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Contributions of Gait and Trunk Movements to Prehension: Perspectives From World- and Body-Centered Coordinates

Ronald G. Marteniuk and Christopher P. Bertram

The present paper reviews a series of prehension experiments recently conducted at Simon Fraser University's Human Motor Systems Laboratory, and attempts to place them into the larger context of multi-segmental control theory. Two related lines of experiments are reported: (a) experiments involving prehension during walking, and (b) experiments involving trunk-assisted reaching. Three-dimensional analyses of movements were performed via both world- and body-centered coordinates. Our results are supportive of the idea that both types of tasks are carried out using task-specific synergies. Furthermore, we assert that the actions of these synergies are comprised of variable contributions of different movement systems and result in smooth, world-centered endpoint trajectories. We show evidence that this "motor equivalence" is the result of increasing the complexity of a given task. Finally, the implications of the present findings on prevailing motor control theory are discussed in terms of the theoretical mechanisms underlying the coordination of the transport and grasp components of prehension.

Key Words: prehension, gait, coordination, motor equivalence, spatial coordinates

Introduction

In the most general terms, the study of prehension is the study of how the hand reaches for and grasps objects. Realistically though, prehension can involve anything from a person simply reaching for a pen to a baseball player sprawling across an infield in pursuit of a line drive. Even reaching for an object remotely via an instrument (e.g., Ibbotson, MacKenzie, & Mason, 1999) is essentially an act of prehension. Although researchers have been investigating prehension since the 1930s (e.g., Hooker, 1938), the bulk of the work on the subject has come in the years since Jeannerod's influential papers in 1981 and 1984. In the 20-odd years

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The authors are with the School of Kinesiology at Simon Fraser University, Burnaby, Canada V5A 1S6.

since Jeannerod's original work, we have come to learn a great deal about the control processes underlying human prehension. For example, it is widely accepted that the act of prehension is comprised of the two separate, yet temporally coupled, sub-components of the transport and the grasp.

Many of the experimental paradigms adopted to study the hand have employed movement limiting devices such as chest straps (e.g., Gentilucci, Chieffi, Scarpa, & Castiello, 1992) and headrests (e.g., Jeannerod, 1984) in an attempt reduce the prehensile act to a movement involving only the hand and arm. Although such reductionist approaches can be beneficial, it is nonetheless important to realize that in natural settings the hand seldom, if ever, moves in isolation from the rest of the body. One might ask whether the results (and the underlying control processes they imply) obtained from these "controlled" situations can be generalized to prehension as it occurs in our everyday lives. Ideally then, it could be suggested that the optimal way to observe human movement is to allow the body and its many degrees of freedom to move naturally in experimental settings. Of course the downside to such an approach is that it is often a troublesome and impractical matter to measure more natural movements in a precise way.

Recently in our lab, we have designed a series of experiments with the dual purpose of minimizing unnatural movement constraints and attempting to meaningfully quantify the relationships between the movement segments. Underlying much of this work are two issues, one theoretical and the other methodological. The theoretical issue deals with the notion of motor equivalence, which has been described as variable means to invariant ends (Abbs & Cole, 1987; Bernstein, 1967; Lashley, 1930). One way to identify motor equivalence is to observe the relatively variable component submovements that lead to relatively invariant overall movement performance. Our view is that the prehension studies that have artificially restricted the movement of other body parts during the prehension act may have missed the contribution from these additional degrees of freedom. We suspect that the picture of how prehension is controlled may be enriched by asking how these other degrees of freedom enter into the coordination of prehension acts. As well, it may help us to extend our current theoretical formulations of prehension, which are largely based on the seminal work of Jeannerod (1981, 1984).

Quantifying the absolute movement of the various body segments is an important step in understanding movement coordination. However, we have come to realize that additional, perhaps more important, information can be gained from observing how the individual segments move in relation to one another. Toward that end, a certain methodological framework underlies much of the work we wish to review in this paper. This approach is directly related to our desire to ascertain if, during a prehension task, the hand exhibits relatively invariant spatial trajectories while the other degrees of freedom related to torso and leg movements would vary in their contributions to the hand in order to preserve the consistent end-point trajectories. To accomplish this, we have employed two methods for determining the movement of the hand during a prehension task. We used an OPTOTRAK (Northern Digital, Waterloo) camera system and two frames of reference to analyze the resulting kinematics: (a) a traditional, world-centered frame of reference; and (b) a body-centered frame of reference (Bertram, Mason, Mackey, MacKenzie, & Marteniuk, 2000). The first method is one used by most, if not all, studies on prehension where hand movements have been quantified by describing the movements in x, y, and z coordinates relative to the workspace of the task (also called world- or room-centered coordinates). Here, the origin of each of the axes are usually arbitrarily assigned some location on the table upon which the objects to be grasped are placed. The other view of the hand, which we call body-centered, uses the torso as a dynamic frame of reference. Here, an infrared emitting diode (IRED) is placed on the torso, and the distance between this IRED and the IRED on the wrist is recorded for each frame of movement. This effectively eliminates the dynamics of the torso (including any contribution from gait) from the dynamics of the hand. In effect, it allows viewing the movement of the hand independently from the movements of the rest of the body.

