Grasping Occam's Razor

Jeroen B.J. Smeets, Eli Brenner, and Juul Martin

Abstract Nine years after proposing our "new view on grasping", we re-examine the support for the approach that we proposed. This approach consisted of two steps. The first step was to formulate three assumptions that made it possible to model grasping in the same way as one would model movements of a single digit. The second step was to implement an existing model for movements of a single digit (minimum jerk model) in accordance with these assumptions. In both cases we applied Occam's razor: we used as few entities as possible to explain as many phenomena as possible. Here we evaluate both steps in the light of recent experimental results. We show that there is ample support for assuming that the movement of the fingertip is controlled in the same way in a reach-to-grasp movement as in other movements performed to interact with objects. The predictions based on the implementation of the minimum jerk model were surprisingly good in many situations, although they were clearly wrong in some other situations. Since more complicated models do not perform better, we conclude that currently our approach gives the best description of grasping.

Introduction

Pluralitas non est ponenda sine neccesitate are the famous words of the English philosopher William of Ockham (ca. 1285–1349), which can be translated into "one should not increase, beyond what is necessary, the number of entities required to explain anything". In this chapter, we will discuss how these words relate to using models to understand motor control in general, and grasping in particular.

There are two ways to look at motor control. The first one is that movements are shaped by properties of the substrate. Some of these properties are biomechanical: bones are connected with each other by joints that allow only specific

J.B.J. Smeets (✉)
Research Institute MOVE, Faculty of Human Movement Sciences, VU University Amsterdam, van der Boechorststraat 9, NL-1081 BT Amsterdam, The Netherlands
e-mail: J.Smeets@fbw.vu.nl

D. Sternad (ed.), *Progress in Motor Control*,
DOI 10.1007/978-0-387-77064-2_27,

movements, muscles have limited forces, and the forces cannot change faster than certain time constants allow. The fact that the brain is highly structured is also a very relevant fact for this perspective and analysis. The brain is not a homogeneous general-purpose computer but is divided into substructures such as cerebellum and basal ganglia. Each substructure has a well-defined architecture that seems designed to perform specific operations. This leads to well-known divisions of functions over different parts of the brain (for a recent review, see Castiello, 2005). For instance, grasping has been shown to be mainly controlled by the contralateral motor cortex (Brinkman and Kuypers, 1973), and the primary motor cortex exerts more direct control on the intrinsic hand muscles than on the more proximal extrinsic muscles (Lemon et al., 1995).

If you want to build a model of grasping that takes all these properties into account, one could simulate the interaction between all structures involved in the task, and see whether the model can mimic observed motor behavior. Such models can help us determine whether a certain mode of control is feasible given our knowledge of anatomy and neurophysiology. In this manner, it has been shown that both equilibrium point control (Feldman and Levin, 1995; Gribble and Ostry, 2000; Kistemaker et al., 2006) and vector integration to endpoint (Bullock and Grossberg, 1991) are plausible models for motor control. These models show *how* all known elements could work together to yield certain behavior. Such models are not supposed to survive Occam's razor. If you can for instance explain all grasping behavior equally well with a model that ignores tendon compliance as with a model that considers this property, nobody will argue that the model that neglects this property is better because it contains fewer parameters.

Another approach to motor control is confined to the level of behavior (positions, velocities, angles), without reference to the anatomy and physiology of the underlying neuromuscular apparatus. One of the arguments for using this approach is that evolution only selects at the level of behavior. One can therefore assume that the anatomy and neuronal control has evolved to perform everyday tasks optimally. Both, the vector integration to endpoint and equilibrium point control models can also be formulated at this level of description (e.g. de Lussanet et al., 2002). Models rooted in this way of thinking ignore the question of how the movements are made, but rather study the regularities in the movements, independent of the underlying neurophysiology. For example, movements are found to be smooth (Hogan and Flash, 1987) and precise (Harris and Wolpert, 1998) and they slow down when curving (Lacquaniti et al., 1983). Such models generally optimize some behavioral variable (Todorov, 2004). They yield insights that are complementary to the first group of models: they teach us *why* we behave as we do. In other words, they examine what the evolution and the fine-tuning during motor development do to behavior. The fact that movements are smooth is thus not considered to be caused "accidentally" by simple properties of control combined with special hardware, but to be the result of optimizing the hardware together with the control signals to achieve this important property. The challenge is to figure out why smoothness is important, and thus why the minimum jerk model is so successful. Other models in this category are those that consider nonlinear dynamical properties of behavior essential, as for example demonstrated by Kelso, Turvey and colleagues in interlimb coordination (Haken et al., 1985). The trade-off between speed and accuracy formulated in Fitts' law (Fitts, 1954) is another model with a simple account of observed behavior. These models are deliberately simple, although they could also be made more complex in order to improve the fitting of the data. Occam's razor can therefore be applied to such models.

All the above models were developed based on tasks that were analyzed in only one or two dimensions. Does a 3D analysis of motor behavior change the performance of various models? For some models, going from 2D to 3D is a very easy exercise. For instance, the minimum jerk model is formulated independently for each dimension (Flash and Hogan, 1985). When this model is applied to three dimensions, the results of the 2D model can be extended simply by adding one more dimension. The reason for this simplicity is that this model requires constraints for each degree of freedom, i.e., position, velocity and acceleration at two instances of the movement. If a degree of freedom is added or removed, the constraints associated with this degree of freedom are also added or removed. For other models, adding more dimensions is not so straightforward. For instance, the information content of a movement is easily defined in one dimension, but this definition becomes more problematic in two or three dimensions, making it difficult to extend Fitts' Law to more dimensions (Smyrnis et al., 2000; Murata and Iwase, 2001; Bohan et al., 2003).

The problem is that many tasks that are well specified in 2D become underspecified in 3D. An example is pointing in a certain direction with an extended arm. In this task, only two angles of the arm are relevant: its azimuth and elevation. However, the extended arm has a third degree of freedom which is the rotation around its own axis, i.e., supination and pronation the hand. A 3D analysis of this task can reveal the rule that determines the third degree of freedom in terms of the two specified degrees of freedom. Testing models by examining such rules is of course only valid for models that take into account the orientation of body segments. Hence, a model that only describes pointing in terms of positions and not orientations (like the minimum jerk model) cannot be tested in this way (see also the chapter by Gielen).

Grasping as an Example of a Complex Movement

Jeannerod was the first one to realize that a grasping movement, also referred to as prehension, is a good example of coordination between body segments. In his initial publication, he suggested that grasping could described as consisting of information processing in two visuomotor channels (Jeannerod, 1981). He argued that one channel related visual information of egocentric object properties (such as position and orientation) to controlling the transport of the arm by proximal muscles. A second channel related intrinsic object properties (such as shape and size) to the control of grip aperture by distal muscles. In this approach, modeling grasping movements has to include descriptions how these two components are coordinated (Hoff and Arbib, 1993; Zaal et al., 1998). This description with its relation of anatomical and neurophysiological findings to behavior has become the standard approach to understand grasping.

Grasping behavior has some characteristics that are always present, independent of the exact nature of the task (reviewed in Smeets and Brenner, 1999b). The best known of these characteristics is that the hand does not always open to the same maximum aperture before closing around the object: the peak grip aperture scales with object size. Interestingly, this scaling is not complete but has a gain of 0.8: if the object is 10 mm larger, the peak grip aperture is only 8 mm larger. Another robust finding is that the peak grip aperture occurs in the second half of the movement, between two-thirds and three-quarters of the total movement time. The peak grip aperture occurs slightly later when grasping larger objects. Moreover, some studies have tried to make grasping more difficult, for instance by imposing time constraints, by making the surface slippery, or by removing (part of the) visual information. Such manipulations generally lead to a larger peak grip apertures earlier in the movement. A last important finding is that the two visuomotor channels seem to be independent: changing object size does not affect the transport component, and changing the distance to the object leaves the grip formation unaffected.

