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Role of vision in aperture closure control during reach-to-grasp movements

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Abstract

We have previously shown that the distance from the hand to the target at which finger closure is initiated during the reach (aperture closure distance) depends on the amplitude of peak aperture, as well as hand velocity and acceleration. This dependence suggests the existence of a control law according to which a decision to initiate finger closure during the reach is made when the hand distance to target crosses a threshold that is a function of the above movement-related parameters. The present study examined whether the control law is affected by manipulating the visibility of the hand and the target. Young adults made reach-to-grasp movements to a dowel under conditions in which the target or the hand or both were either visible or not visible. Reaching for and grasping a target when the hand and/or target were not visible significantly increased transport time and widened peak aperture. Aperture closure distance was significantly lengthened and wrist peak velocity was decreased only when the target was not visible. Further analysis showed that the control law was significantly different between the visibility-related conditions. When either the hand or target was not visible, the aperture closure distance systematically increased compared to its value for the same amplitude of peak aperture, hand velocity, and acceleration under full visibility. This implies an increase in the distance-related safety margin for grasping when the hand or target is not visible. It has been also found that the same control law can be applied to all conditions, if variables describing hand and target visibility were included in the control law model, as the parameters of the task-related environmental context, in addition to the above movement-related parameters. This suggests that that the CNS utilizes those variables for controlling grasp initiation based on a general control law.

Keywords

Prehension; Kinematics; Coordination; Aperture; Finger

Introduction

The role of vision during reach-to-grasp movements has been examined extensively. Both the magnitude of grip aperture and temporal characteristics of the transport component are altered when normal vision is not available during the movements. It is typically found that the duration of the transport component increases in reach-to-grasp movements without vision (Connolly and Goodale 1999; Gentilucci et al. 1994; Jakobson and Goodale 1991; Schettino et al. 2003; Watt and Bradshaw 2000; Winges et al. 2003). An increase in the duration of the deceleration

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phase of the reach or an increase in the duration of closing grip aperture was found when visual feedback was blocked during the entire or initial part of movement (Jackson et al. 1995; Schettino et al. 2003, 2006; Winges et al. 2003), when vision of the hand was blocked (Berthier et al. 1996; Churchill et al. 2000; Connolly and Goodale 1999; Gentilucci et al. 1994; Schettino et al. 2003), or when monocular vision was used (Jackson et al. 1997; Servos et al. 1992; Watt and Bradshaw 2000). Regarding the grasp component, the maximum finger aperture was increased for prehension movements made without vision (Jackson et al. 1995; Jakobson and Goodale 1991; Wing et al. 1986), without vision of hand (Berthier et al. 1996; Churchill et al. 2000; Gentilucci et al. 1994), with peripheral vision (Sivak and MacKenzie 1990), or monocular vision (Jackson et al. 1997; Watt and Bradshaw 2000). This wider grip aperture is thought to occur due when participants increase the safety margin for grasping the object successfully. Despite the previous studies, the role of visual feedback of the target in controlling the transport and grasp components remains elusive. The methodology used previously did not allow dissociating the role of visual feedback of the target from that of the hand, because both sources of visual information were removed at the same time (Darling and Miller 1993; Jackson et al. 1995).

Previous studies indicated that transport–grasp coordination is more adequately described based on spatial rather than temporal characteristics of reach-to-grasp movements (Alberts et al. 2002; Rand and Stelmach 2005; Rand et al. 2004; Wang and Stelmach 1998, 2001). The location of the hand relative to the target object, where the aperture closure was initiated during reaching (aperture closure distance) was similar under various task conditions (Alberts et al. 2002; Rand and Stelmach 2005; Rand et al. 2004; Wang and Stelmach 1998, 2001). This suggests that the motor system utilizes the hand-target distance information for initiating aperture closure. Therefore, vision of the target and/or the hand may be more important for transport–grasp coordination than it would have been if the transport–grasp coordination were based on a preprogrammed temporal relationship. However, to our knowledge, the effect of blocking *target* vision on aperture closure distance has not been examined yet. The dependence of aperture closure distance on *hand* visibility was examined in only one previous study, in which it was reported that the aperture closure distance lengthened significantly when the hand was not visible compared to the condition of full vision (Churchill et al. 2000).

We have recently shown that despite that the aperture closure distance appears relatively invariant across different task conditions, this parameter still significantly depends on the amplitude of peak aperture, as well as hand velocity and acceleration (Rand et al. 2006a, b). In an effort to explore how the central nervous system (CNS) controls the initiation of aperture closure, the dependence of aperture closure distance on those parameters was interpreted based on the theoretical concept of a control law (Davis 2002). A control law describes the dependence of control action (e.g., expressed in joint torques or muscle activity) on the parameters of the motor plant, which in our experimental paradigm includes the dynamics of the arm and its relationship with the reach target. This theoretical concept was successfully used for modeling neural control of arm movements (Shimansky et al. 2004). We hypothesized that the initiation of aperture closure is governed by a certain control law, a function defined on certain state parameters of arm-target dynamics, such as the hand distance to target, hand velocity, aperture, etc. Specifically, if this hypothesis is correct, finger closure is initiated during the reach when the distance to target crosses a threshold that is a function of amplitude of peak aperture, hand velocity, and acceleration. The previous studies by Rand et al. (2006a, b) confirmed that this theoretical concept adequately describes aperture closure initiation during the reaching. This control law formulation was also used for investigating whether the transport–grasp coordination for initiating aperture closure is based on spatial characteristics of arm movement or movement timing (Rand et al. 2006b). It was demonstrated that the transport–grasp coordination for grasp initiation is based on predominantly spatial characteristics of arm movement instead of temporal characteristics (Rand et al. 2006b).

The present study further examined spatial coordination between the hand transport and grasp component for the initiation of aperture closure based on the above control law hypothesis. The purpose of the study was to investigate the role of vision on the spatial coordination of reach-to-grasp movement, and more specifically whether the control law changes when the vision of the target and the hand is manipulated. For this purpose, visual information about the hand and/or target during reach-to-grasp movement was systematically manipulated. If the control law is changed due to a removal of visual feedback of the hand and/or the target, it would manifested itself either as reduced transport–grasp coordination (i.e., weak correlation) among the state parameters for initiating aperture closure (aperture closure distance, the amplitude of peak aperture, hand velocity, and acceleration), or as a specific consistent change in the relationship among those parameters. If the data support the above hypothesis and if changes in the control law due to the manipulations of visual feedback are observed, it would suggest that the CNS utilizes the control law for triggering the initiation of aperture closure during the reach. Preliminary findings of this study were presented elsewhere (Rand et al. 2006c).

Materials and methods

Participants

Ten young adults participated in this study (seven males and three females; the mean (SD) age was 22.1 (1.7) years old, age range between 20 and 26 years old). All participants were right-handed. This study was approved by Arizona State University's Institutional Review Board overseeing the use of human participants in research. All participants signed consent forms prior to participation.

Procedure

Participants were comfortably seated at a table. The start position was located ~15 cm from the participant's midline and 5 cm from the edge of the table. The start position was a 2.5 × 2.5 cm^2 rough surface area. All participants performed reach-to-grasp movements with their dominant hand. Participants were instructed to keep their thumb and index finger together, place the ulnar side of the hand on the table, and rest their index finger and thumb at the start position before each trial.

A cylindrical target (height 10 cm, diameter 2 cm) was placed 30 cm from the start position along the midline of the trunk for half of the trials (front target condition), and at 30 cm from the start position at a 45° angle to the left of the midline of the trunk for the remaining half of the trials (left target condition). Two targets were used to examine generalization of vision manipulation effects across different target locations. The front direction of the target location was often used in previous studies (Churchill et al. 2000; Gentilucci et al. 1994; Schettino et al. 2006; Watt and Bradshaw 2000). The left target location was chosen because the reaching for grasping motion would require less maneuvering of the wrist compared to that required for grasping the front target. The hand posture at the starting position was in line with the left target, but not with the front target. Such a factor could differentiate the vision manipulation effects between two target locations, revealing their dependence on task difficulty.

