Getting a grip on grasping

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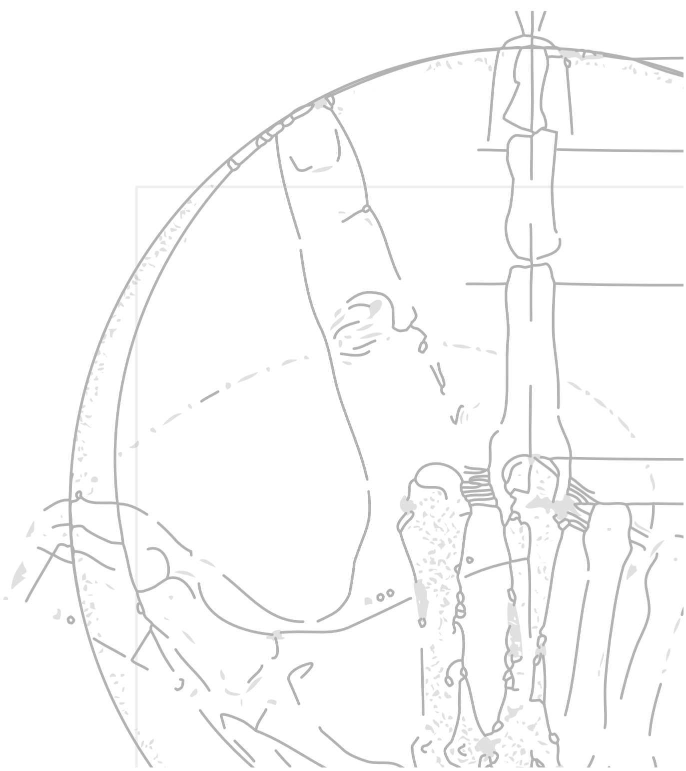
Contents

1

General introduction



Manual dexterity enables humans to grasp a variety of things like, for example, the book you are holding right now. Somehow you managed to pick it from the bookshelf and had the booklet tumbled off the shelf you probably would have caught it just as easily. Catching and prehension (i.e., the coordinated act of reaching and grasping) are seemingly simple acts that we carry out, thoughtlessly, many times a day. But how do we control these movements? How do we manage to close our grasping hand around an object in just the right time and place? The aim of this thesis is to get a better understanding of how grasping movements are controlled in catching and prehension. Theoretical knowledge that is also relevant when applied to the innovative fields of prosthetics and robotics. This introduction is meant to provide some background on the experimental work reported in this thesis.

The framework for the studies presented in this thesis is provided by a vast body of research on the visual guidance of goal-directed movements. In earlier studies on tasks like hitting, catching, and prehension (e.g., Bootsma & van Wieringen, 1990; Bootsma & Peper, 1992; Savelsbergh, Whiting, & Bootsma, 1991) it is argued that time-to-contact information plays an essential role in the guidance of these interceptive actions. Also with respect to the coordination in prehension it has been suggested that this time-to-contact information, which is directly perceivable and specifies the time remaining until the object and the observer meet (Bootsma & Peper, 1992; Lee, 1976; Savelsbergh et al., 1991), plays a role in the continuous informational coupling of reaching and grasping (Zaal & Bootsma, 2004; Zaal, Bootsma, & van Wieringen, 1998). The advantage of using one source of information for the control of both the reaching and the grasping movement (i.e., the controlled variables) is that the coordination between the two would not require a separate control, but that it emerges as the movement develops. The perspective of emerging behavior (as opposed to predefined behavior) is provided by dynamical systems theory. Zaal and colleagues (Zaal & Bootsma, 2004; Zaal et al., 1998) combined elements of the theories of direct-perception and dynamical systems to provide us with a dynamic model to study the control of hand-closure initiation in catching and grasping.

As sketched out in the above, 1) the controlled variables, 2) the information, and 3) the control law (i.e., the way that the information is used for movement control) form the fundamental underpinnings of the model(s) for catching and prehension that will be studied in this thesis. To start with the first of these, the question to address in this thesis is what are the controlled variables in prehension? An intriguing question especially when considering the many degrees of freedom involved in controlling the movements of hand and arm. Realizing that the hand alone, a highly complex structure consisting of 27 bones, 18 joints, and 39 muscles, already offers over 20 degrees of freedom (Mason et al., 1986) illustrates the challenge of understanding how the motor system copes with all its degrees of freedom (cf. Bernstein 1967). This issue in motor control has been studied in a wide variety of ways. One way, which is adopted in the current thesis, is to focus on the system in its functional (or behavioral) context. This way the problem of coordination control is narrowed down to the simple question what is it in the movement of our hand and arm that is actually controlled? To answer this question one does not have to refer to the anatomy and physiology of the neuromuscular machinery as one could also refer to the level of behavior. This approach allows us to make inferences regarding the control system underlying catching and prehension based on kinematic studies of the movements' end effectors (i.e., the position, velocity, and accelerations of -for instance- the wrist and fingers).

Reaching and grasping or double pointing?

The question what are the controlled variables in prehension had been revived in 1999 by Smeets and Brenner. After 20 years of prehension research that had been based mainly on Jeannerod's (1981, 1984) hypothesis that prehension should be considered as the coordinated act of a reaching and a grasping movement, Smeets & Brenner (1999) proposed 'a new view on grasping'. Their alternative explanation was that prehension might just as well be seen as the simultaneous pointing movements of the thumb and the index finger. Whereas in Jeannerod's (functional) view, the hand aperture (i.e., the distance between thumb and index finger) had always been considered to be one of the controlled variables in grasping, according to Smeets and Brenner's 'double pointing hypothesis', this hand aperture is really an emergent property related to the time course of the positions of the two digits moving to their respective end points.

The hypothesis that thumb and index finger are controlled independently denies a functional relationship between the two. However, empirical observations suggest that often movements do relate to each other. Consider in this respect the example of speech production. An important aspect of speaking involves a high number of facial muscles that move the upper and lower lip. When pressing a finger against one of the lips (i.e., mechanically perturbing its movements), an immediate compensation of the other lip occurs, such that the audibility is preserved (Kelso et al., 1984). The observation of a functional coupling between the movements of the lips seems to be in line with Jeannerod's (functional) view on reaching and grasping. However, to (re)establish what are the controlled variables in prehension, the alternative hypothesis deserved a test.

Adjusting the grasp just as rapid as the reach

According to the concept of prehension being the coordinated act of reaching and grasping, people transport the hand to the location of the object while at the same time opening and closing their hand. Some 30 years ago, it was again Jeannerod (1981) who suggested that grasping is temporally ordered on the time scale provided by reaching. Empirical evidence for this predefined (or offline programmed) hierarchy of reaching over grasping seemed to come from perturbation studies (e.g., Castiello, Bennett, & Stelmach, 1993; Gentilucci, Chieffi, Scarpa, & Castiello, 1992; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991), which showed that when object location or size were changed at movement onset, adjustments in the reach component were much faster than adjustments in the grasp component. Knowing how fast the components of prehension respond to perturbations might tell us something about the transit speed of the neural circuitry but in addition to that, it would also give us insight in how, at a behavioral level, reaching and grasping are organized. If adjusting the grasp component would, indeed, take longer than adjusting the reach component, the assumption of a hierarchy of reaching over grasping might be tenable.

One could, however, question whether the above mentioned studies have really invited the grasp component to show its lower limit in responding to perturbations. That is to say, the experimental manipulations reported in these studies all occurred at movement onset but maybe, shorter adjustment times would have been observed if the perturbations had occurred later during the movement. If one could show that adjustments to the grasp component can be just as rapid as adjustments to the reach component, this would support an alternative means to consider the way the grasp component might adjust to size perturbations. This alternative view hypothesizes that a response to perturbations in, for instance object size results from the online control of the hand aperture (cf. Zaal, Bootsma & van Wieringen, 1999). Accordingly, this alternative scheme would fit the smooth adjustments to a perturbation seen when there is plenty of time to adjust but also rapid adjustments in the situation that the perturbation occurs late in the movement.

What and how?

The experiments reported in this thesis were designed to study the hypothesized online control of the hand aperture in catching and grasping. As pointed out in the above, we first have to identify the information that is used for the timing of hand closure in catching and grasping. But how do we achieve something like that? One approach to identify what visual information is used for the control of a goal-directed movement is to observe the consequences of manipulating the information involved in that particular task. In order to assess the use of time-to-contact information for controlling hand opening and closing in catching, Savelsbergh and colleagues (e.g., Savelsbergh et al., 1991) manipulated that information by having approaching balls shrink in size.[1] The timing of hand closure was found to be delayed in the shrinking-balls condition which suggested that time-to-contact information was indeed involved in the control of catching (but see: Wann, 1996). However, if one aims at identifying what information is used for the timing of, for instance, the initiation of hand closure in catching one should at the same time consider the issue of how it is used. Unfortunately, researchers often implicitly assumed a specific control law (relating the information to the controlled variable) in which movements are triggered upon reaching a criterion value of time-to-contact. This assumption

[1] Fundamental to the theory of direct-perception is that information regarding the physical environment-actor relation (the specificandum) is optically available through specific perceptual variables (the specificator). In the current thesis it is assumed that in this way participants perceived the first-order time-to-contact information which they use for the timing of hand closure initiation.

makes the assessment of the use of information become hazardous. That is, if kinematic analyses demonstrate that the timing of certain landmark events is quantitatively not in agreement with the hypothesized use of, for example, time-to-contact information, one of three conclusions might be true (but it cannot be known which is actually true). First, the hypothesized information is not used. Second, the information is used but in a different way. Or third, both the hypothesis concerning the information as well as its use have to be rejected. The current thesis tried to avoid the pitfall of this hypothesis doubling (cf. Bootsma, Fayt, Zaal, & Laurent, 1997) by explicitly considering both the issues of what is the information and of how it is used.

In the context of prehension, Zaal and colleagues (Zaal & Bootsma, 2004; Zaal et al., 1998) considered different informational variables used in different ways and showed that, in contrast to all current competing hypotheses, the timing in the coordination of reaching and grasping was most consistent with the dynamic use of first-order time-to-contact information. The next step is to precisely test the use of time-to-contact information by directly manipulating it in order to determine its use. First-order time-to-contact is defined as the current distance between hand and target divided by the rate of change of that distance. Thus, by manipulating the target's approach trajectory (make it approach the grasping hand in different ways) one easily perturbs the time-to-contact. The above mentioned nonlinear control law with first-order time-to-contact information (Zaal & Bootsma, 2004; Zaal et al., 1998) should be able to predict quantitatively the timing of the initiation of hand closing in different conditions. By comparing the model's predictions with the participants' behavior, one should be able to assess the model's ability to explain the timing of hand closure initiation in catching and in grasping.

Comparing grasping in prehension to catching

Prehension of approaching targets and catching approaching targets are traditionally considered as two separate movement acts. The key difference seems to be in the movement of the hand, which is negligible in catching and substantial in prehension. Interestingly, grasping in prehension and catching also share many aspects. A main characteristic that the two tasks have in common is that the initiation of hand closing has to be coordinated with the closure of the hand-object gap. Therefore, it could well be that grasping in prehension and catching use the same information and the same control law. One of the hypotheses that will be tested in this thesis is that in both catching and prehension, the timing of the initiation of hand closing will be based on the same information and the same control law. Or in other words, that grasping in prehension and catching are controlled by the same principles. This scheme would yield the more parsimonious situation in which a single control system is shared by two kinds of tasks.

Outline of this thesis

The research reported in this thesis addresses the four questions that were raised in the introduction above. The first question concerned the controlled variables in prehension. When picking up an object, what is it in the movement that is actually controlled? Do we transport the hand to the location of the object while at the same time opening and closing our hand, or is this grasping movement an emergent property of the simultaneous pointing movements of thumb and index finger? If there are reservations about the aspects of the movement that are subject to control, it seems premature to write a control law relating the information to the controlled variable. Since part of this thesis will involve testing these control laws, it seems vital to address (or rule out) the possibility that Smeets and Brenner's new view on grasping is the right view. For this test, reported in *Chapter 2*, an experimental setup was developed in which a target object could be made to suddenly change size by quickly sliding in or out either side of the object (like a matchbox). This way, the end position of one of the digits was suddenly changed while leaving the end position of the opposing digit unchanged. Whereas the double-pointing account would predict that the movement trajectory of only one digit should be perturbed by the unilateral change in object size, according to the traditional account on reaching and grasping adjustments to the movement trajectories of both digits are expected.

