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RESEARCH ARTICLE

Quantitative model of transport-aperture coordination during reach-to-grasp movements

Miya K. Rand · Y. P. Shimansky · Abul B. M. I. Hossain · George E. Stelmach

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Abstract It has been found in our previous studies that the initiation of aperture closure during reach-to-grasp movements occurs when the hand distance to target crosses a threshold that is a function of peak aperture amplitude, hand velocity, and hand acceleration. Thus, a stable relationship between those four movement parameters is observed at the moment of aperture closure initiation. Based on the concept of optimal control of movements (Naslin 1969) and its application for reach-to-grasp movement regulation (Hoff and Arbib 1993), it was hypothesized that the mathematical equation expressing that relationship can be generalized to describe coordination between hand transport and finger aperture during the entire reach-to-grasp movement by adding aperture velocity and acceleration to the above four movement parameters. The present study examines whether this hypothesis is supported by the data obtained in experiments in which young adults performed reach-to-grasp movements in eight combinations of two reach-amplitude conditions and four movement-speed conditions. It was found that linear approximation of the mathematical model described the relationship among the six movement parameters for the entire aperture-closure phase with very high precision for each condition, thus supporting the hypothesis for that phase. Testing whether one mathematical model could approximate the data across all the experimental conditions revealed that it was possible to achieve the same high level of data-fitting precision only by including in the model two additional, condition-encoding parameters and using a nonlinear, artificial neural network-based approximator with two hidden layers comprising three and two neurons, respectively. This result indicates that transport-aperture coordination, as a specific relationship between the parameters of hand transport and finger aperture, significantly depends on the condition-encoding variables. The data from the aperture-opening phase also fit a linear model, whose coefficients were substantially different from those identified for the aperture-closure phase. This result supports the above hypothesis for the aperture-opening phase, and consequently, for the entire reach-to-grasp movement. However, the fitting precision was considerably lower than that for the aperture-closure phase, indicating significant trial-to-trial variability of transport-aperture coordination during the aperture-opening phase. Implications for understanding the neural mechanisms employed by the CNS for controlling reach-to-grasp movements and utilization of the mathematical model of transport-aperture coordination for data analysis are discussed.

Keywords Prehension · Kinematics · Coordination · Control law

Introduction

The visually observed stability of the relationship between hand transport (transport component) and finger aperture (grasp component) during reach to grasp (Jeannerod 1984; Jeannerod et al. 1995) has inspired efforts to find a formalized description of coordination between those two movement components. If a constructive description is

M. K. Rand (✉) · A. B. M. I. Hossain · G. E. Stelmach
Motor Control Laboratory, Department of Kinesiology, Arizona State University, Box 870404, Tempe, AZ 85287-0404, USA
e-mail: rand@asu.edu

Y. P. Shimansky
Harrington Department of Bioengineering, Arizona State University, Tempe, AZ 85287-9709, USA

found that is invariant across a wide variety of experimental conditions, it can be used as a model for the normal pattern of transport-aperture coordination. That model would provide a basis for differentiating between the norm and pathologies with respect to the regulation of those movements. In addition, such a description is likely to offer valuable insights into the neural mechanisms of controlling reach-to-grasp movements.

Several different approaches to formulating a description of transport-aperture coordination have been suggested. The early observations that grasp formation and kinematics of the arm transport are temporally interlinked (Jeannerod 1981, 1984) were supported by a few subsequent studies (Marteniuk et al. 1990; Rand et al. 2000; Wallace and Weeks 1988; Wallace et al. 1990). More specifically, transport-aperture coordination was described as a temporal correlation between the peak of grip aperture and the peak of wrist velocity, or between the peak of grip aperture and the peak of wrist deceleration (Castiello et al. 1998, 1999; Churchill et al. 1999, 2000; Gentilucci et al. 1991; Jeannerod 1984; Saling et al. 1996; Timmann et al. 1996). However, because the temporal relationship significantly varied depending on certain parameters (the size of the target, the amplitude, and speed of transport), that approach to describing transport-aperture coordination did not produce a sufficiently universal and constructive description. It was also observed that maximum aperture occurred at a relatively fixed percentage of time with respect to the total movement duration under various transport durations or speeds (Marteniuk et al. 1990; Rand et al. 2000; Smeets and Brenner 1999; Wallace and Weeks 1988; Wallace et al. 1990). However, a contradicting observation that the duration of aperture closure was relatively constant under different task conditions was made in some other studies (Bootsma and van Wieringen 1992; Gentilucci et al. 1992; Paulignan et al. 1991; Watson and Jacobson 1997; Zaal et al. 1998).

Alternatively, it was suggested that the grasp and transport components are coordinated based on spatial parameters, as grip aperture was highly dependent on the distance between the hand and the target (Haggard and Wing 1991, 1995). Previous studies performed in our laboratory supported this view by demonstrating that the hand–target distance at which aperture closure was initiated during hand transport was more invariant across various task conditions than the related temporal parameters (Alberts et al. 2002; Rand and Stelmach 2005; Rand et al. 2004; Wang and Stelmach 1998, 2001). That invariance suggests that the hand–target distance information is important for the CNS to determine the initiation of aperture closure. Our most recent studies demonstrated that the hand–target distance at which aperture closure was initiated actually varied systematically depending on several movement parameters, such as transport velocity and acceleration (Rand et al. 2006a, b, 2007a). Thus, it has appeared that transport-aperture coordination at the time of grasp initiation cannot be in general described by only one spatial parameter, and therefore, requires a more complex form of description, namely as a special relationship between several parameters of hand transport and finger aperture viewed as state space coordinates.