Is grasping as undetermined as pointing? For grasping circular objects, the orientation of the hand is unconstrained even in 2D; the hand can be oriented in any direction. Yet, it has been shown that the orientation of the hand depends on the position of the object in the workplace (Paulignan et al., 1997) and the direction of approach (Roby-Brami et al., 2000). These results can be interpreted in terms of "comfort", but this aspect has never been modeled. If the objects are not circular but elongated, the task becomes much more determined: only grasps to the major and minor axis are stable. Whether the major or minor axis will be chosen depends on the orientation of the object relative to the orientation in which circular objects are grasped, with a preference for grasping the minor axis (Cuijpers et al., 2004). The finding that the choice of the grip depends on the orientation of the object means that the grip aperture cannot be based on intrinsic object properties only. Evidently, if the object is grasped along the long axis, the grip aperture must be much larger than if it is grasped along the minor axis. This means that at the behavioral level, the distinction between the visuomotor channels is not clear-cut. In the next section we will introduce an alternative view.

In most studies objects are grasped with a precision grip (using only index finger and thumb) and the movements are analyzed in two usually horizontal dimensions. Many studies examine the whole-hand grip and analyze the movement in the vertical plane only. Deviations of the transport component from a straight line and the orientation of the grip are typically not considered. For the undetermined situation (grasping spheres) the analyses have never been extended to three dimensions. In this case, the analysis would be six-dimensional: three dimensions for transport and three for grip. The reason for not performing this complex analysis is probably that objects that are generally used in grasping tasks (cylinders or bars) are extended in the direction that is not analyzed. Adding this direction to the analysis does not lead to an infinite but only two additional final orientations of the hand: supination or pronation. The choice between these orientations has been studied and comfort seems to determine the choice (Rosenbaum et al., 1992). However, the focus of Rosenbaum's research was not the inclusion of the third dimension, but rather the demonstration that comfort at later stages of the movement, i.e., the ease with which the grasped object is placed on a table, is taken into account at the onset (see also Rosenbaum et al. in this section). Hence, although this study examined movements performed unconstrained in three dimensions, it has not shed light on the coordination of the two components in 3D. Whether the same holds for models of grasping will be discussed later in this chapter.

The New View on Grasping

In 1999, we published a model for grasping with a precision grip (Smeets and Brenner, 1999b). The aim was to account for the various experimental findings on grasping with thumb and index finger by one simple model based on optimizing behavior, rather than on the characteristics of the underlying substrate. As discussed above, the behavioral distinction between transport and grasp is not clear. We therefore chose another approach and argued that the entities that are controlled might be the thumb and index finger instead. We wondered whether optimizing the movements of the two digits that touch the object would simulate behavior that is similar to natural grasping. In doing so we formulated three assumptions:

(1) The selection of target positions for touching the object is a separate process from making the movement; it is therefore not part of the model.
(2) Grasping an object with a precision grip is equivalent to simultaneously touching the object with index finger and thumb. Cast in terms of Occam's razor: modeling grasping does not require other entities than modeling touching movements of a single digit.
(3) Touching an object is most precise if the surface is approached perpendicularly; the movements of the digits in touching and grasping will therefore tend to end perpendicular to the surface.

In order to formulate testable predictions based on these assumptions, we need a model for the digits' movements. The minimum jerk model was chosen as description of smooth movements, because it yields an analytical description of the digits' trajectories that can be easily compared with experimental data (Flash and Hogan, 1985). However, as will be seen later in this chapter, this choice is not essential. The input for the resulting "digit model" for grasping is the start position and the contact position at the object (for each digit), the orientation of the object's surface at the contact position, and one free parameter: the so-called *approach parameter* a_p. The model produces smooth trajectories that tend to end perpendicular to the object's surface; a large value of a_p leads to an approach that is close to perpendicular.

The digit model produces the complete trajectories of both digits as a function of time (expressed as a fraction of the total movement time). We could show that this very simple model yields an analytical description of grasping behavior that matches the main findings in the grasping literature (Smeets and Brenner, 1999b):

(1) An apparent independence of transport and grip components.
(2) An increase of peak grip aperture with object size with a slope of 0.8, and a later peak grip aperture for larger objects.
(3) An increase in peak grip aperture for more difficult movements, and an earlier peak grip aperture for more difficult movements.

One of the important conclusions from the original paper is that a model based on the control of individual digits results in behavior that is quite complex for those

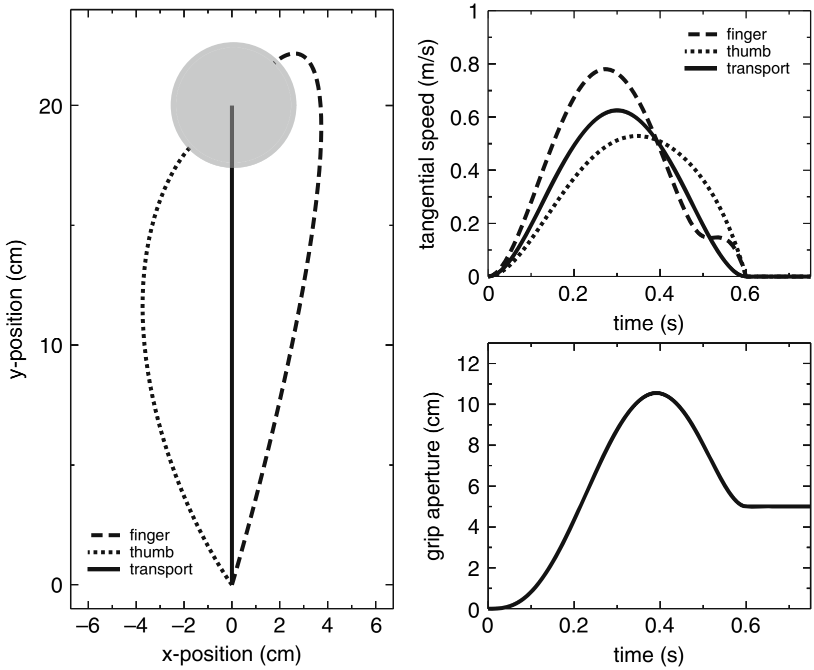

Fig. 1 Example of model predictions: grasping a 5 cm diameter disk that is 20 cm away in 0.6 s, with $a_p = 2$ m. The model produces the curved trajectories of the digits (*dashed curves*). The transport component (continuous curve in the *left* and *right-upper panel*) is defined as the average of the trajectories of the two digits. The grip component (*right-lower graph*) is defined as the distance between the two digits. The transport and grip components derived from the digits' trajectories present a simpler description of the movement than the trajectories that the model optimizes

individual digits: it results in curved movement paths and asymmetric speed profiles which can have multiple peaks (see Fig. 1). These trajectories can be used to predict trajectories for the transport component (the average of index finger and thumb) and the grip component (the distance between index finger and thumb).

To emphasize, the model optimizes the trajectories of the individual digits, hence the transport and grip components are emergent properties. Nevertheless, the predicted behavior is much simpler in terms of a transport and grip component: a straight line with a bell-shaped velocity profile for the transport component and a single-peaked grip-aperture. Moreover, changes in one of the input parameters of the model (like object-size or distance) only affect one of the two components. Thus, the digit model's behavior gives the impression (as does human behavior) that the transport and grip are controlled through independent visuomotor channels (Jeannerod, 1981, 1999). However, unlike in human movements, in the model we know exactly how the trajectories are generated: they are *not* based on such channels but on the control of the individual digits. Consequently, the experimental finding that grip aperture changes independently from the hand transport is not evidence against the digit model. Stated more generally: regularities in behavior of some variables do not imply that these variables are controlled. St-Onge and Feldman (2003) formulated this as: "synergies can emerge without special central commands".