In *Chapters 3* it is studied how rapid the grasp component adjusts to a sudden change in object size. The objective for doing this was the apparent difference in response times between the reaching and the grasping components (i.e., grasping responds slower to perturbations than reaching) which seemed to support a hierarchical view on the control of reaching and grasping. In order to reveal -if existent- shorter grasp adjustment times than previously reported an experiment was designed in which the object-size changes were planned to happen at one of four moments during the movements. This way, lower limit adjustment times might be observed when time to change is pressing whereas response times might turn out to be longer when time would permit. Such adjustments would fit a view of the control of grasping (and reaching) in which the kinematic details of prehension are considered to be emergent rather than preplanned in a hierarchical fashion (e.g., Bullock & Grossberg, 1988; Schöner, 1990; Ulloa & Bullock, 2003; Zaal et al., 1999).

In *Chapters 4* and *5*, the next and exciting step is reported of actually testing the use of the information and the control law by manipulating the information and evaluating quantitative predictions. In *Chapter 4*, a first attempt is reported at showing that grasping in prehension and catching use the same information and the same control law. As it turned out that the initiation of hand closure could well be based on first-order time-to-contact in the prehension task but not in the catching task, in which participants were asked to keep the grasping hand stationary while catching the approaching object, a final study, reported in *Chapter 5*, was conducted that focused on the nature of the hand-object relation in catching. The main question to be answered in this chapter was whether introducing nonlinearities into this hand-object relation would result in grasping behavior that could be accounted for by the nonlinear use of first-order time-to-contact information.

The four empirical studies that form the heart of this thesis are designed to answer the many questions that were raised in this introduction. What are the controlled variables in prehension? Are reaching and grasping hierarchically organized? Do grasping in prehension and catching use the same information? And if so, do they also use the same control law? By answering each of these questions within the dynamic framework set out in this introduction I aim to gain insight into how our grasping movements are controlled in catching and prehension. I hope that, in the end, these studies on the inter-related aspects of visual control (i.e., the controlled variables, the information, and the control law) will contribute to a comprehensive (functional) theory of the role of vision in the control of goal-directed movements.

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2

Prehension is really reaching and grasping

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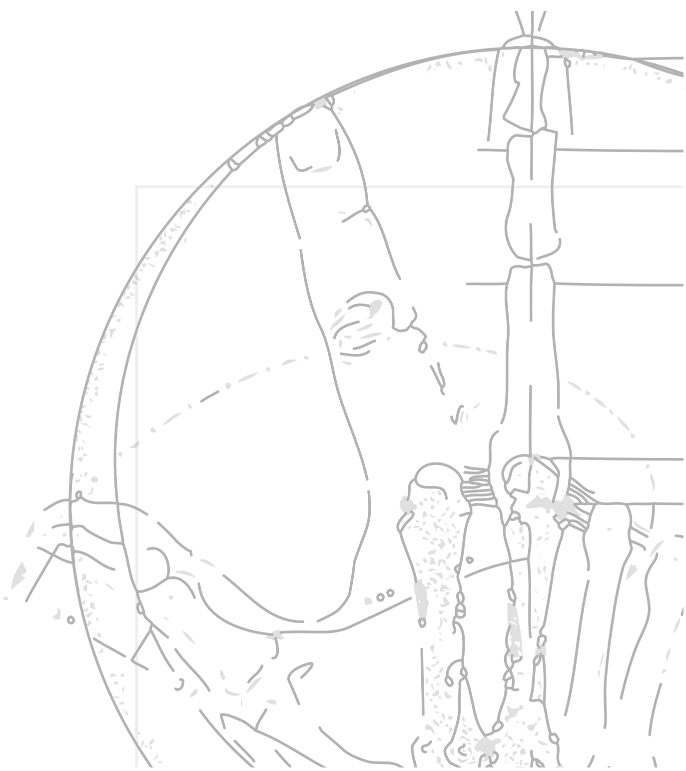

Abstract

Prehension has traditionally been seen as the act of coordinated reaching and grasping. However, recently, Smeets and Brenner (1999) proposed that we might just as well look at prehension as the combination of two independently moving digits. The hand aperture that has featured prominently in many studies on prehension, according to Smeets and Brenner's 'double-pointing hypothesis', is really an emergent property related to the time course of the positions of the two digits moving to their respective end points. We tested this double-pointing hypothesis by perturbing the end position of one of the digits while leaving the end position of the opposing digit unchanged. To this end, we had participants reach for and grasp a metallic object of which the side surfaces could be made to slide in and out. We administered the perturbation right after movement initiation. On several occasions, after perturbing the end position of one digit, we found effects also on the kinematics of the opposing digit. These findings are in conflict with Smeets and Brenner's double-pointing hypothesis.

Introduction

Traditionally, prehension has been understood as the act of coordinated reaching and grasping. The reaching component of prehension is concerned with bringing the hand to the object to be grasped, whereas the grasping component refers to the opening and closing of the hand. This suggested division of labor stems from the seminal studies performed by Marc Jeannerod, about 25 years ago, which, for the first time, reported details of the kinematics of prehensile movements (Jeannerod 1981, 1984). Countless studies have addressed all kinds of aspects of prehension, taking this division in components as their starting point. Recently, however, Smeets and Brenner (1999) started advocating an alternative to this view of prehension. They suggested that it is not reaching and grasping that make up prehension, but that the individual digits move independently to their respective sides of the object to be grasped, and that what looks like a grasping component is really something emerging from individual digits' trajectories. The purpose of the study presented here was to critically test Smeets and Brenner's 'double-pointing hypothesis'. Before presenting the experiment, however, we will briefly review the proposals originally made by Jeannerod and the complaints that Smeets and Brenner formulated regarding the traditional division of prehension into a reaching and a grasping component.

As mentioned earlier, with his first systematic analysis of the kinematics of prehension, Jeannerod (1981, 1984) set the stage for a large number of studies of the control and coordination of reaching and grasping (for reviews, see Castiello 2005; Jeannerod 1988; MacKenzie & Iberall 1994). Jeannerod's proposal that a reaching (or transport) component and a grasping (or manipulation) component make up prehension was based on a number of arguments, such as anatomical arguments that different muscles and brain areas are involved in the control of reaching and grasping (e.g., see Jeannerod 1999; Jeannerod et al., 1995). One of the most prominent among the arguments, however, was that the two components would rely on different types of information about the object: Jeannerod's 'visuo-motor channels hypothesis' (Jeannerod 1981, 1988, 1999; Paulignan & Jeannerod 1996) held that the reaching component operates exclusively on information about extrinsic properties of the object (such as its egocentric distance and direction) and the grasping component operates exclusively on information about intrinsic object properties (such as its size, shape, and surface properties). In this sense, the two components (i.e., the two visuo-motor channels) were hypothesized to be independent. This is why many studies designed to test the independence of the two components of prehension involved perturbations of intrinsic object properties, such as size (e.g., Castiello et al., 1993; Paulignan et al., 1991a) or of extrinsic object properties, such as location (e.g., Gentilucci et al., 1992; Paulignan et al., 1991b), to see if the perturbations would have an effect on the component that should not be dependent on information of either object property. Object-size perturbations, for instance, should only affect the grasping component in Jeannerod's model.

With two components making up one act (that of prehension), not only their independence but also their coordination becomes an issue. Most often, when the coordination of prehension has been addressed, hypotheses regarding the moment of peak hand aperture, the moment that hand opening goes into hand closing, have been put forward (for an overview, see Zaal & Bootsma 2004). For instance, it has been proposed that peak hand aperture would occur at the moment of peak deceleration of the reaching movement (Jeannerod 1984), at a fixed time (Gentilucci et al., 1992) or distance (Rand & Stelmach 2005; Rand et al., 2006; Wang & Stelmach 1998, 2001) before hand-object contact, or that coordination is based on time-to-contact information (Bootsma & Van Wieringen 1992; Zaal & Bootsma 2004; Zaal et al., 1998). In our opinion, the latter hypothesis is the most promising of the ones currently available, but it certainly still needs a critical test. To do so, however, the conceptualization of prehension into a reaching and grasping component must be valid. This is where Smeets and Brenner's (1999) hypothesis that prehension should be seen as the combination of independent digit's movements rather than the combination of reaching and grasping becomes problematic. If prehension is not about reaching and grasping, formulating hypotheses about their coordination (or independence) is pointless. This was the direct inspiration for the current study. But before we turn to the experiment that we performed, let us see what made Smeets and Brenner propose a new view on prehension.

Smeets and Brenner (1999) formulated a number of points of dissatisfaction with the original division of labor between a grasping and reaching component as initially proposed by Jeannerod (1981). Smeets and Brenner pointed out that the distinction between intrinsic and extrinsic object properties was problematic. For instance, the orientation of an object could be (and has been) seen both as an intrinsic and as an extrinsic object property. To identify the respective visuo-motor channels on the basis of their exclusive reliance on information about these two types of object properties, Smeets and Brenner argued, was impossible. Furthermore, Smeets and Brenner explained that the anatomical arguments for the distinction of reaching and grasping components were invalid as well. To argue that reaching (hand transport) and grasping (shaping the hand) rely on to the use of proximal and distal muscles, respectively, an argument used by Jeannerod to distinguish the two components of prehension, did not convince Smeets and Brenner, who pointed at the fact that, for instance, polyarticular muscles in the lower arm (which are proximal muscles) are involved in movements of the digits.

As an answer to what they called the 'classical approach' of Jeannerod (1981), Smeets and Brenner (1999) presented an 'alternative approach'. Their approach essentially proposes to think of prehension as the independent movement of the contributing digits[1] to their respective planned end positions. These digits, as Smeets and Brenner argued, typically arrive at the surface more or less perpendicularly. If one would look at the average path of the two digits, this would be the straight path that might look like a reaching movement; looking at the distance between the two independently moving digits as a function of time would show the well-known hand-aperture profile (and might be incorrectly interpreted as such, according to Smeets and Brenner). To demonstrate how this control of independent digits looking like reaching and grasping might work, Smeets and Brenner modeled the kinematics of the individual digits with the minimal jerk model (Flash & Hogan 1985), but now with a non-zero deceleration at the moment of digit-hand contact. This latter, final deceleration, scaled by movement time squared, made up an 'approach parameter'.

[1] In most cases, when studying prehension, participants are asked to pick up objects between their thumb and index finger, the, so-called, precision grip. We will discuss the different models with this type of grip in our minds.

Smeets and Brenner demonstrated in their original study as well as in others (e.g., Smeets & Brenner 1999, 2001, Smeets et al., 2002) how by varying the approach parameter and movement time the model fitted empirical data. To appreciate the close resemblance of the model behavior with experimentally established relations among 'intrinsic' and 'extrinsic' object properties and the kinematics of prehension, Smeets and Brenner invited us to translate the average trajectory of the thumb and index finger into a hand transport trajectory and the difference of the trajectories of the thumb and index finger into a grasping trajectory, of course, only for the purpose of comparing the model to observed kinematics. Simulations of the model showed that reaching is not affected by variations in 'intrinsic' object properties, that grasping component is not affected by variations in 'extrinsic' object properties, that peak hand aperture occurs later in the movement for larger objects, and that an increase in the approach parameter, for instance because a slippery object surface asks for a more perpendicular approach of the digits, leads to a larger peak hand aperture occurring relatively earlier in the movement.