To develop a mathematical representation of that relationship, we previously applied the theoretical concept of an optimal control law (e.g., Naslin 1969) to describe transport-aperture coordination for initiating the aperture closure during reach-to-grasp movements. A control law describes the dependence of control action (expressed, e.g., 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. 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. Specifically, we presumed that finger closure is initiated during the reach when the distance to target (D) crosses a threshold (D_{thr}) that is a function of grip aperture (G), hand velocity (V_{w}), and hand acceleration (A_{w}) measured at the time of finger closure initiation:

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

It was assumed that aperture closure was not initiated when $D > D_{\mathrm{thr}}$. The previous studies by Rand et al. (2006a, b, 2007a) confirmed that this theoretical model adequately describes the relationship between movement parameters at the initiation of aperture closure during the reach and is highly consistent across trials and subjects. This form of describing transport-aperture coordination has proved very useful for quantifying effects of different experimental conditions, which often can be presented as a general shift of the hand–target distance threshold and interpreted as an increase or decrease in safety margin (Rand et al. 2006c, 2007a). Importantly, such an effect cannot be expressed based on a difference in the value of just one kinematic parameter, because such a parameter usually varies within a wide range between different trials and subjects.

The fact that Eq. 1 fits experimental data across different subjects and conditions with high precision has led us to a hypothesis that a similar, more general equation must fit the entire aperture-closure phase and perhaps the aperture-opening phase as well. If so, that equation can provide a constructive way of describing transport-aperture coordination during the entire movement that includes both aperture-opening and closure phases. This hypothesis is based on the following considerations. Since reach-to-grasp movements are performed very frequently, the corresponding skill must be very well learned, meaning that the movement is highly optimized. It can be easily shown that, if the control system is optimal, there has to be tight coordination between independently controlled processes that are required to finish simultaneously with each other and have a definite final state. In the case of reach-to-grasp movements, there are two such processes: hand transport and grasping, the final state of which is determined by the target's location and size, respectively. It is shown in the "Appendix" that under the above conditions transport-aperture coordination can be described by the following equation (Model 1, same as Eq. 13 in "Appendix").

$$D = D(A_w, V_w, G, A_g, V_g), \quad (2)$$

where V_g and A_g are grip aperture velocity and acceleration, respectively, and the other variables are the same as above (see Eq. 1). This equation can be viewed as a generalization of Eq. 1 from the point of aperture-closure initiation (where $V_g = 0$) to the entire movement. Thus, if the control of transport-aperture coordination is optimal (or almost optimal), one can expect that the experimental data fit Eq. 2 with high precision. We test this theoretical prediction using our experimental data and explore the dependence of the precision with which the data fit Eq. 2 on the movement phase and experimental condition.

The exact form and the coefficients of Eq. 2 could be derived analytically if formulas for the criteria of hand transport and grip aperture optimality were known. However, those formulas are not known. In this situation, the hypothesis to be verified based on the experimental data is that *the same* equation (i.e. Eq. 2) holds for each point in time throughout the reach-to-grasp movement across different trials and different subjects. To verify that hypothesis, we have sought the least complex universal approximator[1] of the above function $D(A_w, V_w, G, A_g, V_g)$ that could fit the experimental data with high precision. Preliminary findings of this study were presented elsewhere (Rand et al. 2007b).

Materials and methods

The data analyzed in this study were obtained in a previous experimental study (Rand et al. 2006b). The experimental procedures are summarized as follows. Eleven young adults [22.3 ± 2.0 (mean ± SD) years old] signed an informed consent prior to participation in this experiment. Each subject was seated comfortably at a table and was required to reach for grasp with the index finger and thumb, and lift a cylinder target (2.1 cm in diameter, 10 cm height) off the table. Reaching amplitude was either 15 cm (near) or 30 cm (far). Based on the experimenter's verbal instruction, subjects modified their general movement speed across four conditions: *slow*, *comfortable*, *fast but comfortable*, and *as fast as possible*. In the rest of the text, these four conditions are referred to as *slow*, *normal*, *fast*, and *maximum*. Ten trials per condition were analyzed. Arm and finger positions during reach-to-grasp movements were recorded at a rate of 100 Hz by using an Optotrak 3D system (Northern Digital). Infrared light emitting diodes (IREDs) were placed over the wrist, tip of the index finger, the tip of the thumb and the target. Further details are described in Rand et al. (2006b).

Data analysis

For the assessment of relationship between movement parameters that corresponds to transport-grasp coordination, the following six parameters were measured for each sampling point throughout the prehension movement in each trial: (1) hand–target distance (D), (2) grip aperture (G), (3) the velocity of grip aperture (V_g), (4) the acceleration of grip aperture (A_g), (5) the wrist velocity (V_w), and (6) the wrist acceleration (A_w). These six parameters completely describe the (one-dimensional) dynamics of hand transport and that of finger aperture.[2] Hand transport was assessed based on the position of the wrist IRED. Wrist velocity during the reach was the tangential velocity calculated as the first derivative of wrist position. Wrist acceleration was calculated as the derivative of wrist velocity. Grip aperture was defined as the distance between two IREDs positioned on the thumb and index finger, respectively. Grip aperture velocity and acceleration was calculated as the first and second derivative of grip aperture data, respectively. The hand–target distance was calculated as a distance between two wrist IRED positions: one at the time of sampling and the other at the time of target contact. Based on the aperture profile, movements were divided into aperture-opening phase (from movement onset to

[1] The least complex approximator is the one with the smallest number of coefficients requiring optimization to fit the data. The simplest possible approximator is a linear function, where the optimization of the coefficients is made through linear regression. It corresponds to an artificial neural network consisting of only one neuron that computes a weighed sum of the inputs.

[2] To someone who is used to thinking about motor control in terms of kinematic parameters as continuous sequences of values within a specific time interval, it might seem that, since, for instance, acceleration as a function of time can be computed as a time derivative of velocity, it must be sufficient to include only one such parameter in equations. In the case of the equation describing transport-aperture coordination, however, *instantaneous* values of such parameters are involved, and therefore, a different logic applies. Knowledge of hand velocity at a certain time point t in general does not allow one to calculate hand acceleration and vice versa. For this reason, these kinematic variables are viewed in theoretical mechanics as state coordinates independent of each other.

maximum aperture), and aperture-closure phase (from maximum aperture to target contact).

