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RESEARCH ARTICLE

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Independent movements of the digits in grasping

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Abstract Reaching out for an object is often considered to consist of the control of two components: transporting the hand to the object's position, and scaling the grip to the object's size. We recently proposed an alternative view. According to this view, grasping consists of controlling the digits, not the hypothetical transport and grip. This alternative view assumes that the opening of the hand emerges from the trajectories of the digits. We therefore studied the movements of the digits in grasping. We asked subjects to grasp disks (diameters ranging from 5 to 8 cm) at marked positions with two digits. The positions were at opposite sides of the disk, at the same distance from the starting position, so that the orientation of the surface was the same for both digits. The subjects grasped the disks either with the index finger and thumb of the dominant hand, with the same digits of the non-dominant hand, or bimanually with both index fingers. Our predictions are: that the well-known relation between object size and grip aperture holds for each digit; that the same relation holds if the object is grasped with two hands instead of with the thumb and finger of one hand; that maximum deviation, variability and duration of the digit movements are related; and that variations in the timing of the maximum deviation of one digit are independent of those in the other digit. In accordance with our predictions, we found that the maximum deviation of both digits increased with 0.75 times the object radius, independent of the hand(s) used. The movements of the thumb were more variable than those of the index finger, which was reflected by a larger deviation earlier in the movement. The timing of the maximum deviation of the two digits was independent. These results on the digits' movements are consistent with our view that grasping can be understood as the largely independent movements of the digits. The results are not in conflict with the hypothesis that the grip is controlled during grasping, but can only be explained by extending that hypothesis post hoc.

Keywords Human · Prehension · Arm movement · Motor control · Co-ordination

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Introduction

Grasping is generally described as a combination of two more or less independent components: transport and grip. We recently showed that several key aspects of grasping can easily be understood if one assumes that grasping is no more than simultaneous smooth movements of finger and thumb to appropriate positions, with the restriction that they will end moving more or less perpendicular to the object's surface (Smeets and Brenner 1999a). Note that with movements of the digits we mean their movement relative to the outside world, not relative to the hand or wrist. By modelling the two key aspects of this new view on grasping (smooth movement and perpendicular approach), one can make quantitative predictions for the movements of the individual digits. Four of these predictions will be tested in this paper. To do so, we will compare the movements of the digits in unimanual and bimanual grasping.

Rosenbaum and colleagues (Rosenbaum et al. 1999a, 1999b) have developed a model which shares several main features of our model. Although their model differs from ours in its level of description and complexity, both models are based on the assumption that grasping is essentially a combination of two pointing movements and can thus be described by models for pointing. A second common feature of these models is that they both base the trajectory formation on arguments of obstacle avoidance. The main difference between the two models lies in the way the redundancy problem is solved. In Rosenbaum's scheme, the whole posture is determined in one process. Our scheme only covers the trajectories of the end-effectors (i.e. the tips of the finger and thumb). Determining how the joint angles must change to obtain such trajectories is deferred to a separate process. There is some experimental evidence that trajectories of end-effectors are largely independent of the underlying joint movements (Morasso 1981; Flash 1987; Wolpert et al. 1994; Schillings et al. 1996; Marteniuk et al. 2000). We believe that this evidence justifies performing an analysis of trajectory formation without simultaneously considering the redundancy problem.

Our view on grasping is quite distinct from the framework that is generally used to perform grasping experiments. The classic view (Jeannerod 1981; Arbib 1981) assumes that the wrist is transported to a position near the object and that the digits move relative to each other to form the grip. The movements of the digits relative to the environment are not explicitly specified. However, the movements of the finger and thumb are generally not regarded to be equivalent: the index finger is assumed to do the major part of grip formation, while the thumb follows the wrist (Paulignan et al. 1991). A second view has been advocated by Wing and colleagues (Haggard and Wing 1997; Wing and Fraser 1983). They take this non-equivalence to its extreme by assuming that the thumb is transported to a position on the object and that the grip is formed by movement of the index finger relative to the thumb.

The main difference between our view and these two alternatives is that we assume that the digits move independently to positions on the object, whereas the other two views assume that the digits move relative to each other. The present experiment and analysis are designed to test our assumptions about the digits' movements. We have argued (Smeets and Brenner 1999a) that the position and orientation of the contact surface are the main determinants of the digit's path. If subjects are asked to grasp a cylinder (a very common task in grasping research), they grasp the objects with the hand in a characteristic orientation: with the thumb closer to the body than the finger (Paulignan et al. 1997). In this situation, the orientation of the contact surface is quite different for the two digits. According to our model, these differences in orientation are responsible for the clear differences between the movements of the two digits (see Figs. 4, 5 in Smeets and Brenner 1999a). In the present study we avoid these complications by indicating two positions on the disks such that the contact surfaces are oriented parallel to the movement direction (see Fig. 1A).