As we discussed earlier, if the hypothesis of Smeets and Brenner (1999) is true that it is the digits themselves that are controlled in prehension and not a reaching and grasping component, much of the research on prehension, most notably the studies on the independence of the reaching and grasping component and the studies on the coordination of the two putative components, have been pointless. That is why, we think, a well-funded appraisal of either Smeets and Brenner's 'new view' or of the 'classical approach' is called for. Although there have been a number of theoretical and methodological arguments against Smeets and Brenner's new view (e.g., Marteniuk & Bertram 1999; Newell & Cesari 1999; Rosenbaum et al., 1999; Steenbergen 1999), we felt that an empirical test would be the strongest argument in favor of either approach. This is the reason why we set out to test Smeets and Brenner's account of prehension. The logic behind our test is the following. If Smeets and Brenner have been correct with their hypothesis that the two digits that are used to pick up an object with a precision grip (between thumb and index finger) move independently to their respective end positions on the object, changing the end position of one of the digits, say, the thumb, would not have an effect on how the other digit, in this case the index finger, would move to its, unchanged, end position. In other words, changing the end position of one digit during the movement should not affect the kinematics of the other digit. For the experiment, we developed an object of which both side surfaces could be made to quickly slide in or out independently (see the Supplementary Movie)[2]. We had participants reach for and grasp this object. In some trials, we had one of the two side surfaces slide in or out right after the movement had started, such that one digit had to move to a new position whereas for the other nothing had changed. By comparing the kinematics of both digits with that of unperturbed trials, we were able to test Smeets and Brenner's hypothesis.

Materials and methods

Participants

Eleven right-handed participants (5 men and 6 women, ranging in age between 20 and 29 years) participated in the experiments. All had normal or corrected-to-normal vision, were naive to the exact purpose of the experiment, and gave written informed consent.

Apparatus

Participants were required to reach to grasp between their thumb and index finger of their right hand an oblong object. The object was located at 35 cm distance along the sagittal plane from a starting location, which was about 2 cm from the edge of the table. Both side surfaces of the object to be grasped could be slid in or out their common case (see Supplementary Movie). Using pressurized air, this sliding in or out took about 100 ms. The common case was 2 cm high, 4 cm deep, and 4 cm wide. Sliding out one side surface added 1.5 cm to the width of the object.

The long axis of the object was positioned at an angle α with the horizontal along the frontal plane (see Figure 1). Before the actual experiment was conducted, we had the participant grasp a cylindrical object to determine

[2] The online version of this article (doi:10.1007/s00221-007-0968-2) contains supplementary material, which is available to authorized users.

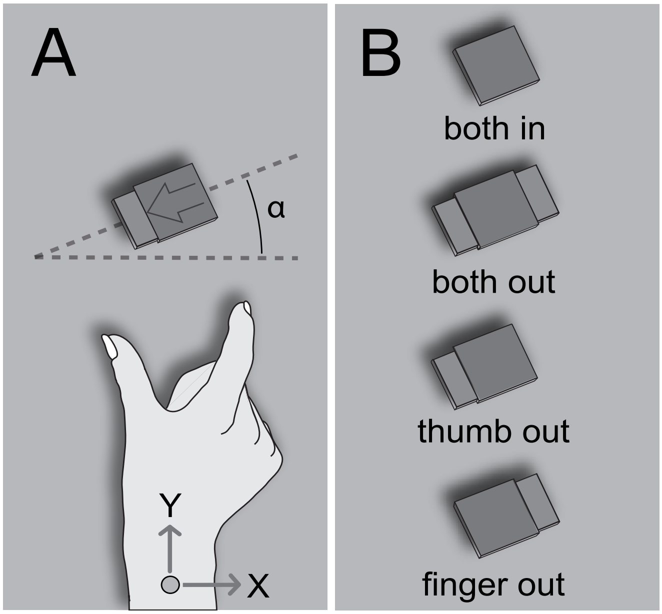

Figure 1. Overview of the experimental manipulations. (a) Participants were to reach to grasp an oblong object. The orientation of the long axis of the object was at an angle α with the x-axis, the axis perpendicular to the horizontal along the sagittal plane, which was the y-axis. (b) The side surfaces of the target object could be made to slide in or out of their common case. The perturbations yielded a change from one of four possible object configurations to another object configuration. See the text for details.

the angle α that was most natural for the specific participant. This angle was used for that participant throughout the experiment. Angle α varied across participants from 5° to 40° (mostly 20° or 40°).

An Optotrak™ system tracked the positions of infrared light emitting diodes (IREDs) at a rate of 100Hz. The IREDs were placed (1) on the lateral lower corner of the index finger nail, (2) on the medial lower corner of the thumb nail, (3) immediately proximal to the styloid process of the radius at the wrist, and (4) on the dorsal aspect of the hand immediately proximal to the metacarpo-phalangeal joint of the index finger.

Design and procedure

The participants' task was to reach to grasp the target object as quickly but accurately as possible. The object was not to be lifted at the end of the movement. The experiment started with a block of 80 trials in which the object did not change its configuration during the trial (static block). We randomly presented to the participants the object in one of four configurations (see Figure 1b): (1) with both side surfaces in their retracted position (static both in), (2) with both side surfaces in their extended position (static both out), (3) with the left side surface slid out and the right side surface slid in (static thumb out), or (4) with the left side surface slid in and the right side surface slid out (static finger out), each configuration 20 times. The static block was followed by a perturbation block, in which in 20% of the 120 trials one of the side surfaces was slid out (or in). The perturbation block consisted of eight types of trials, four in which either side surface slid in or out just after the participant had started his or her movement and the four static configurations that we detailed before (see Figure 1b). That is to say, the perturbation trials involved (1) trials in which the object changed from a 'both-sides-in' to a 'thumb-out' configuration (perturbation thumb out), (2) trials in which the object changed from a 'both-sides-in' to a 'finger-out' configuration (perturbation finger out) , (3) trials in which the object changed from a 'both-sides-out' to a 'finger-out' configuration (perturbation thumb in), and (4) trials in which the object changed from a 'both-sides-out' to a 'thumb-out' configuration (perturbation finger in).

At the start of each trial, we asked the participants to make the tips of the thumb and index finger of the right hand touch at the starting location. After a signal from the experimenter, the participant was free to choose the moment to start reaching for the object. As mentioned before, in 20% of the trials, randomly interspersed with the static trials, a perturbation of the future end position of one of the digits was administered. This perturbation was triggered by the initiation of the reaching movement of the participant. For that purpose, Optotrak data was used on-line, to compute an average position of the thumb and index finger. After taking the derivative with respect to time of this position, yielding an average digit speed, we determined the moment that this average digit speed reached a threshold of 20 mm/s. At that moment, a signal was given to move the specific side surface for that condition, after which it took some 100 ms for the side surface to have slid in or out completely.

Data analysis

Data analysis was performed off-line. Because of missing markers or malfunction of the sliding in or out of the side surfaces of the object, we removed 8 trials of the static blocks and 31 trials of the perturbation blocks from the data set, leaving us with 2161 trials for analyses. We took out high-frequency noise from the recorded data using a low-pass recursive second-order Butterworth filter at a cut-off frequency of 5 Hz. Next, we computed velocities and accelerations of the IREDs on both digits, using finite-difference techniques. We only considered movement along the x- and y-axes (i.e., the movement components along the horizontal plane; see Figure 1). The speeds and accelerations that we present are the square roots of the squared speeds and accelerations in x- and y-direction. For each digit separately, we determined the moment its movement started and stopped (we used a speed threshold of 100 mm/s), and the moments of peak acceleration, peak speed, and peak deceleration. In addition, we computed the hand aperture as the distance between the thumb and index-finger positions and determined the peak hand aperture.

To assess the effect of our manipulations, we concentrated on the moment of peak deceleration[3] in each digit's reaching movement. For each digit separately, we determined (1) the moment of peak deceleration, and at that moment (2) the amount of deceleration, (3) the speed, (4) the x-position, and (5) the y-position. We compared this quintuple of dependent measures of the trials in which a side surface had been slid out or in with that of the trials of the perturbation block of the corresponding static configuration before sliding in or out had occurred. That is to say, because we were interested to see if perturbing the future end position would have an effect on the kinematics, we compared the perturbation condition with the static condition of the situation as if no perturbation had taken place. For instance, if the perturbation meant a sliding out of the right surface (perturbation finger-out-condition), we compared the trials with such perturbation with the trials of the perturbation block in which all surfaces were in their retract position (both-sides-in condition), which was the initial configuration of the perturbation trials. An

[3] As will become apparent when we present the results, we repeated the same analyses for the moment of peak acceleration and peak speed.

effect of the perturbation of targeted end position for a digit would show up as a significant effect of the perturbation in the doubly-multivariate analyses of variance (ANOVAs) that we performed. We were specifically interested in effects of the perturbation on the kinematics of the digit on the side that had not been perturbed. All in all, this meant that we performed four sets of two ANOVAs on the sets of dependent measures associated with peak deceleration: for each of the four perturbation conditions, for the thumb and index-finger kinematics separately, we compared the sets of kinematic variables of the perturbation condition with that of its corresponding static condition of the perturbation block.

Results

As mentioned before, the design of the experiment comprised of a static block, in which the object did not change its configuration during the participant's movement, followed by the perturbation block, in which occasionally one of the side surfaces of the object slid in or out after the participant had started the movement. Table 1 presents the average movement durations and peak velocities of the thumb, and the peak hand apertures of all these conditions. Three things are worth mentioning. First, Table 1 shows that movement durations and peak velocities were essentially the same for the object in all its static configurations. In contrast, peak apertures scaled with the size of the object: peak aperture was smallest when both side surfaces were retracted, largest when both side surfaces were extended, and in between when one of the side surfaces was retracted and the other extended. Second, the same pattern of results can be seen for the corresponding trials of the perturbation block. Finally, movement durations and peak velocities of the perturbation trials were comparable to those of the static trials of the perturbation block. Peak apertures of the perturbation trials were comparable to the middle values of peak apertures of the static trials. This makes sense when we consider that the perturbation always yielded a change to a configuration with one side surface in its retracted position and the other in its extended position. In sum, nothing was dramatically different between the static conditions of the static block and the perturbation block, and movement durations, peak velocities, and peak apertures of the perturbation conditions were comparable to those

Table 1. Means and average within-participant standard deviations (within brackets) of the movement time (MT) and peak speed (PS) of the thumb, as well as peak hand aperture (PA) in the static block and in the perturbation block.

Condition	static block			perturbation block		
	MT (ms)	PS (mm/s)	PA (mm)	MT (ms)	PS (mm/s)	PA (mm)
static both in	594 (46)	1103 (79)	89 (5)	587 (43)	1115 (80)	90 (4)
static thumb out	591 (40)	1097 (67)	99 (4)	591 (41)	1098 (67)	100 (4)
static finger out	591 (40)	1073 (61)	99 (4)	582 (39)	1082 (68)	99 (4)
static both out	583 (41)	1087 (63)	107 (4)	579 (37)	1092 (72)	108 (4)
perturbation thumb out				591 (40)	1106 (78)	99 (3)
perturbation finger out				582 (45)	1100 (86)	99 (3)
perturbation thumb in				594 (38)	1096 (68)	96 (5)
perturbation finger in				606 (42)	1105 (57)	96 (4)

of the static conditions of perturbation block. Now, we are ready to turn to the main question that the experiment was designed to answer: did changing the end position of one digit affect not only the kinematics of this digit but also that of the opposite digit?

To assess the effect of perturbing the future end position of each digit, we compared the kinematics of the perturbed situation with that of the situation as if no perturbation would have occurred (the comparisons were made within the perturbation block). For instance, when we looked for an effect of sliding out the thumb side of the object, we compared the kinematics of this situation (perturbation-thumb-out condition; see Figure 1b) with the kinematics of the situation that both sides remained retracted during the movement (static-both-in condition of the perturbation block). For this comparison, we focused on the moment of peak deceleration of the respective digits (the thumb and index finger). Table 2 gives the kinematic variables that we included in our comparison. We considered the time that peak deceleration occurred, the position of the digit at that moment (x- and y- coordinates), the speed of the digit at that moment, and the amount of deceleration itself.

Sliding out the thumb side of the object had an effect on both the kinematics of the thumb and of the index finger. The comparison of the thumb kinematics of the perturbation-thumb-out condition with that of the static-both-in condition of the perturbation block yielded a highly significant perturbation effect, $F(5,6) = 67.108$, $p < .001$. Importantly, however, a perturbation effect was present also in the kinematics of the index finger, $F(5,6) = 6.201$, $p < .05$. In other words, sliding out the thumb side of the object did affect the kinematics of the opposing digit, the index finger, for which nothing had changed in terms of the position that it was to be moving to.