Fitting experimental data into a mathematical model of relationship between movement parameters

For best fitting the experimental data into the mathematical model represented by an equation that describes hand–target distance as a function of other, movement- and condition-related parameters, both linear and nonlinear regression methods were used. In both cases, the coefficients of the function approximator were determined based on the standard method of least squares (through the minimization of the sum of approximation error squares).

Aperture-closure phase To test whether the experimental data fit Model 1 (Eq. 2), the coefficients of the model were identified based on all data points obtained during the aperture-closure period from all trials and all subjects. Those model coefficients were subsequently used to calculate the approximation (residual) error for each data point of the entire phase. Because the biomechanical properties of the arm and the hand are quite similar across human subjects, it is reasonable to assume that movement control optimization will result in approximately the same pattern of transport-aperture coordination in different subjects. For this reason, we combined trials from all subject into one group (for each condition) for data analysis in this study. In a forthcoming paper dedicated to the analysis of the variability of transport-aperture coordination, we will explore both the intertrial variability of it for each subject and its intersubject variability.

To compare the magnitude of data-fitting residual errors during the aperture-closure phase between different conditions, the model of transport-aperture coordination was applied to approximate data for each condition separately. The magnitude of residual errors was calculated (as the square root of mean square) for each condition across all data points of the aperture-closure phase from all trials performed under that condition by all subjects. Since the model's coefficients were determined based on the standard method of minimizing the sum of approximation error squares, the mean value of the residual errors across all the above data points was zero, and therefore, the residual error magnitude was equal to the standard deviation of the residual errors. For that reason, that magnitude was statistically compared between different conditions using Levene's test for variance homogeneity.

To find out whether the approximation of hand–target distance during the aperture-closure phase can be improved by adding conditional variables encoding reaching amplitude and speed to Model 1, the reaching amplitude (R_a) was encoded as 1 (*near*) or 2 (*far*) and the movement speed condition (M_s) was encoded as 1 (*slow*), 2 (*normal*), 3 (*fast*), or 4 (*maximum*). One or both of these conditional variables were added to Model 1 as following. Model 2 includes the reaching amplitude, R_a:

$$D = D(V_w, A_w, G, V_g, A_g, R_a). \tag{3}$$

Model 3 includes the movement speed, M_s:

$$D = D(V_w, A_w, G, V_g, A_g, M_s). \tag{4}$$

Model 4 includes both the reaching amplitude and the movement speed:

$$D = D(V_w, A_w, G, V_g, A_g, R_a, M_s). \tag{5}$$

Subsequently, the magnitude (the square root of average square) of residual errors was calculated for each model and then statistically compared between Model 1 and other models using Levene's test for variance homogeneity.

Aperture-opening phase To examine how well the Model 1 describes the transport-aperture coordination during the aperture-opening phase, the following procedures were executed across all subjects and all trials for each condition separately: (1) the values (D, G, V_g, A_g, V_w, and A_w) at each sampling point during the aperture-opening phase were normalized based on average duration of the opening phase across all trials; (2) a mean duration of aperture closure across all trials was calculated to determine the width of the time window for residual error calculation during opening phase; (3) the model coefficients were identified based on best-fitting all sampling points within a sliding window starting from the first sampling point of the aperture-opening phase; (4) the residual errors were then calculated based on the model coefficients; (5) the same procedure as (3) and (4) were repeated for each of the subsequent window positions until the window end reached the last data point of the aperture-opening phase. Additionally, to illustrate statistically significant differences among residual errors across the windows, the confidence interval at which residual error values became significantly different from the mean value was determined for each window by using the unpaired t test ($P < 0.05$).

In addition, for visual assessment of the difference in the magnitude (average absolute value) of residual errors between the aperture-opening and aperture-closure phases, the median magnitude of the residual errors for the aperture-closure phase was determined for each condition. For this purpose, the residual error absolute values across all data points within the aperture-closure phase (after its time-normalization) were divided into three subgroups based on the error magnitude (smallest one-third, greatest one-third, and middle one-third). Then, the average error value across the middle subgroup was calculated.

Nonlinear approximation of the function determining the dependence of the relationship between movement parameters on experimental condition

In addition to linear approximation of the relationship between movement parameters described by Model 4 (Eq. 5) for the aperture-closure phase, a nonlinear approximation technique based on artificial neural networks (ANN) was utilized to verify whether residual errors resulting from data-fitting could be significantly reduced.

The complexity (i.e. the number of neuron-like units) of a feedforward ANN approximating the data was selected as minimal among ANN capable of implementing Model 4 and thereby representing the dependence of transport-aperture coordination on the conditional variables with a sufficient level of accuracy. Specifically, the residual error magnitude was considered sufficiently small if it was not statistically greater than the average (across different conditions) accuracy of Model 1 when used to approximate the data for each condition separately. It was found (see "Results" for detail) that an ANN with two hidden layers of nonlinear, neuron-like units with 3 and 2 units in the first and the second layers, respectively, (ANN "3 + 2") met the above conditions. The optimization of ANN synaptic coefficients was performed based on the standard error back-propagation method. The dataset was divided into two subsets of randomly selected movement parameter vectors that are approximately equal in size: one for training the ANN and one for its validation. The limit for the number of optimization iterations was set at 5×10^5. Usually training is supposed to be stopped when the square-root average approximation error across the validation dataset starts increasing (to avoid overfitting). However, in our case, it never increased[3]; therefore, the training was always stopped after all the iterations had been performed. The residual errors produced on the validation dataset were used as ANN-based approximation output. Subsequently, the magnitude of the residual errors was calculated and then statistically compared between different ways of data approximation using Levene's test.

The same nonlinear approximation technique based on the above ANN "3 + 2" was used for the aperture-opening phase to examine whether the residual errors of data-fitting could be significantly reduced compared to those obtained with a linear implementation of Model 1.

[3] This was so apparently due to the fact that the number of patterns for ANN training was very large (10,000) compared to the number of unknown coefficients (i.e. synaptic weights), which was not greater than 35 for the set of ANN candidates. Therefore, the probability of overfitting was practically zero.

