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Multijoint grasping movements

Simulated and observed effects of object location, object size, and initial aperture

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Abstract Studies of human prehension have revealed characteristic patterns of grasping kinematics. We sought to gain insight into the determinants of those patterns by means of a computer simulation and accompanying behavioral experiment concerning multijoint, planar grasping behavior. The simulation was based on a recent theory of posture-based motion planning which hypothesizes that movement preparation entails time-limited, multiple task-constraint satisfaction. Prehension was modeled with a stick-figure animation involving 12 series of 81 grasping movements. Circular objects to be grasped were located at three angles (45°, 90°, and 135°) and at three distances (20 cm, 30 cm, and 40 cm) relative to the initial location of the hand in the workplane. Additionally, three object sizes (2 cm, 4 cm, and 6 cm in diameter) and three initial aperture sizes (0.3 cm, 3.3 cm, and 7.0 cm) were used. Analyses of the simulated grasping movements focused on the time course of the hand opening, the tangential velocity of the wrist, and the rotations of the joints in the arm, hand, and fingers. The results showed that the model accurately mimicked detailed kinematics of prehension observed in earlier studies. With respect to the frequently reported relationship between object size and hand opening, the simulations further re-

vealed an effect of initial aperture. This predicted effect was confirmed in an experiment in which four participants performed analogous planar grasping tasks. An analysis of the time course of the opening of the hand showed that maximum aperture covaried with initial aperture. A conclusion of this work is that a major determinant of grasping kinematics is avoidance of collisions with objects that are to be grasped.

Keywords Reaching movements · Grasping movements · Prehension · Manual control · Computational model · Human

Introduction

Experimental studies of human prehension have yielded a coherent picture of the kinematics of grasping movements. The opening or preshaping of the hand is functionally tuned to features of the object to be grasped and is evident early in the movement (Jeannerod 1981, 1984; Pellegrino et al. 1989; Rosenbaum et al. 1992). The fingers spread apart wider than the object (Jeannerod 1981, 1984), the maximum aperture occurring at approximately 60–80% of the movement time (Castiello 1996; Jeannerod 1981, 1984; Wallace and Weeks 1988). The size of the maximum aperture varies linearly with object size, but with a slope less than 1 – typically approximately 0.8 (Bootsma et al. 1994; Brenner and Smeets 1996; Chieffi and Gentilucci 1993; Goodale et al. 1994; Marteniuk et al. 1990; Paulignan et al. 1991, 1997; Servos et al. 1992; Smeets and Brenner 1999; Zaal and Bootsma 1993). The distance between the initial hand location and the object does not affect the maximum aperture size (Bootsma et al. 1994; Chieffi and Gentilucci 1993; Marteniuk et al. 1990; Paulignan et al. 1991; Zaal and Bootsma 1993; for an exception, see Jakobson and Goodale 1991). The maximum aperture also occurs proportionally later in the movement the larger the object to be grasped (Churchill et al. 2000; Gentilucci et al. 1991; Von Hofsten and Rönnqvist 1993; Marteniuk et al. 1990)

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and the larger the distance between initial hand location and object location (Jakobson and Goodale 1991). As the fingers spread apart, the arm speeds up and then slows down. Often, but not always, this results in a low-velocity transport phase of the wrist (Jeannerod 1981, 1984; Wallace and Weeks 1988). Finally, the maximum aperture tends to occur near the start of the low-velocity transport phases (Jeannerod 1981, 1984).

These kinematic features of human grasping movements have led to a number of models which assume different control processes. Originally, the model of Jeannerod (1981, 1984) asserted that there are two independent visuomotor processes for dealing, respectively, with the transport and the grasping components of prehension. The temporal invariance between the transport and manipulation components was seen in Jeannerod's model to reflect the temporal coordination of the two components during execution (for a recent review of the visuomotor channels hypothesis, see Jeannerod 1999).

Subsequently, Hoff and Arbib (1993; see also Arbib 1997) extended Jeannerod's model and proposed the first quantitative account of prehension based on the minimum-jerk principle of Flash and Hogan (1985). Hoff and Arbib suggest separate activation signals for the relative timing of the transport and manipulation components such that minimum jerk motions of the relevant effectors could be achieved.

Zaal and Bootsma (1993) and Zaal et al. (1998, 1999) have analyzed human prehension from the viewpoint of nonlinear system dynamics. Their approach has provided new insights into the extent to which the timing of grasping movements can be determined by the intrinsic dynamics of arm and hand coordination without appealing to any specific neuromotor control processes.

Another attempt to identify determinants of grasping movements was undertaken by Smeets and Brenner (1999). Their approach is based on experiments showing that the variability of the spatial path of the finger tip and thumb tip decreases near the end of grasping movements (Haggard and Wing 1997; Wing and Fraser 1983; Wing et al. 1986). Reflecting further on this result, Smeets and Brenner (1999) have proposed that human prehension can be viewed as the simultaneous performance of two smooth reaching movements, one performed with the finger tip and the other with the thumb tip, both of which tend to approach the object being grasped perpendicularly to its surface.

The approach pursued here has aspects in common with the one proposed by Smeets and Brenner (1999), but, instead of constraining the movements of the finger tip and thumb tip on the basis of a minimum jerk principle, we allowed for satisfaction of multiple, task-dependent constraints. Our approach also generalized to any set of effectors. Indeed, the model has been used before to model complex movements in reaching, writing, and aspects of grasping different from those covered in the present article (see Rosenbaum et al. 1995, 1999, in press). The general approach is described in the next section, Theory. Then relevant simulations are described,

and a behavioral experiment is presented thereafter. The article ends with a discussion of the implications and remaining questions of this investigation.

Theory

The theory on which the present simulations are based is specified by Rosenbaum et al. (1995, 1999, in press), so here we give a brief summary only. A core assumption is that motion planning involves time-limited, multiple-task constraint satisfaction. The actor is assumed to construct a task-specific constraint hierarchy, and thus may decide to make a slow, spatially accurate movement rather than a fast, relatively inaccurate movement. They may also decide to generate as little force as possible or as much force as can be produced. Avoiding collisions with intermediate obstacles may likewise be part of the constraint hierarchy depending on whether the actor is – to use two extreme examples – in a china shop or on the football field. The idea behind the constraint hierarchy is not to predict what factors actors care or do not care about in different task situations; that is a matter of motivation and instruction. Instead, the theory respects the fact, or indeed emphasizes the fact, that a critical component of skill is the capacity for changing how one wants to perform in different circumstances.

According to the theory, a movement is planned on the basis of the constraint hierarchy, relying on two processes. The first is evaluation of candidate goal postures. The second is evaluation of candidate via postures for collision avoidance. Both processes rely on a stored posture base consisting of representations of learned, previously adopted goal postures. Evaluation of candidate goal postures occurs as follows. From the stored posture base, the stored posture that is most suitable for the task at hand, as defined by the constraint hierarchy, is chosen as the currently most promising stored posture. The most promising stored posture is found by searching for a hand posture that is tuned to the object size in a subregion of the posture base that corresponds to the hand joints, and then by searching for an arm posture that brings the hand at the object location in another subregion of the posture base that represents the arm joints. The combination of the most promising hand and arm postures may result in a new posture which was not stored in the posture base as such. This implies that in the posture base information is stored in a functionally distributed sense and unique, previously unadopted postures may emerge. If additional planning time is available, other possible goal postures near the most suitable goal posture (in posture space) are evaluated. These postures are generated in an ever-widening shell, such that the more planning time there is, the wider the shell becomes. If extra planning time is impossible, subjects are predicted to select less auspicious goal postures and movements to them than would otherwise be the case, resulting potentially in more collisions with obstacles.

Subjects are assumed to be able to generate a new goal posture by means of a time-limited search process

within the posture base. In the theory, the posture base corresponds to a multidimensional joint space representing the subject's effector system. As the search for a more suitable goal posture continues, a successively larger area of the joint space, starting from the best candidate found so far, is explored for a better solution. When time is up, the best of all possible candidate goal postures is chosen as the goal posture and a default transition from the starting posture to the goal posture is planned.

The default postural transition is based on a simple principle: All joints start and stop moving simultaneously according to bell-shaped joint angular velocity profiles. This principle corresponds to producing a smooth, straight-line movement in joint space. Recent evidence from Nakano et al. (1999) indicates that this principle does a surprisingly good job of describing postural transitions in point-to-point, obstacle-free movements and has been assumed in at least one other previous model (Soechting et al. 1995).

Sometimes simple movements like those just described may result in collisions with intermediate obstacles or even with the object to be grasped. This can occur if the hand or fingers contact the to-be-grasped object prematurely or in the wrong orientation. In these cases, additional motion planning time may be needed to select a different transition between the starting and goal posture. During this extra planning time, subjects try to find a detour that satisfies the collision-avoidance constraint. In our model this detour is found by seeking a detour through joint space. A special "via posture" is sought to help define this detour, and it is sought in essentially the same way as a goal posture. The via posture is used to generate a two-stage movement that proceeds from the starting posture to the via posture and then back to the starting posture, while the main movement is carried out from the starting posture to the goal posture. This back-and-forth movement does not add any net excursion to the transition between the starting and goal posture, but it can yield a composite movement that is sufficiently curved to ensure collision avoidance (see also Meulenbroek et al. 1996). For a summary of the behavioral and neurophysiological basis of the theory just described, see Rosenbaum et al. (in press) and Vaughan et al. (1998).