Table 2. Means and average within-participant standard deviations (within brackets) of the time (*t*), position (*x* and *y*), speed (*s*), and acceleration (*a*) at the moment of peak deceleration of the thumb and the index finger in the perturbation block.

Condition	Thumb					Index Finger				
	t (ms)	*x* (mm)	*y* (mm)	*s* (mm/s)	*a* (mm/s^2)	*t* (ms)	*x* (mm)	*y* (mm)	*s* (mm/s)	*a* (mm/s^2)
static both in	373 (30)	-35 (7)	273 (15)	692 (74)	5209 (832)	395 (36)	32 (8)	324 (18)	674 (111)	5796 (907)
static thumb out	381 (28)	-33 (6)	275 (16)	666 (78)	5105 (720)	399 (34)	42 (7)	326 (17)	679 (94)	5580 (770)
static finger out	381 (29)	-45 (6)	269 (14)	660 (74)	5022 (687)	397 (31)	31 (7)	321 (16)	672 (92)	5492 (772)
static both out	381 (30)	-42 (6)	270 (16)	663 (78)	5100 (779)	393 (31)	40 (7)	322 (16)	698 (89)	5509 (819)
perturbation thumb out	372 (37)	-37 (7)	269 (16)	700 (92)	4941 (705)	391 (38)	36 (9)	319 (19)	724 (110)	5565 (979)
perturbation finger out	367 (39)	-42 (7)	262 (17)	690 (94)	5172 (874)	382 (36)	29 (6)	317 (16)	701 (101)	5727 (899)
perturbation thumb in	376 (38)	-37 (7)	269 (19)	692 (107)	4901 (790)	398 (41)	36 (7)	322 (19)	679 (117)	5589 (911)
perturbation finger in	369 (25)	-42 (6)	269 (13)	683 (60)	5231 (658)	392 (34)	32 (7)	321 (16)	678 (105)	6501 (787)

Sliding in the index-finger side of the object also led to adaptations of the kinematics of the opposing digit, that is, of the thumb. Comparing the kinematics of the perturbation-finger-in condition with the static-finger-out condition, we found differences in the kinematics of the index finger, $F(5,6) = 6.188$, $p < .05$, as well as of the thumb, $F(5,6) = 6.207$, $p < .05$.

In the other perturbation situations, we did not find effects of the perturbation on the kinematics of the opposing digit. Sliding out the index-finger surface affected the index-finger kinematics: comparing the perturbation-finger-out condition with the static-both-in condition resulted in a significant perturbation effect on the index-finger kinematics, $F(5,6) = 9.144$, $p < .01$, but no significant effect on the thumb kinematics. The comparison of the perturbation-thumb-in condition with the static-thumb-out condition, to look at the effect of sliding in the thumb side surface, yielded no significant perturbation effect on either the index-finger kinematics or the thumb kinematics.

The comparisons to assess the effects of our perturbations were made using doubly multivariate repeated-measures analyses of variance. This method compares, within participants, sets of dependent variables (in the analyses that we presented, a quintuple of kinematic variables determined at the moment that deceleration reached its peak value). Because this method is not a familiar one in the literature, we felt that we had to gauge the power of the method to detect differences, to convince ourselves that the effects that we found were not the result of a oversensitive method picking up random noise. We performed the analyses that we presented earlier, but now on the kinematics at the moment of peak acceleration and at the moment of peak speed. At the moment of peak acceleration, no effect should be found, because this moment is too close to the moment of perturbation. Indeed, none of the comparisons of the kinematics at the moment of peak acceleration yielded a significant perturbation effect. At the moment of peak speed, we did find significant perturbation effects in two situations. We found a significant perturbation effect when comparing the thumb kinematics in the perturbation-thumb-out condition with the static-both-in condition, $F(5,6) = 7.736$, $p < .05$, and also when comparing the thumb kinematics in the perturbation-finger-in condition with the static-finger-out condition, $F(5,6) = 4.487$, $p < .05$. These effects amount to finding perturbation effects on the kinematics of the thumb already at the moment of peak speed, which is at about 250 ms into the entire movement of roughly 600 ms, in conditions that also showed perturbation effects later in the movement, at the moment of peak deceleration.

Discussion

Our main finding was that in two of our perturbation conditions, changing the future end position of one of the digits not only had an effect on this digit's own kinematics but also on the kinematics of the opposing digit. This was the case when the thumb side of the object was slid out right after movement initiation, and in the case that the index-finger side of the object was slid in. In both conditions, we found an effect of both the thumb and index-finger kinematics. This is in direct conflict with the hypothesis of Smeets and Brenner (1999) that prehension is really two digits moving independently to their respective end positions. If this hypothesis would be true, the kinematics of the digit for which nothing had changed in terms of future end position should have remained unchanged as well. This was clearly not the case.

We found the effect of our perturbation in some conditions but not in others. For instance, sliding out the surface on the thumb side had an effect on the thumb kinematics as well as on the index-finger kinematics. The mirror-symmetric perturbation of sliding out the surface at the index-finger side did only result in an effect on the index-finger kinematics and not on the thumb kinematics. Furthermore, if we found effects of our perturbations on the kinematics earlier than peak deceleration (i.e., at peak speed), these effects were all on the thumb kinematics and never on the index-finger kinematics. One way of interpreting this finding is that thumb and index finger might have a different role in prehension. As proposed earlier by Wing and Haggard (Haggard & Wing 1997; Wing & Fraser 1983), the thumb movement might represent the reaching component of prehension, which would make that the index-finger movement should be seen relative to the thumb movement, and this relative movement would represent the grasping component. Less speculative than this interpretation would be our conclusion that the fact that we did not see the effects of the perturbations in each and every condition, combined with the fact that the kinematic consequences were quite subtle (see

Table 2), tells us that the effects that we observed were not the consequence of biomechanical linkages between the digits through a shared hand. If the biomechanical link would be responsible for effects of perturbations showing up in the opposing digit, we would have seen the effects always in both digits or always in none of the digits, and not only in the digit for which the future end position changed.

We did find the perturbation effect on the kinematics of the opposing digit. Therefore, we can reject Smeets and Brenner's hypothesis. Does this mean that we should accept the 'traditional' hypothesis then, as proposed by Jeannerod in the early 1980s (Jeannerod 1981, 1984) and adopted by many after those classical studies? Note that the study that we report here was designed to be able to reject the hypothesis of Smeets and Brenner (1999) that the two digits involved in grasping an object with a precision grip move independently to the opposing side surfaces of the object. Technically, this means that we are not in a position to accept the null hypothesis that prehension is functionally organized in a reaching and a grasping component. For instance, one thing that our data did not permit us to demonstrate is that the adaptations of the kinematics of the non-perturbed digit were functional in nature. Future work might focus on showing such functionality of adaptations, much like the work by Kelso and colleagues (1984), who studied speech production. In their experiment, Kelso and co-workers perturbed the lower yaw of participants who had to produce specific speech utterances. The study showed that a perturbation of the lower yaw was immediately followed by remote compensatory movements of upper lip, but only when that happened to be the functionally appropriate response (i.e., the response that made that the utterance was still produced). This is a nice illustration of how the yaw and the upper lip are functionally coupled. As said, we are not yet in a position to demonstrate the same kind of functional coupling between the thumb and index finger, making up a grasping component of prehension.

When we realize that there is no real other alternative than prehension either being reaching and grasping or being pointing and pointing, rejecting the latter alternative logically would lead to accepting the former. Furthermore, we know from previous studies that hand aperture adapts in a functional way to object-size perturbations (e.g., Castiello et al., 1993; Gentilucci et al., 1992;

Paulignan et al., 1991a). Therefore, we conclude that Jeannerod was right after all, and that prehension should be seen as the act of coordinated reaching and grasping. That is not to say, that we believe that prehension is organized in terms of a reaching and grasping 'visuo-motor channels' (Jeannerod 1981, 1984, 1999; Paulignan & Jeannerod 1996; see also Arbib 1981; Hoff & Arbib 1993), one operating on the basis of intrinsic object properties and the other operating on extrinsic object properties. We agree with Smeets and Brenner (1999) that the distinction between intrinsic and extrinsic object properties is problematic. Not only can we think of properties that are hard to classify as either intrinsic or extrinsic (Smeets and Brenner mention object orientation), but also another literature (in the tradition of so-called affordance research; see Gibson 1979; Warren 1984; Warren & Whang 1987) suggests that for the person wishing to pick up an object its size per se is not the relevant variable, but more so its size in relation to relevant body metrics (e.g., Cesari & Newell 1999, 2000a; Van der Kamp et al., 1998; Newell et al., 1989; Richardson et al., 2007). For instance, the transition for picking up an object with a two or three-finger grip happens at the same ratio of object size and hand width for small children and adults, such that this transition happens at other object sizes for persons with differently sized hands (Newell et al., 1989). Interestingly, when faced with a series of objects of monotonically changing size, people change their behavior from grasping with one hand to grasping with two hands, even to grasping with two persons, at the same body-scaled size ratio (Richardson et al., 2007). From this perspective, one can impossibly speak of object size to be an intrinsic property. The relevant property has both object and body dimensions as constituents, which would make it both intrinsic and extrinsic. The labeling of object size as being an intrinsic object property seems off. That is not to say, however, that grasping does not rely on specific information to be controlled. We are convinced it does. In our mind, prehension is reaching and grasping, both controlled on the basis of specific information, but reaching and grasping are not tied to intrinsic and extrinsic object properties.

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3

Effects of changing object size during prehension

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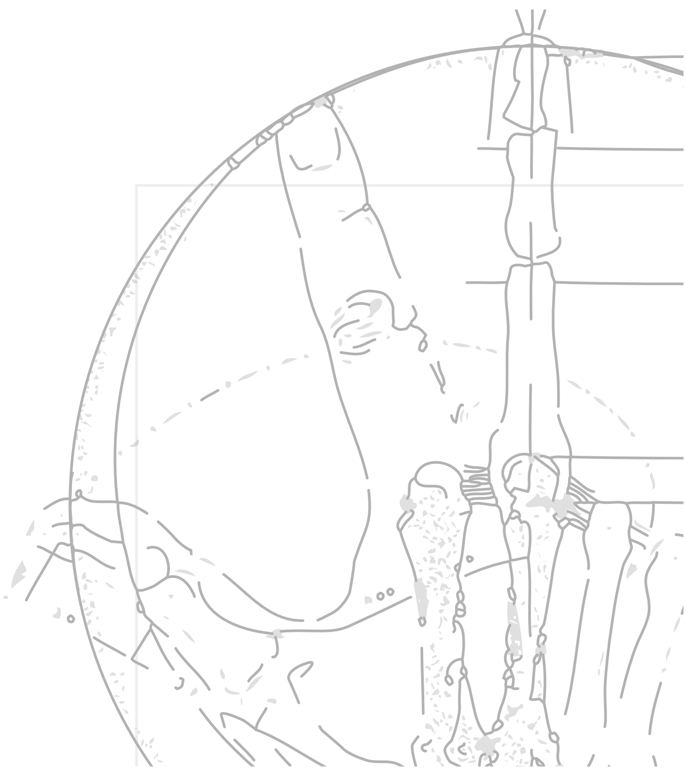

Abstract

The authors tested how fast the grasp component of prehension was able to adjust to a sudden change in object size. Participants grasped an object, the size of which could suddenly increase. Whereas previous researchers usually applied perturbations through a change in illumination at movement onset, the present perturbations involved a change in the object's physical size at 1 of 4 moments during the movement (125, 200, 275, and 350 ms after movement onset). The results showed that grasp adjustments came in many forms and could be as fast as 120 ms. The implications for the understanding of the coordination of reaching and grasping in prehension are discussed.

Introduction

When picking up an object, people transport the hand to the location of the object while at the same time opening and closing their hand. One issue is the coordination of these reach and grasp components of prehension. Approximately 25 years ago, Jeannerod (1981) suggested that grasping is temporally ordered on the time scale provided by reaching. For this hierarchy of reaching over grasping (cf. Gentilucci, Chieffii, Scarpa, & Castiello, 1992; Jeannerod, 1981, 1999), empirical evidence seemed to come from perturbation studies, which showed that when object location or size were changed at movement onset, adjustments in the reach component were much faster than adjustments in the grasp component (e.g., Castiello, Bennett, & Stelmach, 1993; Gentilucci et al., 1992; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991). In the present study, we addressed this apparent difference in the time both components needed to respond to perturbations. More specifically, we designed an experiment that was able to reveal shorter grasp adjustment times than previously reported.