Results

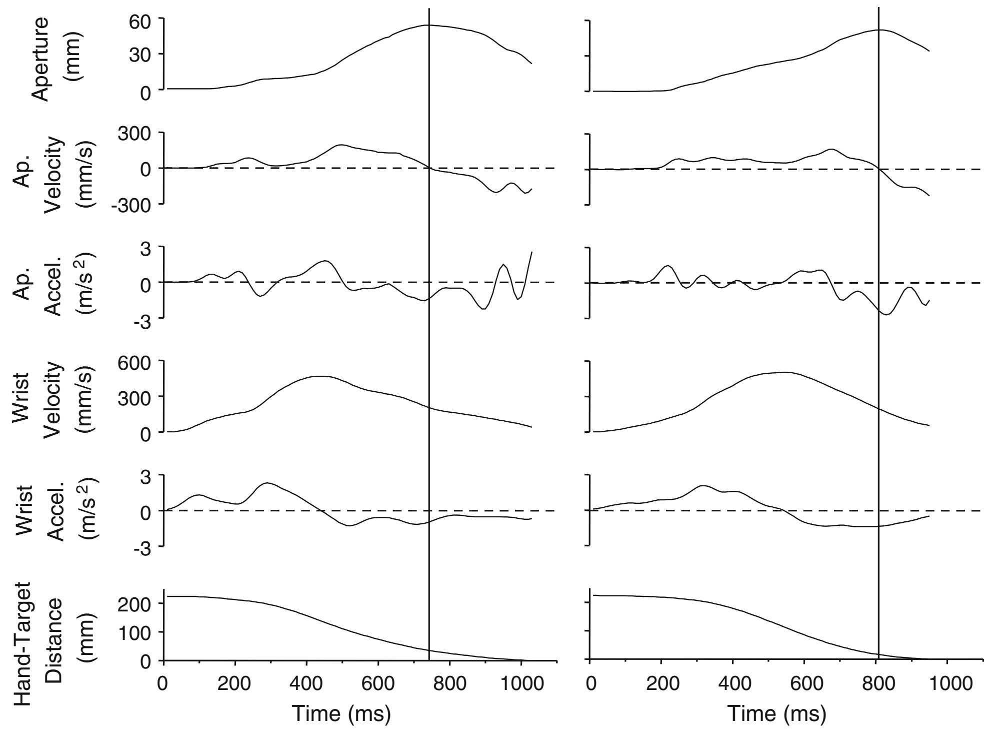
General characteristics of reach-to-grasp movements under the four speed conditions (*Slow* [S], *Normal* [N], *Fast* [F], and *Maximum* [M]) and two movement-amplitude conditions were described in detail in the previous study (Rand et al. 2006b). In brief, the average transport time decreased from the *slow* to the *maximum* condition (S: 1,854, N: 882, F: 540, and M: 385 ms for the *near target*; 2,348, 1,057, 618, and 466 ms for the *far target*, respectively). This change was accompanied by the increase in peak velocity of the hand transport movement (S: 151, N: 284, F: 436, and M: 620 mm/s for the *near target*; 238, 513, 847, and 1,139 mm/s for the *far target*, respectively) and by the increase in the amplitude of the maximum finger aperture (S: 41, N: 52, F: 67, and M: 81 mm for the *near target*; 40, 51, 69, and 84 mm for the *far target*, respectively). The current study is focused on the analysis of transport-aperture coordination during the aperture-opening phase and the aperture-closure phases.

From a theoretical perspective, Model 1 (see "Introduction") must be valid for the entire reach-to-grasp movement. However, the corresponding relationship between movement parameters is substantially nonlinear, since, e.g., correlation between hand–target distance and finger aperture is negative during the aperture-opening phase and positive during the aperture-closure phase. In addition, the former phase is usually described as fast and less accurate in contrast with the latter phase, which is significantly slower and is characterized by higher precision. For these reasons, the testing of the hypothesis that Model 1 accurately describes coordination between hand transport and grasp aperture in terms of relationship between the corresponding movement parameters was performed for the above two phases separately. It is started from the aperture-closure phase, because higher precision of transport-aperture coordination during that phase is expected based on other behavioral observations made in previous studies (Ansuini et al. 2007; Haggard and Wing 1997; Santello and Soechting 1998; Schettino et al. 2003; Winges et al. 2003; see also Mason et al. 2004; Theverapperuma et al. 2006, in primates).

Aperture-closure phase

The profiles of hand transport- and grasp-related movement parameters for the aperture-closure phase were relatively complex and substantially varied from trial to trial (Fig. 1). Nevertheless, fitting the data into a linear version of Model 1 showed that it was possible to present hand–target distance as a function of the other five movement parameters with relatively high precision (Fig. 2). By optimizing the coefficients of Model 1 for the aperture-closure phase and

Fig. 1 Examples of kinematic profiles from two consecutive reach-to-grasp movement trials performed under the *far-target* and *normal-speed* condition. Grip aperture, velocity and acceleration of grip aperture displacement, wrist velocity, wrist acceleration, and hand–target distance are plotted against hand-transport time. The *vertical line* in each plot indicates the time of maximum aperture (i.e., the time of aperture closure initiation)



applying those coefficients to the entire movement for residual error calculation, it was revealed that the residual errors were rather large at the beginning of the movement and gradually reduced to a minimum by the end of the aperture-opening phase (i.e., by the time of the initiation of aperture closure) (Fig. 2). The residual error magnitude was very small throughout the aperture-closure phase for both the *near-* and *far-target* conditions, indicating that the transport-aperture coordination was highly precise throughout that entire phase and consistent across different trials and subjects. These characteristics were the same for all speed conditions.