For each trial, the target object was lit up for a random duration between 1 and 2 s before a beep sound ("go"-signal). In response to the "go"-signal, the participants reached for the object, grasped it with the thumb and index finger, and lifted it a few cm off the table. The participants were instructed to move at a comfortable speed. Different vision conditions tested were: (1) hand visible, target visible (TV-HV), (2) hand visible, target not-visible (TNV-HV), (3) hand not-visible, target visible and (4) hand not-visible, target not-visible. For the target visible conditions, the target remained lit up for the duration of the trial, while for target not-visible trials, the target light was turned off simultaneous with the “go” signal. Participant’s thumb and index finger were covered with glow-in-the-dark fabric for the hand visible conditions. More specifically, the dorsal side of the thumb and index fingers was covered from the metacarpo-phalangeal joint to the tip of the finger with a piece of the glow-in-the-dark fabric (~1.5 cm wide). The palmar side of the participant’s finger tips was not covered by the fabric to keep the contact surface to the object the same across all conditions. All conditions were conducted in complete darkness. An additional condition, context visible/hand visible/target visible (CV), was included. The CV condition included the glow-in-the-dark fabric and was conducted in dim lighting so that the participant could see the surroundings. The CV is a control condition to the TV-HV condition in order to see if performance with both hand and target visible condition is different in the dark compared to that under dim light where the experimental surrounding are also visible. Prior to the recording session, participants practiced several trials to familiarize themselves with the experimental procedure.

A block of 12 trials were performed for each condition, in which the last ten trials were used for data analysis. The method of blocking the trials was selected for the current experiment because it allowed the participants to anticipate the reliable presence (or absence) of visual feedback and to plan the reach and grasping movements accordingly. An alternative method where trials are randomized across conditions has been found to induce a behavioral pattern where the participants always performed the reaching task as if they were reaching without vision, even in those trials where visual feedback was continuously available (Jakobson and Goodale 1991). For this reason, trial randomization does not seem suitable for revealing changes of kinematic characteristics produced by various vision-related manipulations.

The participants performed 12 trials with the front orientation and then 12 trials with the left orientation or vice versa. The order of all vision-related conditions was randomized and counter-balanced between participants.

Wrist and finger positions during reach-to-grasp movements were recorded using an Optotrak 3D system (Northern Digital, Waterloo, ON, Canada). Infrared light emitting diodes (IREDS) were placed over the wrist, tip of the index finger, and the tip of the thumb. An additional IRED was placed on the target in order to record its position and movement. Positions of the IREDS were sampled at a rate of 100 Hz.

Data analysis

Kinematic characteristics related to the grip component and the transport component were analyzed. The transport component was assessed based on the position of the IRED on the wrist. Wrist velocity during the reach was tangential velocity calculated as the first derivative of wrist position. Derivatives were calculated based on the sliding window technique, where the data points within the window (the window width was 7 points) were approximated with a quadratic polynomial. The polynomial was then used for calculating the analytic derivative at the window’s center (or other points, when at the beginning or end of the data array representing the curve). Thus, calculating derivatives using this method also provided data filtering. The grasp component was assessed based on the positions of the IREDs on the index and thumb fingertips. Grip aperture was defined as the resultant distance between these two IREDs. The end of grasp was identified as the point in time where both fingers came in contact with the object and grip aperture stopped decreasing. The end of the transport was defined as the end of grasp. The onset of transport and aperture was calculated by performing an automated movement-parsing algorithm (Teasdale et al. 1993; algorithm B). The onsets of the transport were verified by visual inspection by the experimenter and any errors were corrected.

Temporal measurements included: transport time, time to peak velocity, deceleration time (the time from the peak velocity to the end of grasp), the aperture opening time (the time from movement onset to peak aperture), and aperture closure time (the time from peak aperture to the end of grasp). In order to assess the spatial coordination between the grasp and transport components, the following spatial parameters were measured: transport distance (the resultant distance from movement onset to the end of grasp), aperture opening distance (the resultant distance from movement onset to peak aperture), and aperture closure distance (the resultant distance from peak aperture to the end of grasp). These distances were calculated as a cumulative resultant trajectory length between two positions of the wrist IRED.

A mean value across all trials for each participant was calculated for each condition. The difference between the CV and TV-HV conditions was assessed by using a 2 (target direction) × 2 (conditions) ANOVA. Data from all conditions except the CV condition were tested by using a 2 (target direction) × 2 (target visibility) × 2 (hand visibility) ANOVA with repeated measures. When an interaction effect was found, a post hoc comparison was performed by using a paired *t*-test with Bonferroni correction ($\alpha = 0.05$) in order to identify significant differences between individual cell means.

A model of the control law governing aperture closure initiation (see Introduction) was examined for all conditions except the CV condition. We hypothesized that the aperture closure is initiated when the hand distance to target crosses a threshold that is a function of the aperture magnitude, wrist velocity and wrist acceleration, which was measured at the time of finger closure initiation. According to this control law model (Model 1), the condition for the onset of aperture closure can be presented formally as

$$D = D_{\mathrm{thr}}(G, \quad V_{\mathrm{w}}, \quad A_{\mathrm{w}}), \tag{1}$$

where D is the distance of the hand from the target, G the grip aperture, V_{w} the wrist velocity, and A_{w} is the wrist acceleration. D_{thr} is the distance-to-target threshold. It is assumed that aperture closure is not initiated, while a state where $D > D_{\mathrm{thr}}$.

To test the validity of the above control law model, aperture closure distance, grip aperture amplitude, wrist velocity, and wrist acceleration were measured at the time of maximum aperture (the initiation of the aperture closure). These four parameters constitute a relatively full description of the state of the motor plant, namely the dynamics of the arm and its relationship with the reach target at the time of the initiation of aperture closure. This approach has been successfully used in our previous study (Rand et al. 2006a, b). The coefficients of the control law model were identified based on the standard method, namely by minimizing the least square deviation of the model's prediction from the actual, experimentally measured values of the target variable (the aperture closure distance). The R^2 values and the absolute residual errors were then calculated based on all trials and all participants by using a linear regression analysis. For this analysis, data which were outside ±3.5 standard residual based on the regression analysis performed for Model 1 for each condition were eliminated as outliers. As the result, five trials in total were removed.

Furthermore, to test whether the approximation of aperture closure distance was improved when conditional variables describing hand and target visibility as well as target direction are included into the model, the target visibility condition (Tv) and the hand visibility condition (Hv) were labeled as 1 (visible) or 0 (not visible) for each trial. Target direction condition (Td) was also labeled as 1 (front) or 0 (left) for each trial. One or more of these conditions were added to Model 1 as follows. Model 2 includes target visibility, Tv, into Model 1:

$$D = D_{\mathrm{thr}}(G, \quad V_{\mathrm{w}}, \quad A_{\mathrm{w}}, \quad \mathrm{Tv}). \tag{2}$$

Model 3 includes hand visibility, Hv, into Model 1:

$$D = D_{\mathrm{thr}}(G, \quad V_{\mathrm{w}}, \quad A_{\mathrm{w}}, \quad \mathrm{Hv}). \tag{3}$$

Model 4 includes target direction, Td, into Model 1:

$$D = D_{\mathrm{thr}}(G,\ V_{\mathrm{w}},\ A_{\mathrm{w}},\ \mathrm{Td}). \tag{4}$$

Model 5 includes target visibility, Tv, and hand visibility, Hv, into Model 1:

$$D = D_{\mathrm{thr}}(G,\ V_{\mathrm{w}},\ A_{\mathrm{w}},\ \mathrm{Tv},\ \mathrm{Hv}). \tag{5}$$

Model 6 includes target visibility, Tv, hand visibility, Hv, and target direction, Td into Model 1:

$$D = D_{\mathrm{thr}}(G,\ V_{\mathrm{w}},\ A_{\mathrm{w}},\ \mathrm{Tv},\ \mathrm{Hv},\ \mathrm{Td}). \tag{6}$$

Next, the absolute residual errors were statistically compared between Model 1 and other different models by using ANOVA.