Paulignan, Jeannerod, and colleagues (Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991) presented a set of two perturbation studies in which the size or the location of a target object were changed at movement onset. Targets were dowels made of translucent material that could be illuminated. Location perturbations were realized by unexpectedly switching the illumination from a central dowel to a neighboring dowel as soon as the participant began to move (Paulignan, MacKenzie, et al., 1991). Size perturbations involved the change of the illumination of a dowel of small diameter to a concentric dowel of a larger diameter, or the other way around, also at movement onset (Paulignan, Jeannerod, et al., 1991). Perturbations of location led to adjustments in both the reaching and the grasping (Paulignan, MacKenzie, et al., 1991). The first detectable effect of the perturbation in the reach component was found fewer than 100 ms following the perturbation: significantly earlier and lower values of the wrist's peak acceleration were found in the perturbed trials. In contrast, adjustments in the grasp component were reported to occur not earlier than 200 ms after the location perturbation: the first peak in the hand aperture profiles of the perturbed trials differed from those of control trials without a perturbation. In short, it took the grasp component much longer to adjust to the perturbation than the reach component. The size perturbation study (Paulignan, Jeannerod, et al., 1991) led to similar findings. When target size increased, peak wrist velocities, occurring approximately 200 ms after the perturbation, were different in the control and perturbation conditions. For the grasp component, Paulignan and colleagues reported valleys in the profiles of the rate of change of hand aperture, in many instances resulting in the occurrence of two peaks in the hand aperture profiles. These valleys were found at approximately 330 ms after the size perturbation. Therefore, when object size was perturbed, the grasp component was significantly slower in responding to the perturbation than the reach component.

In comparing the response times of the reach and the grasp component to perturbations, the assumption seems to have been that the observed adjustment times were the fastest the two components of prehension could offer. Apart from the double peak in the hand aperture time series, which often occurred, the perturbations of object size in the Paulignan, Jeannerod, et al. (1991) study also resulted in a lengthening of movement duration. These two results combined might suggest a response to the perturbation along the lines of the abortion of an original plan, which was substituted by an updated movement plan to realize the new goal or the superposition of a corrective movement on top of the originally planned one (cf. Flash & Henis, 1991). If the control of the grasp component would be organized according to either of these scenarios, we would expect that the response to the perturbation would be instantiated as soon as possible after the perturbation. The response times to size perturbation as presented by Paulignan and colleagues (Paulignan, Jeannerod, et al., 1991) could then be interpreted as the fastest the grasp component would be able to deliver. Paulignan and colleagues seem to have adopted this reasoning.

Another means to consider the way the grasp component might adjust to size perturbations would be to view the response to such perturbations as resulting from the online control of the hand aperture (cf. Zaal, Bootsma, & van Wieringen, 1999). The grasp component would respond to perturbations by doing the thing it always does: making sure that the hand is shaped appropriately (in a precision grip, having the appropriate hand aperture) in time for a successful closing and seizing of the object. In this scheme, there might not be a reason to respond immediately after the perturbation, if time would allow. That is, if there were plenty of time for the grasp component to adjust to the new object size, the adjustment would not necessarily have to be realized right away, but a smooth adjustment to the perturbation would be expected. However, in the situation that the perturbation occurs late in the movement, this scheme predicts a rapid adjustment of the action. Thus, in this control scenario, different response times are expected for different moments at which the object is perturbed.

In the latter conceptualization of the control of grasping, in which the adjustment to a perturbation originates from online control, the response times as reported by, for example, Paulignan and colleagues (Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1990; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991), who perturbed the object at movement onset, would not necessarily reflect the minimal time that the grasp component would need to adjust to the perturbations. The reported response times might be long because the grasping system was simply not in a hurry to respond.

One way to invite the grasp component to show its lower limit in responding to perturbations would be to have the object change size late in the movement when time to change is pressing. For this reason, we designed an experiment in which object-size changes could happen at one of four moments during the movements. This way, we anticipated to observe that the lower limit of the time that the grasp component would need to respond to perturbations as well as longer response times when time permitted. Furthermore, to make the task less artificial, we did not use changes in illumination from one object to another to realize the size perturbations, but we changed the actual physical size of the object to be grasped.

Method

Participants

Participants were 11 right-handed volunteers (9 men, 2 women; range 19-23 years, mean age = 20.3 years). All had normal or corrected-to-normal vision, were naive to the purpose of the experiment, and gave their informed consent. They were paid a small fee for their participation.

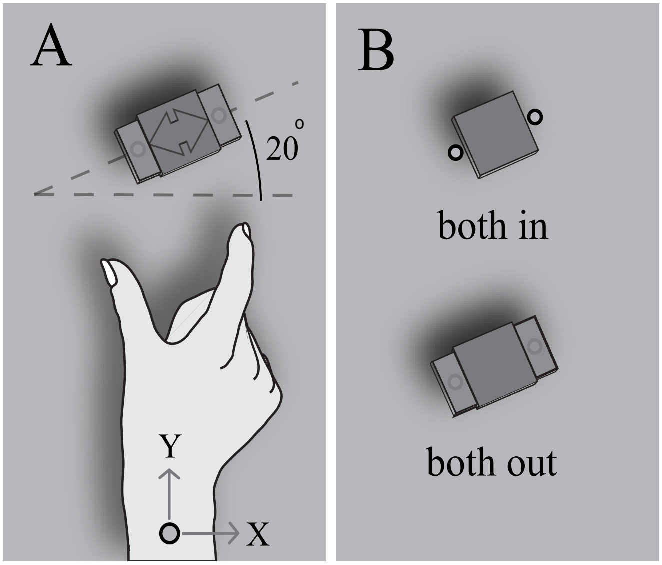

Figure 1. Overview of the experimental manipulations. (A) Participants were to reach to grasp an oblong object. The orientation of the long axis of the object was at a 20° angle, with the horizontal along the frontal plane. The infrared light emitting diodes on the table to the side of the object were used to detect the actual moment of the perturbation. (B) The side surfaces of the target object could slide out of their common case at four occasions during the movement. The perturbations yielded a change from the "both in" configuration to the "both out" configuration.

Apparatus

For the present study, we used an oblong object, both short side surfaces of which could be made to slide out quickly using pressurized air (see van de Kamp & Zaal, 2007). The actual sliding out of the side surfaces occurred at high speed (within 40 ms) and synchronously (within 20-30 ms of each other). When both side surfaces were in their retracted positions, the object measured 2 × 4 × 4 cm (height × depth × width). By sliding out both side surfaces, the width of the object became 7 cm.

The center of the object was 35 cm from the point at which the thumb and index finger had to be positioned at the start of each trial. This latter point was close to the table edge. The long axis of the object was put at an angle of 20° with the horizontal along the frontal plane (see Figure 1), to allow a comfortable grasping posture (cf. van de Kamp & Zaal, 2007).

The positions of five infrared light emitting diodes (IREDs) were tracked at a rate of 100 Hz with an Optotrak™ system. The IREDs were placed on the lateral lower corner of the index finger nail, medial lower corner of the thumb nail, skin immediately proximal to the styloid process of the radius at the wrist, and two IREDs on the table surface next to the short sides of the object (see Figure 1). The latter IREDs were covered when the sides of the object were in their extended positions and were used to provide a measure of the moment at which the side surfaces of the object had slid out. The covering of the table IREDs occurred roughly halfway between the sliding movement of the side surfaces, which means that the start of this movement occurred 10-20 ms before the covering of the table IREDs. The sliding out of the side surfaces was triggered by the online detection of the onset of the movement. To this end, we determined when the average speed of the thumb and the index-finger markers had passed a threshold of 20 mm/s. Following the detection of the initiation of the movement, the object started to change size after one of four delays (125, 200, 275, and 350 ms).

Participants wore soundproof headphones that played white noise during the trials to block auditory information about the size change of the object.

Design and procedure

At the start of each trial, the participant was instructed to have the tips of the thumb and index finger of the right hand touch at the starting location. After a signal from the experimenter, the participant was free to choose the moment to start reaching for the object. The participant was asked to reach to grasp the object between the thumb and index finger of the right hand as quickly but accurately as possible. The object was not to be lifted at the end of the movement. The reason for this was that the pneumatic system lost pressure after sliding out the side surfaces, which meant that picking up the object in its extended configuration was impossible without pushing the sides in again.

The experiment consisted of two blocks of randomized trials. In the first block of 20 trials, the static block, the object did not change size; the side surfaces of the object were either in their retract or extended position. The static block was followed by the perturbation block of 160 trials. In a perturbation trial, the initial configuration of the object was always with the side surfaces in their retracted position. In 20% of the trials, both side surfaces were slid out during the movement. In all, the perturbation block consisted of five conditions: four perturbation conditions (8 trials in each condition) in which the size of the object was changed after one of the four delays and one static condition (128 trials) in which the object kept its original (small) size.

Data analysis

We analyzed 1940 trials. In 3 trials of the static block and in 37 trials of the perturbation block, some IRED data was missing or we encountered problems with the sliding out of the side surfaces of the object. These trials were not analyzed further. Position data were smoothed with a low pass recursive Butterworth filter, with a cut-off frequency of 20 Hz. Hand aperture was defined as the distance between the thumb and the index-finger position along the x- and y-axes (see Figure 1A).We computed the hand aperture velocity with a three-point finite difference algorithm. The start and end of the movement were defined as the moments when hand opening and closing speed increased above or decreased below a threshold of 20 mm/s, respectively.[1] Movement duration was the time from the start to the end of the movement. We computed the peak hand aperture, time of peak hand aperture after movement onset, and relative time of peak hand aperture. Furthermore, we defined the time of perturbation as the time from movement onset until the moment that the IREDs on the table -to the side of the object- were covered by the extending side surfaces (see Table 1).

Detecting adjustments in the grasp component

Previous perturbation studies of prehension have assessed the effect of the perturbations by looking for effects on specific kinematic landmarks (e.g., Castiello et al., 1993; Gentilucci et al., 1992; Paulignan, Jeannerod, et al., 1991;

[1] We used two thresholds in the present study: (a) the hand-aperture-speed threshold, used in the offline analyses and applied to filtered data, to define the start and end of the grasping movement and align the hand-aperture time series and (b) a digit speed threshold, applied to the unfiltered data and used in an online fashion to trigger the actual size perturbation. The hand-aperture-speed threshold was reached, on average, a little later than the digit-speed threshold. The times of the perturbations reported in Table 1 were with reference to the hand-aperture-speed threshold.

Paulignan, MacKenzie, et al., 1991). For example, the effects of changing object location in the study of Paulignan and colleagues (Paulignan, MacKenzie, et al., 1991) could be seen in a change in peak wrist acceleration. Similarly, Paulignan, Jeannerod, et al. (1991) assessed a change in object size by looking at the time that a valley appeared between the two peaks in the hand-aperture profile of perturbed trials. For this type of analysis to work, one needs landmarks in kinematic time series to be able to compare these in perturbed and unperturbed situations. The consequence of this is that the number and distribution of landmarks throughout the movement dictates the temporal resolution of the method to detect the effect of perturbations. With only a limited number of potential landmarks (e.g., peak acceleration, peak hand aperture), the method has a restricted sensitivity. For this reason, we chose to use another method of assessing the effect of the size perturbations.

Table 1. Means and average within-participant standard deviations of the Time to the Perturbation (TP), Movement Duration (MT), Peak Hand Aperture (PA), and Absolute and Relative Time to Peak hand Aperture (TPA) for all conditions of the Static and Perturbation Blocks.