Application of the theory to grasping

The theory just described has been formalized in a computer model rendered as a stick-figure animation capable of generating multijoint, planar grasping movements (see Rosenbaum et al., in press). The stick figure has a 9-degrees-of-freedom (df) planar arm. Four degrees of freedom correspond to the proximal joints of the arm: the shoulder, elbow, and two wrist joints, one connecting the forearm to the index finger, the other connecting the forearm to the thumb. Five degrees of freedom correspond to the distal joints of the index finger ($n=3$) and the thumb ($n=2$). Linkages between the joints (e.g., the three joints in the index finger forming 1 df and those in the thumb forming 1 df) also exist to speed up computations, but the simulation results are just as comparable when no linkages are assumed as when they are.

To model grasping here, we used a constraint hierarchy, stipulating from most important to least important: (1) collision avoidance, i.e., apart from the final moment of contact with the to-be-grasped object, collisions with the object had to be avoided during motion; (2) spatial accuracy, i.e., at the moment of movement completion, the finger tip and thumb tip had to touch the object at opposite sides of the circular object; (3) movement cost reduction, i.e., the total cost of movement summed over the duration of movement (also generated by the model) and summed over all the joints, each of which was given its own weight, had to be kept as low as possible (cf. Vaughan et al. 1998). With these constraints for controlling the motion planning processes, grasping was simulated as follows.

An object was positioned in the workplane such that it was within the stick figure's reach as determined by the minimum angles and angular ranges of motion of the stick figure's joints (see Table 1). Given the initial starting posture of the stick figure, a candidate hand goal posture was sought such that the aperture of the hand approximately matched the size of the object. The search took place in a multidimensional posture space whose dimensions corresponded to the nonlinked mechanical dfs of the stick figure. The number of stored postures in the present simulations was 200, but the number could be as low as 1 (i.e., the current starting posture, which is also the last goal posture adopted). The reason for using 200 rather than 1 stored posture was to mimic proficiency

Table 1 Simulation parameters: grain, 0.01; number of postures in memory, 200; deadline, 15 planning cycles (see text); instructed movement time, 50 arbitrary units (a.u.); length of forearm 18 cm

| Joint | Label | Minimum angle (deg) | Range of motion (deg) | Expense factor (a.u.) |
|--------------------------------|-------|---------------------|-----------------------|-----------------------|
| Shoulder | Shld | -60 | 170 | 18 |
| Elbow | Elbw | 0 | 160 | 18 |
| Wrist to finger | WrstF | -60 | 120 | 18 |
| Wrist to thumb | WrstT | 50 | -35 | 18 |
| Metacarpophalangeal joint | Mtcp | 0 | 35 | 3 |
| Proximal joint of index finger | Indx1 | 0 | 40 | 3 |
| Distal joint of index finger | Indx2 | 0 | 45 | 3 |
| Proximal joint of thumb | Thmb1 | 0 | -40 | 3 |
| Distal joint of thumb | Thmb2 | 0 | -45 | 3 |

and a balanced involvement of the instance retrieval and instance generation search processes for candidate goal and via postures.

Once a suitable hand posture was found based on the aperture coming as close as possible to the object size, a candidate arm goal posture was sought that would bring the suitably shaped hand to the object location. The search for the arm goal posture was conducted in the same set of 200 stored postures as the hand goal posture search, although, in this second stage, the search was restricted to the subspace representing the arm joints (see Rosenbaum et al. 1995). The reason for breaking the goal posture search into hand and arm posture searches is based on evidence that, at the neural level, hand and arm postures are represented separately (Rizzolatti et al. 1988). Furthermore, it has been shown that hand postures are specified before arm postures (Klatzky et al. 1995) and kinematic and reaction time data strongly suggest that hand and arm postures are mentally represented before grasping movements are initiated (Pellegrino et al. 1989; Rosenbaum et al. 1992).

Once a suitable arm-and-hand goal posture was found, a trajectory through joint space was sought in combined arm-hand posture space. If internal simulation of the postural transition from the starting to the planned goal posture on the basis of forward kinematics suggested that there would be a collision with the to-be-grasped object, a search for a via posture was mounted. This via posture search consisted of the same instance-retrieval and instance-generation processes as used for the search for the goal posture and was governed by the same collision-avoidance and travel cost-minimization constraints as were used in the goal posture search. These constraints were applied to the entire movement rather than to the goal and via postures alone. Moreover, both the goal and via posture search processes were limited in time (a maximum of 20 search cycles in the posture base). Each search cycle took place in a gradually larger region of the posture base (i.e., in steps of 1% of the range of motion of the joints constituting the dimensions of the posture base).

Simulations

Methods

The simulations consisted of 12 runs of 81 grasping movements each. Each run began with a different initial set of random stored postures ($n=200$); these can be thought of as representing different subjects. The different initial posture bases were obtained by changing the seed of a random generator at the start of each simulation run. The simulation was repeated 12 times to introduce a random factor in the study, allowing for the use of analyses of variance (ANOVAs) in the data evaluation. All grasping movements ($n=972$) were simulated by using fixed starting angles of the shoulder, elbow, and wrist (see Fig. 1). The initial hand location was always in front of the body midline, approximately 10 cm in front of the stick figure's nose. At the start of motion, the hand always pointed to the left (approximately 180°). Each grasping movement was modeled with a constant movement time of 50 time samples. The minimum joint angles, the ranges of motion

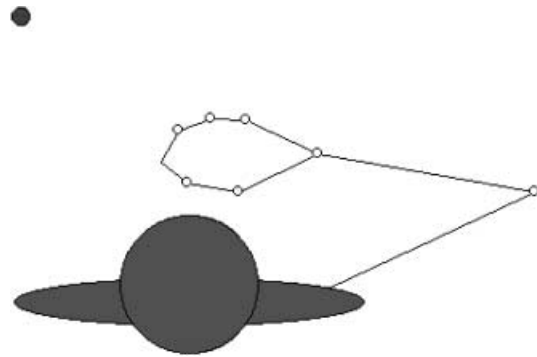


Fig. 1 Typical starting posture. Only the aperture between finger tip and thumb tip was varied across trials (not shown). The aperture here amounts to 0.3 cm. The object to be grasped (*black circle*) is located at 135° relative to the middle between finger tip and thumb tip, at a distance of 20 cm; the object size is 2 cm in diameter

of the nine joints, the joints' expense factors (the weights reflecting the extent to which unit angular displacements of the joints contributed to the total movement cost), and other simulation constants that we used are listed in Table 1.

Task variables and dependent variables

Task variables were object location ($n=9$), object size ($n=3$), and initial aperture ($n=3$). Object location consisted of two variables defined in the two dimensions of a polar coordinate system whose origin was the midpoint between the tips of the index finger and thumb. Thus, object location consisted of the two variables, object angle (45° , 90° , or 135° relative to the stick figure's frontal plane), and object distance (20 cm, 30 cm, or 40 cm from the origin). Object size was either 2 cm, 4 cm, or 6 cm. Additionally, the angles of the finger and thumb joints of the stick figure's starting posture were varied across trials such that the initial aperture of the starting posture was either 0.3 cm, 3.3 cm, or 7.1 cm. In Fig. 1, the initial aperture was 0.3 cm. Note that the initial aperture could either be smaller, approximately equal to, or larger than the object size.

The dependent variables were: (1) the aperture-time functions of the grasping movements; (2) the tangential wrist velocity in centimeters per second; (3) the aperture overshoot in centimeters, defined as the maximum aperture realized during the grasping movement minus the object size; (4) the moment of aperture overshoot expressed as a percentage of the movement time; (5) the net joint excursions in degrees, that is, the goal minus the starting angle for each joint separately; and (6) the difference between the via angle and the starting angle, again for each joint separately.

Predictions

Based on earlier findings of prehension studies summarized in the Introduction, our first prediction (i.e., the first phenomenon we hoped to simulate) was that, with increasing object size, the aperture overshoot would decrease. This corresponds to the finding that the slope of the regression line between maximum aperture and object size is less than 1.0. For an overview of slopes and intercepts reported in the literature, see Smeets and Brenner (1999). Second, we expected that, with increasing object size, the moment of maximum aperture would occur later, that is, nearer the end of the grasping movement. We also made two new predictions. First, we expected objects located to the left of the body midline to elicit a smaller effect of the collision-avoidance constraint on the grasping kinematics than objects on the right side of the body midline. The basis of this prediction was as follows: Given the initial hand location (the hand pointing leftward), objects on the right side of

the body midline were located “behind” the hand. For a creature moving only in the horizontal plane, this means that the shoulder and elbow joints must make relatively large deviations to prevent the hand from colliding with the object. Second, we reasoned that if the initial aperture is smaller than the object size, the likelihood of the hand colliding with the object should be smaller than when the initial aperture is larger than the object size. The reason for this prediction is that a small hand-opening takes up less space and is thus less likely to collide. Consequently, grasping kinematics related to collision avoidance should be differentially affected by initial aperture.

Data analysis

Aperture overshoot (centimeters) and moment of maximum aperture (in percentage of total movement time) were evaluated by means of an ANOVA according to a factorial design of 12 simulation runs (the random variable) \times 3 object angles (45° , 90° , and 135° relative to the initial hand location) \times 3 object distances (20 cm, 30 cm, and 40 cm relative to the initial hand location) \times 3 initial aperture sizes (0.3 cm, 3.3 cm, and 7.0 cm).

Results

Errors and outliers

In 10 of the 972 simulations, it was impossible to find a collision-free trajectory within the time allotted for the motion-planning phase. All of these 10 cases occurred in the 45° object angle condition (i.e., the condition in which the object was located “behind” the initial hand location). In 17 other cases, all of which started with the maximum aperture and the object behind the hand at 45° relative to the hand’s initial axis, the model found no via posture. In these cases, the grasping movement was therefore executed as a straight-line movement through joint space, without any detour through a via posture, which resulted in the hand colliding with the object to be grasped. We will reconsider these error trials in the Discussion section. In 97% of the simulations, a successful collision-free grasping movement was generated.