To verify whether the relationship between D, G, V_w, and A_w estimated in trials from the TV-HV front-target condition was significantly different from the relationships in other conditions, a residual error analysis was performed. A residual error was calculated for each participant for each condition as follows: (1) based on values from all participants and all trials, a multiple linear regression analysis was applied for the aperture closure distance (D) as a function of the three parameters (G, V_w, and V_a) for the TV-HV front-target condition; (2) an intercept constant (k_0) and slopes (k_1, k_2, and k_3) were calculated from the regression analysis involving the three parameters; (3) by using this constant and the slopes, the residual error (E) was calculated by using the equation $E = k_0 + k_1G + k_2V_w + k_2V_a - D$ for all trials for each condition. Next, these residual errors were compared across conditions by using a 2 (direction) × 2 (target visibility) × 2 (hand visibility) ANOVA.

Results

First, the context visible condition and the target-visible hand-visible condition were compared to see if the participants changed their performance when they were able to see the surrounding environment. A 2 × 2 ANOVA revealed that there was no statistically significant difference between the two conditions for all parameters ($P > 0.05$). Thus, despite the circumstantial differences under which the participants performed prehensile movements, the performances were similar for both conditions.

General characteristics of reach-to-grasp movements

The mean values for all experimental conditions (target visibility, hand visibility, and target direction) are shown in Table 1. In terms of the effects of target visibility manipulation, significant Target visibility × Direction interactions were found for transport time, $F(1,9) = 15.82$, $P < 0.01$, and peak velocity, $F(1,9) = 5.84$, $P < 0.05$. Post hoc analyses showed that the transport time was longer for both the front and left target and peak velocity tended to be slower ($0.05 < P < 0.1$) but only for the front target (see Fig. 1, panels A and B) when reaching for a not-visible target. Regarding the effects of hand visibility manipulation, the mean transport time was longer when the hand was not visible than when it was visible, $F(1,9) = 7.43$, $P < 0.05$. No significant effect was observed on peak velocity ($P > 0.05$).

Does the transport slowing due to the removal of target/hand visibility occur during aperture opening or aperture closure? Aperture opening time was not affected by any of the visual conditions, whereas aperture closure time increased when the vision of the target or the hand was blocked (Table 1, target visibility: $F(1,9) = 28.62$, $P < 0.001$; hand visibility: $F(1,9) = 5.18$, $P < 0.05$). These results suggest that vision of the target as well as the hand is important in the control of the hand decent onto the target and finger closure movement.

The amplitude of grip aperture modulation during the reach depended on the hand and target visibility as well as the target direction (Table 1). Significantly wider maximum grip aperture were made during the reach when the target was not visible, $F(1,9) = 73.90$, $P < 0.001$, when the hand was not visible, $F(1,9) = 24.75$, $P < 0.01$, and when the front target was grasped, $F(1,9) = 15.07$, $P < 0.01$. This strategy of widening the grip aperture under the absence of visual feedback is in agreement with previous studies and likely is used to increase a safety margin for grasping at the end of reach (Berthier et al. 1996;Churchill et al. 2000;Gentilucci et al. 1994).

Spatial coordination between the transport and grasp component for aperture closure initiation

The spatial coordination between transport and aperture formation was examined by determining whether maximum grip aperture (and hence the initiation of aperture closure) occurred at a consistent distance from the onset of reach (aperture opening distance) or from the target to be grasped (aperture closure distance) (Table 1). Removal of vision of the target resulted in a statistically significant shortening of opening distance, $F(1,9) = 5.77$, $P < 0.05$, and a significant lengthening of the closure distance $F(1,9) = 5.18$ $P < 0.05$. This indicates that participants initiated aperture closure at a location further away from the target when the target was not visible. No significant hand visibility effect was found for the opening and closure distances ($P > 0.05$).

In addition, the aperture opening distance was also significantly decreased for the front target compared to the left target, $F(1,9) = 58.73$, $P < 0.05$. This accounts for the decrease of the total transport distance for the front target, $F(1,9) = 122.7$, $P < 0.001$. The shortening of the total transport distance is likely caused by an extra wrist extension movement performed when reaching for the front target so that the hand extended the reach of the arm segment, thereby reducing the total transport distance traveled by the wrist. Target or hand visibility manipulations did not affect the transport length ($P > 0.05$).

In contrast to a substantial change in aperture opening distance, there were no changes in the aperture closure distance across two target directions ($P > 0.05$), showing the stability of aperture closure distance compared to the opening distance. The result of the stable aperture closure distance compared to the aperture opening distance is in agreement with previous studies (Alberts et al. 2002; Rand and Stelmach 2005; Rand et al. 2004; Wang and Stelmach 1998, 2001).

Additional factors that influence aperture closure initiation

To test the control law hypothesis (see Introduction), the relationship between the aperture closure distance and the amplitude of peak aperture, wrist velocity, and wrist acceleration, was examined. Figure 2a–c plots the closure distance against each of these parameters for all participants and all trials for the TV-HV front-target condition to graphically demonstrate the relationship between these parameters. In general, aperture closure distance was positively correlated with each of the three parameters. A clear relationship was found for eight participants (Fig. 2a–c filled squares), while two other participants tended to follow a different pattern (Fig. 2a–c, open squares). That pattern of positive correlation was maintained even when the target or the hand was not visible. Since such patterns under different conditions were similar to each other, only examples from the TNV-HV condition are shown in Fig. 2d–f. As one can see in Fig. 2a–c, two participants, who did not show clear pattern of positive correlation in the TV-HV condition, produced peak aperture, wrist velocity, and acceleration within the range shown by other participants. However, they tended to produce much greater aperture closure distance than other participants. This alternative strategy was also reported previously (Wang and Stelmach 2001). Nevertheless, the performance of those two participants became more similar to that of the other participants when target and/or hand was not visible, demonstrating a positive correlation between the aperture closure distance and wrist velocity (Fig. 2e) as well as acceleration (Fig. 2f) under those conditions.

Modeling aperture closure initiation based on a control law

The validity of the control law described as Model 1 was tested by applying a regression analysis across all trials and across all participants for each condition (except for CV). The analysis showed that the relationship between the aperture closure distance, aperture amplitude, wrist velocity and acceleration was statistically significant and that the R^2 value was high for all conditions (Table 2). These results support the hypothesis that the initiation of aperture closure is governed by a certain control law. The results from the subgroup of eight participants who showed similar patterns of correlation between movement parameters (Fig. 2) corresponded to the results from all participants taken together (Table 2).

The analysis of data from the two participants who utilized the alternative strategy revealed that the relationship between the aperture closure distance and the other three parameters was significant for each condition with high R^2 values (Table 2). This result suggests that despite the fact that these two participants did not execute the movement in a similar manner as the other eight participants did, they still used a control law based on above four parameters for the initiation of aperture closure. However, for these two participants, the mean absolute residual error under full vision was much greater than in other conditions for both the front and the left target (Table 2). Since the peak aperture and wrist acceleration did not show a clear correlation with aperture closure distance in the full vision condition (Fig. 2a, c), the contribution of these parameters to the control of initiating aperture closure was reduced.