Condition		Static Block				Perturbation Block			
	TP (ms)	PA (mm)	TPA (ms)	TPA (%)	MT (ms)	PA (mm)	TPA (ms)	TPA (%)	MT (ms)
static both out		112 (4)	376 (36)	66 (6)	570 (51)				
static both in		94 (4)	334 (42)	60 (7)	556 (57)	93 (7)	347 (52)	61 (8)	570 (65)
perturbation delay 1	110 (33)					115 (5)	403 (46)	67 (7)	603 (65)
perturbation delay 2	190 (30)					111 (6)	430 (57)	72 (8)	601 (69)
perturbation delay 3	260 (37)					104 (6)	432 (84)	74 (9)	580 (90)
perturbation delay 4	334 (38)					102 (7)	463 (145)	76 (12)	613 (153)

With a set of unperturbed trials and a set of perturbed trials, the most generic method to look for the effect of the perturbation is to overlay both sets of trials and find the point where the perturbed trials start deviating from the unperturbed trials (e.g., Brenner & Smeets, 1997; Day & Lyon, 2000; Haggard, 1994; Soechting & Lacquaniti, 1983). Following Brenner and Smeets, we used one-tailed Mann-Whitney U tests ($\alpha = .01$) to determine when the hand apertures of a set of perturbed trials were significantly different from the hand apertures of the unperturbed trials. The moment of grasp adjustment was defined as the first time the perturbed and unperturbed hand apertures were significantly different and remained so as time progressed. Last, we calculated the grasp adjustment time, which was the time between the moment of the actual perturbation, as measured by the covering of the IREDs on the table next to the sides of the object and this moment of grasp adjustment.

Results

Figure 2 presents examples of hand-aperture time series of perturbation trials of 3 participants. In all cases, hand aperture of the perturbed trials increased in response to the increase in object size. A variety of responses could be seen. In some cases, the shape of hand-aperture profiles did not change much, but peak hand aperture was simply scaled to the new object size (e.g., see Delay 1 trial, Figure 2A). When perturbations occurred later, we sometimes observed a hand-aperture time series with a peak that was scaled to the initial object size, after which there was hardly any -or no- closing of the hand (e.g., see Delay 4 trial, Figure 2B) or with a peak that was delayed in time (e.g., see Delay 4 trial, Figure 2C). In few trials, we observed double-peaked hand aperture profiles: trials in which, after having started to close their hand, participants opened it again, resulting in a second peak in the hand-aperture time series (e.g., see Delay 3 trial, Figure 2C). Hence, hand-aperture profiles of perturbed trials came in many forms.

Figure 3 presents the average grasp adjustment times for each of the four perturbation conditions. When perturbations came early in the movement, adjustments were seen at approximately 175 ms after the perturbation, on average. When the perturbations came late in the movement, these responses tended to show up earlier. In the condition with the perturbations at the

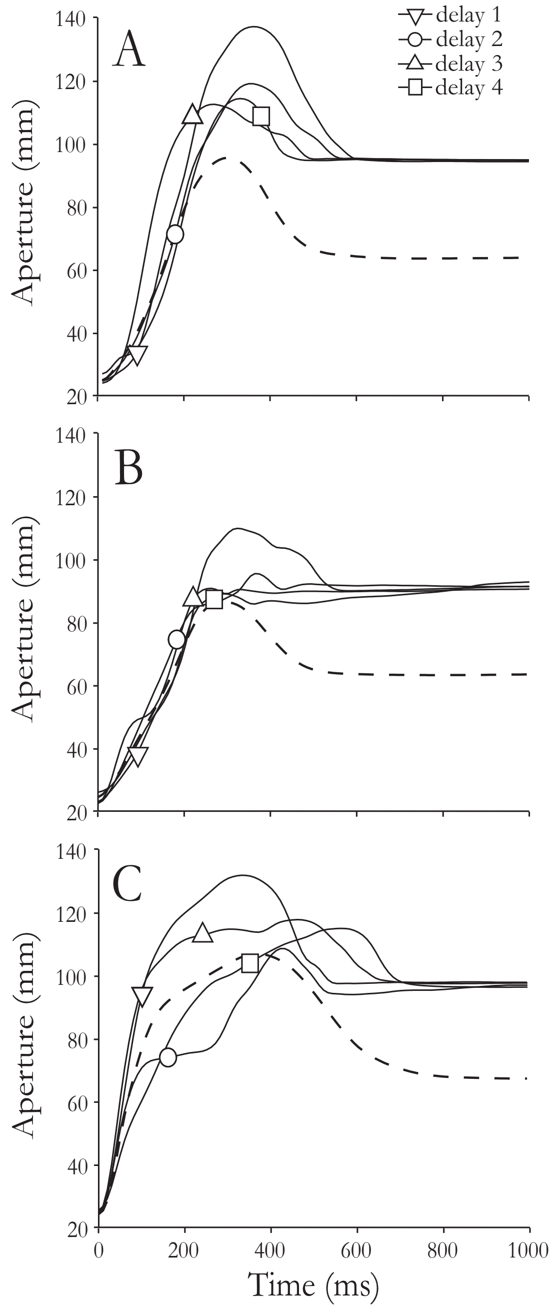

Figure 2. Examples of hand-aperture time series of perturbation trials of 3 participants, (A) 6, (B) 4, and (C) 11, respectively. The dashed lines give the average hand-aperture time series of all unperturbed trials in the perturbation block (dashed lines). The solid lines represent individual perturbation trials. The symbols indicate the moments that the perturbation occurred in each individual trial.

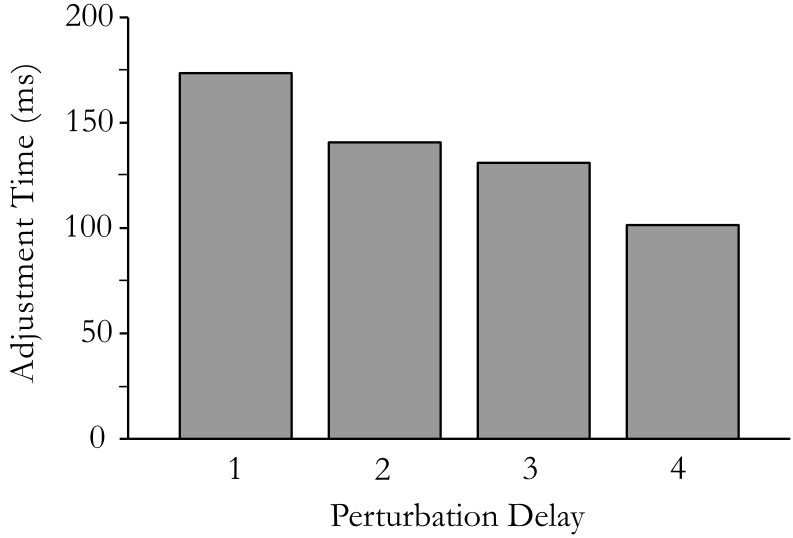

Figure 3. Mean grasp adjustment times as a function of perturbation delay.

longest delay, we saw the fastest grasp adjustment times of approximately 100 ms, on average. A repeated-measures analysis of variance (ANOVA) with a within-participant factor of perturbation condition (Delays 1-4) indicated that the average time to respond to the perturbation decreased as a function of the length of the delay, $F(3, 30) = 16.8$, $p < .001$, with a significant linear contrast, $F(1, 10) = 49.9$, $p < .001$. Note that this effect of a decrease in grasp adjustment times the later in the movement the perturbation was applied can, at least partly, be explained by differences in the variability across trials in hand apertures. This variability was highest around peak hand aperture and decreased when going toward the end of the movement. Differences in means (and medians) have to be larger to be statistically reliable in the case of higher variability. This implied that to reach statistical significance, differences between hand apertures of the perturbed and unperturbed trials had to be larger around peak hand aperture than later in the movement.

To see the effects of the object-size manipulations on the other dependent kinematic measures, such as movement duration and peak hand aperture, we performed a next set of repeated-measures ANOVAs. For these analyses, we removed the trials that had movement durations outside the normal 99% range

(4 trials of the static block and 18 trials of the perturbation block) and trials for which we were unable to determine the end of the movement (14 trials of the perturbation block), leaving 213 trials of the static block and 1691 trials of the perturbation blocks for these analyses. Starting with the static block (see Table 1), in which participants reached for the target object with the side surfaces either in their retracted or extended position, the ANOVAs, with object size (small *vs.* large) as a within-participant factor, indicated that object size did not have a significant effect on movement duration, but that it did have an effect on peak hand aperture, $F(1, 10) = 216.8$, $p < .001$, and the time that peak hand aperture occurred, absolute time: $F(1, 10) = 43.6$, $p < .001$; relative time: $F(1, 10)=20.2$, $p < .005$. This pattern of effects is in line with previous reports (e.g., see Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Marteniuk, Leavitt, MacKenzie, & Athènes, 1990; Smeets & Brenner, 1999).

When we compared the trials with the unperturbed target object in the perturbation block with the trials with the same target in the static block (see Table 1), the ANOVAs, now with block (static *vs.* perturbation block) as a within-participant factor, showed no effects on movement duration, peak hand aperture, or the moment peak hand aperture occurred (in absolute and relative time). Thus, knowing that a perturbation in object size might happen did not change the grasping behavior of participants significantly.

Turning our attention to the effects of the size perturbations, the ANOVAs -with as within-participant factor perturbation condition (no perturbation or a perturbation after Delays 1-4)- revealed no effect of the perturbations on the movement duration. As could be expected, the ANOVA did show a significant effect on peak hand aperture, $F(4, 40) = 51.7$, $p < .001$. Planned comparisons showed that peak hand apertures of all four perturbation conditions were different from that of the unperturbed condition (all p's $< .005$). In addition, we found that the size perturbations significantly affected the peak hand aperture with regard to its absolute time, $F(4, 40) = 13.4$, $p < .005$, as well as its relative time, $F(4, 40) = 14.2$, $p < .001$. Planned comparisons indicated that all peaks in the hand-aperture time series of the perturbed trials, on average, came later (in absolute and relative time) than the peak hand aperture of the unperturbed trials (all p's $< .005$). As seen in Table 1, average peak hand apertures and their (relative) times of occurrence of the perturbed conditions looked much like those of the condition of the static block in which the target object had the same configuration (see: static both-out in Table 1) as the final one in the perturbation trials.

Taken together, in response to a sudden increase in object size, the peak in the hand aperture, on average, developed a greater amplitude later in time. In other words, the final peak hand aperture was scaled to the new object size. The exact way that the adjustment of the hand aperture took place varied across participants, across trials, and as a function of when in the movement the perturbation had happened. The fastest grasp adjustment times could be seen when perturbations came late in the movement.

Discussion

The present study was designed to see how fast the grasp component of prehension is able to adjust to a perturbation in object size. Previous studies (e.g., Castiello et al., 1993; Gentilucci et al., 1992; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991) had reported that the grasp component would adjust much slower to perturbations than would the reach component, which had been taken to imply a hierarchy of these two components of prehension (cf. Gentilucci et al., 1992; Jeannerod, 1981, 1999): The reach component would be responsible for the timing of the movement and the grasp component would have to follow. The present study demonstrated that adjustments to the size perturbations came in many different forms and that these adjustments could well be within approximately 100 ms. These fast adjustment times were found especially when the perturbations came late in the movement. When we take the 10-20 ms into account between the time that the object's side surfaces started to slide out and the moment that the perturbation was detected because the extending side surfaces had covered the IREDs on the table, it seems fair to conclude that the grasp component is able to respond easily within 120 ms.

Previous studies on human prehension reported adjustment times to object-size perturbations from approximately 175 to 500 ms (Castiello et al., 1993; Jeannerod, 1981; Paulignan, Jeannerod, et al., 1991), which are longer than the 120 ms that we found. What might be the reason for this discrepancy in findings? Several factors related to the methods of experimentation and analysis of the data can be identified. With the exception of Jeannerod's early studies, in which he realized the size perturbations by quickly rotating an elliptically shaped object, previous experiments involved visual perturbations (Castiello et al., 1993; Paulignan, Jeannerod, et al., 1991; see also Gentilucci et al., 1992; Paulignan, MacKenzie, et al., 1991). As introduced by Paulignan and colleagues (Paulignan, Jeannerod, et al., 1991), changes in object size were brought about by changing the illumination from a central high dowel to a concentric lower object of a larger diameter that fit around the central dowel, or vice versa (e.g., Paulignan, Jeannerod, et al., 1991)[2]. In contrast, the present study involved a real change of the object.