Example of simulated grasping movement

Figure 2 shows a cartoon of a typical grasping movement. Figure 3 shows the corresponding excursions of the proximal joints (Fig. 3A), the corresponding excursions of the distal joints (Fig. 3B), the associated aperture-time function (Fig. 3C), and the associated tangential wrist-velocity function (Fig. 3D). To facilitate comparisons, the joint excursions shown in Fig. 3A, B are normalized with respect to the starting posture; that is, the joint angles at the start of the movement were set to zero. Figure 3C shows that the aperture overshoot peaked at approximately 60% of the movement time. Figure 3B shows that the aperture overshoot was mainly due to the biphasic movement of the index finger; that is, extensions of the joints of the index finger until the maximum aperture was reached were followed by flexion of these joints until completion of the grasping movement.

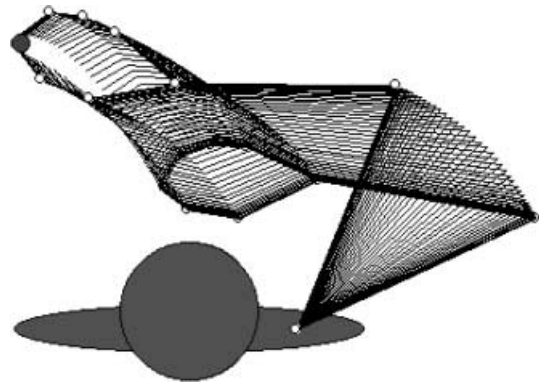


Fig. 2 Cartoon of typical grasping movement

Three of the components of the typical grasping kinematics that have been reported in human performance studies were consistently generated in the simulations. First, there was a wider opening of the hand than the object. Because this wider opening of the hand arose in our simulations from the need to avoid collisions until movement completion (Fig. 3C), it is reasonable to hypothesize that this same constraint is what accounts for the overspreading of the hand during actual grasping. This idea of a safety margin in prehension has been suggested before (Wing et al. 1986).

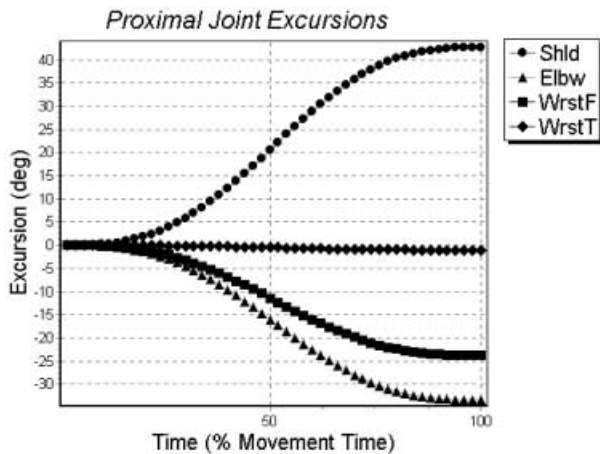
The other component of typical grasping kinematics that emerged in the simulations was that the moment of maximum aperture occurs during the second half of the grasping movement (Fig. 3C). This feature of the simulated grasps arose from the combined effects of the collision-avoidance constraints and movement-smoothness constraints, suggesting that human grasping, which shows this same sort of delay, stems from the same constraints.

A third noteworthy feature of the grasping movement shown in Figs. 2 and 3 is that it did not contain a low-velocity phase of the wrist (Fig. 3D). In fact, such a low-velocity phase is not always seen (Wallace and Weeks 1988).

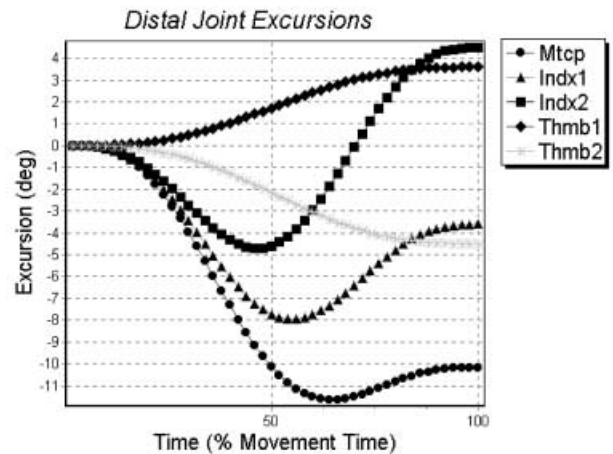
Effects of task variables on aperture-time functions

Figure 4 shows the effects of the task variables on the aperture-time functions. Figure 4A, B shows that object angle and object distance hardly affected the aperture-time functions. Figure 4C, D, however, shows that, owing to task constraints, the aperture-time functions varied as a function of object size and initial-aperture size, respectively. Apart from the obvious task-variable related differences between the aperture-time functions, one invariant feature of these functions stands out. On average, aperture overshoots occurred in all conditions, even when the initial aperture was larger than the object size. Figure 4C also shows that, as object size increased, the moment of maximum aperture shifted forward in time. In contrast, as the initial aperture increased, the

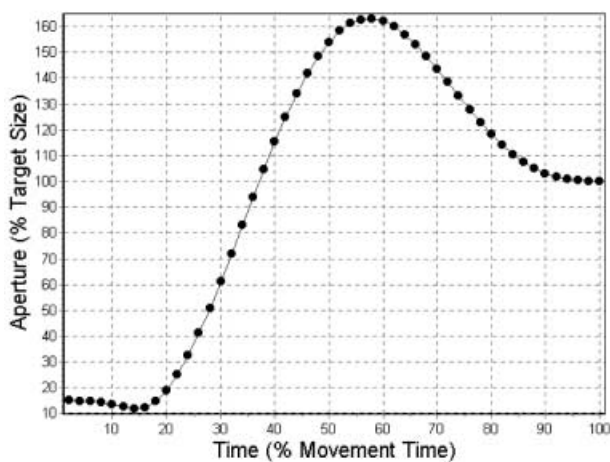
A



B



C



D

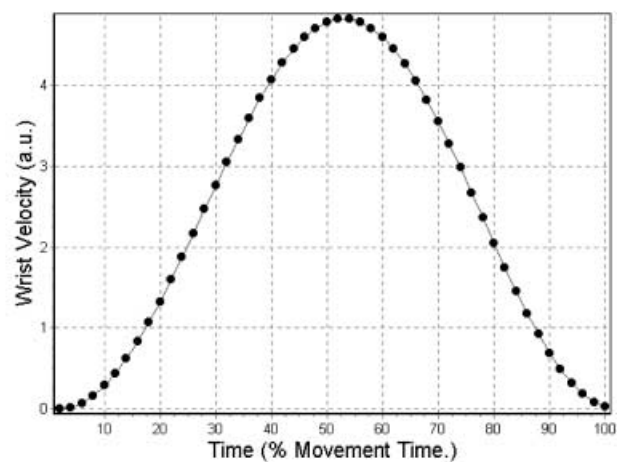


Fig. 3A–D Kinematics corresponding to movement displayed in Fig. 2. **A** Proximal joint excursions; **B** distal joint excursions; **C** aperture-time function; **D** tangential wrist velocity function (*Shld* shoulder, *Elbw* elbow, *WrstF* wrist to finger, *WrstT* wrist to thumb, *Mtcp* metacarpophalangeal joint, *Indx1* proximal joint of index finger, *Indx2* distal joint of index finger, *Thmb1* proximal joint of thumb, *Thmb2* distal joint of thumb)

wrist velocity functions, not their shape (Fig. 5B). Object size (Fig. 5C) and initial aperture size (Fig. 5D) did not systematically affect the tangential wrist-velocity time functions.

moment of maximum aperture occurred earlier (Fig. 4D). In terms of relative object size, these effects are comparable, because as the initial aperture size increases, the object size relative to the initial aperture size decreases.

Effects of task variables on tangential wrist velocity

Effects of the task variables on the tangential wrist velocity functions appear in Fig. 5. Reach direction affected the tangential wrist velocity, as expected (Fig. 5A). The low-velocity phase emerged in the condition in which the object was located more or less “behind” the hand. Object distance only affected the amplitude of the

Effects of task variables on aperture overshoot

The effects of the task variables on aperture overshoot are shown in Fig. 6. As seen here, mean aperture overshoot did not vary as a function of object angle ($F_{2, 22}=1.35$, n.s.). Aperture overshoot increased slightly as object distance increased: 2.17 cm, 2.43 cm, and 2.43 cm for the 20 cm, 30 cm and 40 cm, respectively ($F_{2, 22}=9.83$, $P<0.01$). As expected, mean aperture overshoot decreased as object size increased from 2 cm to 4 cm to 6 cm: 3.26 cm, 2.25 cm, and 1.51 cm, respectively ($F_{2, 22}=867.31$, $P<0.01$). This result corresponds to the frequently reported finding that the slope of the best-fitting straight line fitted to the graph relating maximum aperture overshoot to object size is less than 1. Finally, Fig. 6 shows that aperture overshoot increased with increasing initial aperture size ($F_{2, 22}=867.31$, $P<0.01$). For initial