The magnitude (square root from average square) of residual errors across all subjects and all trials was calculated for each condition to compare the accuracy of Model 1 between different conditions (Fig. 3). The residual errors were greater for the *far target* than for the *near target*. The difference in the variance of residual errors between *near-* and *far-target* conditions was significant for each speed condition (Levene's test, $P < 0.001$). At the same time, the residual errors were greater for the faster-speed conditions (Fig. 3). Levene's test confirmed that, for both *near-* and *far-target* conditions, the *maximum* condition had significantly greater variance of residual errors than the *fast* condition ($P < 0.001$), which had greater variance than the *slow* and *normal* conditions ($P < 0.001$). The greater residual errors indicate some deviation of transport-aperture coordination from optimality under that condition. Analysis of movement kinematics under the faster-speed conditions revealed that aperture closure was not completed by the time of target contact in the majority of those trials in which residual errors were relatively high.

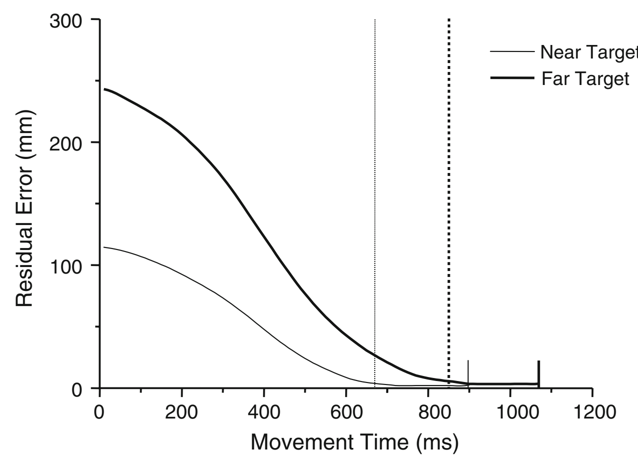


Fig. 2 Variation of the magnitude (average absolute value) of data-fitting error during the entire movement for the *normal-speed* conditions. The residual errors were determined using a linear implementation of Model 1. The model's coefficients were calculated based on a dataset comprising all subjects, all trials, and all data points within the aperture-closure phase and then applied to the entire movement. To plot the residual error magnitude for each condition and each of the two movement phases, the residual error curve was averaged across all trials performed under that condition. The curve averaging was made after normalizing its time duration in each trial to the average duration of the respective movement phase. The *thin and the thick lines* correspond to the near-target and the far-target condition, respectively. The *long vertical lines* indicate the time of aperture closure initiation. The *short vertical lines* indicate the end of hand transport

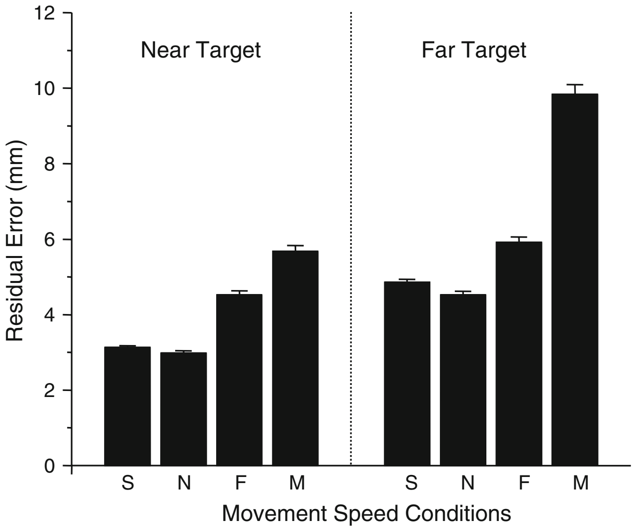


Fig. 3 Residual error magnitude for fitting the aperture-closure phase data to Model 1. The magnitude (square root of average square) of residual errors is plotted for each condition. S, N, F, and M refer to *slow*, *normal*, *fast*, and *maximum* condition, respectively. *Error bars* represent standard error of the data-fitting mismatch

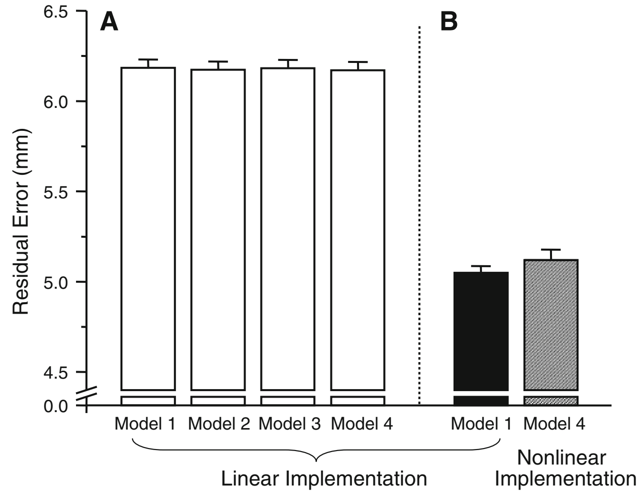


Fig. 4 Comparison of data-fitting error magnitude for the aperture-closure phase between different models of transport-aperture coordination. The magnitude (square root of average square) of residual errors is plotted for each model. **a** The results obtained using linear implementation of Models 1–4. Model 1 does not include any condition-encoding parameters. Models 2, 3, and 4 include the condition-encoding parameter(s) of reach-amplitude, movement-speed, and both, respectively (see "Materials and methods" for more detail). **b** Comparison between the results (*black color*) obtained using linear implementation of Model 1 (which was applied to each of the eight conditions separately with subsequent averaging across all those conditions) and the results (*gray color*) obtained using nonlinear, artificial neural network (ANN)-based implementation of Model 4. *Error bars* represent standard error of the data-fitting mismatch. The residual error magnitude for Model 4 in **a** was significantly greater than that for both Model 1 and Model 4 in **b** ($P < 0.001$, Levene's test). The difference in residual error magnitude between Model 1 and Model 4 in **b** was not statistically significant

Generalization of Model 1 by including conditional parameters

There is a possibility that the CNS utilizes condition-encoding parameters (reaching amplitude and movement speed) together with the movement-related parameters (D, G, V_g, A_g, V_w, and A_w) for controlling the movement. If so, the accuracy of the model approximating hand–target distance as a function of the other parameters could be improved by adding to the model the parameters that encode speed and amplitude conditions as independent variables. To test this hypothesis, one or both conditional variables were included into Model 1, forming Models 2–4 as described in "Materials and methods." These models were applied to a dataset comprising all conditions, all trials, and all subjects. The magnitudes (square root from average square) of residual errors resulting from linear versions of all those models were similar (Fig. 4a). Statistical analysis showed that the variance of residual errors obtained using linear-approximation of Models 2–4 did not differ significantly from that of Model 1 (Levene's test, $P > 0.6$). Thus, the inclusion of one or both conditional parameters describing movement amplitude and speed did not significantly improve linear implementation of Model 1 indicating that transport-aperture coordination was very similar under different speed- and amplitude-related experimental conditions.

