constant, which supports the notion of state-space control. Regarding the relationship among the body segments involved, temporal measures such as relative time to peak aperture, and peak velocity of the arm and trunk were altered by the changes in both object size and reach speed. It was also found that the time to peak trunk velocity was coupled with the time to peak arm velocity as well as with the time to peak aperture. Based on these results, it appears that the trunk is closely linked not only to the arm motion, but also to the aperture formation. Collectively, these findings suggest that, during trunk-assisted prehension, the arm and the trunk are coordinated by neuromotor synergies that appear to position grip aperture for a stable closure to grasp the object.

Keywords Prehension · Motor control · Closure distance · Trunk · Synergy

Introduction

Reach-to-grasp movement is one of the most frequently performed activities in daily life. It has been extensively studied to obtain a better understanding of how the nervous system coordinates multijoint movements, and kinematic and neurophysiological evidence suggests that reaching and grasping involve separate mechanisms (e.g.,

J. Wang · G. E. Stelmach (✉)
Motor Control Laboratory, Arizona State University,
P.O. Box 870404, Tempe, AZ 85287–0404, USA
e-mail: Stelmach@asu.edu
Tel.: +1-480-9659847, Fax: +1-480-9658108

Lawrence and Kuyper 1968; Mountcastle et al. 1975; Rizzolatti et al. 1988; Wallace and Weeks 1988; Jakobson and Goodale 1991; Gentilucci et al. 1992; Jeannerod et al. 1995; Lemon et al. 1995; Kudoh et al. 1997; Smeets and Brenner 1999). Most studies that examined reach-to-grasp movements involved tasks for which the subjects simply reached for an object by extending the arm. In daily life, however, individuals are confronted with situations where an object is located beyond the arm's reach, so the trunk becomes involved in the arm transport to extend the reach. In such a situation, the motor control system needs to not only control the grasp and transport components of the moving arm, but also coordinate the trunk with the arm. Tyler and Hasan (1995) have shown that the nervous system does not activate trunk muscles across all target directions to counteract postural disturbances at the initiation of reaching movements, suggesting that, even when the trunk is not actively involved, it is still activated for reasons other than just postural stabilization. Thus, investigations that employ the tasks in which the trunk becomes more actively involved, such as trunk-assisted prehension, may provide insights into how the nervous system coordinates a redundant number of degrees of freedom.

A limited number of studies have employed trunk-assisted pointing (Kaminski et al. 1995; Ma and Feldman 1995; Pigeon and Feldman 1998) or prehensile movements (Saling et al. 1996; Wang and Stelmach 1998a), most of which focused on the temporal relationship between the arm and trunk. Wang and Stelmach (1998a), however, demonstrated findings with respect to the spatial relationship between the aperture formation and transport component. We showed that the aperture opening distance (i.e., length of hand-path trajectory between onset and peak aperture) increased systemically as the overall hand-path trajectory length increased, while the aperture-closure distance (i.e., length of hand-path trajectory between peak aperture and contact of the object) remained invariant, regardless of whether the hand was delivered to the object by the arm, trunk, or both. We, thus, suggested that the distance between the moving hand and the object (i.e., closure distance) may be an important

variable controlled by the nervous system to maintain co-ordination between the grasp and transport components. Since the invariance in closure distance was only examined for one movement amplitude in that experiment, this hypothesis was not sufficiently tested. This study, thus, examined whether the invariance in closure distance can be observed for two different movement amplitudes.

Two additional variables were also examined in this study: reach speed and object size. The effect of reach speed was examined because the extent to which the trunk participates in the prehensile movement has been shown to vary depending on the reach speed (Seidler and Stelmach 2000). It seemed that the results with regard to the movement amplitude might vary depending on the reach speed; thus, the effect of two different reach speeds were investigated in this study. Regarding the effect of object size, Saling et al. (1996) showed that the change in object size did not affect trunk kinematics. However, when we consider the anatomical and kinematic relationships between the hand and arm and also between the arm and trunk, it is unlikely that the trunk motion is not linked with the aperture formation at all. It was assumed that the failure to find the effect of object size on trunk kinematics in Saling et al.'s experiment was probably due to the object sizes used in their experiment (22 and 67 mm in diameter) not being different enough. In other words, the smaller object might not have been small enough to alter the trunk kinematics. Thus, the present experiment used smaller objects: 1 mm and 38 mm in diameter for small and large sizes, respectively.

Therefore, the present study varied movement amplitude, reach speed, and object size to test the hypothesis that aperture-closure distance is a stable variable controlled by the nervous system. If closure distance is a stable variable for prehensile actions, such invariance in closure distance should be observed regardless of changes in movement amplitude, reach speed, and object size. If this can be documented, it is likely that the closure distance plays an important role in coordinating reach-to-grasp actions. Such findings, thus, will provide further support for the notion that spatial regularity exists in the relation between the grasp and transport components during prehensile movements, that is, state-space control (Haggard and Wing 1995, 1998; Wang and Stelmach 1998a).

Materials and methods

Subjects

Eight healthy college students (four males and four females; age 20–26 years; all right handed) were recruited from the Arizona State University. Informed consent forms were obtained prior to their participation in the study. None of them had a previous history of neurological or visual problems.

Experimental paradigm

There were three factors tested in this experiment: movement amplitude (Near and Far), reach speed (Slow and Fast), and object size (Small and Large). Subjects were seated on a chair and asked to reach and grasp either of two objects, which was placed on a table directly in front of their trunk at a distance of either 50 or 70% of their maximum reaching distance from the starting position of the hand (i.e., approximately 30 and 42 cm, respectively). These movement amplitudes were determined such that the trunk could participate in reaching without any specific instruction. The maximum reaching distance was measured for each subject as the distance between the resting position of the hand and the position of the tip of the middle finger when the subject sat on the chair and reached with the index finger on the table as far as they could by extending both arms straight and bending the trunk forward. For the reach-speed and object-size manipulation, subjects were asked to reach for the object of either 1 or 38 mm in diameter at a comfortable speed (Slow) or as fast as possible (Fast). Thus, for each condition, subjects were seated and asked to reach and grasp the object as the object size, reach speed, and movement amplitude were varied according to the given condition. The height of the chair was adjusted for each subject so that the forearm was maintained near a horizontal level in a resting condition. Subjects were encouraged to move the arm and trunk directly towards the target without any rotation or lateral motion (see Fig. 5). Several practice trials were given before each condition, and 12 trials were collected for each condition.