For an experiment in which the constraints are the same for finger and thumb, our model predicts that the movements of the digits will be the same. A problem with this prediction is that the constraints will never be exactly the same. For instance, the contact area of the thumb is larger than that of the finger. Moreover, although our model does not cover this issue explicitly, we acknowledge that constraints on the movements of the joints could lead to differences in movement strategies between finger and thumb (Rosenbaum et al. 1999a). We therefore chose a different comparison to test: that the average movement of an index finger when grasping an object with finger and thumb should be equal to the average movement of that index finger when grasping an object with the index fingers of both hands. This is the first prediction that was tested.

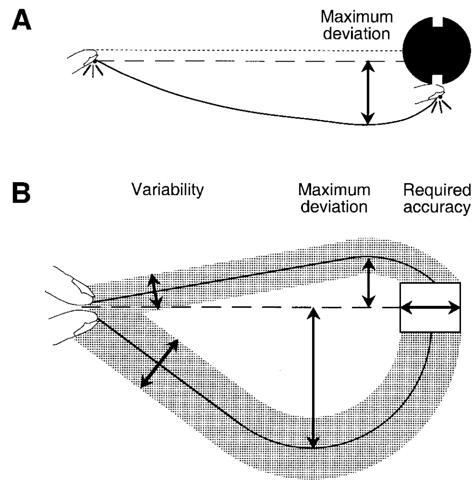

Fig. 1 **A** Definition of the maximum deviation. The *white squares on the disk* indicate the contact positions for the digits. **B** Comparison of the movements of two digits towards contact surfaces of equal size. Whether the movements are accurate enough at contact depends not only on the variability in movement path, but also on the angle of approach. The lower (more variable) digit has to approach the surface closer to orthogonal to have the same accuracy at contact as the other digit. For smooth movements, this more orthogonal approach leads to a larger deviation earlier in its movement path (see Appendix)

One of the major achievements of our model (Smeets and Brenner 1999a) is that it predicts the relationship between object size and grip formation based on the contact positions of the digits. The model also predicts the movements of the individual digits. Given the (unusual) contact positions of the digits in the present experiment, the model equation for the dependency of the maximum deviation (the difference between the actual path and a straight line; see Fig. 1A) on object radius has the same form for both digits (Eq. 3, 4). The differences between finger and thumb that were mentioned in the previous paragraph might enter this equation as a different value for the approach parameter a_p. The slope of the relationship between object size and maximum deviation depends only marginally on the approach parameter. Our second prediction is therefore that the maximum deviation of both digits will vary linearly with object radius, with a slope of approx. 0.75 (see Appendix).

A fundamental aspect of our view is that the variability in the movement path has independent sources for each digit. If, for some reason, the spatial variability should differ between the digits (see Paulignan et al. 1991, 1997), this will be reflected in the way the object is approached (Fig. 1B). We predict that the digit with more variability in its trajectory will have a larger deviation earlier in the movement (third prediction, see Appendix).

Independent control also implies that the maximum deviation of each digit is determined by properties of the object and the digit itself, independent of the movement of the other digit. Variability in the planning and control of the movement should therefore leave the trajectories of the digits uncorrelated. Obviously, the task constrains both digits to contact the object at the same time, so only the relative timing of the trajectories is predicted to be independent. Our view that the digits are controlled independently of each other neglects the fact that the two digits have part of the motor apparatus (i.e. the arm) in common. Noise at this final common level (e.g. in the motoneurones of elbow muscles) can introduce a correlation. Given the geometry of the task, such variability will introduce a negative correlation in the amplitude of the maximum deviations, with a negligible effect on the timing. We therefore predict that the correlation between the maximum deviations of the digits is equal to or (slightly) smaller than zero, without any correlation in their timing. This fourth prediction should hold for both unimanual and bimanual grasping.

We will test these four predictions that are based on the assumption that the digits move independently during grasping. Most of the predictions are not explicitly in conflict with other views on grasping, because models based on those views do not explicitly specify how the digits move. However, our model predicts certain relationships that can be tested and that other models can only deal with in a post hoc fashion.

Methods

Subjects

Seven students (five right-handed, two left-handed) of the Fogarty exchange program participated in the experiment. They gave their informed consent prior to their inclusion in the study. The data from one right-handed subject were not included in the analysis (see Data analysis). All subjects were naive to the purpose of the experiment and had no earlier experience in grasping experiments. Informed consent was obtained from all participants.

Apparatus

Four disks of 3 cm height and diameters of 5 cm, 6 cm, 7 cm and 8 cm were used. Their masses were 85 g, 120 g, 165 g and 215 g. The disks were painted black and had two (1.2-cm-wide) yellow markers on them. In the experiment, a disk was positioned at 40 cm from the starting position (Fig. 2). It was oriented in such a way that the line through the marked positions on the disk was always perpendicular to the line connecting the centre of the disk to the starting position. In this way, the relation between the orientation of the contact surface and the starting position was the same for both digits.