We will take the above issues now and imbed them into the review of two separate but related types of experiments. The first series of experiments deals with the issue of coordination between upper and lower limbs during pointing and prehension tasks (Figure 1A). Following this, we will look specifically at torso and arm coordination when subjects are seated while reaching for and grasping objects placed on a table (Figure 1B).

We will attempt to bridge these two related lines of literature on the grounds that both types of multiarticulate movements employ task-specific synergies to aid in the completion of the task goal. Furthermore, we will discuss how the phenomenon of motor equivalence clearly emerges in response to increases in task complexity.

Combining Locomotion With Upper Limb Tasks

We begin our look at the issue of motor equivalence and prehension by noting that, to date, the literature on combined upper and lower limb activities is minimal. Moreover, the work that has been done has focused primarily on such issues as the role of the arm swing during locomotion both functionally (e.g., Jackson, Joseph, & Wyard, 1983) and from an evolutionary perspective (e.g., Georgopoulos & Grillner, 1989). One experiment that looked specifically at combining an upper

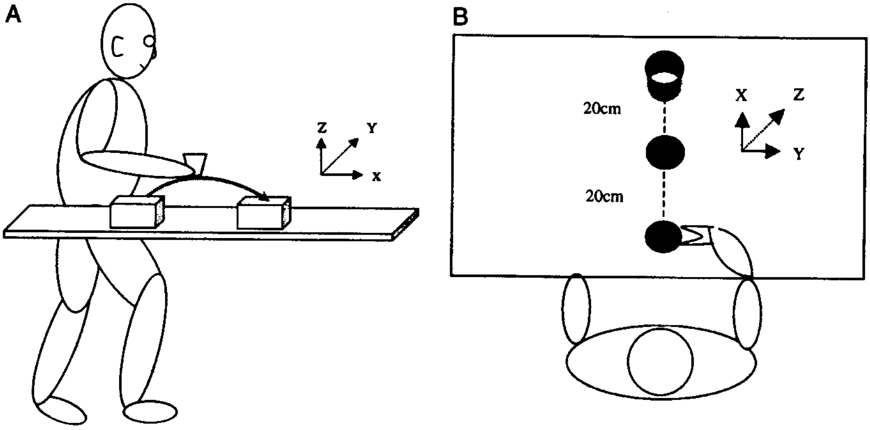

Figure 1 — The upper panel (A) depicts a typical experimental set-up for combined upper and lower extremity tasks described in this paper. In this case, the subject has lifted a cup of water from a starting position and is transporting it to a target located at a distance anterior to the start. Figure 1B depicts an overhead view of a typical experimental set-up for a trunk-assisted prehension task. In this case, the subject is seated at a table, poised to reach for a cup located beyond arm's length.

limb task with locomotion was conducted by Carnahan, McFayden, Cockell, and Halverson (1996). Their experiment involved having subjects walk past a table and grasp one of two objects (a pencil or an aluminum can). These results were compared to other task conditions in which subjects walked without performing grasping movements, and to conditions in which subjects merely stood next to the table and grasped objects. The authors noted that when subjects were asked to perform the prehension tasks while walking, their gait kinematics remained surprisingly consistent across all of the walking conditions. More specifically, no differences were found in stride time, stance time, swing time, or joint angles as a result of grasping either the large or the small object while walking. However, the arm was found to reach greater peak velocities (during the reach) when walking as compared to reaching while standing, indicating that the reach was superimposed onto the normal swing of the arm. These results led the authors to postulate the existence of a movement hierarchy, whereby the stability of gait supercedes the stability of prehension (Carnahan et al., 1996).

Some pilot data from our lab suggested that the above work might not be generalizable to other prehension conditions employing simultaneous locomotion. Thus, to systematically approach the issue of the relationship between prehension and gait, we (Marteniuk, Ivens, & Bertram, 2000) began by using a Fitts task, where subjects performed an aiming movement both while standing and while