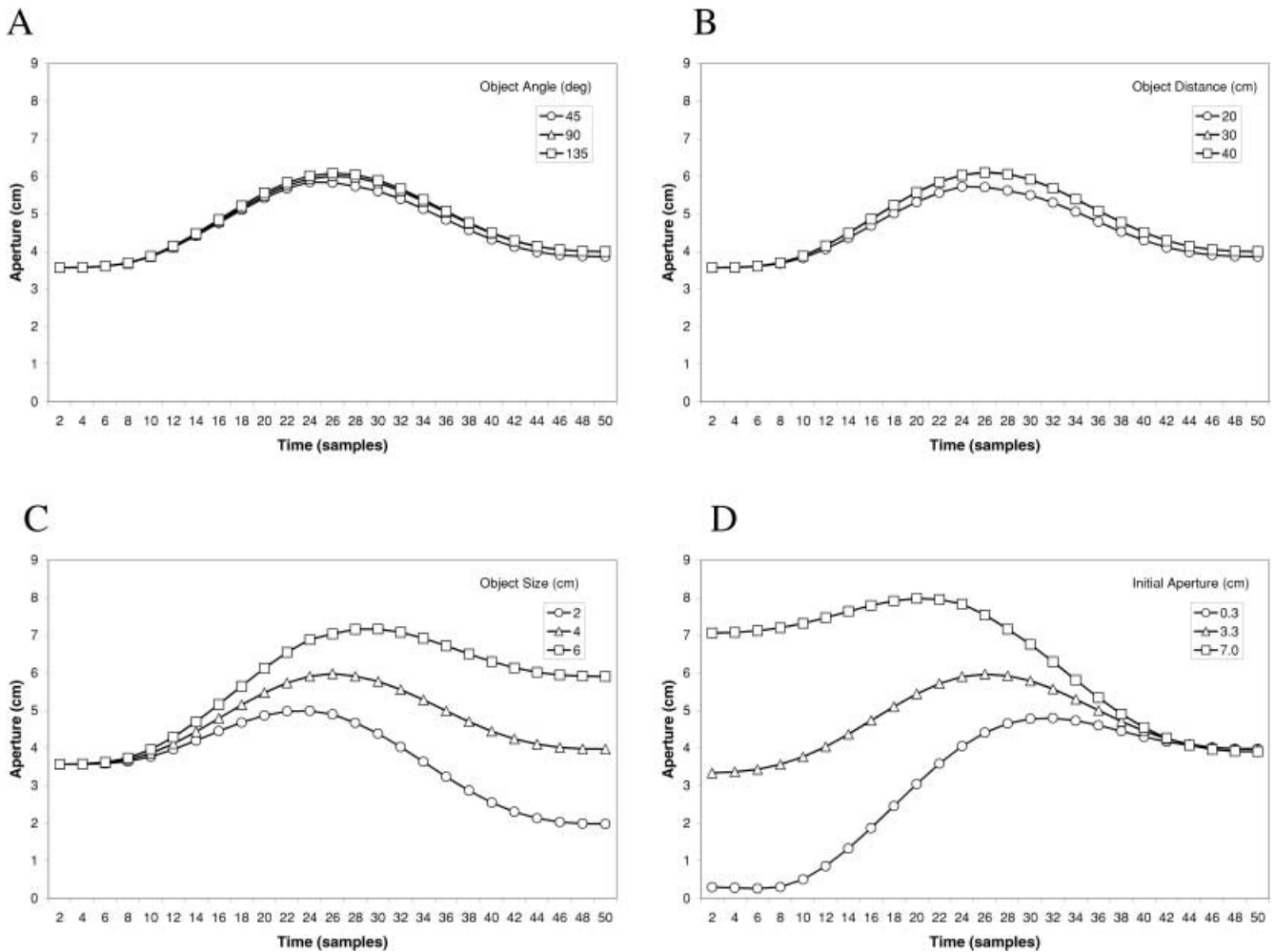


Fig. 4A–D Mean aperture-time functions as a function of object angle (A), object distance (B), object size (C), and initial aperture (D)

apertures of 0.3 cm, 3.3 cm, and 7.0 cm, the aperture overshoots were 0.89 cm, 2.06 cm, and 4.07 cm, respectively.

The effects of the task variables on the aperture overshoot interacted in a predictable manner. When the initial aperture was large (7.0 cm), the decrease of the aperture overshoot due to increasing size of the to-be-grasped object was most pronounced. However, when the initial aperture was small (0.3 cm), the decrease of the aperture overshoot due to increasing object size was smaller ($F_{4,44}=310.27$, $P<0.01$). Similar types of interactions were found between other combinations of task variables, but these interactions were marginal and did not provide more insight into the relative strengths of the effects of the task variables on the size of the aperture overshoot.

The main effects of the task variables on the moment of maximum aperture (see Fig. 7) were as follows. The moment of maximum aperture increased slightly as a function of object angle. For objects located at 45°, 90°, and 135° relative to initial hand location, the moment of

maximum aperture changed from 51% to 54% of the (fixed) movement time ($F_{2,22}=23.32$, $P<0.01$). Object distance had a similar small effect on the moment of maximum aperture ($F_{2,22}=15.45$, $P<0.01$). As expected, when object size increased, time of maximum aperture came later. The maximum aperture occurred at 47.5%, 53.4%, and 59.1% of the movement time for object sizes of 2 cm, 4 cm, and 6 cm, respectively ($F_{2,22}=211.61$, $P<0.01$). When the initial aperture increased, the moment of maximum aperture occurred earlier (65.1%, 54.4%, and 40.0% of the movement time for 0.3 cm, to 3.3 cm, to 7.0 cm initial-aperture conditions, respectively; $F_{2,22}=777.59$, $P<0.01$).

As was the case with the effects of the task variables on the aperture overshoot, the effects of the task variables on the moment of maximum aperture interacted in a predictable manner. As the initial aperture increased, the moment of maximum aperture decreased, particularly when the object was located at a 45° angle relative to the initial hand location ($F_{4,44}=20.57$, $P<0.01$).

Effects of task variables on joint excursions

Figure 8 summarizes the effects of the task variables on the mean excursions of the joints (i.e., the angles adopted

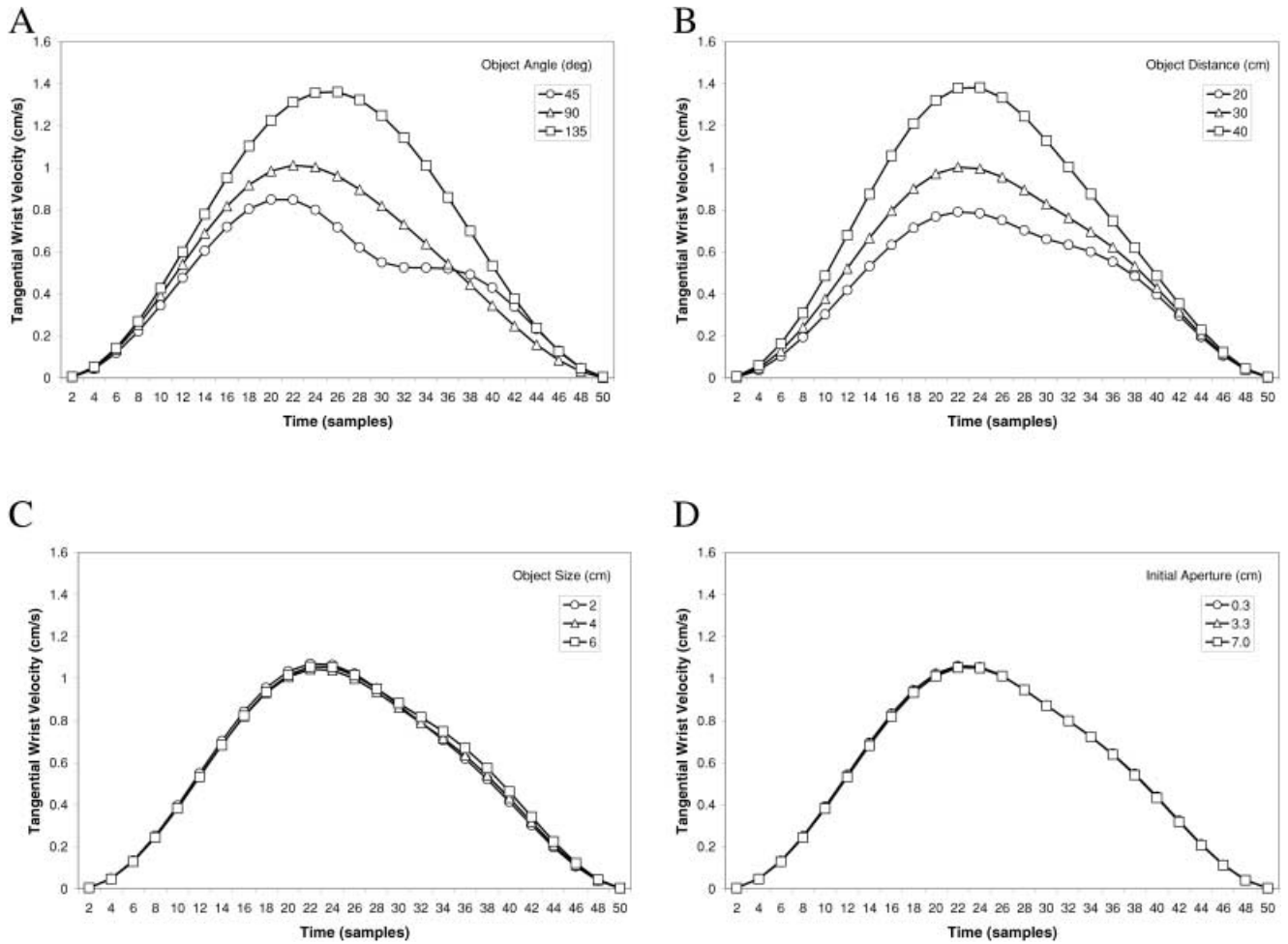


Fig. 5A–D Mean tangential wrist-velocity functions as a function of object angle (A), object distance (B), object size (C), and initial aperture (D)

Fig. 6 Mean aperture overshoot (in centimeters) as a function of object angle, object distance, object size, and initial distance, object size, and initial aperture. Error bars reflect ± 1 SD around the mean; each bar reflects aperture data of 324 grasping movements