Additional Model Predictions: Perturbations and Visual Illusions

After we published the digit model, we realized that it could predict more than ordinary grasping. We subsequently applied the model to two other domains: the response to changes in object properties and visual illusions. Experiments on the effects of changing size and location of an object during prehension movements are among the classics in the grasping literature (Paulignan et al., 1991b,a). The main result of these experiments is that if an object changes position at the onset of a reach-to-grasp movement, both the transport speed and the grip aperture are adjusted. In contrast, if the size of an object is changed at the onset of the movement, only the grip aperture is adjusted (Fig. 2A–D). The authors interpreted these results as indicating that the two assumed visuomotor channels were organized hierarchically: the transport channel does not run in parallel with the grip channel, but is at a higher level: what happens in the transport channel influences the grip channel, but not the other way around. The authors thus introduce an additional entity (hierarchical interaction) to explain their results.

This difference in effect between perturbing object size and perturbing position seems to contradict the digit model because the end-positions of the two digits change after both perturbations. In order to see whether this experimental finding is really in conflict with the model, we simulated these experimental conditions (Smeets et al., 2002a). We implemented both changes as changes in the digits' target positions using the abort-and-replan scheme for minimum jerk

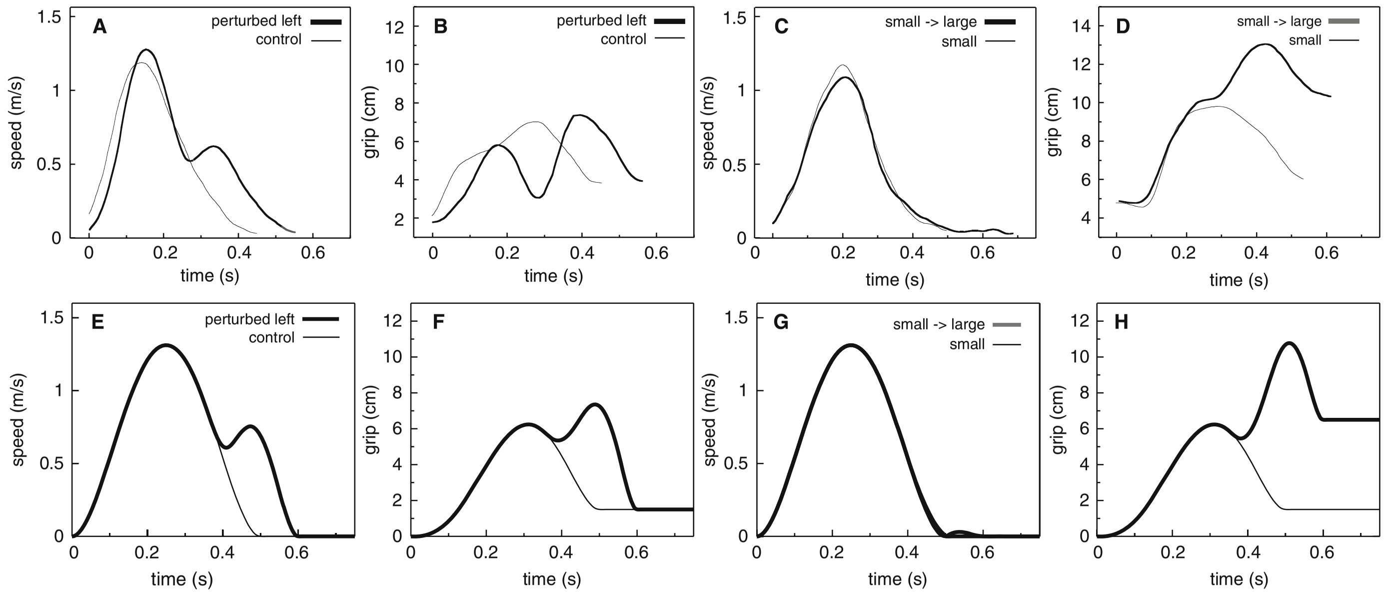

Fig. 2 Correction for perturbations. **A-D**: Velocity profiles and grip aperture of example trials from the studies of Paulignan et al. (1991 a,b) **E-H**: Model simulations for the same perturbations

movements (Henis and Flash, 1995). According to this scheme, a new movement replaces the old movement at a certain instant. In our simulation the timing of this replacement was the same for both digits and both perturbations. Although the same scheme governed the formation of each digit's trajectory in both cases, the shape of the combined response was different because it depended on the direction in which the digits' targets shifted. They either shifted in the same direction (object position perturbation) or in opposite directions (object size perturbation); hence, the transport and grip components of our model movements looked quite different for the two object perturbation conditions. Our model of the individual digits' movements predicted that only the grip aperture changed for perturbations of size, whereas it predicted that both the grip aperture and transport component changed for perturbations of position (Fig. 2E–H). Therefore, our model accounted for the data of Paulignan et al. (1991b,a) without the introduction of additional entities.

Over the last decade, grasping has frequently been taken as an example that supported the proposed separation between visual information processing for perception and action. This is because peak grip aperture is generally much less affected by illusions than one might expect on the basis of the perceptual effects (Aglioti et al., 1995; Carey, 2001). In earlier work we argued that in principle there is no reason to assume such separate processing to explain experimental results that indicate separate processing for perception and action (Smeets and Brenner, 1995; Brenner and Smeets, 1996). The first step in our argument is realizing that what we perceive does not necessarily obey the laws of physics: if an illusion affects the perceived size of an object, it need not affect the perceived locations of points on the object's surface (Gillam and Chambers, 1985; Smeets et al., 2002b). We explained the lack of effect of size illusions on grasping by arguing that according to our model the *size* of an object is irrelevant; the *locations* of the intended contact points are used instead (Smeets and Brenner, 1999b).

Unfortunately, if different attributes are influenced by an illusion in different degrees, it is very difficult to make predictions for its effect. One needs to know which attributes are used for the task (de Grave et al., 2004), and that the elements that cause the illusion have no other effects than the ones under study (e.g. changes in the perceived size). Some authors have argued that the context-elements that are responsible for the illusion might be regarded as obstacles for goal-directed actions such as grasping, which might influence grip aperture (Haffenden et al., 2001; de Grave et al., 2005). We cannot be sure why an influence is found, but we can evaluate various assumptions (e.g. our model assumes that the attribute "size" is not used). Since our model predicts complete trajectories, we can apply a more severe test than only evaluating the predictions for peak grip aperture. In the next two paragraphs we will use our model to evaluate the effect of two illusions.

As a first example, we consider a frequently studied size illusion called the Ebbinghaus illusion (Fig. 3A). The idea behind this illusion is that adding flankers influences the perceived size of the central object: the central object seems larger if the flankers are small than if the flankers are large. It has