Finger movements were recorded at 250 Hz using an Optotrak 3010 motion-analysis system. Markers were taped on the nails of the two digits, which were used to grasp the disks. To facilitate detection of the onset and the end of the grasping movement during the analysis of the movement data, two switches were mounted in the table. One 1.5-cm-diameter switch was below the starting position, and was released when the subject started to move. A second switch was under the disk, so that it was released when the disk was lifted.

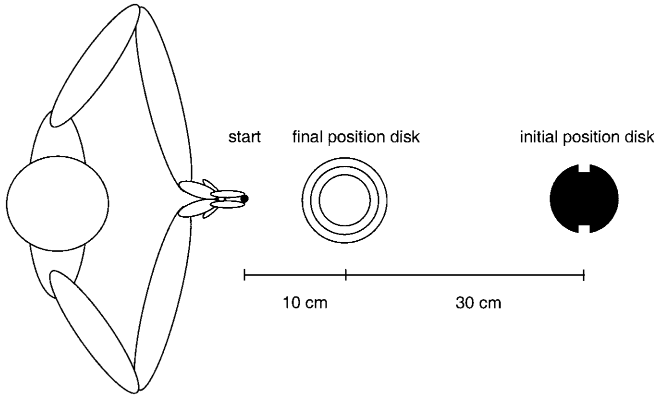

Fig. 2 Experimental set-up. The subject is drawn in the starting posture for bimanual grasping

Procedure

Subjects were seated behind a table and were asked to grasp a disk using a precision grip. They started a trial with the two digits in contact with each other pressing the switch at the starting position. They were instructed to move towards the disk after a go signal, grasp it at the marked positions, pick it up and place it on a target 10 cm from the starting position (see Fig. 2). To let the subjects grasp as naturally as possible, we gave them no further instruction on the reach-to-grasp phase; we instructed them to place the disk accurately on the target instead. Subjects were seated on a chair, which they were encouraged to reposition to sit on as comfortably as possible.

Grasping with the index fingers of both hands is different from one-handed grasping in many ways. The experiment was designed to minimise the effects of the differences in dexterity and mechanical stability between the two ways of grasping. To get an impression of the possible effects of the less dextrous performance of two-handed grasping, we included a condition in which subjects grasped with their non-dominant hand.

When grasping with two hands, the linkage between the two digits is much longer and consists of many more joints than when grasping with digits from one hand. This results in a lower mechanical stability, so that subjects may have to grasp more accurately. We reduced the length of and number of joints in the linkage between the digits in the bimanual grasp by instructing subjects to clasp their hands and stick out their index fingers (see Fig. 2). Although this results in a rather unusual grasping posture, subjects had no difficulty picking up the target in this manner.

The grasping was thus done in three conditions: using index finger and thumb of the dominant hand, using index finger and thumb of the non-dominant hand, and using the index fingers of both hands. Each condition was tested in a separate block, with a short break in between to rearrange the markers. Within each block there were four disk sizes, which were presented in random order, making sure that each disk size was grasped 10 times. The order of the conditions was counterbalanced across subjects.

Data analysis

After the experiment, we checked whether the markers had always been visible. We rejected trials in which markers were hidden from view for more than eight samples. For one subject in one condition, the way the markers were positioned made them disappear from view in 31 out of 40 trials. Trials from this subject were not used in further analysis. Trials were also rejected whenever the subject started to move before data collection started, started without contact of the digits (distance between markers more than 2.0 cm), or did not use the tip of the digits for the grasp (distance between markers at contact more than 3.0 cm larger than object diameter). After applying these criteria, 654 trials remained. For each block of each of the six remaining subjects, at least 30 of the 40 trials could be analysed.

For the analysis, we used only the component of the movement parallel to the table. We started the analysis by reconstructing the positions of missing marker samples using linear interpolation. To determine the onset and end of the digits' movements, we used a velocity threshold of 10 cm/s. To describe the behaviour of the individual digits, we introduced a measure comparable with grip aperture: the deviation of a digit (see Fig. 1). This is the distance between a point on the digit's path and the line connecting the start and disk position (i.e. the onset and end of the average of the digits' trajectories). For descriptions in classic terms, we used grip aperture, which is defined as the (horizontal) distance between the markers. The grip aperture was corrected for the distance between the markers and the digits' surfaces by subtracting the value at movement onset from it. The digits' deviations were corrected in a similar way by subtracting half of the grip aperture at movement onset from them.