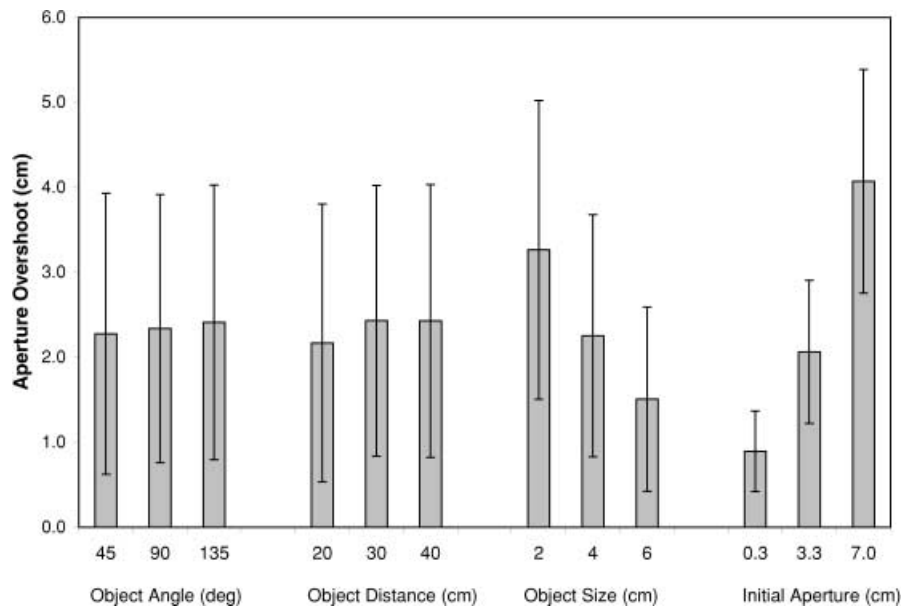


Fig. 7 Mean moment of maximum aperture (in percentage of movement time) as a function of object angle, object distance, object size, and initial aperture. Error bars reflect ± 1 SD; each bar reflects the mean data of 324 grasping movements

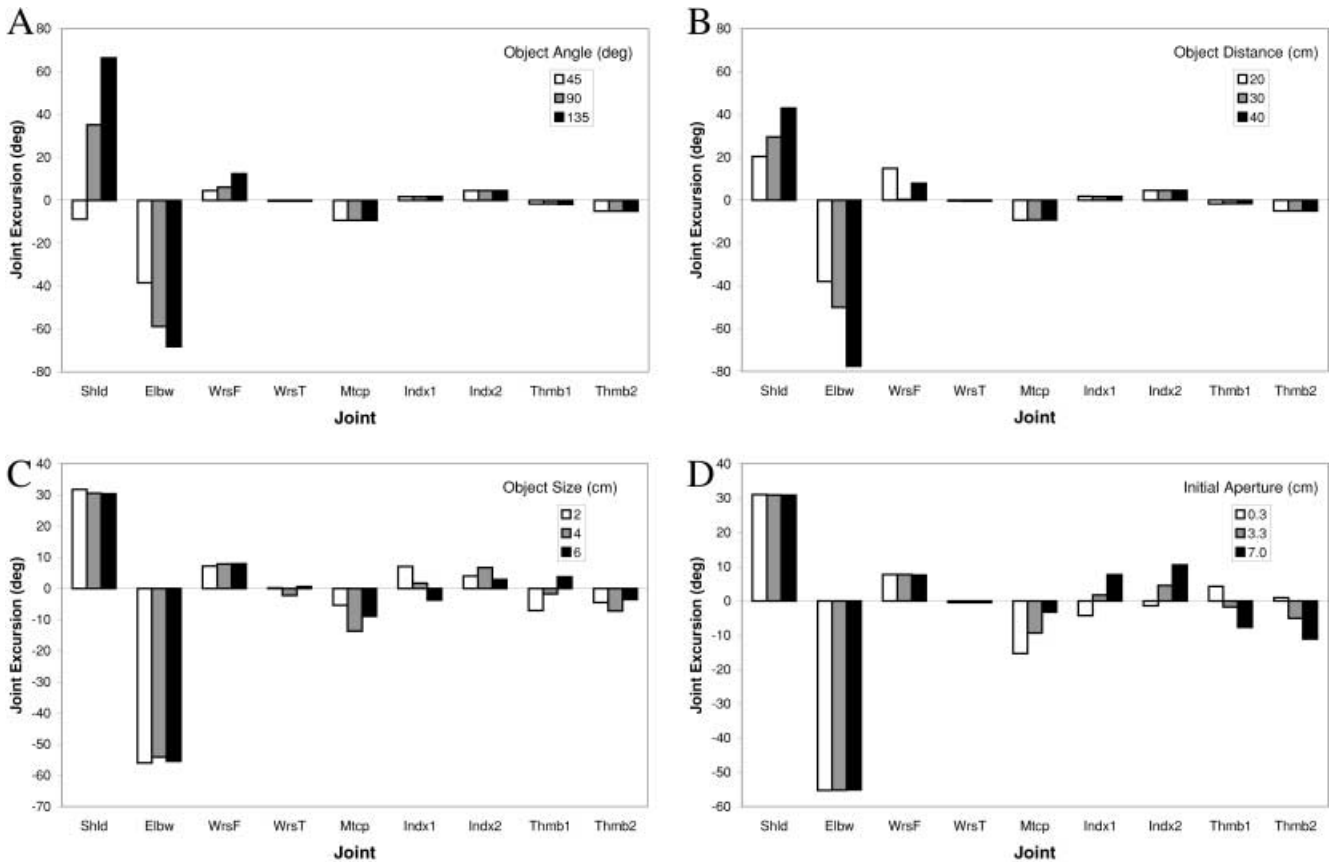
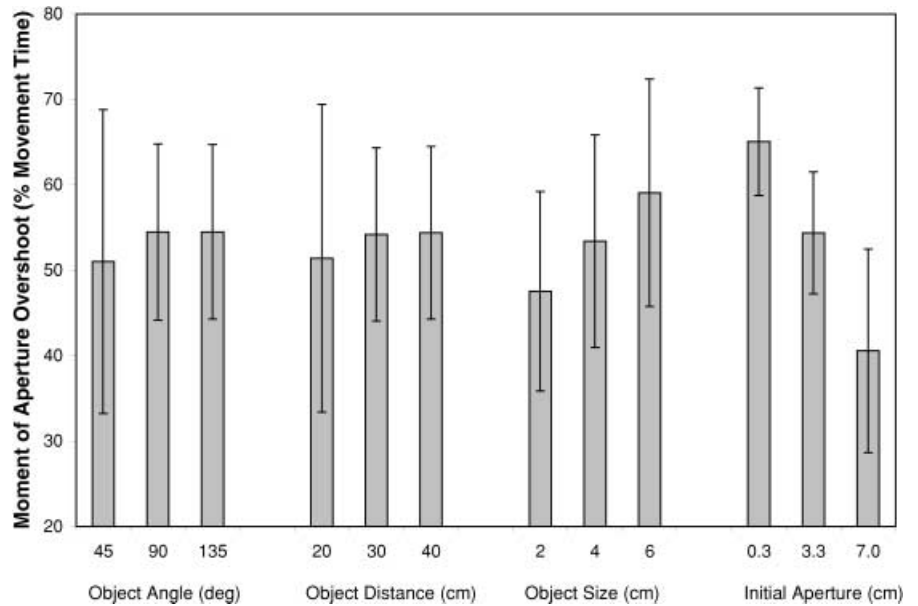


Fig. 8A–D Mean joint excursions (degrees) as a function of object angle (A), object distance (B), object size (C), and initial aperture size (D). On the *x*-axis, the joints are labeled in a proximal order, with the index finger joints preceding the thumb joints (see Table 1)

upon completion of the grasping movements minus the starting angles). As seen in Fig. 8A, for the 135° and 90° object angle conditions, shoulder adduction (positive shoulder excursion) was needed, but for the 45° object angle condition, shoulder abduction (negative shoulder excursion) was needed. Figure 8A, B shows that object angle and object distance had strong differential effects