Data analysis

The movements were recorded using an Optotrak 3D system with three independent cameras (Northern Digital, Waterloo, Ontario). Four infrared-emitting diode (IRED) markers were attached to each subject: index finger nail, thumb nail, metacarpal of the index finger (approximately two-thirds of the length from the distal end), and the middle of the sternum. Data were sampled at 100 Hz for 2 s, filtered through a second-order Butterworth digital filter with a cutoff frequency of 6 Hz.

Collected data were used to obtain kinematic measures for three different components: the grasp component, wrist component, and trunk component. For the grasp component, peak aperture, aperture duration (the time taken between the onset and offset of aperture), time to peak aperture (i.e., opening time), and closure time were calculated. In addition to these temporal measures, distance kinematic measures were considered, since a spatial pattern of coordination between the grasp and the transport components has been suggested (Haggard and Wing 1995; Saling et al. 1998; Wang and Stelmach 1998a). Using the data of the thumb marker as it traveled along an axis joining the home and the target positions, the length of hand-path trajectory was calculated between the onset of grip aperture and the peak aperture (i.e., opening distance) and also between the peak aperture and the contact with the object (i.e., closure distance) (Fig. 1). For the trunk component, trunk-movement duration (time taken between the onset and offset of trunk motion), peak velocity, and absolute and relative time to peak velocity were calculated. Regarding the wrist component, data from the wrist marker reflected not only the wrist motion, but also the trunk motion because the transport of the hand in these conditions was carried out by both the wrist and trunk motions. Therefore, the data on the wrist component were subdivided into two components: endpoint motion and arm motion. Kinematic data obtained directly from the wrist marker were used for the endpoint component. Arm motion relative to the trunk was measured by taking the difference between the wrist and trunk markers at every sample point. Movement duration, peak velocity, and absolute and relative time to peak velocity were calculated for each component.

For each dependent measure, a mean value was calculated for each subject for each condition and an ANOVA was performed using these mean values. In addition to this, Pearson correlation coefficients and partial correlations were calculated to examine the relationship of the trunk motion to the aperture and to the endpoint and arm motions. Pearson correlation coefficients were used to examine whether the trunk motion was temporally related to other body segment motions, while partial correlations were used to compare the relative contribution of the trunk and arm motions to the endpoint motion.
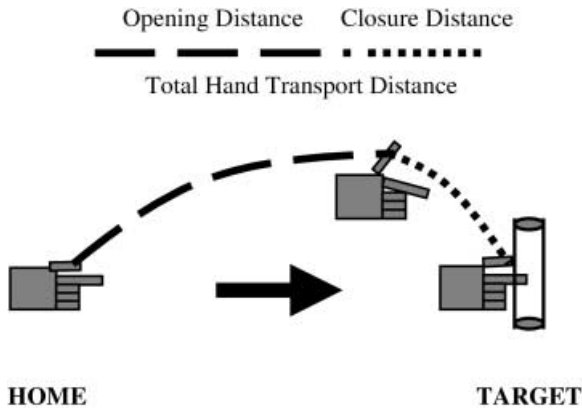
Fig. 1 Aperture-opening and -closure distance during a reaching motion

Results

Figure 2 shows a representative example of the changes in the grip aperture as well as the endpoint, arm-, and trunk-velocity profiles over time. Both the endpoint and the trunk velocity showed a relatively bell-shaped profile, although the arm-velocity profile was not always bell-shaped (i.e., it sometimes demonstrated a sinusoidal profile, showing negative values for a brief period – this was when the trunk moved faster than the wrist). There was no fixed pattern found in terms of the order between onsets of the endpoint and trunk motions. The trunk mo-tion tended to precede the endpoint motion for the majority of trials regardless of condition, although the time delay between the two onsets was small. As for the order between offsets, it is apparent that, in conditions where the large object was used, the endpoint motion stopped as the hand grasped the object while the trunk continued to move for approximately 100–200 ms. In conditions where the small object was used, however, both the endpoint and the trunk velocity reached zero before the hand grasped the object. With regard to the arm motion, its onset and offset occurred very closely in time to those of endpoint motion.

Temporal kinematics of the transport components

For the transport component, no significant interaction effect was found for any of the parameters, except that the Speed × Amplitude interaction was significant for the time to peak endpoint velocity ($P<0.05$). As the movement amplitude increased, the time to peak endpoint velocity increased significantly for the Slow condition, whereas it did not increase for the Fast condition. Although not statistically significant, the Speed × Amplitude interaction also almost reached the significance level for the time to peak velocity of the arm and the trunk, showing a trend similar to that of the time to peak endpoint velocity. Mean and standard-deviation values of selective parameters for each condition are presented in Table 1.