The main difference between the above two participants and other participants under the full vision condition was that their grip aperture started decreasing at a point much further away from the target, as was shown by large aperture closure distances (Fig. 2a–c). Furthermore, it was found that the correlation between the aperture closure distance and absolute residual errors obtained from the control law model applied across all trials and all participants under the full vision condition was rather strong for the two subjects ($P < 0.01$, mean correlation coefficient 0.89, mean $R^2 = 0.8$). This indicates that the greater the aperture closure distance, the less precise the prediction by the control law model in the full vision condition. These observations suggest a possibility that there was a certain factor causing the “premature” initiation of aperture closure, other than an active control of a phasic increase in the activity of muscles responsible for closing the aperture. However, this assumption cannot be verified based on the data obtained in the current experiment.[1]

Modulation of the control law by manipulations of hand and target visibility and target direction

To determine whether the relationship between the aperture closure distance and aperture amplitude, wrist velocity, and acceleration was changed due to the manipulation of visual feedback of the hand and target, residual errors were calculated for each participant for each condition based on the regression coefficients computed for the TV-HV front-target condition (see Method section). The average residual errors across all participants were plotted for all conditions in Fig. 3a, b. When either vision of the target or the hand was not available, residual errors significantly increased (target visibility: $F(1,780) = 135.39$, $P < 0.001$; hand visibility: $F(1,780) = 96.46$, $P < 0.001$), indicating that the control law significantly changed compared to that in the TV-HV. For better viewing of the effects of these manipulations across two target direction conditions, residual errors of all left target-related conditions were calculated based on the regression coefficients obtained for the TV-HV condition, left-target and plotted in Fig. 3c, so that the results of both the front (Fig. 3a) and the left (Fig. 3c) target can be seen in relation to the TV-HV condition. The residual errors were calculated by subtracting experimentally measured values from the corresponding values predicted by the control-law model. The high negative residual errors for not-visible conditions indicate that the relationship between the aperture closure distance and the other three parameters was changed in a manner such that this distance was lengthened relative to these parameters when the vision of the hand or the target was not available. This implies that the threshold for the initiation of aperture closure was shifted to increase the safety margin for grasping when vision was not available. In addition, the residual errors significantly increased for the left-target conditions (Fig. 3b) as compared for the front-target conditions (Fig. 3a, $F(1,780) = 38.34$, $P < 0.001$), showing that the relationship between the aperture closure distance and the other three parameters was also changed so that this distance was shortened relative to these parameters for the left-target conditions.

Control law generalization by including conditional parameters

The above-demonstrated dependence of the control law on hand and target visibility and target location implies a possibility that the CNS utilizes condition-encoding parameters (hand and target visibility as well as target direction) together with the above movement parameters (aperture closure distance, aperture amplitude, wrist velocity, and acceleration) in controlling the initiation of aperture closure. If so, the approximation of aperture closure distance across the conditions with one control law would be improved when the conditional variables are added as independent parameters to the movement parameters for performing regression analyses. To test this hypothesis, one or more conditional variables were included into the control law model in addition to the movement parameters, and the corresponding regression analyses were carried out based on all trials across all conditions (except the CV condition) for all participants (Models as 1–6 in Materials and Methods section). As shown in Table 3a, the utilization of the three movement parameters in the control law model (Model 1) applied to all conditions produced a reasonably high R^2 value (0.66), indicating a strong dependence between those parameters and the closure distance. Similarly, high R^2 values ranging from 0.66 to 0.69 were obtained for the other models (Models 2–6), in which one or more conditional parameters were included in addition to the movement parameters (Table 3a). Compared to Model 1, the average absolute residual errors were significantly reduced when the model added the target visibility condition (Model 2), the target and hand visibility conditions (Model 5), and the target and hand visibility conditions as well as the target direction condition (Model 6) ($t(787) = 3.28$, $P < 0.01$ for Model 2; $t(787) = 4.94$; $P < 0.001$ for Model 5; and $t(787) = 5.26$, $P < 0.001$ for Model 6, Table 3a, see also Fig. 4). The residual errors were also reduced after a variable encoding hand visibility condition was added to the set of input parameters (Model 3) compared to Model 1 ($t(787) = 1.85$, $0.05 < P < 0.1$).

On the other hand, when a conditional parameter encoding the target direction was included in addition to the movement parameters (Model 4), the average absolute residual errors was not significantly different from those that resulted from Model 1, which only included movement parameters ($P > 0.05$). This indicates that the conditional parameter describing target direction did not improve the approximation of aperture closure. However, it is possible that the effect of including target direction was relatively small compared to those of target and hand visibility, thereby resulting in non-significant changes of residual errors. To eliminate the effects of manipulations of target and hand visibility, the same analysis was applied for the full vision (TV-HV) condition across both target direction conditions (Table 3b). In this case, the average absolute residual error was significantly reduced when the target direction was added (Model 4) compared to that of Model 1 ($t(194) = 2.234$, $P < 0.05$). This indicates that direction to the target also significantly modifies the control law for grasp initiation.

When the same analyses were applied to the subgroup of eight participants who showed similar parameter correlation (Fig. 2), higher R^2 values (ranging from 0.70 to 0.76) and smaller residual errors (ranging from 7.95 to 8.94) compared to those of all participants were found across models (Table 3a, b). The results of the foregoing comparisons between Model 1 and other models for only eight participants were the same as the results of all participants included except that the difference between the Model 3 and Model 1 based on all conditions became significant ($t(633) = 2.16$, $P < 0.05$), and that the difference between the Model 4 and Model 1 based on TV-HV condition became a trend ($t(158) = 1.70$, $P = 0.09$) in the case of 8 participants.

In summary, inclusion of each conditional parameter improved the accuracy of the control law model. A model that included all conditional parameters (Model 6) produced the highest R^2 value and the smallest average residual error among all models (Table 3a). Therefore, the CNS, when initiating aperture closure, seems to account for the environmental conditions related to the availability of vision of target and hand as well as for the difference in target direction by modulating the control law with additional parameters encoding those conditions.

A control law that includes conditional variables describing hand and target visibility as well as target direction in addition to the movement parameters (Model 6) can be used as a general control law for all experimental conditions. How accurate is that model? The absolute residual errors using Model 6 were obtained based on all trials and all conditions across all participants, while the errors using Model 1 were obtained based on all trials across all participants for each condition separately. The results showed that the average absolute residual error for Model 6 (10.61, Table 3a) was significantly greater than that for Model 1 (9.85, Table 3c, $t(787) = 4.09$, $P < 0.001$), indicating that Model 6 used for all conditions is less precise as Model 1 used for each condition separately. This difference indicates that the control law that includes all the condition parameters describing the availability of vision of the hand and the target as well as target direction is significantly non-linear (see Discussion for further details). Overall, the analysis of data from the eight participants showed results similar to those obtained for all the participants taken together (Table 3a, c).

Discussion

This study examined the effects of blocking the participant's view of the target and/or the hand during the control of reach-to-grasp movements. Visual information about the target provides static spatial information about the goal of a reach-to-grasp movement, while information about the hand as an effector is provided through vision and proprioception. The data analysis has revealed that the removal of visual feedback from the target, or the hand, or both significantly affected movement parameters (hand-target distance at aperture closure initiation, grip aperture amplitude, wrist velocity, and wrist acceleration) and their interrelationship. The explicit inclusion of the variables describing the vision-related and target direction-related conditions in the control law model of that relationship made the model invariant with respect to the difference in these experimental conditions.

Absence of visual feedback from the target or the hand affects the duration of aperture closure phase but not aperture opening phase

Removal of the vision of the hand increased transport duration, mainly due to prolongation of the aperture closure phase, which is in agreement with previous studies (Berthier et al. 1996; Churchill et al. 2000; Gentilucci et al. 1994; Schettino et al. 2003; Winges et al. 2003). Our results extend those obtained in the previous studies by demonstrating that blocking visual information about the target also increased transport duration as well as the time spent for the aperture closure movement phase. This suggests that on-line processing of visual information about the target and the hand is important for controlling aperture closure movement (Santello et al. 2002; Schettino et al. 2003; Servos and Goodale 1994; Winges et al. 2003). An increase in the time duration of the aperture closure phase was also reported when proprioceptive information about hand was unavailable (Gentilucci et al. 1994). Thus, the strategy of slowing the movement under conditions in which sensory information about the target or the arm is reduced is often used to ensure the accuracy of reach and grasping. At the same time, the duration of the transport phase from movement onset to the time of peak aperture (aperture opening time) was not significantly affected by manipulating hand visibility and was only marginally affected by manipulating vision of the target. These results support the idea that the initial part of the reach-to-grasp movement is mostly preplanned and executed without on-line feedback (Gentilucci et al. 1994).