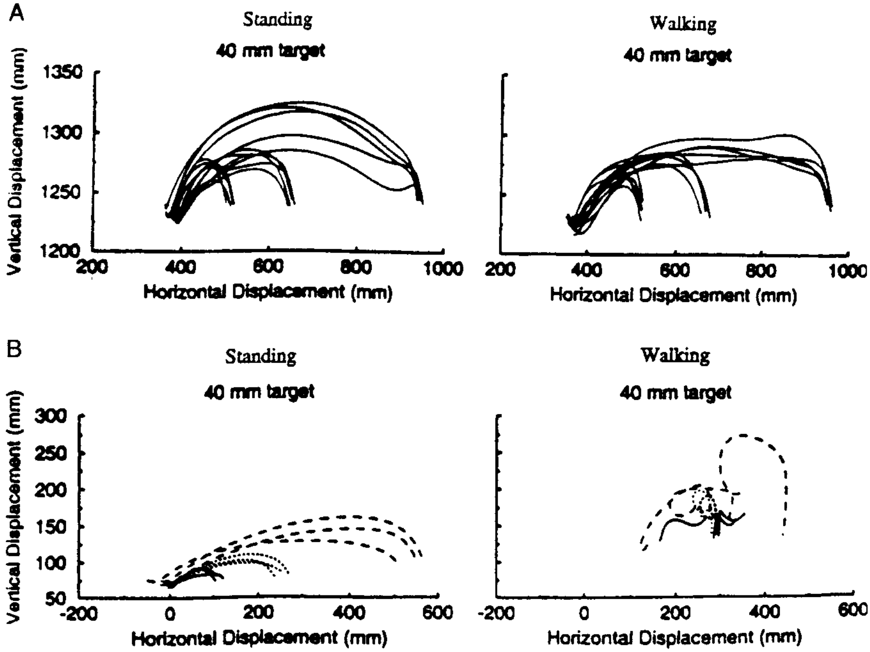

Figure 2 — Spatial plots involving the forward (horizontal) and the vertical displacements of the hand viewed from a fixed, world-centered frame of reference and also from a body-centered frame of reference. Figure 2A depicts data from a typical subject in both the standing and walking conditions, as viewed from a world-centered coordinate system. Figure 2B depicts data from the same subject during both the standing and walking conditions, as viewed from a body-centered coordinate system.

walking past targets of varying sizes and amplitudes. Analysis of hand and torso kinematics yielded several interesting findings.

Figures 2A and 2B present typical data that contrast the spatial path of the hand during the standing and walking conditions for both the world- and body-centered frames of reference. When considering the trajectory of the end effector compared to a fixed, world-centered frame of reference (Figure 2A), it was difficult to distinguish between pointing movements that were performed while walking from those performed while standing. In both conditions, the familiar skewed bell-shaped trajectories were seen, showing the hand moving forward (i.e., away from the torso) while moving first up and then down. However, when the movement of the hand was considered relative to the subject's torso as a moving frame of reference (Figure 2B) a dramatically different picture emerged. In the standing condition, the familiar skewed bell-shaped trajectories were again seen. In the walking condition however, the trajectories were profoundly different, as the net displacement of the hand was backward toward the torso. In addition, looping spatial trajectories were observed in both the 30- and 60-cm movements, reflecting the hand moving towards the torso and up, then forward slightly, then down and back toward the torso again. As could be expected, these differences in the spatial trajectory of the limb resulted in kinematic differences between the standing and walking tasks. This is not surprising, considering that the movements of the hand in the walking task reflect a compensation for the torso's forward displacement during locomotion. Thus, these results show that the bell shaped trajectories achieved from the world-centered view are achieved by a combination of arm and body movement, the two acting in cooperation to produce smooth bell-shaped trajectories.

Further postural analyses revealed that subjects employed clockwise trunk rotation as the target width decreased. This rotation was towards the target and likely was used to keep the end-effector in closer proximity to the target as the body locomoted past its location. An additional benefit of this rotation was possibly to allow the subjects to keep their heads and eyes directed towards the target. These task-specific compensations reflect a strategy of keeping the end-effector, head, and eyes near the target, thereby helping the subjects to successfully complete the movements under the constraints imposed by the task conditions. Furthermore, it is clear that many degrees of freedom were incorporated into the pointing movements performed in this experiment. We believe the bulk of the evidence suggests that all of these degrees of freedom were organized and controlled in an integrated way. The implication here is that the functional requirements of this task lead to the unique planning and execution processes for the involved degrees of freedom.

The next step was to determine if the results for aiming while walking could be extended to a prehension task involving locomotion. Bertram, Marteniuk, and Wymer (1999) showed that performing a prehension task while walking not only affected the upper limbs but the forward speed of the body as well. In this study, subjects were required to walk alongside a table, pick up a cup of water (either covered or uncovered), and transport it to one of two targets (one large, one small) located 30 cm anterior to the lift-off point. The results showed that reaching for and grasping an uncovered cup resulted in subjects slowing their forward progress to accommodate the precision requirements of the task. Likewise, placing the cup (covered or uncovered) on the smaller target resulted in the subjects slowing their forward progress.

Of particular interest were the results of the spatial plot analysis where world- and body-centered views of the hand were contrasted. As can be seen in Figures 3A and 3B, results not too dissimilar from the movement aiming study of Marteniuk et al. (2000) were achieved.