Fig. 2a–d Aperture and velocity profiles of endpoint, arm motion, and trunk motion for Speed and Size combinations. *Solid line* in the *upper panel* depicts the change in aperture; *broken line* in the *middle panel* endpoint velocity; *dotted line* trunk velocity; and *solid line* in the *lower panel* arm velocity. *Vertical solid line* represents the point in time when the fingers contacted the object; *vertical broken line* offset of endpoint motion; and *vertical dotted line* offset of trunk motion. (*Vertical broken* and *dotted lines* were overlapped in **b** and **d**.) Offset intervals between grasp and transport components were longer when the small object was used. Amplitude conditions are not shown in this figure since most temporal measures were not altered very much by the increase in Amplitude, except that the overall aperture and velocity profiles were lengthened over time. (Each *line* represents an individual trial from the same subject)
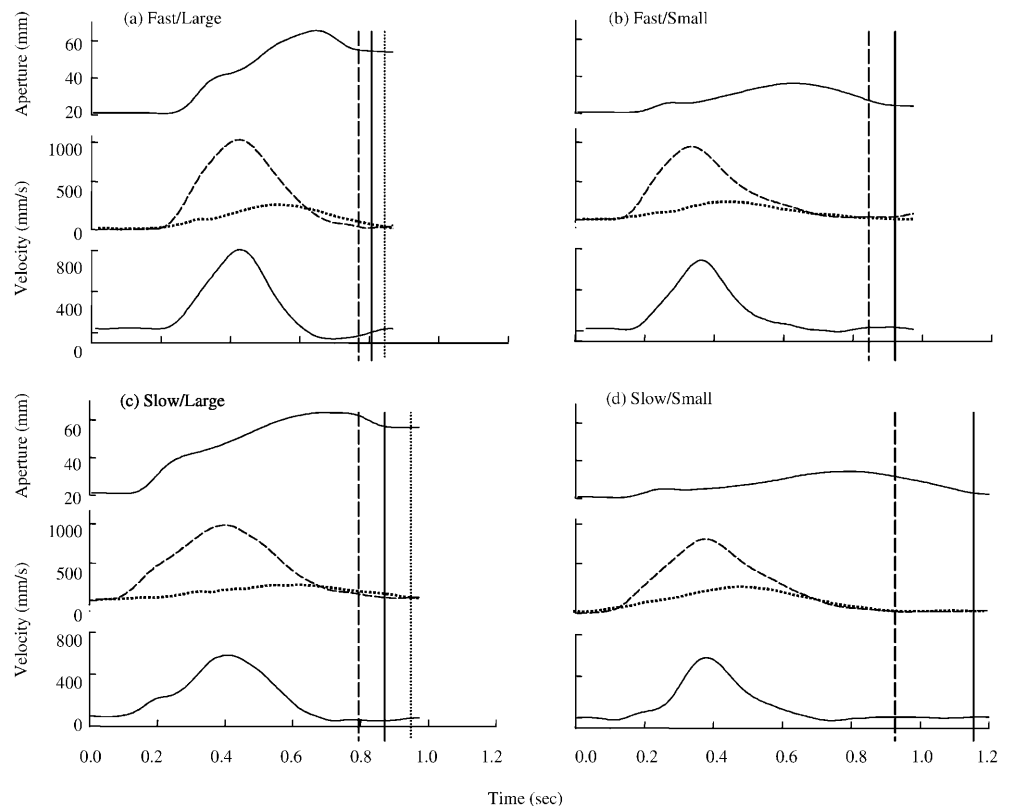
Table 1 Means (and standard deviations) of temporal parameters for different conditions

	Amplitude		Speed		Size	
	Near	Far	Fast	Slow	Small	Large
Endpoint motion						
Peak endpoint velocity[b] (mm/s)	573 (232)	483 (239)	428 (234)	628 (201)	527 (234)	529 (247)
Time to peak endpoint velocity[a, b] (ms)	33 (8)	37 (11)	26 (4)	44 (7)	35 (10)	35 (10)
Arm motion						
Peak arm velocity[b] (mm/s)	419 (166)	507 (162)	542 (152)	383 (147)	446 (163)	480 (174)
Time to peak arm velocity[b] (ms)	31 (9)	34 (11)	24 (5)	41 (6)	33 (10)	32 (10)
Trunk motion						
Peak trunk velocity[b] (mm/s)	302 (133)	518 (143)	499 (166)	321 (136)	417 (176)	403 (176)
Time to peak trunk velocity[a, b] (ms)	47 (11)	52 (13)	39 (4)	60 (7)	50 (12)	49 (13)
Aperture formation						
Peak aperture[c] (mm)	48 (12)	48 (13)	49 (12)	47 (13)	37 (4)	58 (8)
Time to peak aperture[a, b] (ms)	56 (21)	69 (23)	47 (11)	78 (21)	64 (23)	61 (23)
Closure time (ms)[c]	29 (15)	29 (17)	26 (17)	31 (15)	37 (19)	20 (5)

[a]Amplitude significant, [b]speed significant, [c]size significant (at $P<0.05$)

As for the main effects, Size was significant for the movement duration and the relative time to peak velocity of the endpoint, arm, and trunk motions ($P<0.05$). The movement duration of all three transport components was longer for the small object, while the relative time to peak velocity of those three components became shorter for the small object. Speed was significant for the peak velocity, movement duration, and relative time to peak velocity of the endpoint, arm, and trunk motions ($P<0.05$ for relative time variables; $P<0.001$ for the other variables). The peak velocity of all the three components was higher for the Fast condition, whereas movement duration and relative time to peak velocity were longer for the Slow condition. Amplitude was significant for the movement duration of all the three components ($P<0.05$ for the trunk; $P<0.001$ for the endpoint and arm), but not for the relative time to peak velocity of any components. With regard to the time to peak velocity, Speed was significant for all the three components ($P<0.001$), while Amplitude was significant for the endpoint and trunk motions ($P<0.01$). As mentioned earlier, however, the Speed × Amplitude interaction almost reached the significance level for the time to peak velocity of all three components, indicating that as Amplitude increased the time to peak velocity in the Fast condition did not increase as much as it did in the Slow condition. Since the relative time variables are of main interest in this study, changes in the relative time to peak velocity of the endpoint, arm, and trunk motions across conditions are shown in Fig. 3.

Temporal kinematics of the grasp component

For the grasp component, no significant interaction effect was found for any of the temporal parameters. Mean and standard deviation values of selective parameters for each condition are presented in Table 1. As for the main effects, Size was significant for the peak aperture ($P<0.001$), showing that it was smaller for the small object than for the large object. Aperture duration, closure time, and relative time to peak aperture were also influenced by the size of the object ($P<0.001$ for all parameters), showing that the aperture duration and closure time were longer for the smaller object, while the relative time to peak aperture was longer for the large object. Speed was significant for the aperture duration and the absolute and relative time to peak aperture ($P<0.05$ for all parameters), showing that all these time measures were shorter for the Fast condition. Amplitude was significant for the aperture duration and the time to peak aperture ($P<0.01$ for both), showing that they both increased as the movement amplitude increased, although it was not significant for the relative time to peak aperture. Changes in the relative time to peak aperture across conditions are shown in Fig. 3.