The manipulation of hand or target visibility for the left target did not result in significant changes in the average value of movement parameters. In contrast, changes were significant for the front target location. A possible explanation for this difference is that reaching and grasping the front target requires greater amount of sensory information processing than that needed for the left target. That was so likely because, while the hand posture at the starting position was already in line with the left target, reaching for the front target location required extra maneuvering to position the wrist for comfortable grasping. This explanation is consistent with the finding that the safety margin for aperture closure was significantly increased in reaches to the front target compared to that in reaches for the left target.

Spatial coordination between the aperture and transport components

The location of the hand relative to the target at which the aperture closure was initiated (aperture closure distance) was influenced by manipulating target visibility, but not hand visibility. However, the average increase in aperture closure distance when shifting from the *target visible* condition to the *target not-visible* condition was relatively small (1 cm). A similar magnitude of increase was found for the removal of the vision of hand (Churchill et al. 2000). This small but significant alteration of aperture closure distance by manipulating target visibility indicates a possibility that the on-line information of target location is more critical for the control of aperture closure initiation compared to the on-line visual information about the moving hand. However, a firm conclusion about this cannot be made based on the results of the current study for two reasons. The first reason is that there is a discrepancy between the visibility of the hand and that of the target prior to the "go"-signal. Namely, the vision of the target was removed concurrently with the "go"-signal in the target not-visible condition, while the vision of the hand was removed from the beginning of the trial, prior to the "go"-signal, in the hand not-visible condition. This makes it difficult to compare the effects of hand visibility and those of target visibility. The second reason is the fact that the vision of the target or the hand was removed at the "go"-signal in the not-visible conditions instead of at movement initiation. This makes it difficult to distinguish between the contribution of on-line information and that of the information available during the initial programming phase of the movement prior to movement initiation. A future study that manipulates the visibility of the hand and target only after the movement initiation will clarify which on-line information between the hand and the target contributes more to the control of aperture closure initiation.

The removal of hand visibility may not be as critical as that of target visibility, since the participants can still utilize on-line proprioceptive feedback from the hand to determine its location and velocity. It is not clear, however, whether the proprioception generally predominates in providing on-line information about the moving hand for the initiation of aperture closure, or the proprioception optimally substitutes for vision. The higher dependence of prehension control on proprioception over the vision of the hand has been suggested previously (Gentilucci et al. 1994; Jeannerod 1986).

In the target not-visible trials where the target was visible only prior to the "go" stimulus for movement initiation, visual information about target location stored in memory might not be sufficiently accurate to fully substitute for the related on-line visual feedback. The greater aperture closure distance for this condition suggests that the distance between the target and the starting position is underestimated for the visuomotor integration between the target location and hand movement. Alternatively, because of the less accurate information processing of the target's location from memory, the participants might use a strategy to initiate the aperture closure at a distance further away from the target in order to increase the safety margin for aperture closure movements. Interestingly, a recent study (Heath and Westwood 2003) demonstrated that the memory-based representation of target location acquired immediately prior to the "go" signal for movement initiation was used as effectively as on-line target information for the on-line control of reaching movements (Heath and Westwood 2003). However, our data suggest that that is not the case for reach-to-grasp movements. Higher complexity of information processing required for controlling aperture closure during reach-to-grasp movements, compared to that in the case of simple pointing to a target (Bekkering and Neggers 2002) is likely to increase the dependency on the on-line visual information about target location.

The comparison of average closure distance between different conditions showed no statistically significant effect of hand visibility manipulation in contrast to the findings from Churchill et al. (2000), in which peak aperture occurred at further distance from the object under the no-hand visibility condition. One way to resolve this discrepancy is by taking into account the fact that the closure distance is a function of several parameters according to the control law Models (1–6). Indeed, the results of data analysis based on the control law concept have clearly shown that the safety margin for closure distance significantly increases when the hand or the target is not visible. The safety margin increases considerably more when both the hand and the target are not visible. It should be emphasized that these important conclusions could not be made based on separate comparisons of averages for each movement parameter between different experimental conditions. The control law framework for data analysis provided an adequate basis for detecting the effects of visibility manipulation on the control of aperture closure initiation.

Initiation of aperture closure under different conditions is governed by a generalized control law

In agreement with previous studies (Rand et al. 2006a, b), aperture closure distance was highly predictable based on the amplitude of maximum grip aperture, hand velocity, and hand acceleration, which represented the hand/arm dynamics at the time of aperture closure initiation (Fig. 3, Table 2). This suggests that a specific control law, arguments of which include these parameters, governs the initiation of aperture closure. The data analysis based on the control law models enabled us to examine whether changes of hand dynamics due to the manipulation of visual feedback, such as a widened grip aperture by the removal of the visual feedback of either the hand or a target, and increased aperture closure distance by the removal of target visibility (Table 1), were accompanied by the changes of grasp–transport relationship defined by the control law for the aperture closure initiation. It was revealed that the aperture closure distance threshold significantly increased when either the hand or target was not visible (Fig. 3). This implies that the participants increased the distance-related safety margin for grasping under these conditions.

Thus, the relationship between the aperture closure distance and other three movement parameters significantly depends on target location and two systematically varied environmental conditions: the vision of the target and the hand. At the same time, the results demonstrate that the control law for grasp initiation can be generalized to fit multiple conditions by including variables that encode those conditions as additional input parameters in the control law model. It was found that the approximation of aperture closure distance across different conditions was significantly improved when those additional parameters were included in the control law model. This suggests that the CNS utilizes the information regarding the availability of visual feedback of the hand and/or the target, which is obtained prior to the movement initiation, in order to adjust the control law for the grasp initiation to specific environmental conditions. Interestingly, the vision-related parameters improved the approximation of aperture closure distance more clearly than the target direction-related parameters. Hence, the CNS adjusts the control law to a greater extent based on the availability of vision than according to the target direction. The fact that the precision of the general control law across all the conditions (Model 6) was not as high as that of Model 1 when applied to each condition separately indicates a possibility that the relationship among the parameters becomes significantly nonlinear as the parameter values span greater range across several conditions. A non-linear regression technique, such as that based on the utilization of artificial neural networks as universal approximators of continuous non-linear functions, may produce better results. Exploring this possibility is an important direction of future research.

The current data analysis based on the control law models examined the relation among parameters at the time of aperture closure initiation. It seems possible that the same law describes the relationship between movement parameters during the *entire period* of aperture closure (from its initiation to a contact with the target). We plan to explore this interesting possibility in a forthcoming study.

The concept of a control law is considerably more than just a convenient framework for behavioral data processing. The corresponding mathematical models of relationship between behavioral parameters can be viewed also as models for sensory information processing performed by the CNS to make a decision for grasp initiation. Their testing in neurophysiological experiments is another important line of further research.

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References

Alberts JL, Saling M, Stelmach GE. Alterations in transport path differentially affect temporal and spatial movement parameters. Exp Brain Res 2002;143:417–425. [PubMed: 11914786]

Bekkering H, Neggers SFW. Visual search is modulated by action intentions. Psychol Sci 2002;13:370–374. [PubMed: 12137141]

Berthier NE, Clifton RK, Gullapalli V, McCall DD, Robin D. Visual information and object size in the control of reaching. J Mot Behav 1996;28:187–197. [PubMed: 12529202]

Churchill A, Hopkins B, Rönnqvist L, Vogt S. Vision of the hand and environmental context in human prehension. Exp Brain Res 2000;134:81–89. [PubMed: 11026729]

Connolly JD, Goodale MA. The role of visual feedback of hand position in the control of manual prehension. Exp Brain Res 1999;125:281–286. [PubMed: 10229019]

Darling WG, Miller GF. Transformation between visual and kinesthetic coordinate systems in reaches to remembered object locations and orientations. Exp Brain Res 1993;93:534–547. [PubMed: 8519342]

Davis, JH. Foundations of deterministic and stochastic control. Birkhäuser; Boston: 2002.