We used *t*-tests to compare mean values between conditions and paired *t*-tests to compare mean values between digits within conditions. We used regression analysis to determine the relations between object size and various experimental parameters. Regressions were performed for each subject and condition separately. We used (paired) *t*-tests to compare the slopes, intercepts and correlation coefficients of these regressions.

Results

On average, the reach to grasp movement took 693 ms. It was slower in the bimanual condition than in the non-dominant and dominant unimanual conditions (776 ms versus 638 ms and 658 ms; $t(46)=3.9$, $P<0.0005$, and $t(46)=3.0$, $P<0.005$). The orientation of the line connecting the digits did not exactly match the requested orientation (perpendicular to the movement direction). In two-handed grasping, there was a mean error of 4.5°, with a negligible (less than 1°) bias. In the two one-handed grasping conditions, the mean orientation error of the hand was 13.2°, with the thumb closer to the body than the finger. The error for one-handed grasping varied strongly between subjects: means ranging from 3.8° to 21.4°. The orientation error was smaller for larger objects (for one-handed grasping it ranged from 14.9° for 5 cm objects to 11.5° for 8 cm objects). This orientation error could give rise to some small differences between the two digits in the unimanual conditions; the difference in orientation error between conditions could give rise to small differences in the behaviour of the index finger between these conditions.

To check whether our constraint on the positioning of the digits disrupted the normal grasping behaviour, we examined whether our subjects showed the classic relations between object size and grip formation (for a review, see Smeets and Brenner 1999a). Both maximum grip aperture and its relative time increased with object size. On average, maximum grip equalled 5.9 cm plus 0.72 times the object diameter ($r^2=0.56$). The relative time of the maximum aperture increased with object size: the maximum was found at 65% plus 1.2 times object diameter in centimeters ($r^2=0.07$). A first impression based on the grip formation is thus that our task yielded normal grasping behaviour in all three conditions. Contrary to the reason for adding the non-dominant hand condition, there was no better correspondence between the bimanual and non-dominant hand conditions than between the other combinations: on average, the hand opened 0.4 cm less when the non-dominant hand was used than in the other two conditions.

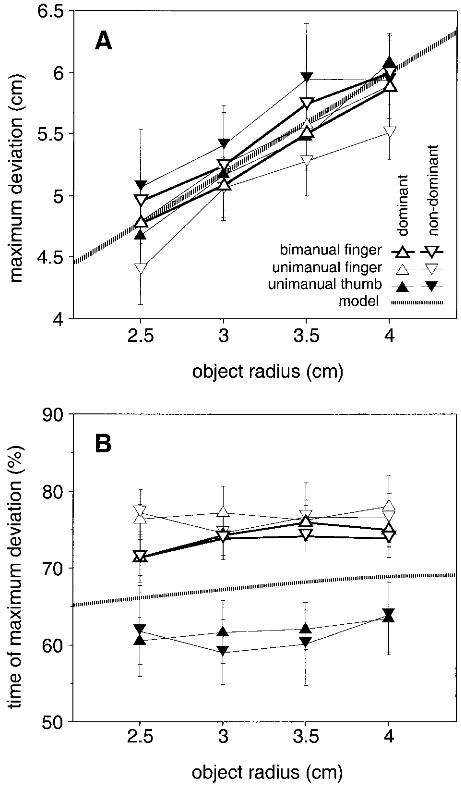

Fig. 3 A Maximal deviations of the individual digits during grasping. **B** The timing of these maximal deviations. The symbols are the means, with *error bars* indicating the inter-subject SEM. The *thick curve* is a model prediction (see Appendix) based on a value for the approach parameter of 1.7 m

Our predictions are at the level of the movements of the individual digits. The qualitative behaviour of both digits as a function of object size was the same in all conditions. The data followed our second prediction: the digits' maximum deviation increased with object radius with a slope of approx. 0.75 (Fig. 3A) and occurred at about two-thirds of the movement (Fig. 3B). Regressions for each subject, digit and condition show that the maximum deviations were (mean±standard error) 3.0±0.2 cm plus 0.74±0.04 times the object radius ($r^2=0.33\pm0.03$). This behaviour is consistently found for all subjects, independent of condition (*t*-tests, Fig. 4A) and for both digits (paired *t*-tests, Fig. 4B). The relative time at which the maximum deviation was found was 66±3% plus 1.4±0.7 times object radius ($r^2=0.04\pm0.01$).