Spatial coordination between the grasp and transport components

In order to examine the spatial coordination between the two components, the relationship between the aperture opening and closure distances was examined. Scatter plots were made to graphically demonstrate the relationship between the opening distance and the overall hand transport distance as well as between the closure distance and the overall hand transport distance. In general, there was a trend that opening distance increased as the overall hand-transport distance increased while the closure distance did not (Fig. 4a). Although the majority of data points fit in such a trend, it also appeared that there were some data points that did not correspond to this trend. A closer examination of the relationship between

Fig. 3 Changes in relative time parameters in response to changing object size and reach speed. (* indicates that this comparison was found to be statistically significant at $P<0.05$; ** significant at $P<0.01$; movement amplitude was not significant for any of these parameters)
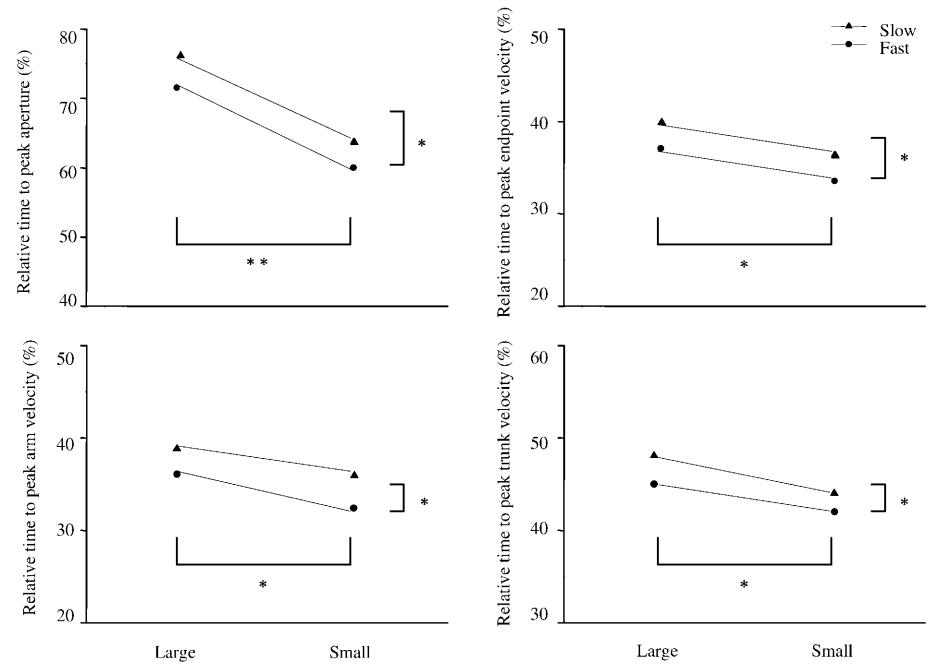
the opening/closure distance and the overall distance within each subject revealed that a very clear trend was observed in six subjects, whereas it was not so robust in two subjects. We, thus, plotted the changes in the opening/closure distance as a function of the overall distance again, with the data of the two subjects separated from those of the other subjects. It appeared that the closure distance was quite invariant, regardless of the overall hand-transport distance in these six subjects (Fig. 4b). Such a trend was also observed in the remaining two subjects, although it was not as apparent as in the other six subjects (Fig. 4c).

Spatial plots for the endpoint and trunk motions are shown in Fig. 5, which illustrates the movement trajectories traveled by the endpoint and trunk markers. From the figure, it is apparent that the change in movement amplitude significantly altered both the endpoint and trunk trajectories (approximately 50 cm for the Far condition and 30 cm for the Near; 25 cm for the Far and 15 cm for the Near, respectively). It also appears that the trunk moved directly towards the target without any rotation or lateral motion (top view), as instructed. Although the trunk did not move towards the target horizontally (side view), the extent to which the trunk descended as it moved forward was minimal (approximately 4 cm for the Far condition and 2 cm for the Near, respectively). Analysis of variance revealed that the opening distance was significantly affected by both Amplitude and Speed ($P<0.001$ and $P<0.05$, respectively), while the closure distance was not altered by any of the three factors. When the data from the six subjects only were considered, however, the opening distance was only affected by Amplitude ($P<0.001$), while the results with respect to the closure distance remained the same. Figure 6 illustrates the changes in the opening and closure distances

across different conditions. As can be seen in Table 2 (data from the six subjects), the opening distance changed from 285 to 469 mm (approximately 65% increase) as Amplitude changed, although the change in closure distance was minimal (approximately 10%).