Gentilucci M, Toni I, Chieffi S, Pavesi G. The role of proprioception in the control of prehension movements: a kinematic study in a peripherally deafferented patient and in normal participants. Exp Brain Res 1994;99:483–500. [PubMed: 7957728]

Heath M, Westwood DA. Can a visual representation support the online control of memory-dependent reaching? Evidence from a variable spatial mapping paradigm. Motor Control 2003;7:346–361. [PubMed: 14999133]

Jackson SR, Jackson GM, Rosicky J. Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. Exp Brain Res 1995;102:519–530. [PubMed: 7737398]

Jackson SR, Jones CA, Newport R, Pritchard C. A kinematic analysis of goal-directed prehension movements executed under binocular, monocular, and memory-guided viewing conditions. Vis Cogn 1997;4:113–142.

Jakobson LS, Goodale MA. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res 1991;86:199–208. [PubMed: 1756790]

Jeannerod M. The formation of finger grip during prehension. A cortically mediated visuomotor pattern. Behav Brain Res 1986;19:99–116. [PubMed: 3964409]

Rand MK, Shimansky Y, Stelmach GE, Bloedel JR. Adaptation of reach-to-grasp movement in response to force perturbations. Exp Brain Res 2004;154:50–65. [PubMed: 14530893]

Rand MK, Stelmach GE. Effect of orienting the finger opposition space in the control of reach-to-grasp movements. J Mot Behav 2005;37:65–78. [PubMed: 15642693]

Rand MK, Smiley-Oyen AL, Shimansky YP, Bloedel JR, Stelmach GE. Control of aperture closure during reach-to-grasp movements in Parkinson's disease. Exp Brain Res 2006a;168:131–142. [PubMed: 16307233]

Rand MK, Squire LM, Stelmach GE. Effect of speed manipulation on the control of aperture closure during reach-to-grasp movements. Exp Brain Res 2006b;174:74–85. [PubMed: 16565810]

Rand MK, Squire LM, Lemay M, Shimansky YP, Stelmach GE. Effect of the presence of vision on finger closure during reach-to-grasp movements. Soc Neurosci Abstr 2006c;32:147.1.

Santello M, Flanders M, Soechting JF. Patterns of hand motion during grasping and the influence of sensory guidance. J Neurosci 2002;22:1426–1435. [PubMed: 11850469]

Schettino LF, Adamovich SV, Poizner H. Effects of object shape and visual feedback on hand configuration during grasping. Exp Brain Res 2003;151:158–166. [PubMed: 12783144]

Schettino LF, Adamovich SV, Hening W, Tunik E, Sage J, Poizner H. Hand preshaping in Parkinson's disease: effects of visual feedback and medication state. Exp Brain Res 2006;168:186–202. [PubMed: 16041510]

Servos P, Goodale MA. Binocular vision and the on-line control of human prehension. Exp Brain Res 1994;98:119–127. [PubMed: 8013579]

Servos P, Goodale MA, Jacobson LS. The role of binocular vision in prehension: a kinematic analysis. Vision Res 1992;32:1513–1521. [PubMed: 1455724]

Shimansky YP, Kany T, He J. A novel model of motor learning capable of developing an optimal movement control law online from scratch. Biol Cybern 2004;90:133–145. [PubMed: 14999480]

Sivak B, MacKenzie CL. Integration of visual information and motor output in reaching and grasping: the contributions of peripheral and central vision. Neuropsychologia 1990;28:1095–1116. [PubMed: 2267060]

Teasdale N, Bard C, Fleury M, Young D, Proteau L. Determining movement onsets from temporal series. J Mot Behav 1993;25:97–106. [PubMed: 15064201]

Wang J, Stelmach GE. Coordination among the body segments during reach-to-grasp action involving the trunk. Exp Brain Res 1998;123:346–350. [PubMed: 9860274]

Wang J, Stelmach GE. Spatial and temporal control of trunk-assisted prehensile actions. Exp Brain Res 2001;136:231–240. [PubMed: 11206285]

Watt SJ, Bradshaw MF. Binocular cues are important in controlling the grasp but not the reach in natural prehension movements. Neuropsychologia 2000;38:1473–1481. [PubMed: 10906373]

Wing AM, Turton A, Fraser C. Grasp size and accuracy of approach in reaching. J Mot Behav 1986;18:245–260. [PubMed: 15138146]

Winges SA, Weber DJ, Santello M. The role of vision on hand preshaping during reach to grasp. Exp Brain Res 2003;152:489–498. [PubMed: 12898088]

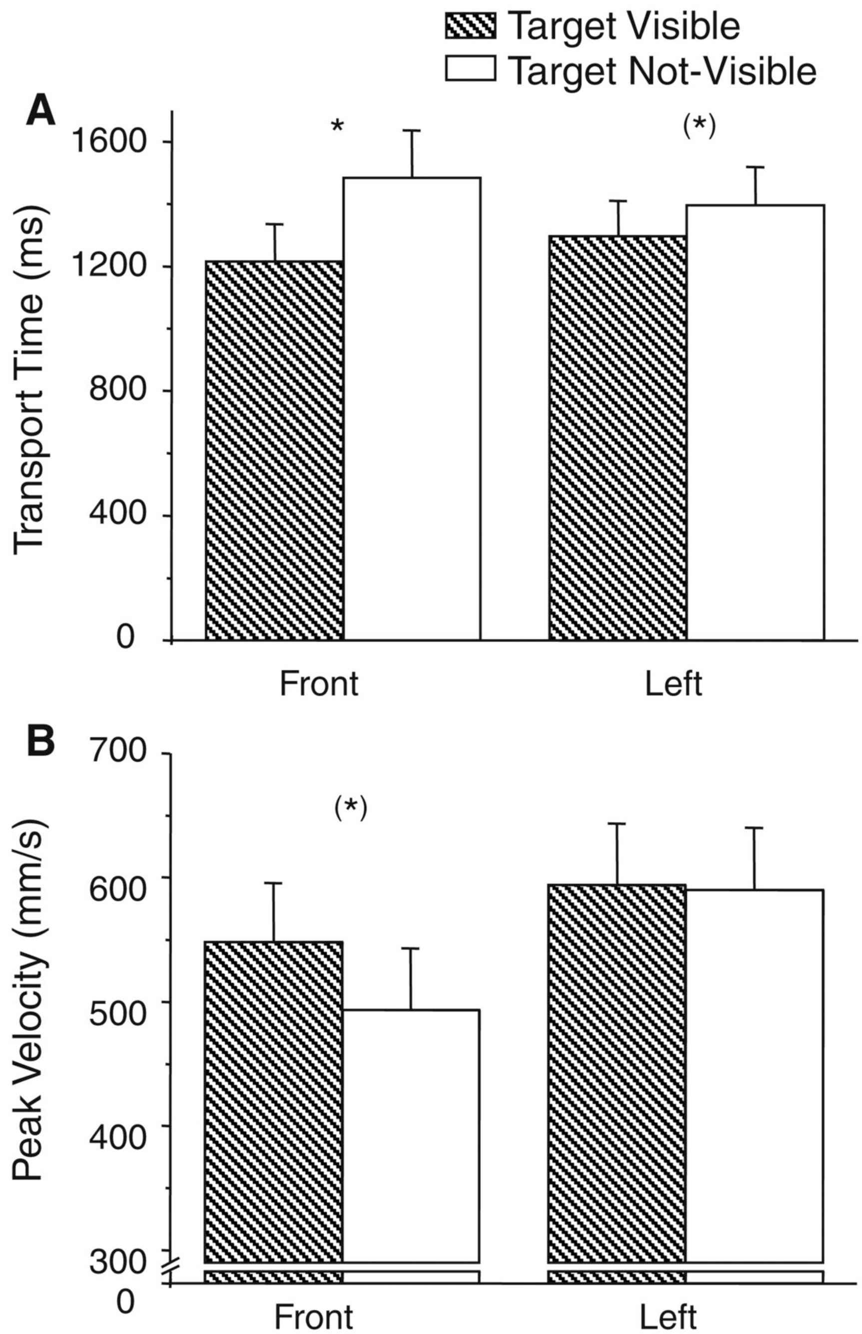

Fig. 1.