Interestingly, Roy, Paulignan, Meunier, and Boussaoud (2006), who studied the responses to size perturbation in the reaching and grasping of macaque monkeys, physically changed the size of the target object. They used a cylindrical tube that fitted around another cylindrical dowel and could be pushed up or down pneumatically; thus, the target object for the monkey was either the larger outer cylinder or the smaller inner cylinder. Roy et al. (2006) also reported faster adjustment times (on the order of magnitude of 160 ms) than the studies that applied visual perturbations. Thus, adjustments in response to physical perturbations might just be faster than adjustments to perturbations induced by changes in illumination of targets.

A second factor that might explain the differences in reported adjustment times might have something to do with the differences in the method of detecting adjustments to perturbations. Previous prehension studies (e.g., Castiello et al., 1993; Gentilucci et al., 1992; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991) involved the comparison of kinematic landmarks of a set of trials of unperturbed movements with those of a set of trials of perturbed movements. Significant differences were interpreted as resulting from the perturbation. For example, the effect of perturbing target

[2] The difference in height of the two targets, in combination with the fact that the bigger target fits around the smaller object, forced the participants in Paulignan, Jeannerod et al.'s (1991) experiment to grasp the target objects at different heights. Any difference in kinematics might also have been affected by this difference in final hand position.

location showed up as a difference in the average timing of peak acceleration of the reach component between unperturbed and perturbed trials (e.g., Paulignan, MacKenzie, et al., 1991). Also, the effect of perturbing target size showed up as a reopening of the hand in the perturbed trials (e.g., Paulignan, Jeannerod, et al., 1991).

For several reasons, we did not apply the method of comparing averaged kinematic landmark data but adopted an alternative method to assess the time it took to respond to a perturbation (cf. Brenner & Smeets, 1997). We compared hand-aperture time series of perturbed trials with those of unperturbed trials and detected the moment these had started to differ. An advantage of this process is that the temporal resolution of the method is much higher than a method that depends on landmarks. There are just a few landmarks that can be studied -peaks in the speed, acceleration, and hand aperture time series- whereas the method used in the present study can decide at any point in time whether this is the moment at which the adjustment has taken place. Second, in the event that there are no double peaks in the hand-aperture profiles, the method can still be applied. Last, the method was suited to deal with the different moments that we perturbed target size. Whereas previous studies had administered the size perturbation at movement onset (e.g., Castiello et al., 1993; Paulignan, Jeannerod, et al., 1991), we had the target change size at four times after movement onset. The method we used allowed us to detect the responses to these perturbations at any time during the movement and not only at times that kinematic landmarks presented themselves.

Actually, a close inspection of Table 1 suggests that the method of detecting differences between perturbed trials and the means of unperturbed trials might be a principally better method than that of looking for significant differences between means of perturbed and unperturbed trials. The latter method would have forced us to conclude that adjustment times of the grasping can be as fast as approximately 35 ms. That is to say, when we inspect Table 1 closely, we see that average peak hand aperture in the unperturbed trials of the perturbation block occurred after 347 ms. Size perturbations added 1-2 cm to peak hand apertures and delayed these by 55-116 ms. These differences were statistically significant for all perturbation conditions. The latest perturbation (Delay 4 condition) happened on average at 334 ms after the start of the grasping movement. Hence, the conclusion should be that the grasp component needs no more than 347 ms (i.e., time of peak hand aperture in the unperturbed trials) minus 334 ms (i.e., time of the latest perturbation), which would equal 13 ms, to adjust to the size perturbation. Even when we corrected this number by adding the time it maximally took from the start of the sliding out of the object's side surface to the moment that we detected the perturbation (i.e., the moment that the IREDs on the table were covered by the extending side surfaces; 20 ms), we still arrived at an adjustment time of approximately 35 ms. A number of 35 ms seemed too low. We have trouble believing that adjustments to size (or other) perturbations can be this fast. We do not fully grasp the reasons why, but it seems that something in the method of comparing means must be going wrong.

We set out to show that the grasp component would be just as fast as the reach component in responding to perturbations. We have demonstrated that grasping can adjust within approximately 120 ms when needed (or desired), which compares with the roughly 100 ms of adjustments of reaching from previous studies (e.g., Paulignan, MacKenzie, et al., 1991). However, given our concerns with the method applied in these studies, we no longer fully trust the latter result. At the same time, we realize that no matter what method is used to demonstrate the fastest adjustment times, the times will most probably not be faster than the 100 ms known from the literature: The same time has also been reported in studies of pointing movements to perturbed locations (e.g., Brenner & Smeets, 1997; Liu & Todorov, 2007; Soechting & Lacquaniti, 1983). In the future, we should conduct a new assessment of the times that the reach component of prehension needs to respond to location perturbations.

We looked in our data set to see if the size perturbations that we administered not only had an effect on the grasping but also on the reaching component. Applying the same method that we used to show adjustments of the perturbations in the grasp component, we found no effects in the reaching component; occasionally, the wrist position at the end of the movement was slightly different in the perturbed trials. This was not a systematic effect and occurred in approximately 15% of the trials. Actually, we did not expect to see effects of size perturbations on the reaching, but we expected to find effects of object location perturbations on the reaching, a manipulation that was not part of the present study. We suggest performing the latter kind of experiment and analyze the data in a similar matter as we did here. We would be interested to see what adjustment times would be possible in the reaching component faced with object location perturbations and compare these times with the time of 120 ms that we found in the present study; it might even be the case that adjustments to the reach component are slower than those of the grasp component. Lower inertia of the fingers than that of the hand and differences in neural transmission times of both components might play out in favor of the grasp component.

Interestingly, Haggard, in his doctoral dissertation (Haggard, 1991; 1994), replicated the location perturbation experiment of Paulignan and colleagues (Paulignan, MacKenzie, et al., 1991), but with real objects moving to a new location rather than visual changes of location. Haggard (1991), using a method to detect a response to a perturbation similar to the one applied in the present study, reported responses in both the reaching and grasping after roughly 200 ms (i.e., the same for both components). Haggard (1991) attributed the fact that he had found longer response times than did Paulignan and colleagues (Paulignan, MacKenzie, et al., 1991), in large part, to the use of acceleration time series in the latter study. He noted that numerical filtering and differentiation of position time series could have made that certain landmarks in the time series seem to appear earlier than they actually did (cf. Haggard, 1994). The onset and offset of movements especially suffer from this detrimental effect of numerical methods. However, the fact that we would have found unrealistically small adjustment times of 35 ms in our data when looking at the averages of hand apertures, with only numerical filtering and no numerical differentiation applied, suggests that perhaps other features of the applied methods might also be responsible for finding anomalous results. Perhaps, as we suggested previously, the method of considering averages is itself responsible. The method of averaging landmarks might be a good method to demonstrate differences among sets of trials but less so to determine adjustment times.

The fact that the grasp component might adjust just as fast to perturbations as does the reach component of prehension has implications for the understanding of the coordination in prehension. Accounts in which the reaching would determine the timing of the grasping (cf. Gentilucci et al., 1992; Jeannerod, 1981, 1999) would loose one of their empirical underpinnings. The previous findings that the reach component responded much faster to perturbations than did the grasp component had been an important argument for the presumed hierarchy of reaching over grasping. The present findings suggest more equal roles for reaching and grasping in their responsibility for the timing of their coordinated result (i.e., prehension; cf. Hoff & Arbib, 1993; see also Bate & Hoffmann, 1995). However, in the few cases that we observed double peaks in the hand aperture profile of the perturbed trials, the closing and reopening of the hand went together with a small retraction of the hand. This would be a clear example of the reach component adjusting to changes happening in the grasp component.

Last, in contrast with previous reports (e.g., Paulignan, Jeannerod, et al., 1991), changing object size did not seem to result in longer movement durations in the present study. Thus, the response to a perturbation might be originating from the online control of grasping (and reaching). When perturbations are not too dramatic and plenty of time remains to adjust to changing circumstances, adjustments to the opening and closing of the hand will happen (smoothly or not) without delaying the moment of hand-object contact. However, perturbations that would put enough pressure on the system would force rapid adaptations. The latter view of the control of grasping (and reaching) would fit models in which the kinematic details of prehension are considered to be emergent rather than preplanned (e.g., Bullock & Grossberg, 1988; Schöner, 1990; Ulloa & Bullock, 2003; Zaal et al., 1999).

In conclusion, the present study showed that the grasp component can respond fast to size perturbations. In addition, we demonstrated that there are several ways to respond to size perturbations, and these can be found across trials and participants. When a perturbation happens early in the movement, it is possible to adapt the grasping smoothly without having to take more time for the movement. When perturbed late in the movement, the need for fast adjustments is much higher, which resulted in grasp adjustment times comparable to the reach adjustment times from the literature. Reaching and grasping have to work together on equal footing to realize a successful prehension of the target object.

Acknowledgments

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4

Getting hold of approaching objects: In search of a common control of hand-closure initiation in catching and grasping

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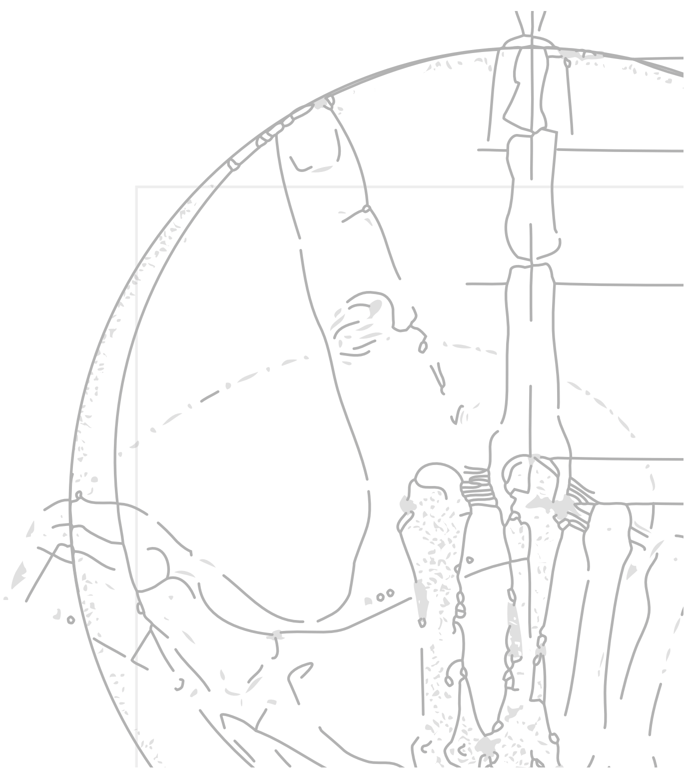

Abstract

Both in the catching and grasping component of prehension, the hand opens and closes before hand-object contact is made. The initiation of hand closure has to be coordinated with the time course of the decrease of the distance between the hand and the target object, i.e., with the reaching component in prehension or the approach of the target in catching. The authors investigated if this initiation of hand closure could be explained by a common control. For this purpose, they fitted the dynamic timing model to data from the two tasks. In both tasks, participants were asked to get hold of an object approaching along the table top at a constant velocity. In the prehension task, participants could reach out to grasp the object; in the catching task, they were required to keep their hand stationary. In comparison with other accounts, the dynamic timing model performed best in explaining the data. The model proved adequate for the prehension task but not for the current catching task.

Introduction

Prehension, the act of coordinated reaching and grasping, and catching have in common that the hand first opens and subsequently closes to take hold of the target object. In prehension, the initiation of the hand closure has to be coordinated with the reaching (i.e., the movement of the hand towards the target). In catching, the initiation of hand closure has to be coordinated with the arrival of the approaching target. Thus, in both tasks, the gap between the hand and the target closes, and the timing of the initiation of closure of the hand has to be coordinated with this gap closure. The objective of the current study was to see if the control of catching and the control of the grasping component of prehension could be understood within the same framework. More specifically, given the success of the dynamic timing model in the context of prehension (Zaal & Bootsma, 2004; Zaal, Bootsma, & van Wieringen, 1998), in which first-order time-to-contact information is used to time the initiation of hand closure, we focused on this model to see if it would predict this timing both in the grasping of prehension and in catching equally well.