Regression analyses were conducted to examine whether the invariance in closure distance was observed under different conditions within each subject. Thus, the standardized regression coefficients (β), which reflect the amount of change in opening and closure distance resulting from a one-standard-deviation change in the total hand transport distance, were calculated for the four Speed × Amplitude conditions for each subject (Speed and Amplitude only were found significant for opening distance). Results showed that, for the opening distance, 28 βs among 32 (four βs per subject; mean of 0.80; range from 0.20 to 1.00) were found significantly greater than zero ($P<0.05$), whereas seven βs among 32 (mean of 0.22; range from 0.00 to 0.67) were found significantly greater than zero for the closure distance. (Regression analyses using a statistical computer program SPSS, version 9, for Windows automatically provided the significance levels of β.) Among the four βs of opening distance that were not greater than zero, however, three βs came from the two subjects whose data points were shown in Fig. 4c; similarly, among the seven βs of closure distance that were greater than zero, two βs came from those two subjects. This result indicates that most βs were significantly greater than zero for the opening distance, although not for the closure distance, suggesting that the opening distance increased systematically with the increase in the total hand-transport distance although the closure distance did not. These coefficients were further subjected to an ANOVA as a standard dependent variable (assumptions for an ANOVA were
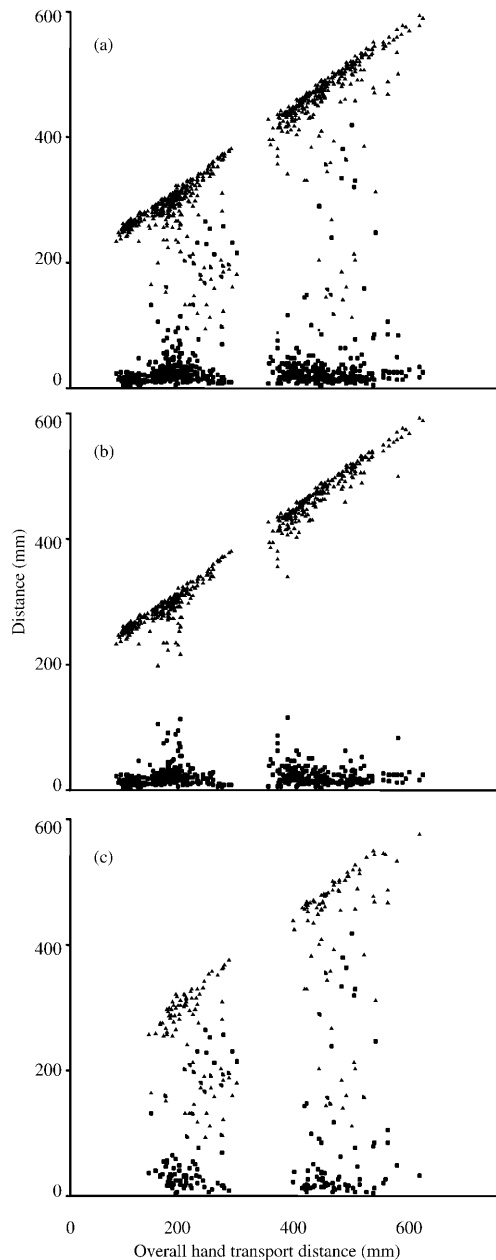
Fig. 4a–c Scatter plots showing the changes in opening (▲)/closure (■) distance as a function of total hand-transport distance. **a** Data from all subjects. **b** Data from the six subjects who demonstrated constant closure distance. **c** Data from the two subjects who did not clearly show such a trend. (Although the two subjects behaved quite differently from the other six subjects with respect to the spatial aspect, their performance with respect to the temporal aspect was not significantly different from the other subjects)

met), which showed no significant effect of Amplitude, Speed, or their interaction for either opening or closure distance. Effect size, o^2, was estimated for each effect: for opening distance o^2 was –0.01, –0.01, and –0.03; for closure distance o^2 was –0.02, –0.02, and –0.02 for Amplitude, Speed, and Amplitude by Speed interaction, respectively. Therefore, these data indicate that the closure distance remained invariant as the hand transport-distance changed and that the amount of change in both opening and closure distance was not statistically different across conditions, which suggests an invariance in closure distance under different conditions where the temporal and spatial features of the transport vary.

Temporal relationship
of the trunk motion to other components

Pearson correlation coefficients were calculated to examine whether the trunk motion was correlated with the grasp aperture as well as with the arm and endpoint motions within each subject. It was found that the correlation coefficients between any two motions were statistically significant for every subject ($P<0.01$). The time to peak trunk velocity was significantly correlated with the time to peak aperture for every subject (mean of 0.71; range from 0.37 to 0.83). In addition, the time to peak trunk velocity was significantly correlated with the time to peak endpoint velocity (mean of 0.86; range from 0.75 to 0.95) and also with the time to peak arm velocity (mean of 0.80; range from 0.68 to 0.91). These correlation data indicate that trunk motion was temporally coupled not only with the endpoint and arm motions, but also with the aperture formation. In addition, the time to peak endpoint velocity was significantly correlated with the time to peak aperture (mean of 0.71; range from 0.39 to 0.84) and with the time to peak arm velocity (mean of 0.88; range from 0.79 to 0.94). The time to peak arm velocity was also significantly correlated with the time to peak aperture (mean of 0.65; range from 0.34 to 0.85). Figure 7 shows the relationships among those parameters.

Contribution of the trunk
to the transport component

The relative contribution of the trunk and the arm motions to the endpoint motion was estimated by calculating, within each subject, the partial correlation between the peak trunk velocity and the peak endpoint velocity, with the peak arm velocity partialled out, as well as the partial correlation between the peak arm velocity and the peak endpoint velocity, with the peak trunk velocity partialled out. The extent to which the arm and trunk participate in, or contribute to, the reaching movement changed in most subjects as reach speed changed, showing that as reach speed increased the partial correlation between the peak trunk and endpoint velocity decreased, whereas the partial correlation between the peak arm and endpoint velocity increased (Table 3). The partial correlations data were subjected to a Wilcoxon matched-pair signed-ranks test, which is a powerful nonparametric test for comparing dependent groups. The results showed that, with the increase in reach speed, the partial correlation between the peak arm and endpoint velocity increased significantly ($P<0.05$), although the partial cor-

Fig. 5 Spatial plots showing the trajectories of the endpoint and trunk motions. Reaching motion to the target involved the natural flexion of the hip and extension of the shoulder and elbow joints. *Upper panel* depicts the endpoint and trunk trajectories for the far-amplitude condition; *lower panel* depicts those for the near condition. (Each *line* represents an individual trial from the same subject)
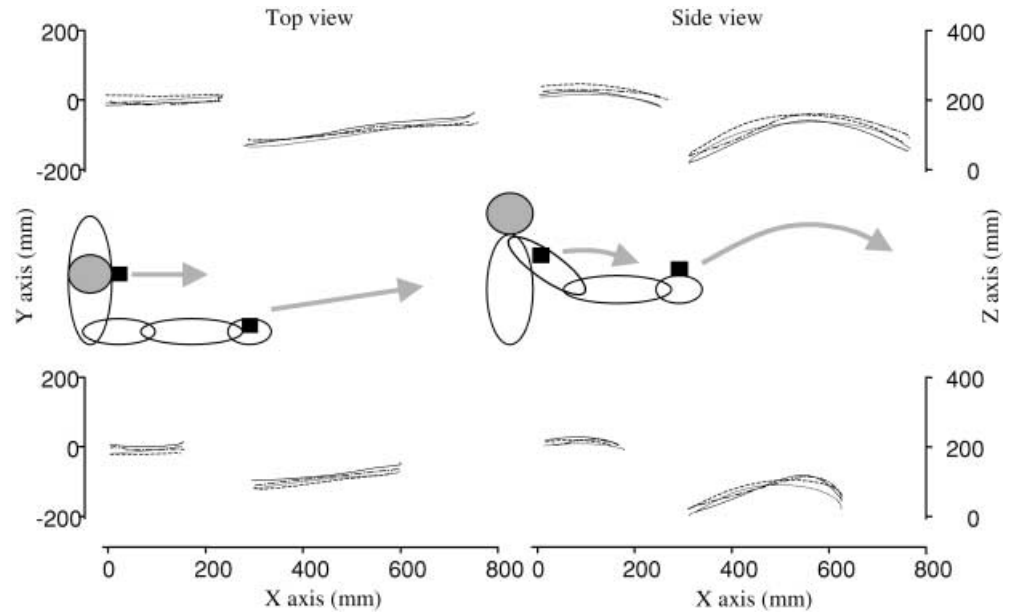