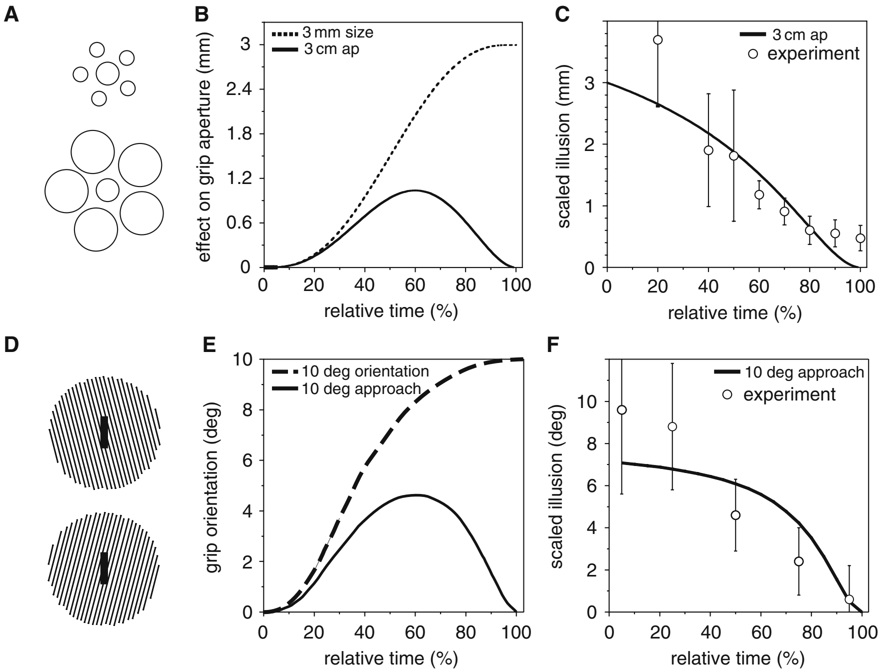

Fig. 3 Model predictions of the time-dependent effect of illusions. **A** The Ebbinghaus illusion: the two central circles are exactly the same, but due to the surrounding flankers the upper one looks larger. **B** The effect of an (illusory) change in size on grip aperture increases monotonically (*dashed line*), whereas an increase in approach parameter has an effect on grip aperture that peaks at 60% of the movement (*continuous line*). **C** If it is assumed that the effect of the illusion on grip aperture is caused by a change in approach parameter, the predicted scaled illusion effect is the ratio between the effects of an approach parameter change and a real size change (*curve*). The symbols show experimental data replotted from (Smeets et al., 2003). **D** Simultaneous tilt illusion. The two central bars are exactly vertical, but due to the surrounding tilted lines, they look tilted. **E** An oriented object will be grasped with a monotonic change in hand orientation (*dashed line*), whereas an (illusory) change in approach angle will cause an effect on hand orientation that peaks at 60% of the movement (*continuous line*) **F** If we assume that the effect of the illusion on grip orientation is caused by a change in approach angle, the predicted scaled illusion effect is the ratio between the effects of an approach angle change and a real orientation change (*curve*). The symbols show data replotted from Fig. 7 of (Glover and Dixon, 2001a)

frequently been reported that small flankers lead to a large grip aperture, in line with the visual illusion (Aglioti et al., 1995; Pavani et al., 1999; Franz et al., 2000; Glover and Dixon, 2002; de Grave et al., 2005). According to our model this size illusion should not lead to a larger peak grip aperture because, according to the model, subjects move their digits to positions. We assume that locations on the object's surface are perceived correctly, irrespective of the size of the flankers. We can only explain the effect of flankers by assuming that they influence the approach parameter, although we have no reason why this should occur; perhaps small flankers make you move more carefully.

In Fig. 3B we show an example of the effect of a change in a_p and a change in object size. The effect is initially similar, but a change in a_p has a decreasing effect on the last part of the movement, whereas the effect of object size increases monotonically.

In order to quantify the effect of an illusion on grasping, one can convert the additional grip aperture caused by the illusion into an equivalent change in object size (i.e. one can find the change in object size that would have the same effect on grip aperture). This scaled illusion effect can be determined for every instant during the movement. The model predicts that if the larger grip aperture arises from an increased a_p, the effect of the manipulation will gradually decrease during the movement (see Fig. 3C). This is what was observed in a grasping experiment using the Ebbinghaus illusion (Glover and Dixon, 2002). However, other authors (Danckert et al., 2002; Franz et al., 2005) did not find such a time-dependent effect of the Ebbinghaus illusion on grip aperture. Our model can explain these discrepancies in the experimental results in terms of differences in the data analyses: different studies used different procedures to align the different movements in time. In the above, we scaled the movements so that both movement onset and contact with the object were aligned. In accordance with an increase in a_p, the model predicts that peak grip aperture occurs earlier for larger grip apertures (Smeets et al., 2003). If one scales the same model movements in such a manner that the moment of peak grip aperture is aligned (following the method used by Danckert et al., 2002), one thus compares different points with each other. The result of this seemingly minor change in data analysis is that the effect of the flankers no longer decreases, but seems to remain constant in time (Smeets et al., 2003).

The time-dependency of illusion effects is not only observed for the well-known Ebbinghaus figure. It was originally observed for the simultaneous tilt illusion (Fig. 3D). The background of the tilted lines leads to an error in perceiving orientation of the central bar, while not affecting the perception of its location. It has also been shown that the effect of the illusion on the orientation of the hand decreases during the movement (Glover and Dixon, 2001b,a). The digit model can easily simulate the grasping of the central bar: a change of the tilt of the background lines does not change the positions for the model movements but only the direction of approach. Can the model also predict the changing effect throughout the movement? We performed the model calculations using a constant approach parameter, and a misjudgement of approach direction depending on the tilt of the background lines (Smeets et al., 2002b). The result was that the effect of the background tilt on grip orientation decreases in the second half of the movement (continuous curve in Fig. 3E). The effect of an actual orientation change (in the model a change in both end-positions and approach direction) on grip orientation increases monotonically (dashed curve in Fig. 3E). Thus the time-dependent effects of illusions on action can be explained by a constant perturbation of one of the input variables of the model (approach parameter or approach direction).

In the research on illusions we made three extreme assumptions: the illusion has no effect on the perceived positions, the effect of the illusion was constant over time, and the illusion affects action in the same way as perception. This strategy was guided by Occam's razor: we removed all assumptions that were not necessary to explain the data. Admittedly, we could not disprove that visual information is processed separately for perception and action (Goodale et al., 1991) or for planning and control (Glover and Dixon, 2001a; Glover, 2004), but we could show that such assumptions are not necessary to explain the experimental results.

Are the Model Assumptions Implausible?

The experiments described above show the predictive power of the model, which makes it a good model in terms of Occam's razor: many experimental results can be described reasonably well with a very simple model. As discussed in the introduction, many scientists are more interested in describing what is happening in the brain than accurately predicting behavior. They might argue that the model is not very valuable, because it is based on potentially implausible assumptions. To counter these criticisms, we performed more experiments that yielded results that showed that these assumptions were not so unreasonable after all.

One of the most counter-intuitive assumptions of the model is that grasping is nothing more than pointing with two digits. This means that the two digits play equivalent roles in grasping and that they should move more or less independently. The first attempt to show that the digits move independently in grasping was published two years after the initial development of the digit model (Smeets and Brenner, 2001). In this experiment subjects were asked to grasp circular objects of various sizes, on which we indicated the two desired contact positions. We choose these positions in such a way that the distance between start and contact was the same for the thumb and the index finger. For this situation, the digit model predicts that the movements of the two digits will be each other's mirror image. We described the movement paths by the maximum deviation from a straight line to the centre of the object. As predicted by the model, this deviation increased with object size with a slope of 0.8 for both digits. The maximum deviations were, however, not exactly the same for the two digits. They occurred earlier and were larger for the thumb than the index finger. This corresponds (within the assumptions of the digit model) to the thumb having a larger approach parameter. According to the reasoning behind the digit model, a larger approach parameter is needed if the movements are less precise. We therefore compared the precision of the two digits by analyzing the standard deviations in the maximum deviation over repeated trials. These were indeed significantly larger for the thumb than for the index finger.

A second prediction of the digit model is that the maximum deviation of the index finger need not be correlated with that of the thumb. We determined for individual subjects and conditions whether variations in the timing and amplitude of the maximum deviation of the thumb were correlated with those of the index finger (Smeets and Brenner, 2001). As predicted, we found no correlation between the digits for the timing of the maximum deviation. For the maximum deviation itself, there was a slight negative correlation (only significant for the dominant hand). This means that the maximum deviation of the index finger was larger in trials in which the maximum deviation of the thumb was smaller. This was probably a consequence of the fact that the two digits were coupled to each other as part of the hand. A similar small correlation has been reported recently for responses to perturbations of target positions in grasping (van de Kamp and Zaal, 2007). In situations where the position for one digit was changed, something in the kinematics of the other digit changed too. However, the effect was only visible in a combined measure, therefore it was not clear what the change in the kinematics was. The fact that the correlation was so small meant that we applied Occam's razor correctly: adding a coupling between the digits to the model would only explain a very small correlation.