Typical skewed bell-shaped trajectories were achieved from the world-centered coordinate system (Figure 3A). However, erratic and variable spatial trajectories were seen from the body-centered view (Figure 3B). Again, this reinforces the notion that during the movement, the hand can be closely coordinated with the degrees of freedom associated with other body movements. It is the functional outcome (i.e., a consistent, relatively invariable spatial trajectory) that is preserved, while the various degrees of freedom that produce these trajectories vary to achieve that outcome. It should be noted that Bertram et al. (1999) used chest velocity and not lower limb kinematics to measure rates of locomotion. Therefore, it is possible that the slowing of the forward velocity was not indicative of lower limb activity but rather of a postural adjustment at the level of the torso.

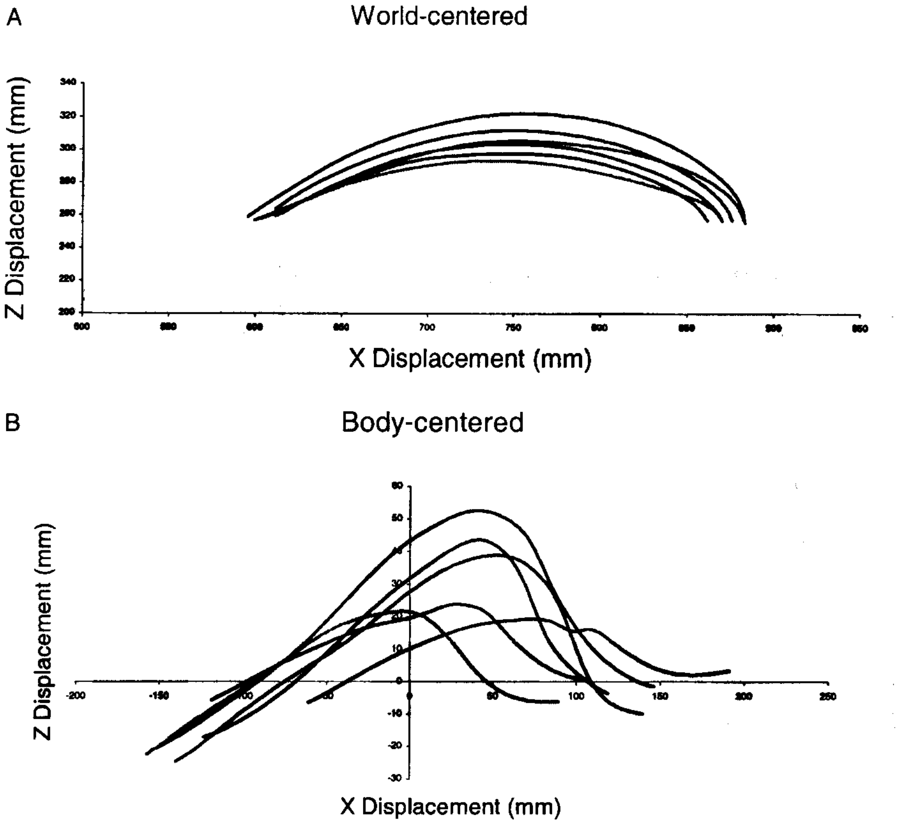

Figure 3 — Spatial plots showing the vertical and horizontal displacement of the hand as it reaches for an uncovered cup. Figure 3A depicts the hand from a world-centered frame of reference. Figure 3B depicts the same data, now viewed using the body as a dynamic frame of reference.

A more recent study conducted in our lab confirmed our earlier suspicions that adding complexity to the upper limb task would in fact result in altered gait patterns (Bertram, Marteniuk, & Mackey, 2000). For this experiment, we had subjects grasp cups of water (either covered or uncovered) and transport them to one of three target amplitudes while walking. Subjects were instructed to approach the cup at a comfortable pace, then transport the cup as quickly and accurately as possible while trying not to spill any of the cup's contents. Footswitches were used to quantify heel contact and toe lift-off during gait so that we could measure stance and swing times of each of them throughout the task.

At the outset, it was noted that there was a large degree of variability in strategies used by our subjects to complete this task. For example, when we looked at which foot was in stance phase at the time of cup-lift, we saw that the left foot was in stance 61% of the time, while the right foot was in stance 39% of the time. However, this pattern of preference was by no means consistent across subjects or even within a subject across conditions. Despite these differing gait strategies, we did however note several consistent adaptations. For example, it was found that regardless of which foot was down at the time of cup lift, reaching for a cup of water (regardless of whether it was covered or uncovered) resulted in increases in time spent during stance phase, as compared to a stance phase prior to interaction with cup. Moreover, our results indicated that stance times while grasping uncovered cups were longer than when subjects were grasping covered cups. Differences in time spent in swing phase failed to reach significance. Therefore, this study showed that when walking, adding significant complexity to a prehension task does in fact result in adjustments at the level of gait, and confirms that the locomotion system can become integrated into the act of prehension.