Table 2 Means (and standard deviations) of aperture opening and closure distances

	Amplitude		Speed		Size	
	Near	Far	Fast	Slow	Small	Large
Eight subjects						
Opening distance[a, b] (mm)	281 (40)	461 (55)	358 (101)	384 (104)	371 (110)	371 (96)
Closure distance (mm)	34 (33)	36 (46)	41 (48)	29 (29)	43 (53)	27 (18)
Six subjects						
Opening distance[a] (mm)	285 (41)	469 (41)	371 (101)	383 (104)	387 (108)	368 (96)
Closure distance (mm)	21 (13)	23 (9)	23 (9)	20 (13)	20 (9)	23 (13)

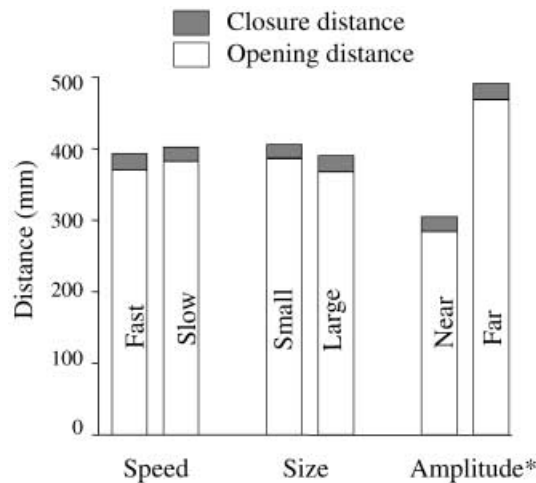[a]Amplitude significant (at $P<0.001$), [b]speed significant (at $P<0.05$)

Fig. 6 Changes in opening/closure distance across Amplitude, Size, and Speed conditions. (Data based on six subjects; * significant at $P<0.001$)

Table 3 Partial correlations between peak-velocity parameters

Subject	Slow		Fast	
	Trunk vs. endpoint	Arm vs. endpoint	Trunk vs. endpoint	Arm vs. endpoint
1	0.33*	0.86*	0.54*	0.97*
2	0.33*	0.74*	0.24	0.66*
3	0.63*	0.57*	0.35*	0.93*
4	0.49*	0.94*	0.29	0.97*
5	0.36*	0.65*	0.09	0.68*
6	0.48*	0.91*	0.04	0.96*
7	0.41*	0.72*	0.54*	0.85*
8	0.73*	0.63*	0.43*	0.87*

*Significantly different from zero at $P<0.05$

relation between the peak trunk and endpoint velocity did not decrease significantly. However, the change in the partial correlation between the peak trunk and endpoint velocity was found to be statistically significant ($P<0.05$) when one of the two subjects, who showed an increase in the partial correlation rather than a decrease (subject no. 1 in Table 3), was removed. Therefore, it appears that, as the temporal constraints are increased, the relative contribution of arm motion to the endpoint motion is increased, although that of trunk motion is decreased. The changes in the object size and the movement amplitude did not appear to change the relative contribution of the trunk and the arm motions to the endpoint motion, since no systematic changes in partial correlation were observed across subjects.
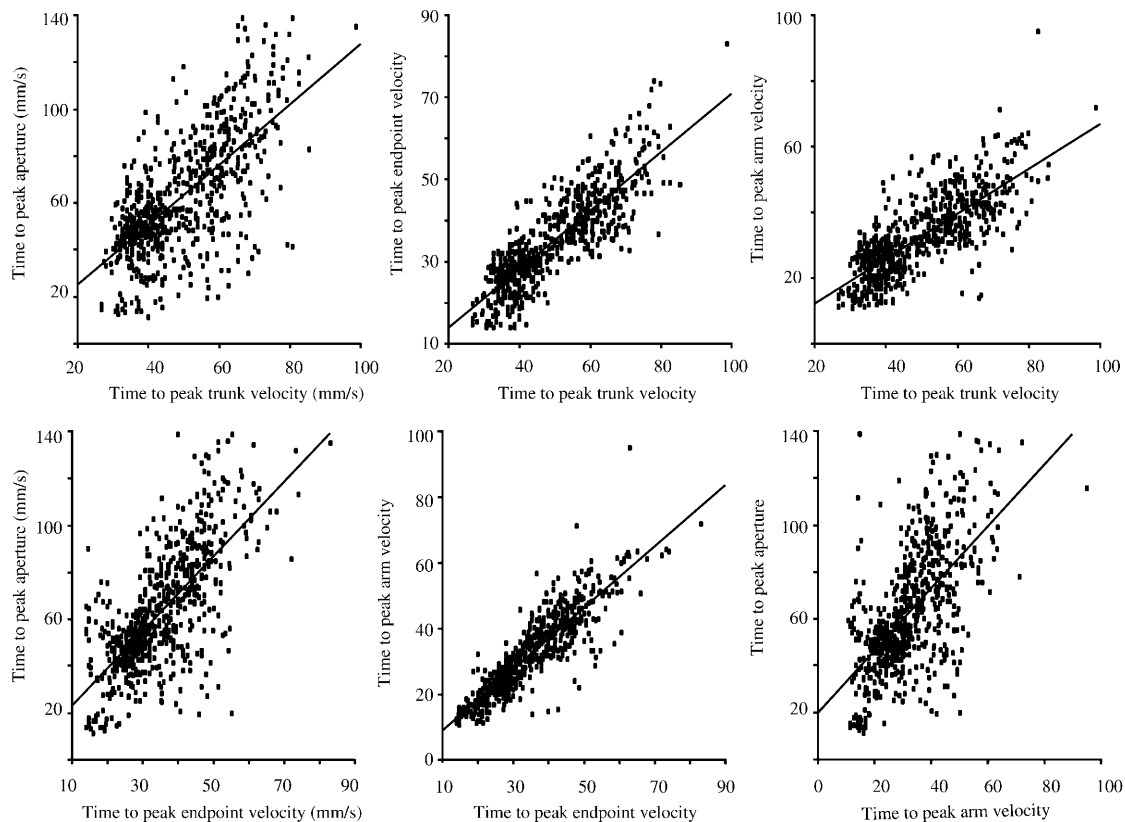
Fig. 7 Scatter plots showing the relations among the grasp formation, endpoint, arm motion, and trunk motion