The digit model assumes that grasping is equivalent to simultaneous pointing with two digits. If subjects are asked to point simultaneously with both index fingers where each finger has to move a different distance, then the finger that has to move the longer distance starts slightly earlier and ends slightly later than the other finger (Boessenkool et al., 1999). If our assumptions are correct, a similar effect should be present in grasping. We tested this in an experiment in which we varied the starting position, while keeping the contact positions on the object constant (Biegstraaten et al., 2006). We found that if the index finger and thumb moved over the same distance, they moved more or less in synchrony. If the thumb had to move over a longer distance because it had to pass the object, the thumb started slightly earlier and ended 37 ms later than the index finger. This result is similar to the effect of starting position on contact times in bimanual pointing movements. One would not expect this result if subjects transported their hand and separately controlled the opening and closing of their grip, as is generally assumed.

The second assumption of the model is even more stringent than just stating that the digits move independently. In order not to introduce any additional entity to explain grasping, we assumed that the movements of each digit involved in grasping are the same as those when that digit moves alone. This assumption seems invalid at first sight: if you move any one of your fingers alone, your movements are straight, unlike when your fingers are engaged in grasping. However, this is not a fair comparison; rather, one should compare movements of the finger for which the constraints at contact are similar. Therefore, we reasoned that the constraints when touching an object without moving it or when pushing it away can be made to be similar to those when grasping. In grasping, similar to pushing, the actor intends to exert forces on the object. On the other hand, unlike in pushing, the actor does not intend to move the object laterally, which makes it more like touching. Touching and pushing, however, differ from grasping in what the other digit has to do. In touching and pushing the movements of the other digit are irrelevant, as long as it avoids contact with the object. In grasping, the other finger has to contact at the same time, exerting force in the opposite direction. To investigate whether this difference has an effect on the movements we compared these three tasks for each subject using exactly the same set-up and configuration in all three tasks.

The set-up was designed in such a way that when grasping the 5 cm cube, or touching the indicated side, the finger and thumb would end on positions that were suited to push the cube perpendicular to the movement direction. The horizontal components of the resulting movements, averaged over all subjects, are given in Fig. 4. The movement paths of the finger and thumb are similar in all three tasks, although they are not each other's mirror image as predicted by the model (right lower panel). The finger starts with a slight outward curve, whereas the thumb starts with a light inward curve. The same is seen in the other two tasks: pushing and touching. In these tasks, the irrelevant digit (dashed curves) moves in a completely different way than when it is relevant, so the asymmetry between finger and thumb cannot be a consequence of the way grasping is controlled, as has been suggested by several authors (Haggard and Wing, 1997; Mon-Williams and McIntosh, 2000). The main difference between the three tasks is that the grip aperture is on average a little bit smaller than expected on the basis of the movements of the digits in the one-digit tasks. This might be due to the fact that (some) subjects cannot open their hand with a distance of more than 10 cm between the finger pads.

The third assumption of the model is that the digits approach the surface perpendicularly. We provided two arguments for this assumption. Firstly, a

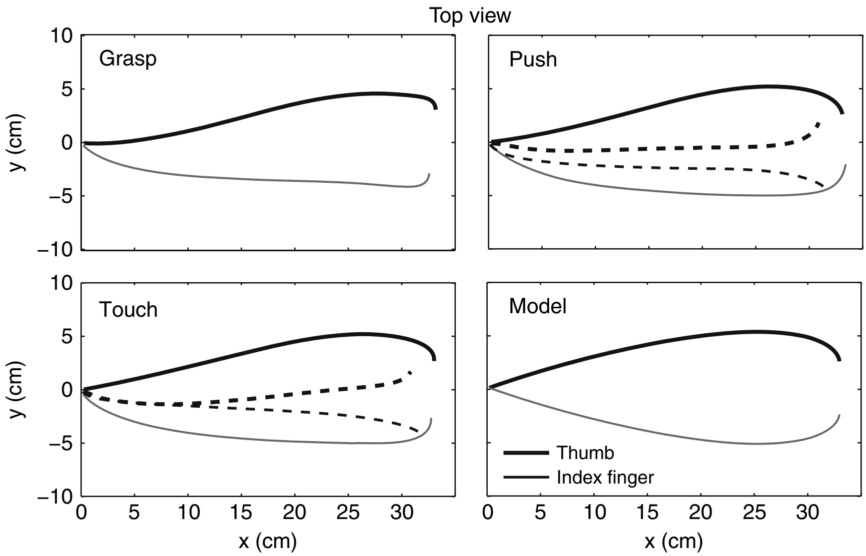

Fig. 4 Movement paths of the finger (*thin curves*) and thumb (*thick curves*). Mean measured paths in three tasks and predictions of the minimum jerk model (for $a_p = 2$ m). In the "touch" and "push" tasks, the curves originate from two different sessions where one digit had to push or touch the object (*continuous curves*), and the other (*dashed curves*) only had to avoid contacting the object. The *thick dashed curves* are from the same session as the *thin continuous curves* and vice versa

perpendicular approach helps in placing the digit accurately: the shallower the angle of approach, the larger is the effect of an error in the digit's path on the accuracy. Secondly, a perpendicular approach helps preventing the digit from slipping when the force increases after contact. The perpendicular approach may appear trivial because closing the grip on the object also seems to require that the digits approach the surface perpendicularly. However, this is only true if the surfaces are perpendicular to the line between the contact points, as they would be for optimally stable grasp positions (Cuijpers et al., 2004). Such positions are present for instance on cubes and cylinders, but may be absent on objects with less symmetric shapes. If the contact positions are not on two parallel surfaces, placing the digits accurately still involves a perpendicular approach, but applying adequate grip forces and closing the grip involves movements in opposite directions at contact. Because only one of the arguments for arriving perpendicularly holds for non-parallel surfaces, control of the digits predicts a tendency to approach perpendicularly, whereas grip control predicts no effect of surface orientation.

In a recent study (Kleinholdermann et al., 2007) we asked subjects to grasp objects in which the angle of the grasping surfaces ranged between –20 and 20°; their shape viewed from the top was thus a trapezoid (see Fig. 5A). Subjects grasped these objects starting from a position above the objects such that the

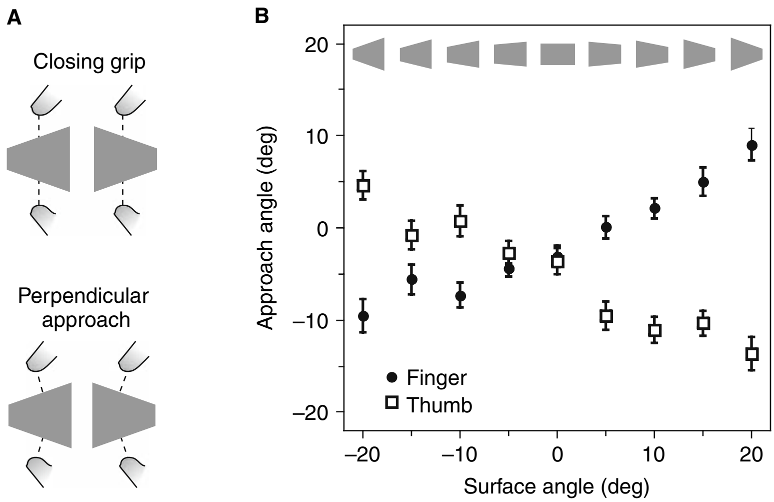

Fig. 5 **A**: For movements from above closing the grip leads to collinear movements of the digits, independent of the object's shape. Approaching surfaces perpendicularly will only do so if the contact surfaces are parallel. **B**: The direction of approach for the index finger (*filled disks*) and thumb (*open squares*) for different orientations of the contact surfaces (see icons at the top of the plot). Each data-point is the average of the median values for two object sizes and 23 subjects; error bars indicate the standard error of these means. If the grip had been closed without taking the surface orientation into consideration, the symbols for both digits would fall on a horizontal line. There is a very clear tendency toward keeping the approach close to perpendicular to the surfaces

corners of the object did not pose obstacles. As seen in Fig. 5B the approach angle varied systematically with the orientation of the contact surface (unlike the prediction of grip-closure). The effect was much larger than for pointing movements that had no contact requirements and it is the consequence of our hypothesis that the trajectories contact the surface perpendicularly (Brenner and Smeets, 1995). This feature varied between subjects, from changing the approach direction as much as the surface orientation to no significant correlation between approach direction and surface orientation at all (the latter was the case for 3 of our 23 subjects). This interindividual difference might be related to the relative importance that subjects ascribe to the spatial accuracy and avoidance of slip.