Conclusions

The finding that adding complexity to a combined upper and lower limb task resulted in adjustments beyond the upper limb (Bertram et al., 1999; Bertram et al, 2000; Marteniuk et al., 2000) raises some interesting questions. Namely, are the upper and lower limbs truly controlled in a hierarchical fashion as suggested by Carnahan et al. (1996), or could there be another explanation? A closer examination of the methodology employed by Carnahan et al. (1996) may hold the answer to this question. As has been previously mentioned, subjects were required to pick up one of two objects while walking past a support surface. The two objects in this case were an empty aluminum can or a pencil. Although the dimensions of these two objects differed (6.5 cm in diameter × 12.3 cm in height versus 0.8 cm in diameter × 14.9 cm in height, respectively), it is quite reasonable to assume that any adjustments needed to grasp the smaller object could be made at the level of the hand. In this case, it is likely that there was simply no need to adjust the locomotion kinematics to account for the relatively small difference in object size.

On the other hand, the methodology of Bertram et al. (1999), as well as Bertram et al. (2000), employed experimental conditions that differed quite significantly in terms of their task complexity. More specifically, transporting a full cup of water without a lid is much more difficult than transporting that same cup of water when covered. Therefore, it could be hypothesized that the recruiting of additional body segments to aid in the successful completion of a task is, at least in part, a function of the difficulty or complexity of that task.

Our idea, then, is that the many degrees of freedom associated with simultaneously performing locomotion and prehension are controlled as an integrated whole. The movements performed in the experiments reported above required the control of many of the bodies estimated 100 to 150 degrees of freedom (van Ingen Shenau, van Soest, Gabreëls, & Horstink, 1995). These redundant degrees of freedom make the control of the movement simultaneously more difficult to coordinate and, at the same time, more flexible (Abbs & Cole, 1987; Gieten, van Bolhuis, & Theeuwen, 1995). Many have theorized about and studied how the human motor apparatus overcomes this redundancy to solve this degrees of freedom problem (e.g., Abbs & Cole, 1987; Bernstein, 1967; Greene, 1982; Newell, Kugler, van Emmerik, & McDonald, 1989; Vereijken, van Emmerik, Whiting, & Newell, 1992), although the solution employed by the CNS has not yet been determined (Gielen et al., 1995). With regard to the experiments we outlined in the previous section of this paper, it would seem that the supposedly *redundant* degrees of freedom were in fact utilized by subjects to allow them to complete the task successfully. For example, subjects used rotational movements about the waist to assist in aiming to smaller targets (Marteniuk et al., 2000). Additionally, we showed that degrees of freedom associated with locomotion also would assist in prehension (Bertram et al., 2000). For both the pointing and prehension studies, it is important to note that these redundant degrees of freedom were only utilized when necessary. That is, subjects did not lean forward to bring the target into reach during the walking condition, since they were moving themselves towards the target (Marteniuk et al., 2000). These task constraints, therefore, helped solve the degrees of freedom problem, as only a subset of the total available degrees of freedom were appropriate for a given experimentally imposed set of constraints (Newell et al., 1989; van Emmerik & Newell, 1990).

In summary, the results we have presented thus far suggest that although the movements of the hand, torso, and gait can be controlled separately, a single, task-specific synergy employing elements of each segment can arise when needed. It would also appear, based on these findings, that the separate effector systems are readily able to reorganize themselves in response to evolving environmental conditions. Furthermore, it is quite remarkable to note that despite the seemingly disorderly nature of this reorganization, the performing hand is nonetheless carried smoothly through space.

Trunk-Assisted Reaching

We turn now to the second type of experiment that is pertinent to our discussion of multi-segmental coordination by examining the relationship between the torso and arm during trunk-assisted reaching experiments. Oftentimes, prehensile situations require that the torso becomes involved in the movement. For example, it would be impossible for most people to reach for and grasp a cup in the middle of a table without a significant degree of trunk flexion. Exactly how the trunk and arm work together in this kind of situation has been the subject of recent experimentation. Ma and Feldman (1995) found that when they asked subjects to move their torsos either forward or back during a reach, hand trajectories were virtually identical to when they made the same movements using only the arm. Furthermore, they discovered that torso movement generally preceded the movement of the hand and continued after the hand had reached its target. These findings led the authors to suggest that reaching movements involving the torso involve two functionally different synergies. One synergy was said to coordinate the muscles and joints of the hand, while the other was left to coordinate the trunk and arm together, thereby resulting in a consistent endpoint position of the hand (Ma & Feldman, 1995).