Although the slopes and intercepts did not differ significantly between the digits, the behaviour of the thumb was clearly not exactly the same as that of the index finger (Fig. 3B). Because the intercept is a rather inaccurate measure of the offset, we compared the difference in be-

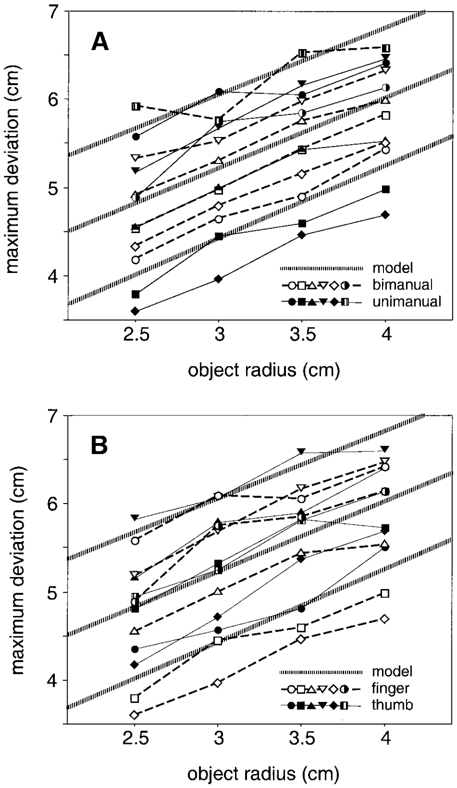

Fig. 4A, B Maximal deviations of the individual digits during grasping. The performance of individual subjects are indicated by *symbols connected with lines*. The *thick curves* are model predictions (see Appendix) based on values for the approach parameter of 1.2 m, 1.7 m, and 2.2 m. **A** The maximal deviation of the index finger (averaged over both hands) in the unimanual tasks compared with that of the same digits in the bimanual task. **B** The maximal deviation of the thumb and finger averaged over the two unimanual tasks

haviour of the two digits in each of the three conditions using paired *t*-tests. The mean maximum deviation of the thumb was 0.5 cm larger than that of the finger when grasping with the non-dominant hand [$t(23)=4.6$, $P<0.05$]. Moreover, the time to maximum deviation was at 61% of the movement for the thumb, and at 76% for the index finger, irrespective of the hand that was used [for both hands: $t(23)=15$, $P<0.0001$]. Otherwise, none of the comparisons between digits or conditions yielded significant differences. Most importantly, the index fingers showed the same behaviour in all three conditions, in accordance with our first prediction.

According to our model, a larger deviation earlier during the movement, as we found for the thumb, should only occur if there is more variability in the trajectory (the third prediction). We therefore calculated the standard deviation in the maximum deviation of each digit for each subject, disk size and condition (Fig. 5A). A paired *t*-test showed that this variability was indeed larger [$t(47)=2.7$, $P=0.008$] for the thumb (0.82 cm) than for the index finger (0.58 cm). We also found unpredicted difference in variability: for the index finger, it was larger [$t(94)=4.0$, $P=0.001$] in the unimanual condition

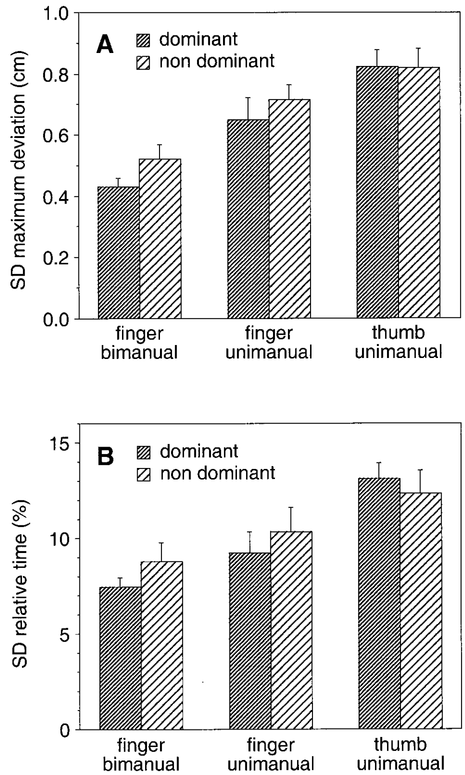

Fig. 5 Correlation between the digit's movements. Correlation coefficients for the maximum deviations (*left part*) and their timing (*right part*). *Error bars* indicate the SEM across subjects and object sizes. The maximum deviation of the digits is slightly (negatively) correlated in the dominant hand condition; the timing of the digit's maximum deviation is not correlated

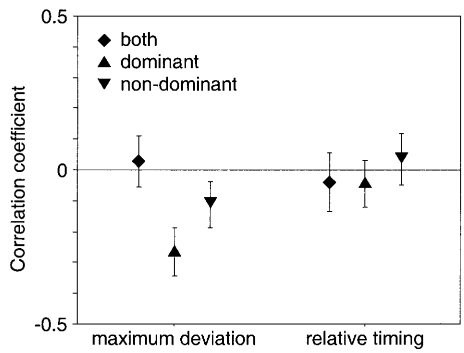

Fig. 6 A Variability in the maximum deviations of the digits. **B** Variability in the timing of these maximum deviations. As measure for the variability we use the SD of the repetitions of movements towards the same object by the same subject. The mean and the SEM (across object sizes and subjects) of these standard deviations

(0.68 cm) than in the bimanual condition (0.48 cm). We found a similar pattern for the variability in the timing of the maximum deviation (Fig. 5B). It too was larger [paired *t*-test $t(47)=2.5$, $P=0.02$] for the thumb (12.7%) than for the index finger (8.9%).