At the same time, using Model 1 for each condition separately across all trials and all subjects produced significantly smaller (Levene's test, $P < 0.001$) residual errors ($\sigma = 5.05$, averaged across the conditions) than those ($\sigma = 6.19$) obtained by applying Model 4 to all conditions together (Fig. 4). This significant difference indicates a possibility that the relationship between movement parameters generalized by including the two condition-encoding parameters is significantly nonlinear. To test that possibility, different nonlinear artificial neural network (ANN) models were utilized as candidates for implementing Model 4 (see "Materials and methods" for details). Residual errors obtained from the ANN-based versions of Model 4 were compared to those obtained from the linear version of Model 1 applied to each condition separately (Fig. 4b). The least complex ANN capable of approximating the data with the same accuracy had 3 and 2 units in the first and the second hidden layers, respectively (ANN "3 + 2"). The resulting residual errors were not significantly different from those produced by the linear version of Model 1 applied to each condition separately (Levene's test, $P > 0.05$). Thus, ANN "3 + 2" was the least complex nonlinear approximator capable of capturing the dependence of transport-aperture coordination on experimental conditions with sufficient accuracy.

Aperture-opening phase

Testing whether Model 1 fits the entire aperture-opening phase revealed that the residual errors were considerably greater than those obtained for the aperture-closure phase, indicating significant trial-to-trial variability of transport-aperture coordination during aperture opening. To determine how that variability changes throughout that phase, its time duration was normalized across trials (for each condition separately) and Model 1 was used to approximate the data within a sliding time widow, the duration of which was set equal to the average duration of the aperture-closure phase. Next, data approximation using Model 1 was performed separately for each position of the sliding window, which was moved with one-frame step of approximately (due to time normalization) 10 ms. The residual error magnitude was small (<2.5 cm) compared to the hand transport amplitude (from the starting position to the target) of 15 or 25 cm, indicating a good fit. At the same time, the error magnitude was substantially greater than that for the aperture-closure phase (Fig. 5). Note that the confidence interval ($P < 0.05$) for the residual errors was sufficiently small to conclude that the residual error magnitude significantly varied throughout the aperture-opening phase. The residual errors increased towards the middle of the opening phase (Fig. 5). This trend was more apparent for the *far-target* and for the *slower-speed* conditions. The residual errors gradually decreased by the end of the phase for all conditions (Fig. 5). The decrease was greater in the *far-target* condition, where the total reach distance was longer.

There still is a possibility, however, that the residual errors reflect the nonlinearity of the parameter relationship, rather than the intertrial variability. To test for that possibility, the middle portion of the aperture-opening phase equal in time duration to the average duration of the aperture-closure phase was used to approximate the data with a nonlinear, ANN-based implementation of Model 1 (ANN "3 + 2"). It was found that the residual errors resulting from data-fitting with that ANN were not significantly different ($P > 0.1$) than residual errors produced by a linear implementation of Model 1. Therefore, the increase in the magnitude of residual errors in the middle part of the aperture-opening phase most likely reflected an increase in the inter-trial variability of transport-aperture coordination.

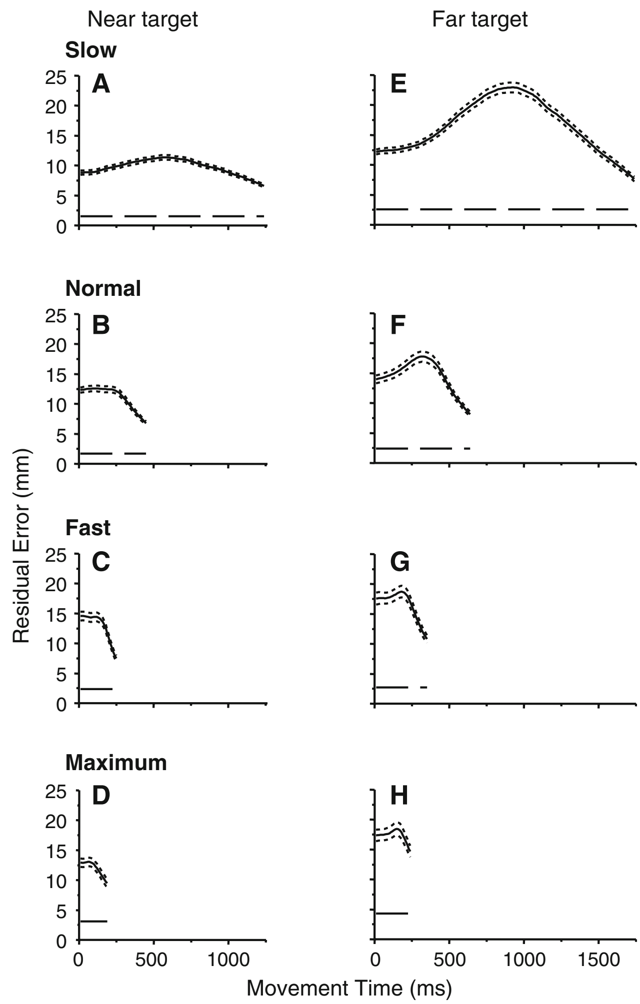


Fig. 5 Variation of the magnitude (average absolute value) of data-fitting error during the aperture-opening phase. The results are shown for different experimental conditions related to *slow* (**a**, **e**), *normal* (**b**, **f**), *fast* (**c**, **g**), and *maximum* (**d**, **h**) general speed of hand transport, as well as to *near-target* (**a–d**) and *far-target* (**e–h**) reach amplitude. For each condition, data-fitting was carried out within a time window moving through the aperture-opening phase. The window width was equal to the mean duration of the aperture closure phase. The residual error magnitude and the confidence interval at which the residual errors were significantly different from the mean residual error ($P < 0.05$) were calculated based on a dataset comprising all data points, all trials, and all subjects. The residual error magnitude and the corresponding confidence interval are shown with *solid and dotted lines*, respectively. The residual error magnitude for the aperture-closure phase is shown with *dashed lines* (for comparison). See "Materials and methods" for further details