Discussion

It has been suggested that prehensile movements utilize state-space control; that is, there is spatial regularity between the grasp and transport components during prehensile action (Haggard and Wing 1995, 1998). This notion has been supported by our previous experiment (Wang and Stelmach 1998a) that manipulated the involvement and coordination of body segments during the reach to the object (i.e., arm only, trunk only, combinations of both). The present experiment confirmed our previous findings, demonstrating that the aperture-opening distance increased systematically as the total hand-transport distance increased, whereas the aperture-closure distance did not. Until this experiment, invariance in closure distance was only observed for one movement amplitude; thus, the present experiment extends the previous findings by showing that closure distance remained constant across two different amplitudes. These findings also extend Saling et al.'s (1998) finding that closure distance was relatively constant regardless of a change in the total hand-transport distance when altered by the presence of an obstacle that required the elevation of the arm on the way to the target object. In their study, the trunk was not involved in reaching, but the total hand-transport distance was lengthened without changing the position of the target object. At this point, it is important to note that the stability in closure distance was observed regardless of whether the coordination between the grasp and transport components was influenced by the involvement of body segments (i.e., arm only, trunk only, or both) or by the changes in movement amplitude, reach speed, and object size. This suggests that the grasp component is specified independently from the transport component (Jeannerod 1992; Lemon et al. 1995; Timman et al. 1996), at least in terms of spatial control, and that the closure distance is a stable variable controlled by the nervous system for prehensile action.

With regard to trunk motion, our data showed that it was temporally coupled to both arm motion and aperture formation. The time to peak trunk velocity was significantly correlated with both the time to peak arm velocity and the time to peak aperture. In addition, the trunk-velocity profile became asymmetrical, i.e., the relative time to peak trunk velocity changed significantly as the object size became smaller. Saling et al. (1996) also examined the effect of object size on the trunk motion, although they failed to show the tight relationship between trunk motion and aperture formation. It may be due to the fact that the two object sizes they used (22 mm and 67 mm in diameter) were not different enough, i.e., the smaller object may not have been small enough to alter the trunk kinematics. When a smaller object (1 mm in diameter) was used in the present study, however, the trunk kinematics were altered, indicating that trunk motion is closely linked to the aperture formation. Thus, it is suggested that, when the trunk becomes involved, trunk mo-

tion is coupled with the arm motion to accomplish the goal of the transport component as well as with the grasp component, probably in a manner similar to which the arm is related to the grasp component, to preserve the coordination between the grasp and transport components.

Saling et al. (1996) suggested that the trunk and arm are controlled separately based on the finding that no fixed onset-movement pattern was observed, even within a subject (i.e., reaching movement was initiated by the trunk in 58% of trials, by the arm in 18%, and unclear in remaining trials). This experiment found similar results with regard to the initiation of movement and further found that the offsets of the arm and trunk motions were differentially affected by the change in object size (i.e., when reaching for the large object, the trunk stopped moving much later than the arm did, although when reaching for the small one, they stopped very closely in time). These findings indicate that the arm and the trunk are controlled independently. This, however, does not necessarily mean that the two are completely independent. Our data also showed that the movement duration and the relative time to peak velocity of both the arm and trunk decreased when the object size decreased and also when the reach speed increased. In other words, the movement duration and relative time to peak velocity of the arm and trunk scaled together with changes in temporal and spatial constraints, suggesting that the arm and the trunk, which make up the transport component, are governed by one synergy. Thus, considering these findings together, it is rather suggested that the arm and trunk are controlled separately and, yet, are regulated by some form of higher-order neuromotor organization.

The interpretation that the two components involved in reaching are governed by one neuromotor synergy is in agreement with the idea that there are two neuromotor synergies involved in reaching motions: one that controls arm movement to the target (i.e., reaching synergy) and the other that coordinates the arm and trunk motions without affecting the endpoint trajectory (Ma and Feldman 1995; Pigeon and Feldman 1998). The notion of the latter, compensatory, neuromotor synergy is supported by our study since our data suggest that arm and trunk motions are coordinated together as a functional unit during reaching. This notion is also supported by a set of data that examined the synchronization pattern of arm and trunk motions during reaching tasks between different age groups of children (Wann et al. 1998). They compared four groups of children (i.e., 3–4 year olds, 5–6 year olds, 7–12 year olds, 7–12 year olds with developmental coordination disorder) and found that the time delay between the onsets of the arm and trunk motions was much longer in the youngest children group and the group with developmental coordination disorder (DCD) than in the other two groups. They also found that the endpoint velocity profile was less symmetrical in the youngest group and the group with DCD, indicating poor coordination of the arm and trunk motions in these children. This finding suggests that the optimal coordi-

nation between the arm and trunk during a reaching motion is accomplished naturally in children without neural deficits, thereby suggesting the development of a compensatory neuromotor synergy with age.