To investigate whether the variations in the maximum deviations of the digits and in their timing were independent (the fourth prediction), we calculated the correlation between the values for the two digits for each subject, condition and object size. There was on average (Fig. 6) a slight negative correlation between the digits (r=–0.12). A two-way (subject × condition) ANOVA revealed a significant ($F_{2, 54}$=4.0, P=0.023) effect of condition; a post-hoc analysis showed that the dominant hand condition differed from the bimanual condition. A one-sample t-test for each of the three conditions revealed that the (negative) correlation was significant [t(23)=3.4, P=0.003] for the dominant hand condition only. For the timing of the maximum deviations of the two digits, the correlation did not differ significantly from zero (ANOVA with factors condition and subject).

Discussion

The results show that grasping with the dominant, non-dominant and both hands is remarkably similar. Parameters that are frequently used to describe the grasp do not differ between these conditions. Tresilian and Stelmach (1997) have already reported the qualitative correspondence between unimanual and bimanual grasping. They have found various quantitative differences between these conditions and report that the variability (SD) in the grip aperture in the bimanual condition was twice as large as in the unimanual condition. This difference was probably due to the weak mechanical link in their bimanual condition. In our bimanual condition, we had subjects clasp their hands. This gives quite a stable link between the index fingers. Consequently, the variability was no longer larger in the bimanual condition in our study; it was even slightly smaller. According to our model, differences in variability will affect other parameters, such as the maximum grip aperture. Indeed, the maximum grip aperture (and its timing) differed between conditions in the experiment of Tresilian and Stelmach (1997). Considering the results of the present study, these differences were probably not due to differences in control, but to differences in the mechanical link between the digits.

Based on our model (Smeets and Brenner 1999a), we made four predictions. The experiments clearly support our first prediction: the average movement of the index finger(s) is the same in all conditions (Fig. 3A, B). The second prediction is also supported: the slope of the regression with object radius is independent of digit and condition. The third prediction was indirect: we predicted that, for comparisons between two digits within a condition, the digit with the largest variability would have a larger maximum deviation that occurs earlier in the movement. Figure 5 shows that the thumb is more variable than the index finger; the prediction is therefore that the thumb will have a larger maximum deviation that occurs earlier in the movement. Figure 3 shows that both thumbs have their maximum deviations earlier than the finger, and that the maximum deviation is larger for the thumb in the non-dominant hand. Although, in qualitative agreement, the effects are not in agreement with the quantitative predictions made in the Appendix: the difference in timing is much too large. The lack of correlation between the timing of the movement of the digits, and the small negative correlation between the amplitudes, conform to the fourth prediction. We predicted that noise in the activation of muscles common to the control of both digits (e.g. m. biceps) could introduce a slight negative correlation between their deviations. As the digits in bimanual grasping have fewer muscles in common, it is not surprising that we only found a negative correlation in unimanual conditions (Fig. 6).

The lack of (positive) correlation between the timing and amplitudes of the digit's maximum deviation may seem very surprising. There is a wealth of literature showing a mutual dependence of effectors in cyclic tasks, and a strong interaction between effectors has also been reported in bimanual pointing tasks. For instance, Kelso et al. (1979) have reported that, in a bimanual pointing task with different accuracy constraints for both fingers, the average movement times of both fingers are more or less equal and changed for both fingers when the accuracy constraint was changed for only one of them. However, when looking at various movement parameters of the fingers within one condition in a similar task, Boessenkool et al. (1999) have reported that the correlation is very low. The similarity between the results of Boessenkool et al. (1999) on pointing and our results on grasping supports our view that grasping is nothing more than pointing with two digits to oriented surfaces. Before discussing these results in relation to the other two views on grasping, we will discuss the results on the variability in some more detail.

The significant negative correlation between the maximum deviations of the digits (Fig. 6) seems at first sight to be at odds with our hypothesis of independent control of the digits' movements. However, our predictions were more subtle. One might hypothesize that the movements of the digits are planned independently, but, at the level of the execution, some dependency is introduced due to the biomechanical link between the movements of the digits. This link differs between conditions: it is purely mechanical in the bimanual case. In the unimanual conditions, there is an additional neuromuscular link: the movements of the finger and thumb through space are to a large extent controlled by the same muscles around wrist, elbow and shoulder. It is thus not surprising to find more negative correlation in the unimanual conditions than in the bimanual condition. The fact that the correlation was significant in only one condition stresses that the biomechanical factors only play a minor role in the control of grasping.