Mean transport time (a) and mean peak velocity (b) for reach-to-grasp movements for front and left targets under target visibility manipulations. The *shaded columns* refer to the target visible condition and the *white columns* refer to the target not-visible condition. Mean values across all participants and SE (*error bars*) are plotted. * $P < 0.05$; (*) $0.05 < P < 0.1$

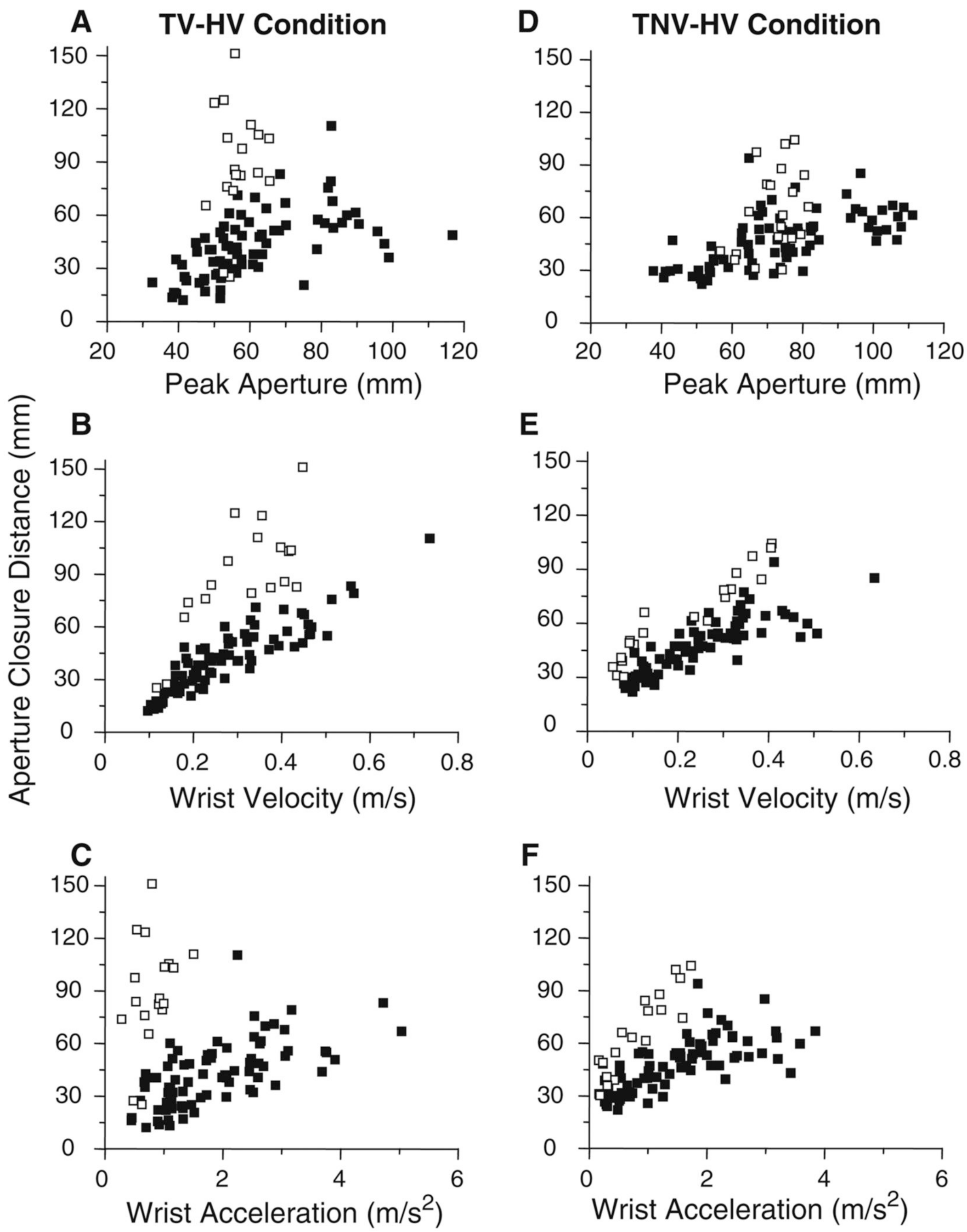

Fig. 2.

Scatter plots for the aperture closure distance as a function of the amplitude of aperture (a, d), the wrist velocity (b, e), and wrist acceleration (c, f) at the time of maximum aperture. The data from all trials from eight participants (*filled squares*) and two participants (*open squares*, who showed different patterns from others) are plotted for the target-visible, hand-visible condition (*TV-HV*, a–c) and the target-not-visible, hand-visible condition (*TNV-HV*, d–f) of the front target

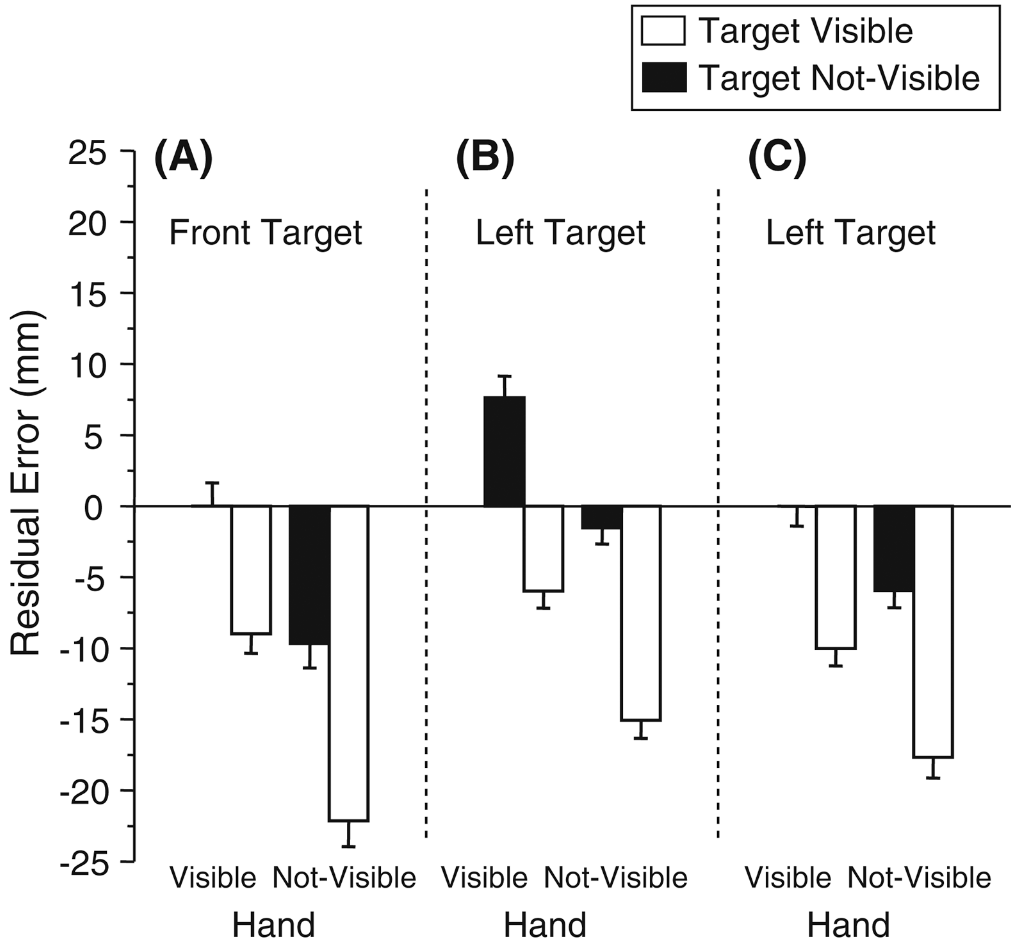

Fig. 3.
Mean residual errors for all conditions of the target and hand visibility manipulations including the visible condition and not-visible condition. Mean residual error values for the front and left target conditions are calculated based on the target-visible, hand-visible (*TV-HV*) front-target condition (a, b). The values for the left target condition are also calculated based on the TV-HV left-target condition (c). Mean values across all participants and SE (*error bars*) are plotted