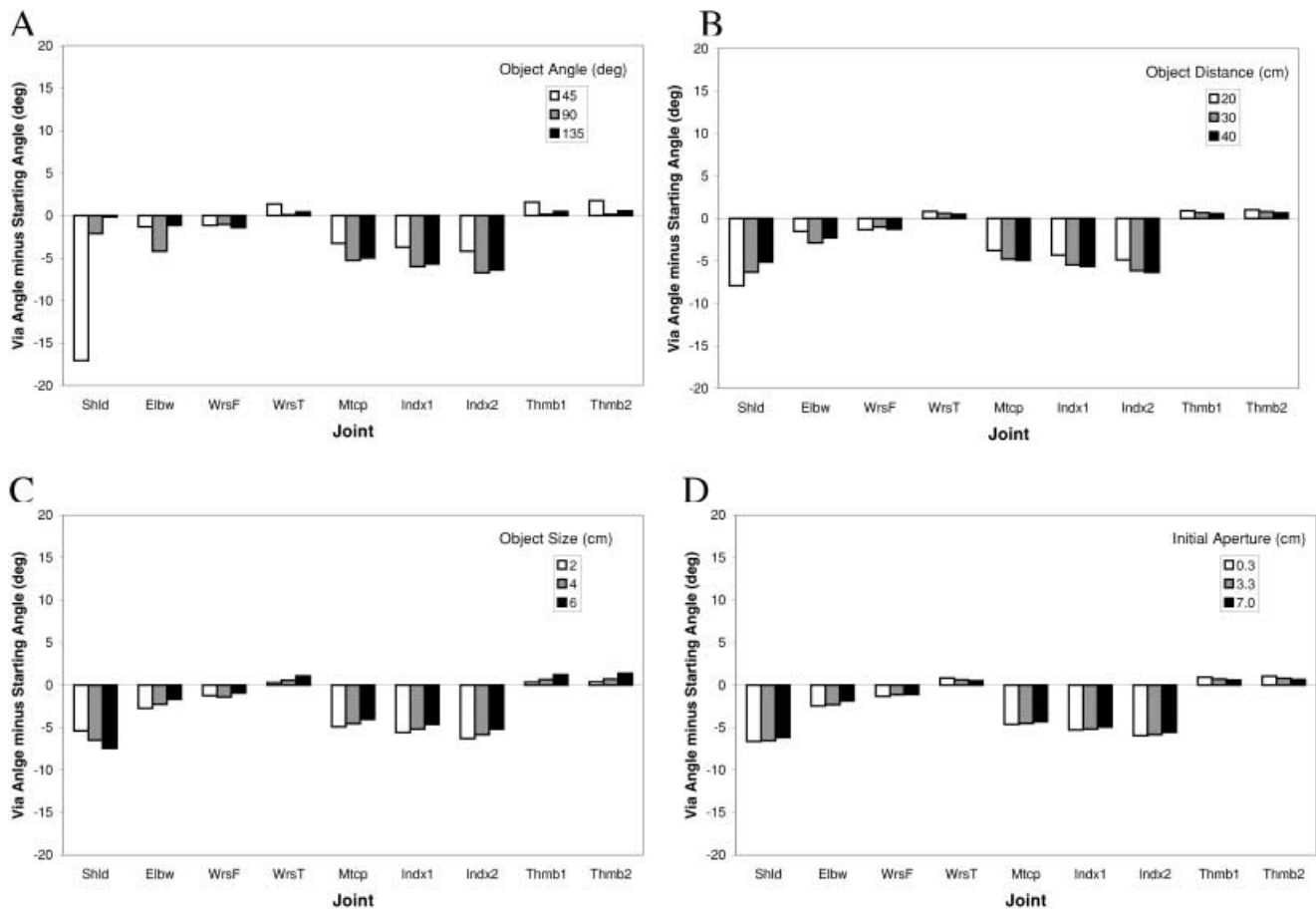


Fig. 9A–D Mean difference between the via angle and the starting angle (degrees) as a function of object angle (A), object distance (B), object size (C), and initial aperture size (D). On the *x*-axis, the joints are labeled in a proximodistal order, with the index finger joints preceding the thumb joints (see Table 1)

on the shoulder and elbow excursions. Figure 8C, D demonstrates that object size and initial aperture size mainly affected the distal joint excursions.

Effects of task variables on difference between via posture and starting posture

Figure 9 shows the effects of the task variables on the distance between the via posture and the starting posture for each joint separately. This variable reflects the extra back-and-forth movement components generated by the individual joints to avoid collisions. Figure 9A shows differential effects of the collision avoidance constraint inherent in grasping objects on the proximal joints (shoulder and elbow) versus the distal joints (wrist, finger, and thumb). For objects located behind the initial hand location (i.e., at the 45° object angle), a significant shoulder abduction component corresponding to -18° difference between via angle and starting angle was required to get the hand behind the object before approaching it. This shoulder abduction was followed by a shoulder

adduction component corresponding to $+18^\circ$ difference between starting angle and via angle; this component is not shown in Fig. 9. The combined back-and-forth movement of the shoulder did not contribute to the net joint excursion of the shoulder, as shown in Fig. 8. This is expected, because the extra back-and-forth of a joint is designed to affect the trajectory without influencing the end position. Such trajectory modification is needed for collision avoidance.

To a lesser extent than the shoulder, the elbow also needed to produce an additional extension-flexion combination to ensure collision avoidance. The other joints all reflected the opening-closing component of the hand joints. For the joints connecting the forearm to the fingers, negative differences between the via angle and the starting angle reflected extension followed by flexion (the size of the latter component not being shown in Fig. 9). For those joints connecting the forearm with the thumb, the positive differences between the via angle and the starting angle also reflected extension because of thumb-finger opposition. Consequently, it is interesting to see that when the object was located to the left of the body midline, the hand opening was mainly realized by the index finger and not by the thumb. For the opposite cases, where the object was located to the right of the body midline, the hand opening was partly realized by finger extensions but also by a more pronounced thumb extension.

Object distance, object size, and initial aperture size had systematic effects on the modeled joint excursions (Figure 9B, C, and D, respectively). In particular, the object-size effects (Fig. 9C) were due to systematic biphasic excursions of the distal joints.

Behavioral experiment

Our simulations revealed a role of initial aperture in determining the maximum opening of the hand. To test this, we conducted a behavioral experiment in which we asked participants to perform the prehension task we simulated. The experiment was originally designed to test the power and sensitivity of our model through an assessment of the correspondence between the shape of predicted and observed work- and joint-space paths. The results of these tests are reported by Rosenbaum et al. (in press) and show that the model accounts satisfactorily for the individual paths of the tip of the index finger and the tip of the thumb in workspace and shoulder-elbow joint-space paths. Here, we focus on an analysis of variations in the magnitude and time course of the hand opening as a function of the task variables, in particular initial aperture. We did not analyze the time course of the distance between the tip of the index finger and thumb as a function of the task variables previously. The present evaluation therefore constitutes a new and separate test of our model's capacity to account for typical prehension kinematics.

Materials and methods

Four right-handed volunteers participated (three men, one woman); their ages ranged from 24 to 32 years.

Each participant was asked to move their hand from a fixed starting position to grasp a cylindrical object. The participant sat at a table raised to shoulder height so all movements could be made with just the shoulder, elbow, wrist, and fingers in the horizontal plane. At the start of each trial, the participant's right arm rested comfortably on the table, with the hand positioned approximately 20 cm in front of the body midline and with the palm perpendicular to the table surface and facing the subject (i.e., the thumb was up and the little finger was in contact with the table). A 3-cm-, 4-cm-, or 5-cm-wide cylinder (height 9 cm) was positioned at each of nine locations corresponding to distances of 20 cm, 30 cm, or 40 cm from the right hand at angles of 45°, 90°, or 135° relative to the near edge of the table from the subject's perspective. The widths of the cylinders differed from the circle sizes used in the computer simulations to accommodate participants' finger and thumb volumes.

At the start of each trial, the initial aperture of the participant's right hand was set. The participant was asked to hold a wooden object of either 0.3 cm, 3.0 cm, or 7.0 cm diameter between the index finger and thumb of the right hand for about 15 s. After the experimenter confirmed that the proper initial aperture was adopted, the participant was asked to remove the wooden object from the right hand with the left hand while taking care that the initial aperture remained unchanged. Next, the experimenter started the movement recording and then gave the participant a verbal "go" signal. The participant was asked to grasp the cylinder quickly and accurately, using a single, smooth movement. Each experimental condition was tested twice, resulting in a total of 162 trials per participant – that is, 3 object angles \times 3 object distances \times 3 object sizes \times 3 initial apertures, tested twice.

Data collection

Movements were recorded in three dimensions with an Optotrak 3020 motion-tracking system (Northern Digital, Waterloo, Canada). Five infrared-emitting diodes (IREDs) were fixed to the participant's right shoulder, elbow, wrist, lateral corner of the index fingernail, and medial corner of the thumbnail. The *xyz* positions of the IREDs were sampled at a rate of 200 Hz with a spatial accuracy of better than 0.2 mm in each spatial dimension. IRED displacement data were filtered off-line with a low-pass, zero phase lag, third-order Butterworth filter (cutoff frequency 8 Hz). The tangential wrist velocity was derived to determine the start and end of the grasping movements. These were determined by the local velocity minima that preceded and succeeded a 5% peak tangential velocity threshold at the beginning and end of motion. The tangential wrist velocity function was defined by the first derivative of the *xyz* displacement function of the IRED fixed to the wrist. The aperture time function was determined by calculating on a sample-by-sample basis the euclidean distance between the two IREDs positioned on the index fingernail and thumbnail.

Data analysis

As with the simulated grasps, data analyses first focused on the aperture time functions. Because in the simulations movement time was kept constant, a normalization of the movement time of the observed grasping movements was required to allow for comparisons and to enable us to average the aperture time functions across object angles, object positions, and object sizes. For this purpose, each observed aperture-time function was resampled into 100 data points by means of spline-based interpolations.

To assess the overall correspondence between the experimental data and the simulations, we also evaluated the main effects of the task variables on the aperture overshoot (centimeters) and the moment of maximum aperture (in percentage of total movement time). The two variables were evaluated by means of separate ANOVAs according to a factorial design of 4 participants \times 3 object angles (45°, 90°, and 135° relative to the initial hand location) \times 3 object distances (20 cm, 30 cm, and 40 cm relative to the initial hand location) \times 3 initial aperture sizes (0.3 cm, 3.3 cm, and 7.0 cm). To reduce the effects of outliers, the statistics resulting from this analysis are given in terms of medians rather than means.