A problem with the discussion of the quantitatively predicted effects of variability is that we only measured the spatial variability of the marker perpendicular to the movement path (at maximum deviation). What matters, according to our model, is the total expected inaccuracy of the digit just before contact. However, the tangential component of the spatial variability is inseparable from variability in timing and thus not measurable. Furthermore, we made the implicit assumption that the variability does not change considerably in the last part of the movement (Haggard and Wing 1997; Paulignan et al. 1997). We also assumed that subjects know how variable their movements are (which can be questioned because of the unusual way of grasping in our experiment). A second problem in interpreting such details of the data is that the markers were not placed on the part of the digit that contacted the surface. We made a correction for this error in the calculation of the deviation of the digits. However, this correction was only a first approximation: the orientation of the digit changed during the grasp, and the contact point of the digit was not the same for all object sizes. Given the differences in shape between finger and thumb, this could have caused some of the apparent differences in behaviour between the digits.

We found about 50% more variability in the thumb than in the finger (this is the value we used for the predictions we make in the Appendix). Although we correctly predicted that the more variable digit (i.e. the thumb) would open earlier, the difference in timing we found in Fig. 3B (about 15%) was more than the few percent we predicted. We also found a lower variability in the maximum deviation in the bimanual condition than in the unimanual conditions (Fig. 5). This could be related to the 130-ms-longer movement time, because slower movements are generally less variable (Fitts and Peterson 1964). However, this reduction in variability was not accompanied by a decrease in the maximum deviation and it occurred earlier, as our model predicts. This may be due to the above-mentioned problems in interpreting the variability quantitatively.

One of the main findings of our experiment is that the finger and thumb moved qualitatively in the same way: the maximum deviation occurred at two-thirds of the movement and increased in a similar way with object size. Even the difference we found between the digits was qualitatively accounted for by our model (third prediction): because the thumb's movement was more variable, its maximum deviation was larger for than for the finger (for the non-dominant hand) and occurred earlier for the thumb than the finger (for both hands). Why the thumb's movement should be more variable was beyond the scope of our model, but it may have been related to its limited dexterity. Altogether we were more impressed by the similarities between the digits and conditions than by the small differences.

Relation with other views on grasping

We conclude that the thumb and finger have an equivalent role in grasping. The differences in curvature that we observed in many experiments are in our view not due to differences in control, but primarily to differences in the orientation of the surface at the positions where the digits contacted the object. Smooth movements ending perpendicular to the surface lead to straight trajectories towards positions on the near side of an object, and to strongly curved trajectories towards positions at the back of the object (see Figs. 4 and 5 in Smeets and Brenner 1999a). This opposes the view of Wing and colleagues. Wing and Fraser (1983) conclude, from the much straighter trajectory of the thumb in natural grasping, that the finger and thumb have different roles. More recently, Haggard andWing (1997) have added more evidence for this hypothesis by showing that the variability in the thumb's path is smaller than that of the wrist and starts to decrease well before the maximum aperture (a result reproduced by Paulignan et al. 1997). Based on Wing's view that the thumb is transported, one can make an explicit prediction about the variability of the finger's path. As this variability is caused by the (uncorrelated) variability in the transport and grip components, it should be larger than the variability of the thumb, which is caused by the variability of the transport component only. Our results show that this is clearly not the case: the variability in the maximum deviation of the index finger is *smaller* than that of the thumb. This prediction based on Wing's view is not only clearly falsified by our experimental results (Fig. 5A), but also by those of Paulignan et al. (1997). They show in their Fig. 6 that, from 60% of the movement time onwards, the thumb is more variable than the index finger.

It is not possible to make quantitative predictions using the classic view (Arbib 1981; Jeannerod 1981), because the movement of the wrist and the distance between the digits (the variables of this view) are not enough to predict trajectories of individual digits. Not only the orientation of the grip, but also the vector connecting the grip to the wrist are needed (Smeets and Brenner 1999a). Moreover, many predictions of our model (the relation between object size and grip formation) are *inputs* of classic models. However, our finding (and that of Tresilian and Stelmach 1997) that bimanual and unimanual grasping is essentially the same are not in the spirit of the classic view. The first aspect of our data that seems to be at odds with the classic view is the lack of correlation in the timing of the digit's deviations. If grip formation follows from movements of the digits relative to each other, we would expect a positive correlation in the maximum deviations and in their timing due to variability in the grip component. For the correlation between the maximum deviations, this could be compensated by the variability in the wrist movement (which is larger; Kudoh et al. 1997). As the movements of the wrist involve a relatively large mass (compared with the grip), it is reasonable to assume that its variability is characterised by low-frequency noise. Such noise affects the amplitude of deviations, but not their relative timing. It is therefore not very likely that a positive correlation in the timing of the maximum deviation of the digits due to common control could be compensated by variability in the wrist movement.