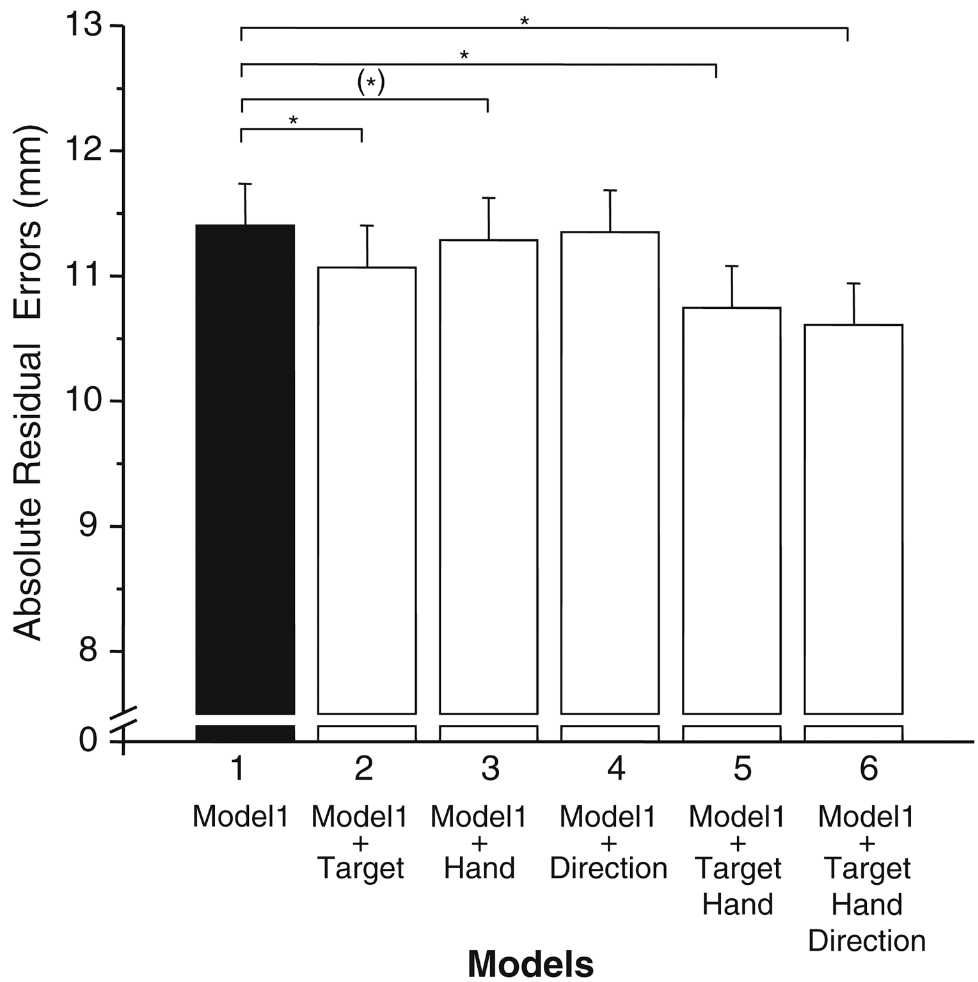

Fig. 4.

Absolute residual errors for all models. Mean values across all trials, all conditions and all participants are plotted. *Error bars* represent standard errors. * $P < 0.01$; (*) $0.05 < P < 0.1$

Table 1

Effect of hand and target visibility on the kinematic parameters of reach-to-grasp movements

	Target		Hand		Direction	
	Visible	Not-visible	Visible	Not-visible	Front	Left
Transport time (ms)	1,257 (115)	1,441 (136)**	1,316 (121)	1,382 (127)*	1,351 (132)	1,347 (116)
Transport length (mm)	285 (7)	282 (6)	284 (7)	284 (7)	265 (8)	303 (6)**
Peak velocity (mm/s)	571 (48)	542 (49)*	560 (50)	553 (47)	521 (47)	592 (49)**
Amplitude of peak aperture (mm)	64 (5)	77 (5)**	65 (4)	77 (5)**	73 (5)	68 (4)**
Aperture opening time (ms)	777 (78)	786 (88)	779 (79)	784 (87)	761 (83)	802 (83)*
Aperture closure time (ms)	480 (63)	654 (70)**	536 (67)	597 (64)*	589 (71)	544 (58)*
Aperture opening distance (mm)	236 (7)	225 (6)*	231 (8)	230 (4)	211 (6)	250 (7)*
Aperture closure distance (mm)	49 (7)	57 (5)*	52 (7)	54 (5)	53 (5)	53 (6)

Values are mean (SE)

df = 1, 9

* $P < 0.05$

** $P < 0.01$

Table 2

R^2 values and mean absolute residual errors across all trials for each condition by using Model 1

Condition	Ten subjects		Eight subjects		Two subjects	
	R^2	Residual errors	R^2	Residual errors	R^2	Residual errors
Front target						
Target visible, hand visible	0.67***	12.15	0.82***	6.49	0.60**	15.85
Target visible, hand not-visible	0.56***	11.13	0.73***	8.00	0.84***	6.68
Target not-visible, hand visible	0.60***	9.35	0.71***	5.77	0.92***	5.27
Target not-visible, hand not-visible	0.51***	11.06	0.64***	9.15	0.87***	5.65
Left target						
Target visible, hand visible	0.83***	9.68	0.92***	4.91	0.92***	11.11
Target visible, hand not-visible	0.86***	7.19	0.86***	6.63	0.98***	3.84
Target not-visible, hand visible	0.83***	8.27	0.82***	7.47	0.95***	6.21
Target not-visible, hand not-visible	0.64***	10.01	0.57***	10.05	0.91***	5.62

** $P < 0.01$

*** $P < 0.001$

Table 3

R^2 values and mean absolute residual errors across all trials of all subjects for each model

	Ten subjects			Eight subjects		
	R^2	Residual errors	*t*-Test	R^2	Residual errors	*t*-Test
(a) *Based on all conditions*						
Model 1	0.66	11.40	—	0.70	8.94	—
Model 2: Model 1 plus Tv	0.67	11.07	*bb*	0.74	8.45	*bbb*
Model 3: Model 1 plus Hv	0.66	11.29	*(b)*	0.71	8.77	*b*
Model 4: Model 1 plus Td	0.66	11.35	ns	0.71	8.92	ns
Model 5: Model 1 plus Tv and Hv	0.68	10.75	*bbb*	0.76	8.02	*bbb*
Model 6: Model 1 plus Tv, Hv, and Td	0.69	10.61	*bbb*	0.76	7.95	*bbb*
(b) *Based on TV-HV condition only*						
Model 1	0.74	11.74	—	0.85	6.13	—
Model 4: Model 1 plus Td	0.75	11.18	*c*	0.88	5.75	*(c)*
(c) *Based on each condition separately*[a]						
Model 1	—	9.85	*ddd*	—	7.31	*ddd*

Tv target visibility condition, *Hv* hand visibility condition, *Td* target direction condition

[a] Residual errors are calculated for each condition separately and then all residual errors are pooled together across all conditions

[bbb] $P < 0.001$,

[bb] $P < 0.01$,

[b] $P < 0.05$,

[(b)] $0.05 < P < 0.1$; *ns* not significant for a comparison of residual errors from Model 1 in the section (a)

[c] $P < 0.05$,

[(c)] $0.05 < P < 0.1$ for a comparison of residual errors from Model 1 in the section (b)

[ddd] $P < 0.001$ for a comparison of residual errors from Model 6 in the section (a)