It has been well documented that the grasp and transport (i.e., endpoint motion without the trunk) components are temporally coupled (e.g., Jeannerod 1981, 1984; Marteniuk et al. 1990; Hoff and Arbib 1993; Bootsma et al. 1994; Timmann et al. 1996). Our findings add to the literature by suggesting that, during trunk-assisted prehension, all the movement components involved (i.e., grasping hand, arm, trunk) are controlled separately and yet are coordinated through temporal and/or spatial domains, which further suggests the involvement of a hierarchical control of neuromotor synergies in prehension (Jakobson and Goodale 1991; Wang and Stelmach 1998a). It appears that the arm and trunk motions, which are governed by separate neuromotor synergies, are functionally unitized by a higher-order synergy as an overall transport component to accomplish the goal of reaching; in turn, this overall transport component is coordinated with the grasp component by another higher-order synergy to accomplish the global goal of reaching and grasping.

This idea can be closely linked to some other findings. Tresilian and Stelmach (1997) demonstrated that the development of the grasp component and its adaptation to changes in object size were very similar, regardless of whether the object was grasped by the thumb and index finger (i.e., unimanual) or by two index fingers (i.e., bimanual), suggesting that there is an effector-independent level of organization governing the coordination of the reach-to-grasp movements. This hypothesis is further supported by a more recent study (Wang and Stelmach 1998b), in which the grasp and transport components were anatomically separated by having the subjects grasp with one stabilized hand an object that was delivered by the other hand (i.e., passing motion). When the data from the passing condition were compared with those from a typical reach-to-grasp condition (i.e., reaching motion), the temporal relationship between the grasp and transport components was similar across conditions. It was also found that the closure distance was very constant regardless of conditions. Thus, these findings suggest that the two components maintain their temporal and spatial relationships no matter how the grip was carried out (i.e., unimanual vs. bimanual, reaching vs. passing), which provides support for the notion of an effector-independent level of organization responsible for coordination between the two components. This notion is also supported by neurophysiological data that, for example, activities of some neurons in the premotor area were related more with an action goal (i.e., similar activities during the grasping of food with either the hand or mouth) than with the effectors that are used for different action goals (i.e., different activities during the grasping and pointing-pushing movement using the hand) (Rizzolatti et al. 1988). Taken all the findings together, therefore, it is suggested that the nervous system utilizes

individual neuromotor synergies to control the movement components involved in prehensile action and that, no matter which effectors or body segments are used for the prehension tasks, the nervous system coordinates in a hierarchical manner the neuromotor synergies responsible for the control of the available effectors to accomplish the goal of movement. Such control processes may reflect the way in which the nervous system deals with multiple body segments in controlling complex movements.

References

Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaal FTJM (1994) The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. Exp Brain Res 98:535–541

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

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

Haggard P, Wing A (1998) Coordination of hand aperture with the spatial path of hand transport. Exp Brain Res 118:286–292

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

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

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

Jeannerod M (1992) Coordination mechanisms in prehension movements. In: Stelmach GE, Requin J (eds) Tutorials in motor behavior II. Elsevier North-Holland, Amsterdam, pp 265–285

Jeannerod M, Arbib MA, Rizzolatti G, Sakata H (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci 18:314–320

Kaminski TR, Bock C, Gentile AM (1995) The coordination between trunk and arm motion during pointing movements. Exp Brain Res 106:457–466

Kudoh N, Hattori M, Numata N, Maruyama K (1997) An analysis of spatiotemporal variability during prehension movements: effects of object size and distance. Exp Brain Res 117:457–464

Langolf GD, Chaffin DB, Foulke JA (1976) An investigation of Fitt's Law using a wide range of movement amplitudes. J Mot Behav 8:113–128

Lawrence DG, Kuypers HGJM (1968) The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. Brain 91:1–14

Lemon RN, Johansson RS, Westling G (1995) Corticospinal control during reach, grasp, and precision lift in man. J Neurosci 15:6145–6156

Ma S, Feldman AG (1995) Two functional different synergies during arm reaching movements involving the trunk. J Neurophysiol 73:2120–2122

Marteniuk RG, Leavitt JL, MacKenzie CL, Athenes S (1990) Functional relationships between grasp and transport components in a prehension task. Hum Mov Sci 9:149–176

Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extra-personal space. J Neurophysiol 38:871–908

Pigeon P, Feldman AG (1998) Compensatory arm-trunk coordination inpointing movements is preserved in the absence of visual feedback. Brain Res 802:274–280

Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M (1988) Functional organization of inferior area 6 in the macaque monkey. Exp Brain Res 71:491–507

Saling M, Stelmach GE, Mescheriakov S, Berger M (1996) Prehension with trunk assisted reaching. Behav Brain Res 80:153–162

Saling M, Alberts J, Stelmach GE, Bloedel JR (1998) Reach-to-grasp movements during obstacle avoidance. Exp Brain Res 118:251–258

Seidler RD, Stelmach GE (2000) Trunk assisted prehension: specification of body segments with imposed temporal constraints. J Mot Behav (in press)

Smeets JBJ, Brenner E (1999) A new view on grasping. Mot Control 3:237–271

Timmann D, Stelmach GE, Bloedel JR (1996) Grasping component alterations and limb transport. Exp Brain Res 108:486–495

Tresilian JR, Stelmach GE (1997) Common organization for unimanual and bimanual reach-to-grasp tasks. Exp Brain Res 115:283–299

Tyler AE, Hasan Z (1995) Qualitative discrepancies between trunk muscle activity and dynamic postural requirements at the initiation of reaching movements performed while sitting. Exp Brain Res 107:87–95

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

Wang J, Stelmach GE (1998a) Coordination among the body segments during reach-to-grasp action involving the trunk. Exp Brain Res 123:346–350

Wang J, Stelmach GE (1998b) Spatial coordination of a prehensile action during reaching and passing movements. Soc Neurosci Abst 24:2110

Wann JP, Mon-Williams M, Carson RG (1998) Assessing manual control in children with coordination difficulties. In: Connolly KJ (ed) The psychobiology of the hand. MacKeith Press, London, pp 213–229