Other New Experimental Results

One of the interesting critiques of the original paper was that the same pattern of hand opening and closing was also seen in catching with a static hand as well as in jaw movements during eating (Savelsbergh and van der Kamp, 1999). The authors argued that these tasks cannot be interpreted as consisting of two touching movements. If so, the fact that our model describes these movements also very well would mean that the similarity between grasping and the model predictions would not support our conclusion that grasping is a combination of touching movements. We argued that eating and catching can also be regarded as touching movements if we view the task in the object's frame of reference (Smeets and Brenner, 1999a). We regard the fact that quite different anatomical structures such as the mouth and the hand yield a similar kinematic pattern as clear support for our claim that this pattern is not caused by visuomotor channels, but emerges from the constraints on contact. If the constraints on contact with the surface are different, the grasping behavior should be quite different. A way to remove the constraints at contact is to let subjects grasp virtual objects that have no physical contact surface. It has been shown several times that the normal grasping pattern is not found in this task: the hand opens much less than in normal grasping with a peak grip aperture occurring at the end of the movement (Goodale et al., 1994; Bock, 1996). On the other hand, changing anatomical relations should have little effect. When a person grasps with a tool that he/she has to squeeze to open, the movements of the digits are totally different from those in normal grasping; yet, the kinematics of aperture of the tool are remarkably similar to the aperture of a human hand, supporting the notion that some features of the grasp movement are coded independently of the used effector (Gentilucci et al., 2004).

A last set of experiments that we would like to discuss relates Fitts' law to grasping. The idea for this experiment was that by placing obstacles on both sides of the target, the grasping movement would slow down. The exact positions of the obstacles influence both the difficulty for controlling the digits (determined by the distance between target and obstacles) as well as the difficulty for grip formation (determined by the distance between the two obstacles). By varying the positions of the obstacles in a smart way, one should be able to determine whether the obstacles constrain grip formation or the movements of the individual digits. Mon-Williams and McIntosh (2000) performed such an experiment. They concluded from their interpretation of the data that obstacles constrain grip formation. In order to reach that conclusion, they assumed that if the digits were constrained, the average difficulty would determine movement time. We argued that it is more logical to assume that the most constrained digit determines the movement time and that a better experiment would vary the positions of both obstacles (Biegstraaten et al., 2003). Both our new experiment and a re-analysis of the original experiments showed that the movement time was better correlated with the difficulty for the most constrained digit than with the difficulty of the grip.

Relation with Other Models

Since the publication of our digit model a few other models for (aspects of) grasping have been proposed. The only modeling attempt that tries to capture the complete grasping movement is that of Rosenbaum, Meulenbroek and colleagues (Meulenbroek et al., 2001; Rosenbaum et al., 2001). Their posture model (posture-based motion planning theory, see chapter by Rosenbaum) contains many more entities than our digit model: it includes not only the tips of the digits, but also limb segments and joints. They used a set of "hierarchical constraints" to make the model grasp which has the same purpose as the approach parameter of the digit model. Due to the rich set of entities it uses, the posture model can describe aspects of the grasping movements that the digit model cannot (e.g. joint angles); hence, it is definitely a valuable model. But does the additional complexity of the model improve the predictions for the movements of the tips of the digits? We have argued before that in some situations the posture model makes the same incorrect predictions as the digit model, such as when a grasping movement starts with the hand already open (Smeets and Brenner, 2002). However, the predictions of the posture model and digit model also differ in one aspect. The posture model predicts a peak grip aperture at 50% of the movement for infinitely small objects (Fig. 7 of Rosenbaum et al., 2001), whereas the digit model predicts peak grip aperture to be at 60% (Fig. 6 of Smeets and Brenner, 1999b). A review of experimental results shows that the digit model is closer to the average experimental result (Fig. 7 of Smeets and Brenner, 1999b).

Simmons and Demiris (2006) proposed to combine our approach of controlling the digits (Smeets and Brenner, 1999b) with the minimum variance approach (Harris and Wolpert, 1998). The idea of the latter approach is to find those patterns of muscle activation that render the most precise movement for given task requirements, assuming that noise in muscle force increases linearly with the activation of muscles. For grasping Simmons and Demiris modeled the task requirements in terms of the constraints at contact. In order to calculate the effects of noise in muscle force, one has to include some anatomical details. This model therefore reflects ideas from the classical approach to grasping: the muscles that control grip aperture are different from the ones that transport the hand. In order to let their model be able to grasp, the authors had to introduce one additional parameter: a via-point for each of the digits, which is equivalent to the approach parameter in the digit model. This hybrid model yields predictions that are very similar to the ones of our digit model.

The model of Jiang et al. (2002) is a third model that is based on constraints. It is the one that is closest to our approach; however, their implementation differed in two aspects (Smeets and Brenner, 1999b): these authors chose a different smoothness criterion (minimum acceleration instead of minimum jerk) and a discrete-time instead of continuous-time controller. Despite these changes, their model produced trajectories that were very similar to the ones that our digit model produced. The fact that this model that capitalizes on the constraints for the digits yields results that are similar to our digit model means that the constraints on the digits are more fundamental for grasping behavior than the way in which the digits are controlled to comply with these constraints.

With our digit model, it is not possible to use Occam's razor any further than we did. At least one free parameter is needed to incorporate the experimental finding that for the same object size, the peak grip aperture depends on factors such as movement speed and the amount of visual information. Yet, there is one model that seems to be even simpler than our digit model: the "rule of thumb" for the temporal relationship between the transport and grasp components (Mon-Williams and Tresilian, 2001). However, the model's simplicity is only in the mathematical formulation, not in the number of entities needed to explain the behavior. Both models need one additional parameter apart from object size to account for observations: in the digit model it is the approach parameter, with the peak grip aperture as its equivalent in the "rule of thumb". As the latter model does not predict more aspects of the grasping movement such as trajectory shapes and peak grip aperture, it uses the same number of entities to explain less. Moreover, even this single aspect is not simulated as accurately by the rule of thumb as by our model (Mon-Williams and Tresilian, 2001, p. 1061); similar to the results of the posture model discussed above, peak grip aperture is simulated to occur at 50% of the movement for infinitely small objects.

A fifth model is even more limited: it only addresses how well an experimenter can predict the final grip aperture during the prehension movement (Hu et al., 2005). Obviously, the accuracy of this prediction improves with the unfolding of the movement. The authors show that a sigmoid captures the experimentally observed increase in accuracy. If one assumes a bell-shaped velocity profile, this sigmoidal increase with time corresponds to a linear increase of prediction accuracy with distance, as observed by Cuijpers et al. (2004). The latter formulation might be more useful, as it is easier to predict the "where" than the "when" of the grasp, at least for grasping static objects.

A final interesting comparison is that between the minimum jerk model (based only on the movement of the end-effector in extrinsic space) and the minimum torque change model that takes into account the various properties of the arm. These models have been compared for normal point-to-point arm movements with mixed conclusions as to whether the movements are planned in intrinsic or extrinsic co-ordinates (Uno et al., 1989; Wolpert et al., 1995). A more recent study that incorporated constraints on the final velocity also could not give a clear answer as both models could reproduce the movements qualitatively, but both made (different) systematic errors in their predictions (Klein Breteler et al., 2001).