Saling et al. (1996) conducted an experiment in which subjects were to reach for and grasp dowels (large or small) placed at such a distance so as to require the forward flexion of the torso for a successful grasp. These authors found further evidence to suggest the presence of independent synergies working together to produce consistent hand trajectories. Specifically, it was noted that the transport and aperture components remained temporally coupled despite the addition of the torso to the movement. Conversely, there was no such coupling between the trunk movement and the grasp. Furthermore, the fact that the trunk kinematics did not reflect the accuracy constraints of grasping a smaller dowel provided further evidence for the notion of independent control mechanisms for the arm and for the torso (Saling et al., 1996). Interestingly however, Steenbergen, Marteniuk, and Kalbfleish (1995) showed that under certain conditions, the torso kinematics could be affected by the accuracy requirements of a task. These authors found that the displacement of the torso significantly increased when subjects reached to grasp cups full of coffee compared to when they reached for empty cups. This result raises an obvious question: Why is the movement of the torso affected by certain constraints but not others?

A closer examination of the trunk-assisted reaching literature may provide an answer. To recall, Saling et al. (1996) had subjects reach to and grasp one of two dowels (one large, one small). It was concluded that the task constraint of object size affected the transport and grasp components of the upper limb movement, while the trunk remained unaffected. Similar to the explanation given in the previous section of this paper regarding locomotion and prehension, a possible alternative explanation for these results could be that the paradigm employed by Saling et al. (1996) (i.e., big dowel/little dowel) did not offer enough complexity so as to elicit significant torso contributions. Therefore, one might expect that if a trunk-assisted reaching study were designed in which one of the experimental conditions was significantly more difficult than the other, differences in the torso would become apparent. Along with Steenbergen et al. (1995), two more recent experiments from our lab confirmed this assertion. First, Mackey, Bertram, Mason, Marteniuk, and MacKenzie (2000) conducted a trunk-assisted reaching study in which subjects were required to either reach for and grasp, or transport cups of water to targets within and beyond the arm's length. For half the trials, the cup of water was covered, while for the other half the lid was removed. Among the results of this study was the finding that removing the lid from the cup resulted in a significant increase in forward torso displacement. This finding supports the Steenbergen et al. (1995) suggestion that when necessary, added torso movement allows for a more stable movement by reducing the movement at the shoulder and elbow joints (i.e., joint-freezing).

Of further interest is not only how the arm and the torso segments move individually, but also how they move in relation to one another. Bertram et al. (2000) presented aspects of the above data in terms of both world-centered and body-centered coordinates. Figures 4A and 4B show the spatial path plots of a representative subject in X (horizontal) and Z (vertical) coordinates.

A preliminary view of the individual subject spatial path plots from a world-centered viewpoint (Figure 4A -reaching for a covered cup) shows quite a large degree of variability in the vertical (Z) direction of the movement. Furthermore, the body-centered plots show substantial variability in terms of the final X position, indicating a variable torso contribution from trial to trial. On the other hand, for the uncovered cup condition (Figure 4B), results show that in body-centered coordinates, there is less variability in the X direction. Therefore, even though the torso