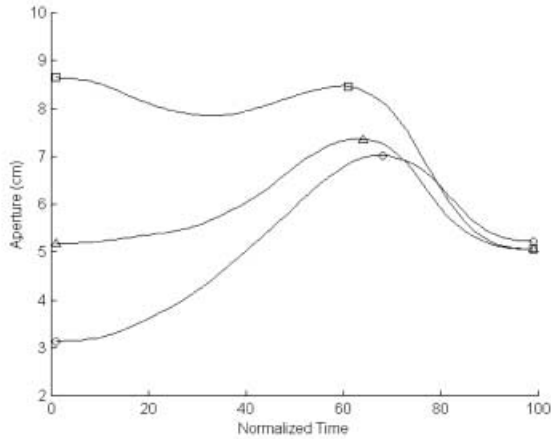
Results

Effects of initial aperture and object size on time-normalized aperture-time functions

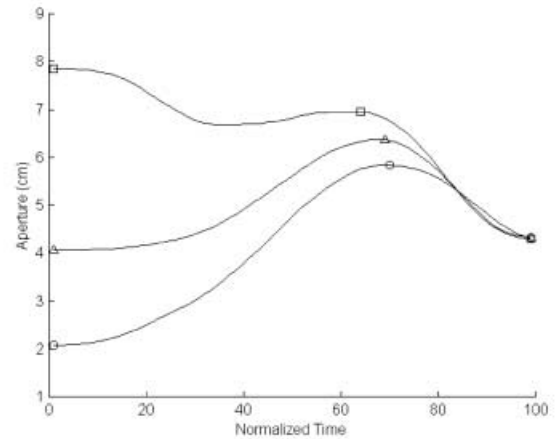
Figure 10 shows the mean time-normalized aperture-time functions as observed in the initial-aperture conditions for each participant. The data are pooled across object angle, object position, and object size. Besides the start and end of the movements, the moments of (local) maximum aperture prior to movement completion are marked in each function also.

The aperture-time functions displayed in Fig. 10 correspond qualitatively to the simulated aperture-time functions shown in Fig. 4D. However, when the initial aperture was larger than the average object size, the time course of the hand opening of the participants showed a characteristic feature that was not predicted. In these cases, the participants first closed the hand until about 30–40% of the movement time, after which they increased their aperture again until a local maximum hand-

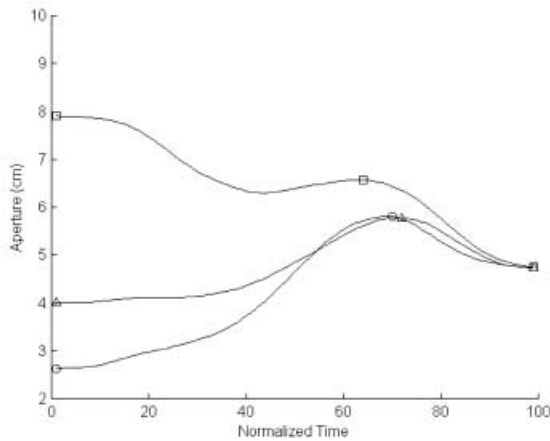
Participant 1



Participant 2



Participant 3



Participant 4

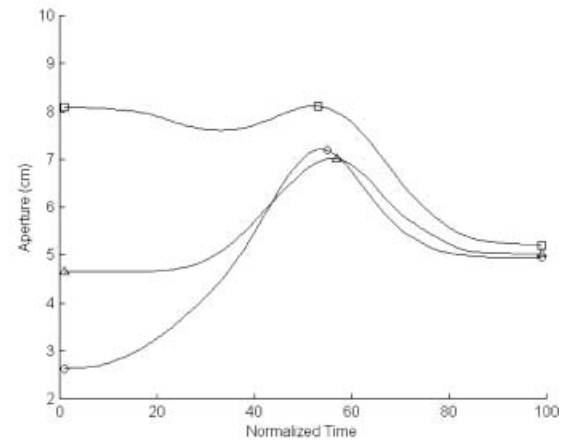


Fig. 10 Mean time-normalized aperture-time functions for each of the four participants. Data are pooled across object angle, object distance, and object size. *Circles*, *triangles*, and *squares* represent the 0.3-cm, 3.3-cm, and 7.0-cm initial-aperture conditions, respectively. In addition to the start and end of the movements, the moment of maximum aperture in each aperture-time function is also marked accordingly

opening was reached at about 60–70% of the movement time. In the final 30–40% of the movement time, the hand closed around the object. We will return to these findings in the Discussion.

Figure 10 also shows that the size of the maximum aperture adopted at around 60–70% of the movement time varied with initial aperture size. Table 2 summarizes this effect for each participant in terms of the observed mean aperture overshoots, i.e., the size of the local maximum aperture prior to movement completion minus the width of the cylinder. Whereas, for the 0.3 cm and 3.3 cm initial-aperture conditions, the observed aperture overshoot did not differ as much as was expected on the basis of the simulations, the observed aperture overshoots appeared to be systematically larger in the 7.0-cm

Table 2 Mean (and SD) of aperture overshoot (centimeters) by initial aperture (0.3 cm, 3.3 cm, or 7.0 cm) of the four participants separately, pooled across the participants, and of the model

| | Initial aperture (cm) | | | | | |
|--------------|-----------------------|-----|------|-----|------|-----|
| | 0.3 | | 3.3 | | 7.0 | |
| | Mean | SD | Mean | SD | Mean | SD |
| Participants | | | | | | |
| 1 | 2.4 | 0.4 | 2.8 | 0.5 | 3.9 | 0.4 |
| 2 | 1.9 | 0.5 | 2.3 | 0.5 | 2.9 | 0.5 |
| 3 | 1.3 | 0.4 | 1.2 | 0.3 | 2.0 | 0.4 |
| 4 | 2.8 | 0.8 | 2.6 | 0.6 | 3.3 | 0.7 |
| Pooled mean | 2.1 | 0.8 | 2.2 | 0.8 | 3.0 | 0.9 |
| Model | 0.9 | 0.5 | 2.1 | 1.8 | 3.6 | 0.8 |

than in the 3.0-cm initial-aperture condition, as predicted.

With respect to the moment of maximum aperture, the data show a similar pattern. Whereas the moments of maximum aperture for each participant differed only marginally in the 0.3-cm and 3.3-cm initial-aperture con-

Table 3 Mean (and SD) of moment of maximum aperture (in percentage of movement time) by initial aperture (0.3 cm, 3.3 cm, or 7.0 cm) of the four participants separately, pooled across the participants, and of the model

| | Initial aperture (cm) | | | | | |
|--------------|-----------------------|----|------|----|------|----|
| | 0.3 | | 3.3 | | 7.0 | |
| | Mean | SD | Mean | SD | Mean | SD |
| Participants | | | | | | |
| 1 | 73 | 4 | 70 | 4 | 67 | 7 |
| 2 | 71 | 7 | 69 | 7 | 64 | 9 |
| 3 | 74 | 8 | 72 | 6 | 66 | 8 |
| 4 | 68 | 7 | 70 | 9 | 65 | 8 |
| Pooled mean | 71 | 7 | 70 | 7 | 66 | 8 |
| Model | 65 | 5 | 54 | 6 | 47 | 3 |

ditions, the predicted difference between the 3.3-cm and 7.0-cm initial-aperture conditions was confirmed, i.e., the moment of maximum aperture occurred earlier in the grasp when the initial aperture was larger (see Table 3).

Effects of task variables on aperture overshoot

The angle at which the cylinder was positioned relative to the initial hand location appeared to determine the aperture overshoot of the participants. In contrast to the simulations, which did not predict an effect, the median observed aperture overshoots significantly increased from 2.34 cm to 2.39 cm to 2.52 cm for the 45°, 90°, and 135° object angle conditions, respectively ($F_{2,6}=15.50$, $P<0.01$). Object distance did not affect the observed aperture overshoot. In the 20-cm, 30-cm, and 40-cm object-distance conditions the median aperture overshoots were, 2.44 cm, 2.36 cm, and 2.45 cm, respectively ($F_{2,6}<1$). Object size, even though marginally significant, affected aperture overshoot in the expected direction. The 3-cm-, 4-cm-, and 5-cm-wide cylinders were approached with median aperture overshoots of 2.70 cm, 2.44 cm, and 2.12 cm, respectively ($F_{2,6}=3.67$, $P=.09$). Finally, the initial aperture manipulation proved to have a considerable effect on the participants' hand opening, as shown by the data for each participant separately (see Table 2). On average, the 0.3-cm, 3.3-cm, and 7.0-cm initial aperture conditions were accompanied by 1.99-cm, 2.29-cm, and 3.02-cm median aperture overshoots, respectively ($F_{2,6}=15.29$, $P<0.01$).

In sum, even though the observed effects of object angle and object location on the aperture overshoot were different from the predicted effects (see Fig. 6), the effects of object size and initial aperture corresponded with the simulations as well as with the findings reported in the literature we have summarized.

Effects of task variables on moment of maximum aperture

Object angle did not affect the moment of maximum aperture. The moments at which the maximum aperture occurred for the 45°, 90°, and 135° object angle conditions in terms of median percentages of movement time were 71%, 69%, and 70%, respectively ($F_{2,6}=1.95$, n.s.). Object distance did affect the moment of maximum aperture. As predicted, the 20-cm, 30-cm, and 40-cm object distance conditions yielded median moments of maximum aperture at 66%, 70%, and 73% of the movement time ($F_{2,6}=105.89$, $P<0.01$). Cylinder size did not have a significant effect on the moment of maximum aperture. For the 3-cm-, 4-cm-, and 5-cm-wide cylinders, the median values of the moments of maximum aperture were 69%, 69%, and 70% ($F_{2,6}<1$, n.s.). The absence of a size effect on the moment of maximum aperture was unexpected and clearly at odds with earlier findings. The reason may possibly be that the range of object sizes used in the experiment was rather small relative to the range of initial aperture sizes. Indeed, an increase in initial aperture clearly induced the moment of maximum hand-opening to occur earlier in the movements, as predicted. For the 0.3-cm, 3.3-cm, and 7.3-cm initial-aperture conditions, the median values were 72%, 70%, and 67%, respectively ($F_{2,6}=16.34$, $P<0.01$).

In sum, in contrast to our predictions and at odds with earlier findings, we did not find an effect of object size on the moment of maximum aperture. The absence of an object angle effect was also in contrast to our simulations which the relative moment of maximum aperture changed from 51% to 54% (see Fig. 7). The object distance and initial aperture effects, however, corresponded to our simulation as well as with earlier findings reported in the literature. Whereas a larger object distance induced the moment of maximum aperture to occur later in the grasp, a larger initial aperture made the maximum aperture occur earlier in the grasp.