Going to 3 Dimensions

The digit model was presented as a 2D-model, following the tradition in grasping research of presenting a top-view of the experiment (Smeets and Brenner, 1999b). As this model is based on the minimum jerk model, an extension to 3 dimensions is straightforward as discussed above. The approach vector is still perpendicular to the surface, and still has only one free parameter (its length). In terms of Occam's razor: we do not need an additional entity for describing the third dimension. How good is this description? It is long known that for simple point-to-point movements, adding the vertical dimension introduces important changes: movements in the horizontal plane are predominantly straight (Morasso, 1981), whereas movements with a vertical component are systematically curved and cannot be described by a minimum jerk model without introducing additional constraints (Atkeson and Hollerbach, 1985).

For prehension movements starting at some position on a table and ending on an object with vertical contact surfaces (like a cylinder or a cube) on that table, the approach vector is horizontal. The constraints added in the vertical direction are thus zero velocity and acceleration at both movement onset and movement offset. Therefore, the model predicts a classic minimum jerk trajectory with a bell-shaped velocity profile (Flash and Hogan, 1985) for the (small) vertical component of the movement. The side-view of the movement should therefore look like a straight line (lower right panel in Fig. 6). However, this is not what we observed in experiments, irrespective of whether subjects grasped, pushed or touched the object (other panels of Fig. 6). Hence, just as the minimum jerk model cannot describe simple point-to-point movements in the vertical plane, the digit model cannot be extended to include the vertical direction. This shortcoming held for grasping, pushing and touching. The only way to extend the model without changing it fundamentally is by introducing additional constraints.

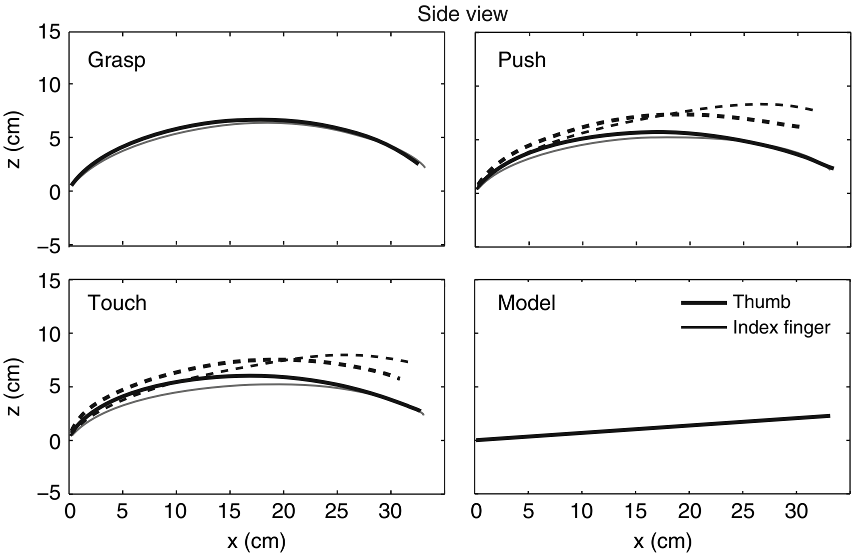

Fig. 6 Side view of the same average movement paths shown in Fig. 4. The vertical components of the movements are very similar for the three tasks, but are not well predicted by our digit model

The large mismatch between model and experiment regarding the vertical component does not imply that the digit-model is refuted. The fact that subjects also touch surfaces by approaching them perpendicularly when moving in three dimensions (Klein Breteler et al., 1998) gives support for the validity of the model for 3D movements. Moreover, the fact that the deviations from the minimum jerk model were equal for grasping, touching and pushing again supports the basic assumption of the digit model that grasping is the combination of two digit movements. Our implementation with a minimum jerk model that only considers the orientation of the contact surface might evidently be too simple. Similar to how adding obstacles in the digits' paths influences the movements, we think that the third dimension when interacting with an object introduces two additional constraints: gravity and the presence of a support surface (the table). Subjects minimize the chances to make contact with the table during the movement and might have some general preference to approach objects on a table from above, because this reduces the likelihood of pushing the object away (Biegstraaten et al., 2006).

Formalizing such relationships would make the model much more complex, and thus would not improve the model in the light of Occam's razor. From a modeling perspective it would be better to perform experiments in which the effects of these additional constraints are minimized. For instance, when grasping an object from a table when starting from above the object, the movements of the digits seem to follow the 3D minimum jerk trajectories much better than is shown in Fig. 6 (unpublished observations).

Conclusion

We showed that based on very few assumptions we could describe a wide range of phenomena related to the reach to grasp movement. However, some clear mismatches also showed that the digit model is not perfect and one might suggest that we have reached the limits of being able to ignore the anatomy of the hand and the complications of joints, forces and muscles. However, we must not jump to this conclusion too fast, because models that take several of these factors already into account do not perform better than the present incomplete digit model in predicting the results of selected critical experiments.

References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Current Biology 5:679–685.

Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained vertical arm movements. Journal of Neuroscience 5:2318–2330.

Biegstraaten M, Smeets JBJ, Brenner E (2003) The influence of obstacles on the speed of grasping. Experimental Brain Research 149:530–534.

Biegstraaten M, Smeets JBJ, Brenner E (2006) The relation between force and movement when grasping an object with a precision grip. Experimental Brain Research 171:347–357.

Bock O (1996) Grasping of virtual objects in changed gravity. Aviation Space and Environmental Medicine 7:1185–1189.

Boessenkool JJ, Nijhof EJ, Erkelens CJ (1999) Variability and correlations in bi-manual pointing movements. Human Movement Science 18:525–552.

Bohan M, Longstaff MG, Van Gemmert AWA, Rand MK, Stelmach GE (2003) Differential effects of target height and width on 2D pointing movement duration and kinematics. Motor Control 7:278–289.

Brenner E, Smeets JBJ (1995) Moving one's finger to a visually specified position – Target orientation influences the fingers path. Experimental Brain Research 105:318–320.

Brenner E, Smeets JBJ (1996) Size illusion influences how we lift but not how we grasp an object. Experimental Brain Research 111:473–476.

Brinkman J, Kuypers HGJM (1973) Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey. Brain 96:653–674.

Bullock D, Grossberg S (1991) Adaptive neural networks for control of movement trajectories invariant under speed and force rescaling. Human Movement Science 10:3–53.

Carey DP (2001) Do action systems resist visual illusions? Trends in Cognitive Sciences 5:109–113.

Castiello U (2005) The neuroscience of grasping. Nature Reviews Neuroscience 6:726–736.

Cuijpers RH, Smeets JBJ, Brenner E (2004) On the relation between object shape and grasping kinematics. Journal of Neurophysiology 91:2598–2606.

Danckert JA, Sharif N, Haffenden AM, Schiff KC, Goodale MA (2002) A temporal analysis of grasping in the Ebbinghaus illusion: planning versus online control. Experimental Brain Research 144:275–280.

de Grave DDJ, Brenner E, Smeets JBJ (2004) Illusions as a tool to study the coding of pointing movements. Experimental Brain Research 155:56–62.

de Grave DDJ, Biegstraaten M, Smeets JBJ, Brenner E (2005) Effects of the Ebbinghaus figure on grasping are not only due to misjudged size. Experimental Brain Research 163:58–64.