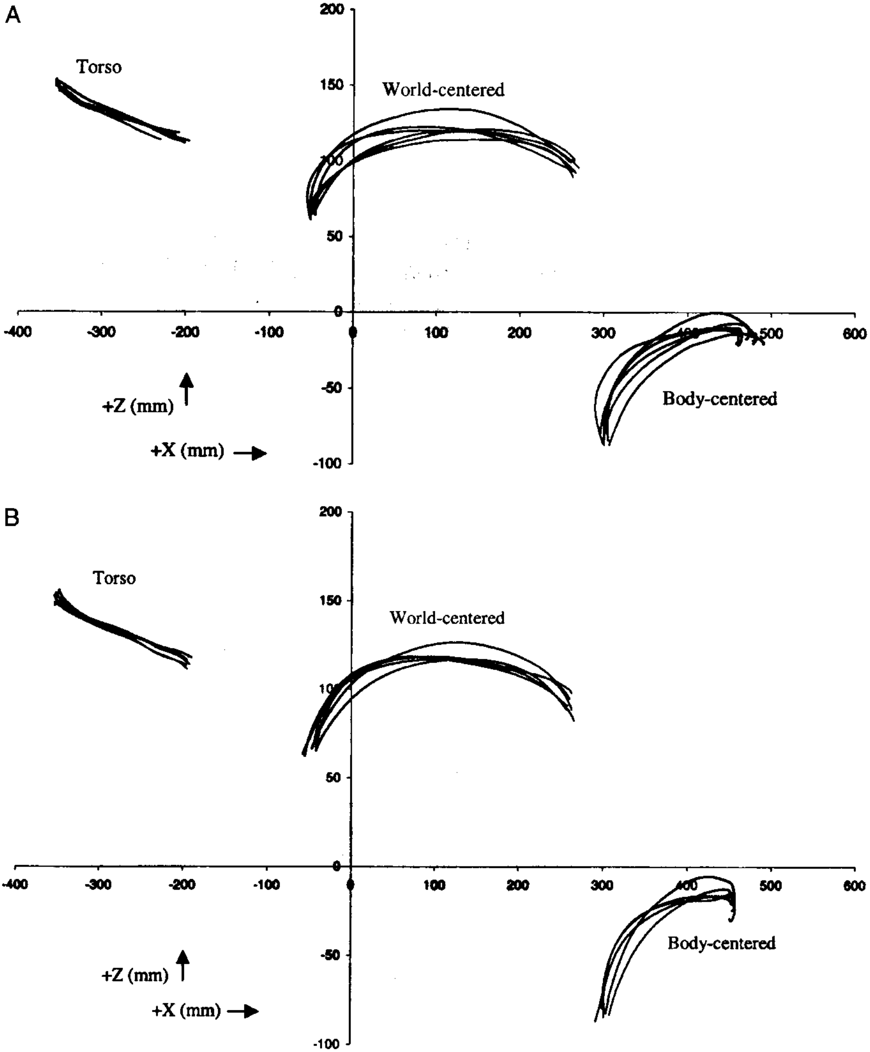

Figure 4 — Spatial path plots involving the horizontal (x) and the vertical (z) displacements of: (a) the torso and (b) the hand viewed from both a world- and body-centered frame of reference. Figure 4A shows six trials and their spatial paths for a representative subject's reach for a covered cup. Figure 4B shows the spatial path plots for the same subject reaching for an uncovered cup.

was moving significantly further when the cup was uncovered, its movements were more consistent on a trial to trial basis. This consistency is depicted in the more tightly grouped world-centered trajectories and would seem to reflect a concerted effort on the part of the motor control system to more tightly coordinate the arm and torso under more complex task conditions. Efforts to more rigorously quantify the patterns observed in these spatial plots are currently underway in our lab.

Conclusions

The above results on trunk-assisted reaching nicely compliment our earlier discussion of combined upper and lower extremity tasks. First, we have argued in both cases that in order to observe the full expression of the motor control system, one must design experiments that simultaneously allow the body to move freely, and that employ conditions of distinct levels of complexity. In doing so, we have shown that adding significant complexity to a task results in the recruitment of additional body segments to assist the arm in achieving a successful grasp. Second, we have suggested that if one is to concurrently observe separate body segments, it is informative to describe the movements of those segments both in terms of their absolute contributions, and also in terms of the movement of one segment relative to the others. The spatial path plots depicted in Figures 4A and 4B, for example, convincingly show how the hand and body work together to produce smooth end-point trajectories. Here again, it became evident that the distal movement segments were capable of a good deal of variable adaptation to ensure successful task completion.

Finally, the results of our trunk-assisted reaching experiments provide further evidence for the notion that compound movements are controlled by task-specific synergies. As was the case with combined upper and lower limb tasks, here again we observed that not only was the body integrated into the movement plan for prehension, but also that the degree to which the torso assisted with the reach hinged upon the complexity of the task.

General Discussion

One important question about the studies reported above relates to asking what are the control mechanisms that would allow such coordination over such a large number of degrees of freedom. It would seem at the outset that the tremendous variability observed in the data discussed thus far would speak against the notion of a single motor program or synergy. It is instead suggested that the compound movements discussed herein are controlled by a more flexible series of motor commands. One such versatile control mechanism is Arbib's (1981) notion of the coordinated control program. Arbib's distributed model was useful for explaining the coupling of the transport and grasp components of prehension. Central to Arbib's claim was the idea that a motor program need not imply specified or fixed-sequence behavior. He suggested instead that movements are allowed to evolve according to peripheral as well as central inputs. Arbib also spoke of high-level goals and lower-level motor outputs as a possible means for controlling degrees of freedom.

Abbs, Gracco, and Cole (1984) further suggested that a motor program is a representation of the dynamic processes of movement, whereby appropriate sensorimotor contingencies are set up to ensure cooperative contributions of multiple actions to achieve a common predetermined goal. Such a construct was set up by the authors to explain the corrections observed in speech perturbation research. Essentially, Abbs et al. (1984) showed that when a perturbation was applied to one sub-component of a speech movement (i.e., the lower lip), adjustments were seen in the lower lip (termed *autogenic*), as well as in the upper lip and jaw (termed *feedforward*). The defining feature of these and other related studies was that despite the perturbations, successful sound production was consistently achieved. Again, it would appear as if the task of the motor system was to achieve the goal successfully, using all means available. Abbs et al. (1984) also drew parallels between speech production and upper limb activities:

> Specifically, involving a multimovement gesture involving subcomponents A, B, and C (elbow, wrist, and finger, or upper lip, lower lip, and jaw), one might hypothesize that the final contribution of each of these subactions is determined by sensorimotor, feedforward controllers operating independently on afferent information from A, B, and C, and guided by an abstract, goal-directed plan of action. (p. 213)

It is a distinct possibility that the sub-components of the compound movements described in this paper could be characterized in a similar way. In other words, sub-components A, B, and C would correspond to hand, torso, and gait, with each independently contributing as necessary to ensure the successful completion of the movement goal. We have attempted to capture the essence of this model of organization in Figure 5.