Discussion

The main result of this study is that the mathematical model of coordination between hand transport and grip aperture presented as a quantitative relationship among the corresponding movement parameters (Model 1 described by Eq. 2) fits the experimental data, thus fully confirming the hypothesis stated in "Introduction." During the aperture-closure phase, the precision of data-fitting is remarkably high across not only different trials and different subjects, but also different conditions related to the average speed and amplitude of reach-to-grasp movements. This outcome is consistent with the view that the aperture-closure phase is slow and accurate (Ansuini et al. 2007; Haggard and Wing

1997; Jeannerod 1981, 1984; Santello and Soechting 1998; Schettino et al. 2003). Movement control has to be highly optimized during that phase, because significant inaccuracy in transport-aperture coordination during it is likely to result in a costly error of target acquisition (e.g., upsetting and perhaps even damaging the target object). From this perspective, the existence of Model 1 and its high precision simply follows from a general assumption of control optimality (see "Appendix").

The data-fitting precision for the aperture-opening phase, while being reasonably good in general, is considerably lower than that for the aperture-closure phase. In addition, it systematically varies across the aperture-opening phase, especially under the conditions of slower movement speed and greater reaching amplitude. The fact that the utilization of a nonlinear approximator for implementing Model 1 failed to produce a significant decrease in residual errors indicates that the observed large magnitude of those errors likely reflects trial-to-trial variability of transport-aperture coordination during aperture opening, rather than its nonlinearity. It is theoretically possible that the nonlinearity of the relationship between movement parameters is considerably more complex than the complexity of the ANN used for its approximation. Although, given the fact that the aperture-closure phase can be linearly approximated with high precision, the above possibility seems unlikely.

One may attribute the decrease in the precision of transport-aperture coordination to the manifestation of the well-described control principle of speed-accuracy tradeoff (Fitts 1954; Schmidt et al. 1979; Woodworth 1899), since the hand transport in the aperture-opening phase is generally much faster than that during the aperture-closure phase (Fig. 1, see also Jeannerod 1981, 1984). However, that decrease is significantly more pronounced under slow-speed conditions and larger movement amplitude (Fig. 5). Therefore, there must be a different reason for that precision decrease. In contrast to the aperture-opening phase, the precision decrease during the aperture-closure phase is fully consistent with the speed-accuracy tradeoff. The accuracy of transport-aperture coordination decreases with an increase in movement speed, which is evident from an increase in the magnitude of residual errors of data approximation based on Model 1 (Fig. 3). This intriguing difference in movement control between the two phases requires a separate study. It will be shown in a forthcoming paper that the phase dependence of motor variability holds important keys to understanding the control of reach-to-grasp movements.

Phase transition between aperture opening and aperture closure

A remarkable feature of the relationship between movement parameters characterizing transport-aperture coordination is that it allows for a very good linear approximation during both aperture-opening and aperture-closure phases treated separately from each other. At the same time, that relationship taken over the *entire movement* is significantly nonlinear, because the correlation between the aperture and the hand-target distance changes its sign after switching from aperture opening to aperture closure. This feature makes the transition between the two movement phases a fairly distinct landmark in the space of movement parameters as state coordinates. It can be described based on a reasonably clear mathematical interpretation. Although that interpretation might look excessively abstract, we have included it below because of its constructiveness and importance for understanding how the CNS controls reach-to-grasp movements.

From a geometrical perspective, the aperture-opening and aperture-closure phases correspond to two different hyperplanes, each of which is a five-dimensional object in the six-dimensional movement parameter space. The transition between the phases corresponds to the intersection between those hyperplanes. The intersection itself is a set of state-space points that forms a four-dimensional hyperplane (compare to a usual 3D space where planes are two-dimensional objects, and the intersection between two such planes forms a one-dimensional object, a line). In linear algebra, each of the two hyperplanes is described by a linear equation:

$$f_1(D, V_w, A_w, G, A_g, V_g) = 0 \tag{6}$$

$$f_2(D, V_w, A_w, G, A_g, V_g) = 0, \tag{7}$$

where f_1 and f_2 are functions describing the hyper-planes corresponding to aperture opening and aperture closure, respectively (compare to Eq. 12 in "Appendix"). Note that the algebraic representation would still hold if the relationship between movement parameters were not linear.

An equation describing a transition from aperture opening to aperture closure can be obtained from the above two-equation system (Eqs. 6, 7) in the following way. Since the aperture velocity (V_g) is zero in the transition from aperture opening to aperture closure, it can be excluded from the above equation system. Then, by solving that system with respect to the aperture acceleration (A_g) and excluding it, one obtains a single equation that describes a (linear) relationship between the remaining four movement parameters:

$$f_3(D, V_w, A_w, G) = 0. \tag{8}$$

By solving Eq. 8 with respect to the hand–target distance, it can be transformed into

$$D = D(V_w, A_w, G), \tag{9}$$

which is exactly the equation that we used previously for describing the initiation of aperture closure (see

"Introduction," Eq. 1). In our previous studies, we found that this equation accurately describes the relationship between movement parameters at the time of aperture closure initiation across different trials and subjects (Rand et al. 2006a, b, 2007a).