de Lussanet MHE, Smeets JBJ, Brenner E (2002) Relative damping improves linear mass-spring models of goal – directed movements. Human Movement Science 21:85–100.
Feldman AG, Levin MF (1995) The origin and use of positional frames of reference in motor control. Behavioral and Brain Sciences 18:723–806.
Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. Journal of Experimental Psychology 47:381–391.
Flash T, Hogan N (1985) The coordination of arm movements: an experimentally confirmed mathematical model. Journal of Neuroscience 5:1688–1703.
Franz VH, Scharnowski F, Gegenfurtner KR (2005) Illusion effects on grasping are temporally constant not dynamic. Journal of Experimental Psychology-Human Perception and Performance 31:1359–1378.
Franz VH, Gegenfurtner KR, Bülthoff HH, Fahle M (2000) Grasping visual illusions: No evidence for a dissociation between perception and action. Psychological Science 11:20–25.
Gentilucci M, Roy AC, Stefanini S (2004) Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? Experimental Brain Research 157:496–506.
Gillam B, Chambers D (1985) Size and position are incongruous: Measurements on the Müller-Lyer figure. Perception & Psychophysics 37:549–556.
Glover S (2004) Separate visual representations in the planning and control of action. Behavioral and Brain Sciences 27:3–24.
Glover S, Dixon P (2001a) Dynamic illusion effects in a reaching task: Evidence for seperate visual representations in the planning and control of reaching. Journal of Experimental Psychology: Human Perception and Performance 27:560–572.
Glover S, Dixon P (2001b) Motor adaptation to an optical illusion. Experimental Brain Research 137:254–258.
Glover S, Dixon P (2002) Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. Perception & Psychophysics 64:266–278.
Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. Neuropsychologia 10:1159–1178.
Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156.
Gribble PL, Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. Experimental Brain Research 135:474–482.
Haffenden AM, Schiff KC, Goodale MA (2001) The dissociation between perception and action in the Ebbinghaus illusion: Nonillusory effects of pictorial cues on grasp. Current Biology 11:177–181.
Haggard P, Wing A (1997) On the hand transport component of prehensile movements. Journal of Motor Behavior 29:282–287.
Haken H, Kelso JAS, Bunz H (1985) A theoretical model of phase transitions in human hand movements. Biological Cybernetics 51:347–356.
Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394:780–784.
Henis EA, Flash T (1995) Mechanisms underlying the generation of averaged modified trajectories. Biological Cybernetics 72:407–419.
Hoff B, Arbib MA (1993) Models of trajectory formation and temporal interaction of reach and grasp. Journal of Motor Behavior 25:175–192.
Hogan N, Flash T (1987) Moving gracefully: quantitative theories of motor coordination. Trends in Neurosciences 10:170–174.
Hu YP, Osu R, Okada M, Goodale MA, Kawato M (2005) A model of the coupling between grip aperture and hand transport during human prehension. Experimental Brain Research 167:301–304.
Jeannerod M (1981) Intersegmental coordination during reaching at natural visual objects. In: Attention and Performance IX (Long J, Baddeley A, eds), pp. 153–169. Hillsdale, NJ: Erlbaum.

Jeannerod M (1999) Visuomotor channels: their integration in goal-directed prehension. Human Movement Science 18:210–218.
Jiang J, Shen Y, Neilson PD (2002) A simulation study of the degrees of freedom of movement in reaching and grasping. Human Movement Science 21:881–904.
Kistemaker DA, van Soest AJ, Bobbert MF (2006) Is equilibrium point control feasible for fast goal-directed single-joint movements? Journal of Neurophysiology 95:2898–2912.
Klein Breteler MD, Meulenbroek RGJ, Gielen SCAM (1998) Geometric features of work-space and joint-space paths of 3D reaching movements. Acta Psychologica 100:37–53.
Klein Breteler MD, Gielen SCAM, Meulenbroek RGJ (2001) End-point constraints in aiming movements: effects of approach angle and speed. Biological Cybernetics 85:65–75.
Kleinholdermann U, Brenner E, Franz VH, Smeets JBJ (2007) Grasping trapezoidal objects. Experimental Brain Research 180:415–420.
Lacquaniti F, Terzuolo C, Viviani P (1983) The law relating the kinematic and figural aspects of drawing movements. Acta Psychologica 54:115–130.
Lemon RN, Johansson RS, Westling G (1995) Corticospinal control during reach, grasp, and precision lift in man. Journal of Neuroscience 15:6145–6156.
Meulenbroek RGJ, Rosenbaum DA, Jansen C, Vaughan J, Vogt S (2001) Multijoint grasping movements. Simulated and observed effects of object location, object size, and initial aperture. Experimental Brain Research 138:219–234.
Mon-Williams M, McIntosh RD (2000) A test between two hypotheses and a possible third way for the control of prehension. Experimental Brain Research 134:268–273.
Mon-Williams M, Tresilian JR (2001) A simple rule of thumb for elegant prehension. Current Biology 11:1058–1061.
Morasso P (1981) Spatial control of arm movements. Experimental Brain Research 42:223–227.
Murata A, Iwase H (2001) Extending Fitts' law to a three-dimensional pointing task. Human Movement Science 20:791–805.
Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M (1991a) Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. Experimental Brain Research 83:502–512.
Paulignan Y, Jeannerod M, MacKenzie C, Marteniuk R (1991b) Selective perturbation of visual input during prehension movements. 2. The effects of changing object size. Experimental Brain Research 87:407–420.
Paulignan Y, Frak VG, Toni I, Jeannerod M (1997) Influence of object position and size on human prehension movements. Experimental Brain Research 114:226–234.
Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farnè A (1999) Are perception and action affected differently by the Titchener circles illusion? Experimental Brain Research 127:95–101.
Roby-Brami A, Bennis N, Mokhtari M, Baraduc P (2000) Hand orientation for grasping depends on the direction of the reaching movement. Brain Research 869:121–129.
Rosenbaum DA, Barnes HJ, Vaughan J, Jorgensen MJ (1992) Time course of movement planning – Selection of hand grips for object manipulation. Journal of Experimental Psychology-Learning Memory and Cognition 18:1058–1073.
Rosenbaum DA, Meulenbroek RJ, Vaughan J, Jansen C (2001) Posture-based motion planning: Applications to grasping. Psychological Review 108:709–734.
Savelsbergh GJP, van der Kamp J (1999) Is it pointing to grasping or grasping pointing? Motor Control 3:298–301.
Simmons G, Demiris Y (2006) Object grasping using the minimum variance model. Biological Cybernetics 94:393–407.
Smeets JBJ, Brenner E (1995) Perception and action are based on the same visual information: distinction between position and velocity. Journal of Experimental Psychology: Human Perception and Performance 21:19–31.
Smeets JBJ, Brenner E (1999a) Grip formation as an emergent property. Response to commentaries on "A new view on grasping". Motor Control 3:316–325.

Smeets JBJ, Brenner E (1999b) A new view on grasping. Motor Control 3:237–271.

Smeets JBJ, Brenner E (2001) Independent movements of the digits in grasping. Experimental Brain Research 139:92–100.

Smeets JBJ, Brenner E (2002) Does a complex model help to understand grasping? Experimental Brain Research 144:132–135.

Smeets JBJ, Brenner E, Biegstraaten M (2002a) Independent control of the digits predicts an apparent hierarchy of visuomotor channels in grasping. Behavioural Brain Research 136:427–432.

Smeets JBJ, Glover S, Brenner E (2003) Modeling the time-dependent effect of the Ebbinghaus illusion on grasping. Spatial Vision 16:311–324.

Smeets JBJ, Brenner E, de Grave DDJ, Cuijpers RH (2002b) Illusions in action: consequences of inconsistent processing of spatial attributes. Experimental Brain Research 147:135–144.

Smyrnis N, Evdokimidis I, Constantinidis TS, Kastrinakis G (2000) Speed-accuracy trade-off in the performance of pointing movements in different directions in two-dimensional space. Experimental Brain Research 134:21–31.

St-Onge N, Feldman AG (2003) Interjoint coordination in lower limbs during different movements in humans. Experimental Brain Research 148:139–149.

Todorov E (2004) Optimality principles in sensorimotor control. Nature Neuroscience 7:907–915.

Uno Y, Kawato M, Suzuki R (1989) Formation and control of optimal trajectory in human multijoint arm movement – Minimum torque-change model. Biological Cybernetics 61:89–101.

van de Kamp C, Zaal FT (2007) Prehension is really reaching and grasping. Experimental Brain Research 182:27–34.

Wolpert DM, Ghahramani Z, Jordan MI (1995) Are arm trajectories planned in kinematic or dynamic coordinates – an adaptation study. Experimental Brain Research 103:460–470.

Zaal FTJM, Bootsma RJ, van Wieringen PCW (1998) Information-based coupling of reaching and grasping. Experimental Brain Research 119:427–435.