Discussion

The simulations and behavioral study described here were designed to shed light on the determinants of human grasping kinematics. The simulations displayed most of the reported properties of kinematics of the hand and arm in prehension. This outcome can be taken to demonstrate the strength of the theory of motion planning on which the simulations were based (Rosenbaum et al. 1995, 1999, in press).

Four predictions were evaluated in the present study, two of which were based on the characteristic pattern of prehension kinematics reported in the literature, and two of which were based on our model. The predictions were as follows: (1) larger object sizes should be accompanied by smaller aperture overshoots; (2) larger objects should induce the moment of maximum aperture to occur later in the grasping movement; (3) objects located to the

right of the body midline should elicit large, biphasic, shoulder and elbow rotations; and (4) grasping kinematics should be differentially affected by initial aperture.

With respect to the first prediction, as expected, object size systematically influenced the aperture overshoot, both in the simulations and, even though only marginally, in the experiment. As object size increased, overshoot decreased. Because aperture overshoot was defined as the maximum aperture minus the object size, this simulated effect corresponds to behavioral evidence (see Smeets and Brenner 1999 for an overview), showing that the linear regression line relating maximum aperture to object size generally has a slope of less than 1. To facilitate comparisons between the present simulation results and the experimental findings reported in the literature, we reanalyzed our simulation results in terms of maximum aperture and conducted a linear regression analysis relating maximum apertures to object sizes. The regression analysis was conducted for the three initial aperture-size conditions separately. The results, presented in Table 4, show that in our simulations initial aperture size strongly influenced the slope of the regression lines. Given that slopes varying between 0.6 and 1.2 have been reported in the behavioral literature (for a review, see Smeets and Brenner 1999), the simulation results might be taken to suggest that the initial aperture size adopted by subjects in earlier experiments may have influenced the results of those experiments. The present behavioral experiment does not confirm this suggestion, however, for, as shown in Table 5, across the participants in the present behavioral study, initial-aperture variations failed to have a consistent effect on the regression equations relating maximum aperture to object size. The less-than-1 slopes need not, according to our model, be due to initial aperture size, however. Instead, they may be due to the relative increase in the distance between starting and goal hand postures under unchanged collision-avoidance conditions, as elaborated later in this article.

With respect to the second prediction, object size influenced the simulated moment of maximum aperture as predicted, even though this effect was not directly coded into the program (i.e., the effect emerged from the model). A number of behavioral studies have shown that maximum aperture occurs proportionally later in the movement with larger objects (Bootsma et al. 1994; Brenner and Smeets 1996; Chieffi and Gentilucci 1993; Churchill et al. 2000; Goodale et al. 1994; Marteniuk et al. 1990; Paulignan et al. 1991, 1997; Servos et al. 1992; Smeets and Brenner 1999; Zaal and Bootsma 1993; Zaal et al. 1998, 1999). The simulated effect can be understood by considering the relations in our model between the starting posture, the goal posture, and the via posture of the hand. If a grasping movement only consisted of a movement from the hand's starting posture to a via posture and back, the moment of maximum aperture would occur at 50% of the movement time. In this case, the hand's goal posture would be identical to its starting posture, and the grasping movement would merely consist of opening and closing the hand. However, when under

Table 4 Results of regression analyses relating maximum aperture to object size for each initial aperture condition separately ($n=324$)

| Initial aperture (cm) | Regression | | R^2 |
|-----------------------|---------------|-------------|-------|
| | Max. aperture | Object size | |
| 0.3 | 0.78 | +1.77 | 0.95 |
| 3.3 | 0.57 | +3.81 | 0.82 |
| 7.0 | 0.34 | +6.86 | 0.73 |

Table 5 Results of regression analyses relating maximum aperture to object size for each initial aperture condition and participant separately. Each regression analysis involved 54 data pairs

| Participant | Initial aperture (cm) | Regression | | R^2 |
|-------------|-----------------------|---------------|-------------|-------|
| | | Max. aperture | Object size | |
| 1 | 0.3 | 0.97 | +2.51 | 0.71 |
| | 3.3 | 1.22 | +1.76 | 0.71 |
| | 7.0 | 0.87 | +4.52 | 0.70 |
| 2 | 0.3 | 0.72 | +3.08 | 0.64 |
| | 3.3 | 0.52 | +4.32 | 0.53 |
| | 7.0 | 0.44 | +5.29 | 0.57 |
| 3 | 0.3 | 0.70 | +2.69 | 0.73 |
| | 3.3 | 0.91 | +1.63 | 0.87 |
| | 7.0 | 1.03 | +1.83 | 0.82 |
| 4 | 0.3 | 0.33 | +6.09 | 0.17 |
| | 3.3 | 0.55 | +4.75 | 0.52 |
| | 7.0 | 0.41 | +6.25 | 0.38 |

similar collision-avoidance constraints the difference between the starting posture and goal posture of the hand becomes larger, as is the case with larger objects, the moment of maximum aperture occurs later. This is because in our model the biphasic movement from the starting posture to the via posture and back is superimposed on the motion between the starting posture and the goal posture. In the present behavioral experiment, we failed to reproduce these object-size effects on the moment of maximum aperture, probably because we used a smaller-than-needed range of object sizes to get the predicted effects.

With respect to the third prediction, the location of the object relative to the hand's starting location had pronounced effects on the simulated shoulder and elbow excursions required to transport the hand to the object without colliding with it. As predicted, this was particularly the case for objects located "behind" the hand. The results of the behavioral experiment showed that, when objects occupied this position, a larger aperture overshoot occurred. This finding suggests that object occlusion may increase uncertainty about collision-free prehension which may be compensated for with larger overshoot. Even though our model did not show this behavior, the behavioral finding provides further evidence for the important role of the collision-avoidance constraint

in prehension control. That the simulation did not adequately predict this effect indicates that the theory needs improvement.

With respect to the fourth prediction (concerning initial aperture size), our simulations yielded an interesting effect, which was confirmed in our behavioral experiment. Both in our simulations and in the behavioral study, as initial aperture increased, aperture overshoot increased. The fact that aperture overshoots occurred even when the initial aperture was larger than the object size is not surprising, because the requirement to avoid colliding with objects to be grasped is an important, albeit implicit, constraint in grasping. Recent experiments (Saling et al. 1996, 1998; Timman et al. 1996) have shown that perturbing hand-opening during grasping or having subjects start a grasping movement with a maximum hand-opening strongly influences the character of prehension movements. In particular, it has been shown that subjects tend to close the hand in these situations before they reopen the hand as it approaches the target object and then close in on it. The aperture time functions shown in Fig. 10 confirm these findings. However, with large initial apertures, the simulations did not yield this kinematic pattern, as seen in Fig. 4D.

How might the latter disparity be interpreted within the framework of our model? One possibility is that when the initial aperture is unusually large, the subject selects two via postures rather than only one to generate a compound grasping movement made up of superimposed submovements. Another possibility is that subjects resort to a strategy of using stored movements. Further research and modeling is needed to distinguish between these alternatives. Yet another alternative worth considering is that subjects may rely on the stretch-shorten cycle of muscle (Shorten 1987), much as they bend down to prepare to jump, or pull the arm back before throwing forward. Currently, such features of muscle control are not represented in our model, but this is only a matter of convenience. The model so far is limited to kinematics. Kinetics are omitted merely to facilitate the exploration of computational processes. The promise of the model, however, given its exclusive reliance so far on kinematics, encourages us to think that the model's framework can provide a basis for explaining outcomes that may have a basis in force control. Note that the model's framework is entirely conducive to the inclusion of kinetics. Another example of the necessity of considering force control relates to the effects of object location on tangential wrist velocity, as discussed above. This effect has been attributed to changes in the effective inertia of the limb as a function of movement direction (Ghez et al. 1997). Although our model does not capture such inertial aspects of trajectory formation, it nonetheless predicts at the kinematic level similar direction-dependent movement features. The lesson to be learned from this outcome is that even though the model does not include kinetics, not all phenomena that seem attributable to kinetics need to be. Working with an impoverished model provides one way of illustrating this.

Another aspect of the simulation results that deserves comment concerns the fact that in human grasping a low-velocity transport phase sometimes is seen (Jeannerod 1981, 1984) but sometimes not (Wallace and Weeks 1988). Our simulations likewise yielded a low-velocity transport phase in some reaches but not others. We can explain the presence or absence of the low-velocity transport phase on the basis of the collision-avoidance requirements of the tasks we studied. Our simulations show that if the goal of avoiding collisions with the to-be-grasped object prompts a subject to generate a biphasic shoulder and/or elbow excursion on top of the linear excursions between the starting and goal angles of these proximal joints, a low-velocity phase is likely to occur (cf. Figs. 5A, 8A, 9A). However, when monophasic shoulder and/or elbow excursions will do the job, a low-velocity phase will not occur (cf. Figs. 5D, 8D, 9D). In the same vein, our results fit with recent findings showing that, in the presence of obstacles at intermediate positions between starts and ends of grasping movements, hand transport slows down but the movements of the fingers remain unaltered (Saling et al. 1998). We observed the same thing here (cf. Figs. 4A and 5A).

To conclude, the present study demonstrates that a recent model of motor planning (Rosenbaum et al. 1995, 1999, in press) can generate a large, realistic range of grasping kinematics. The simulations reported here reproduced frequently reported effects of object location and object size, and it made new predictions, particularly concerning the role of initial aperture size. These new predictions were partially confirmed in a behavioral test, but the test also revealed a weakness of the model. More study will be needed to determine how the lapses in the model, which the present work was designed to expose, may be repaired to yield a more powerful account of human grasping and motor control generally.

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