The above description of transport-aperture coordination for grasp initiation during reach-to-grasp movements is directly supported by the current experimental results. The experimentally observed relationship between movement parameters forms a state space hypersurface that consists of two hyperplanes, one of which corresponds to the aperture-opening phase and the other to the aperture-closure phase. This construction justifies the utilization of the term *grasp initiation*, which can be depicted as the transition between the hyperplanes. Note that it would be much less justified if the hypersurface were smooth (e.g., parabolic), without any distinct landmark-type feature.

Utilization of the transport-aperture coordination model for data analysis

The existence of an equation that describes transport-aperture coordination with high precision is a fundamental result. However, its true value can be measured only in terms of its utilization benefits. What are those benefits? The data analysis approach based on fitting the experimental data into Model 1 apparently solves the old problem of comparing data with two groups where preferred movement speed for each group is different (e.g., young adults vs. older adults, or patients with a specific motor disorder vs. controls). As it has been demonstrated, the model of transport-aperture coordination is highly invariant with respect to average speed of the movement or reaching amplitude. Therefore, it provides a reliable basis for the quantitative comparison of results across different experimental conditions and subject groups (e.g., Rand et al. 2006a, b, c, 2007a).

The generalization of an equation describing transport-aperture coordination to an entire phase of movement provides additional important possibilities for data analysis. For instance, it allows one to study perturbations of transport-aperture coordination caused by different factors, such as a pulse of external force acting of the arm, a sudden shift of the target position, etc. Any violation of normal transport-aperture coordination can be easily detected as a violation of the corresponding equation and accurately quantified as a mismatch error. This makes it possible to determine time intervals during which the violation occurred. The above possibilities, in turn, provide a method for studying adaptation to such perturbations.

The method of analyzing and quantifying transport-aperture coordination that has been developed and used in this study can be easily generalized to more complex situations, where more than two different independent, well-optimized control processes are required to finish simultaneously. With regard to reach-to-grasp movements, for example, the control of hand orientation (to match the orientation of the target) can be added to hand transport and finger-aperture regulation as a third independent control process. Then, following the same logic as described in "Appendix," from three equations (one for each control process) for the corresponding control laws, one obtains a two-equation system modeling coordination between the three control processes. Testing whether that model would describe experimental data with the same extent of accuracy as found in this study is an exciting next step of further research.

Implications for understanding the functional organization of a neural system controlling reach-to-grasp movements

The results of the present study provide several valuable insights into the nature of reach-to-grasp movement control. Since finger aperture is mechanically independent from hand transport, the relationship between kinematic parameters corresponding to Model 1 is not determined by the mechanical properties of the arm. Therefore, it has to be maintained by the CNS as corresponding to an optimal coordination between hand transport and finger aperture. What can be said about neural mechanisms responsible for maintaining the strict relationship between the transport and aperture parameters described by the equation of transport-aperture coordination? A salient feature of Model 1 is its quasilinearity. To find a constructive answer to why the relationship between movement parameters during the opening and closure phases is so close to linearity, one would need to know an adequate model of the optimality criterion for both the control of hand transport and that of finger aperture and to solve the corresponding optimal control problems. A good example of a theoretical analysis along this line can be found in a previous work by Hoff and Arbib (1993).

From a neurophysiological perspective, neural implementation of a linear function requires the least amount of resources, because mathematically, it can be computed with only one neuron-like element. In addition, very importantly, the optimization of the related synaptic weights usually can be performed much faster for a quasilinear function than for a significantly nonlinear one. Consequently, an implementation of reach-to-grasp control using two different sets of linear functions for the aperture-opening and the aperture-closure phases, respectively, and a subsystem that makes a decision to switch control between those phases must allow the CNS to minimize neural resources. Additional neurophysiological and perhaps neuroanatomical studies are required to verify this hypothesis and identify neural substrate for the related computations.

The results of generalizing Model 1 into Model 4 to fit experimental data across several conditions related to the reach amplitude and average speed of reaching show that the approximation accuracy can be significantly increased by including the corresponding conditional variables in the model. This finding points to a possibility that the CNS forms state variables corresponding to such conditions and uses them for the computation of control actions.

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Appendix

Derivation of an equation describing coordination between hand transport and grasp aperture

Reach-to-grasp movements can be viewed as consisting of two independently and optimally controlled processes (hand transport and grasping), which are required to finish simultaneously. Note that their independence here is understood as the independence of the corresponding optimality criteria. Simple examples of such criteria are described, e.g., in Hoff and Arbib (1993). The final state for hand position and aperture is determined by the target's location and size, respectively. A control action for regulating the transport and the aperture can be presented, e.g., as hand transport acceleration and as finger aperture acceleration, respectively (Hoff and Arbib 1993). Hence, an optimal control law for hand transport and grasp aperture can be described by the following set of equations

$$A_w = f_w(D, V_w, T) \quad (10)$$

and

$$A_g = f_g(G, V_g, T), \quad (11)$$

where D, V_w, and A_w are the instantaneous values of hand–target distance, wrist velocity, and wrist acceleration, respectively; G, V_g, and A_g are grip aperture and the corresponding velocity and acceleration, respectively; and T is the amount of time left to target contact. Note that the explicit inclusion of T in the above control laws does not imply that that parameter is prescribed. On the contrary, in this case, it is a variable requiring optimization (Naslin 1969). If two control processes are required to finish simultaneously, the optimization of movement time left to finish has to be performed according to a generalized optimality criterion that can be expressed, e.g., as a weighted sum of such criteria corresponding to the control of hand transport and grip aperture if optimized separately from each other. By excluding T from the above equation set (Eqs. 10, 11), one obtains an equation describing a functional relationship between all other movement parameters:

$$f(D, V_w, A_w, G, A_g, V_g) = 0. \quad (12)$$

This equation is rather general because it does not depend on the results of optimizing T. By solving Eq. 12 with respect to D, one obtains

$$D = D(A_w, V_w, G, A_g, V_g). \quad (13)$$

It should be emphasized that the existence of Eq. 13 is based on an assumption that both the hand transport and grasp aperture are regulated optimally. Therefore, the precision with which any related experimental data can be approximated based on that equation strongly depends on how close to optimality are the control actions regulating the above two processes.

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