Figure 5 is presented as a possible hierarchical-distributed representation of a compound movement involving the hand, torso, and gait. At the top of the hierarchy sits the overall representation of the movement goal. Below the task goal are the individual segments involved that could possibly be recruited in order to successfully carry out an upper limb task involving locomotion. In other words, the *method* of achieving the goal (i.e., hand alone; hand + torso; hand + torso + gait) is subordinate to, and dependent upon, the demands of the task. It is postulated that in the case of a very simple experimental task, the hand alone would be capable of making the necessary adjustments to account for minor changes in a to-be-grasped object. For movements of moderate complexity, adjustments would be made in parallel in the hand and torso. Finally, for very complex or difficult movements, parallel adjustments would be seen in the hand, torso, and gait. The current model is in keeping with the model proposed by Rosenbaum et al. (this issue), in which it is suggested that task objectives are represented as predetermined goal postures, and that highly variable movement patterns can arise to satisfy those goals.

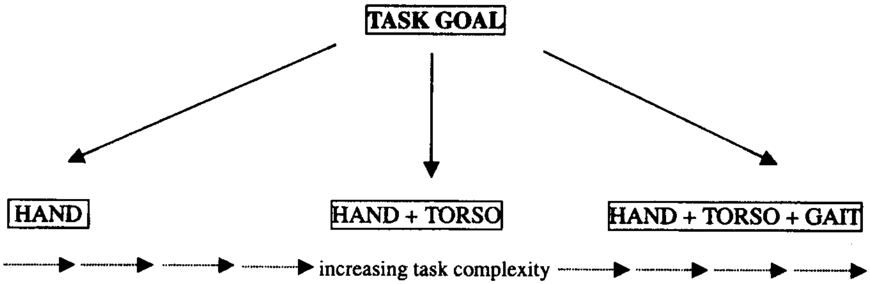

Figure 5 — A hierarchical distributed model depicting the contributions of additional body segments in response to increasing task complexity.

Several of the studies mentioned earlier in this paper support the model presented in Figure 5. For example, the Carnahan et al. (1996) study employed the fairly simple manipulation of dowel size. The results of their combined locomotion/prehension experiment fit the current model in that the majority of the adjustments made to accommodate changes in dowel size were seen at the level of the hand. It should be noted, however, that these authors did not measure kinematic features of the torso. Indeed, it would be interesting to discover if torso compensations would arise as a result of a making simple prehension movement while walking. The work of Marteniuk et al. (2000) is likewise consistent with the present model. In a pointing task involving locomotion, these authors noted that decreasing the size of the target affected both the kinematics of the hand and the contribution of the torso. In other words, when subjects required more precision, the torso contributed more toward helping the hand maintain the speed and accuracy of the task. A prediction based on the current model would suggest that as the upper limb task continued to increase in complexity, adjustments would be seen in gait characteristics. This prediction was realized by Bertram et al. (2000) by demonstrating that complex prehension tasks resulted in lengthening of the stance phases of gait when subjects interacted with the objects.

Finally, the above model also can account for the inconsistencies mentioned earlier in the trunk-assisted reaching literature. To review, Saling et al. (1996) suggested that trunk kinematics are unaffected by changes in dowel size. If one considers that the two dowels were of equal height and similar diameter (2.2 cm and 6.7 cm), it is reasonable to assume that the task was simple enough to have all adjustments made at the level of the hand. Steenbergen et al. (1995) added to the complexity of the trunk-assisted reaching paradigm by making the to-be-grasped objects a full cup of coffee versus an empty cup. In keeping with the present model, the added complexity of the tasks employed by Steenbergen et al. (1995) and Mackey et al. (2000) resulted in adjustments in the kinematics of the hand as well as the trunk.

One conclusion that can be drawn from the combined results of the present experiments is that the end-point (i.e., the hand) trajectories remained reasonably constant despite the large number of contributing degrees of freedom. This was seen nicely by contrasting the world-centered trajectories with the body-centered trajectories (Figures 2, 3, & 4). We have argued that this consistency is derived from the combining of many variable sub-movements into a smooth end-point trajectory. Therefore, we feel the results presented herein provide a very strong demonstration for motor equivalence, and that task complexity is one variable that is related to the emergence of motor equivalence. We believe that the above work begins a systematic exploration of the underlying parameters of motor equivalence, and it is our hope that our future work will help delineate other variables that lead to expressions of this fascinating phenomenon.

One further issue that the above results bear on concerns the theoretical underpinnings of prehension. Jeannerod's (1981, 1984) seminal work suggested that prehension is composed of the independent but temporally coupled sub-components of the transport and grasp, where the transport component is due to the movement of the arm. Our results clearly show the world-centered path trajectory of the transport component can be composed of a combination of the trajectories of the leg, trunk, and arm, all combining to produce a smooth world-centered trajectory of the hand. Clearly Jeannerod's theory must be expanded, or a new theory developed, to account for these results.

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