The second aspect that is not intuitive within the classic view is the similarity between unimanual and bimanual grasping. The classic view is based on the anatomical segregation between grip formation (controlled by distal muscles) and transportation (controlled by proximal muscles). In bimanual grasping, it is not clear what is transported. In Tresilian and Stelmach's 1997 experiment, the grip formation was made with the same effectors (the two arms) as the transport component. That the effectors are not an important factor in grip formation is also evident from the fact that similar behaviour is found when grasping using an artificial hand controlled by shoulder movements (Wing and Fraser 1983), and also in other tasks in which two effectors are co-ordinated to close around an object, such as in eating (Castiello 1997; Savelsbergh and van der Kamp 1999). This has led us to argue that the characteristic pattern of grip formation is a consequence of the task constraints, and not of anatomical constraints (Smeets and Brenner 1999b).

This paper shows that regarding grasping as the independent control of the digits yields predictions that nobody would make on the basis of one of the other two views. On the other hand, most of the predictions are not in direct conflict with the other views. The fact that our experimental results conformed to the predictions shows that our model has clear advantages over the other two views (it can explain more data using fewer assumptions), but cannot disprove them. Our model also has obvious limitations. It assumes that the spatial variations in the movements of the digits are completely independent, which of course is not true. Our experiment showed such dependence by the slight negative correlation between the maximum deviations of the digits when grasping with one hand. However, altogether this anatomical constraint does not appear to have much influence on normal human grasping.

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Appendix

Model for digit movement

Here we formulate a minimum jerk pointing trajectory (Flash and Hogan 1985) towards a surface with a non-zero deceleration at contact, as in Fig. 1. The derivation can be found in the study by Smeets and Brenner (1999a). For the movements in the present experiment (over a distance l in the x-direction, towards a disk with radius r approached in the y-direction) the constraints are:

$x(0)=0$	$x(MT)=l$	$v_x(0)=0$	$v_x(MT)=0$	$a_x(0)=0$	$a_x(MT)=0$
$y(0)=0$	$y(MT)=r$	$v_y(0)=0$	$v_y(MT)=0$	$a_y(0)=0$	$a_y(MT)=a_p/MT^2$

with MT the movement time and a_p the approach parameter. The latter is a spatial measure of the final deceleration. Given these constraints and introducing a normalised time $t_r=t/MT$ the minimum jerk trajectory is:

$$x(t_r) = \left(l\left(6t_r^2 - 15t_r + 10\right)\right)t_r^3 \quad (1)$$

$$y(t_r) = \left(\frac{1}{2}a_p(t_r - 1)^2 + r\left(6t_r^2 - 15t_r + 10\right)\right)t_r^3. \quad (2)$$

The maximum deviation is the maximum value of y:

$$y_{\max} = \frac{27\left(20r + a_p\right)^4\left(15r + 2a_p\right)}{3125\left(12r + a_p\right)^4} \quad (3)$$

$$y_{\max} \approx a_p\left(0.0173 + 0.683r / a_p + 4.147\left(r / a_p\right)^2\right) \quad \left(r << a_p\right) \quad (4)$$

at relative time:

$$t_r = \frac{3\left(a_p + 20r\right)}{5\left(a_p + 12r\right)} \quad (5)$$

$$t_r \approx 0.6 + 4.8r / a_p - 57.6\left(r / a_p\right)^2 \quad \left(r << a_p\right). \quad (6)$$

Both approximations Eqs. 4 and 6 are Taylor series expansions for small values of the object radius.

As the relationship between maximum deviation and object diameter is not linear, parameters obtained by a linear regression depend on the disk sizes used relative to the value of a_p. The first term in Eq. 4 is the offset of the relation between maximum deviation and object size. To obtain a value of this parameter corresponding to the result of the present experiment (about 3 cm), the approach parameter has to be about 2 m. For disks with a radius of 2.5–4 cm, the predicted slope is then 0.73–0.77 (second prediction), and the peak aperture will be at $t_r \approx 0.67\%$.

The larger the approach parameter, the larger the final deceleration and thus (given the smoothness of the movement) the larger the part of the path that is more or less perpendicular to the surface. Within the model, increasing the approach parameter is the only way to deal with more variability (see Fig. 1B). The result of increasing the approach parameter is a larger maximum deviation (Eq. 3, 4) earlier in the movement (Eq. 5, 6), the third prediction. As a quantitative example, we regard grasping a disk with a radius of 4 cm. Using an approach parameter of 2 m, the maximum deviation is 6.5 cm at 67.7% of the movement. A 50% increase in the approach parameter to 3 m leads to 8.1 cm maximum deviation at 65.5% of the movement.

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