Two decades of prehension research offered several proposals that described how the initiation of hand closure might be timed. Unfortunately, most of these proposals did not hold very well under experimental scrutiny. Three of these proposals will be briefly presented in the following. In the first proposal, hand closure was thought to be initiated at a fixed time before hand-object contact, independent of task conditions (Gentilucci, Chieffi, Scarpa, & Castiello, 1992). Several empirical studies tested this hypothesis by manipulating reaching amplitude (Zaal et al., 1998), object width (Zaal & Bootsma, 2004), object size (Wang & Stelmach, 2001), object orientation (Rand & Stelmach, 2005), reach or object velocity (Carnahan & McFadyen, 1996; Rand, Squire, & Stelmach, 2006; Zaal et al., 1998), and the direction of the object's approach (Watson & Jakobson, 1997), which, taken together, demonstrated that in prehension the initiation of hand closure is not time-invariant over a range of conditions.

A second proposal employed a spatial rather than a temporal variable: the initiation of hand closure should happen at a fixed distance from the hand to the target object (cf. Wang & Stelmach, 1998, 2001). Recently, Stelmach and colleagues have amended this original proposal (Rand, Shimansky, Hossain,

& Stelmach, 2008; Rand et al., 2006), after finding that closing distance varied with object orientation (Rand & Stelmach, 2005) and reach velocity (Rand et al., 2006). They proposed that the initiation of hand closure occurs at a closing distance that is a function of, among other variables, reaching amplitude and velocity. Although adding these variables improved the data fitting, it made the account less parsimonious, of course.

A third proposal that we will discuss stems from the line of research that considers the timing of interceptive actions to be based on prospective information about the time remaining until the object and the observer meet (e.g., Bootsma & Peper, 1992; Lee, 1976; Savelsbergh, Whiting, & Bootsma, 1991). In this proposal, the initiation of hand closure is triggered on the basis of first-order time-to-contact information (tau). In prehension, this first-order time-to-contact information specifies the time for the physical gap between the target object and the grasping hand to be closed under prevailing speed conditions. One way the initiation of hand closure could be based on first-order time-to-contact information is that the hand starts closing at a critical value of tau. In prehension, however, this seems not to be the case. For instance, earlier work showed that at the initiation of hand closure, first-order time-to-contact varied with reaching amplitude (Zaal & Bootsma, 2004; Zaal et al., 1998) and object velocity (Zaal et al., 1998). However, Zaal and coworkers (Zaal & Bootsma, 2004; Zaal et al., 1998) showed another way first-order time-to-contact information could be at the basis of the initiation of hand closure, along the lines of Schöner's (1994) dynamic timing model. We will return to this model later, after having had a look at the catching literature.

As in the literature on prehension, also in the context of catching, researchers have considered the proposal that the initiation of hand closure is timed on the basis of a critical value of first-order time-to-contact. Just as in prehension, little support was found for this proposal. That is to say, ambiguous results concerning values of first-order time-to-contact at the initiation of hand closure were found in studies on catching. Whereas an earlier study reported no effects of object velocity (Savelsbergh, Whiting, Burden, & Bartlett, 1992), later studies showed that first-order time-to-contact at the initiation of hand closure varied with object velocity (Bennett, van der Kamp, Savelsbergh, & Davids, 1999; Caljouw, van der Kamp, & Savelsbergh, 2004; Wallace, Stevenson, Weeks, & Kelso, 1992). Also, just as was the case for prehension, it was examined whether the initiation of hand closure is timed on the basis of a critical closing time or closing distance. Findings concerning these hypotheses were inconsistent as well (Laurent, Montagne, & Savelsbergh, 1994; Mazyn, Montagne, Savelsbergh, & Lenoir, 2006; Savelsbergh et al., 1992; Wallace et al., 1992; Wang & Stelmach, 2001).

Together, the proposals introduced so far, do not seem very promising in revealing the control for the separate tasks, let alone for an account for the timing of hand closure common in both prehension and catching. Therefore, we turn to a final proposal, one that has been shown to accurately predict the moment of hand closure in prehension (Zaal & Bootsma, 2004; Zaal et al., 1998) and might apply to catching as well. In the same vein as the critical-tau (threshold) type of control mentioned before, the *dynamic timing model* exploits first-order time-to-contact information. However, in this account, the use of tau is more sophisticated than simply waiting until a critical value has been reached. The idea is that grasping behavior is best understood within a dynamical systems approach, in which the hand-opening and hand-closing states are endowed with stability features. Elaborating on the work of Schöner (1994), Zaal and colleagues (1998, 2004) proposed a formulation of how the stability of the hand-opening state and the stability of the hand-closing state are coupled to first-order time-to-contact. At the beginning of the movement, when first-order time-to-contact between the grasping hand and the target object is long, the hand-opening state is most stable, whereas the hand-closing state is rather unstable. While the reach unfolds, first-order time-to-contact decreases, resulting in a loss of stability of the hand-opening state and a gain of stability of the hand-closing state. At a certain point in time (i.e., the initiation of hand closure), the hand-closing state has become more stable than the hand-opening state and a transition -which has stability features of its own- from the hand-opening state to the hand-closing state takes place (for more details see Schöner, 1994; Zaal & Bootsma, 2004; Zaal et al., 1998). A consequence of this nonlinear dynamics alternative for the use of first-order time-to-contact over the threshold type of control is that hand closure does not necessarily occur at a fixed value of first-order time-to-contact. That is to say, in the situation of non-constant velocities, whereas values of first-order time-to-contact at the moment of the initiation of hand closure might vary across experimental conditions, the dynamic timing model might be able to accommodate these variations (cf. Zaal & Bootsma, 2004; Zaal et al., 1998). Furthermore, the dynamic regulation of the initiation of hand closure makes the system resistant to perturbations, for instance, when the hand needs to be retracted or the target object changes position.

Zaal and Bootsma (2004) considered the standard prehension task of having participants pick up stationary target objects, and showed that closing time, closing distance, and first-order time-to-contact at the moment of hand-closure initiation all varied with factors such as distance and the size of the objects, but no effects were seen when looking at the differences between the model predictions and the actual moments of hand-closure initiation. These differences had been computed on a trial-to-trial basis. In an earlier study, Zaal and colleagues (1998) had studied the picking up of objects that either remained stationary or moved away from the participants in the experiments. They inspected the performance of the dynamic timing model, using compound time-to-contact time series rather than individual ones, and showed that the model predicted the moments of initiation of hand closure quite accurately. Here, we will present an experiment in which participants were asked to either reach for and pick up an approaching target (prehension task) or keep their hand still and wait for the object to arrive into the hand that they needed to open and close to get hold of the approaching object (catching task). Following Zaal and Bootsma (2004), we will evaluate the data on a trial-to-trial basis, to investigate if the dynamic timing model also applies to the situation of approaching objects, both in prehension and in catching.

Methods

Participants

Seven men and eight women, with an average age of 24 years (ranging from 20 to 41 years) participated in the experiment. All were right-handed and had normal or corrected-to-normal vision. Participants were naive to the exact purpose of the experiment, gave their informed consent and were paid a small fee for their participation.

Apparatus

A cylindrical target object was placed on top of a magnet embedded object-carrier. This carrier was made to move along a plain white tabletop (2 m x 2 m) by means of a magnetic coupling to a servo-motor driven mechanism underneath the tabletop (for a similar setup, see Schenk et al., 2000). The exact movement path of the target object was computer-controlled through a user interface that was developed for this purpose (LabView, National Instruments). The positions of four infrared light emitting diodes (IREDs) were tracked at a rate of 100 Hz using an Optotrak system (NDI, Waterloo, Ontario, Canada). The IREDs were placed on the center of the target object, the lateral lower corner of the index finger nail, the medial lower corner of the thumb nail, and the skin immediately proximal to the styloid process of the radius at the wrist.

Procedure and design

We used two tasks (prehension and catching) in which the target object (diameter: 3 cm, height: 1.5 cm) approached the participants with one of three constant velocities (20, 40, and 60 cm/s) and starting from one of two initial distances (75 and 100 cm). With a set acceleration of 600 cm/s^2 it took the object at most 6 cm (100 ms) to reach the constant velocity. Participants sat alongside the table, with their right side touching the table edge and their sagittal plane parallel to the table edge. The object approached along the participants' sagittal plane, some 30 cm away from the edge of the table. At the start of each trial, the right hand, with the tips of the thumb and index finger touching, was positioned on a Plexiglas span; this span allowed the object to pass underneath. In the *prehension* task, participants were to reach for and grasp the object. As soon as the object started to move towards the participant, he or she was free to choose the moment to start the reach to grasp movement. This way, the pick-up location was left to the participant; the only instruction was to carry out a continuous, fast but accurate reaching-to-grasp movement. In the *catching* task, the participants were required to catch the approaching object between the pads of the thumb and index finger while keeping the position of their hand fixed, resting on the Plexiglas span. After liftoff, the object was to be placed on the tabletop somewhere around the pick-up location. During each trial headphone-delivered white noise was played.

The order of the catching and prehension tasks was counterbalanced across participants. Presenting the 6 randomized conditions (3 Object Velocities x 2 Initial Distances) in 12 blocks for the two tasks resulted in a total of 144 trials per participant.

Data analysis

A total of 2080 trials were used for the data analysis. In 3 trials the object was unintentionally dropped, while in 46 trials, either some IRED data were missing or we encountered problems with the object carrier.

Position data was smoothed using a low-pass recursive Butterworth filter with a cutoff frequency of 10 Hz. Speed was computed using a three-point finite difference algorithm. Hand position was defined as the average position of the thumb and index-finger IRED. The start of the reaching movement was defined as the moment at which the tangential hand speed rose above a threshold of 2 cm/s. Hand aperture was defined as the three-dimensional distance between the thumb and the index-finger IREDs. The start and end of the grasping movement were defined as the moment when hand opening and closing speed rose above or dropped below a threshold of 2 cm/s, respectively.

To determine the initiation of hand closure we looked back from the moment of peak closing velocity and detected the first moment that the hand closing speed passed a threshold of 2 cm/s. *Closing distance* was defined as the distance (projected along the dimension of the object approach) between the object and the hand at the initiation of hand closure. *Closing time* was the time from the initiation of hand closure until the end of the grasping movement. *First-order time-to-contact* [1] $TC_1(D)$ at the moment of hand-closure initiation corresponded to the time it would take to make contact with the object if conditions would prevail (i.e., constant velocity) and was computed by dividing

[1] Following Bootsma, Fayt, Zaal, and Laurent (1997), we distinguish the optical time-to-contact information (τ) from the organism-environment property that it specifies, $TC_1(D)$. $TC_1(D)$ is defined as the first-order time-to-contact, the time that distance gap D will be closed when closing velocity would remain constant. Although our ultimate interest is in the information, technically speaking, it is the physical first-order time-to-contact $TC_1(D)$ that we manipulated in the current study, and that we used in our model simulations.

Table 1. Values of the c_{vision} parameter that were used in the simulations when the same parameter was used for both tasks and when different parameters were used for the two tasks of catching and prehension.

Participant	c_{vision} parameter		
	Same	Different	
		Catching	Prehension
1	4.21	5.29	3.90
2	4.27	4.23	4.27
3	4.67	4.85	4.59
4	4.37	5.37	4.14
5	3.75	4.82	3.62
6	4.32	4.70	4.18
7	3.87	4.72	3.63
8	3.96	5.89	3.59
9	3.86	4.95	3.53
10	6.04	6.10	5.80
11	4.40	4.57	3.86
12	4.11	4.14	3.97
13	4.89	5.00	4.89
14	3.50	3.85	3.23
15	3.80	4.64	3.73

the distance (projected along the dimension of the object approach) between the object and the hand by the momentary speed at which this distance was closed.

An important part of our analyses examined the accuracy with which the initiation of hand closure was predicted by the *dynamic timing model* (Schöner, 1994; Zaal & Bootsma, 2004; Zaal et al., 1998). For each trial, we compared the predicted moment of hand-closure initiation with the experimentally observed moment of hand-closure initiation. To arrive at the model prediction, we numerically simulated the model's set of differential equations (see Appendix) using a Runge-Kutta algorithm, with a fixed time step of 0.01 s, equal to the time step of the kinematic data. All parameters of the model were set at a fixed value ($\alpha = 10$; $\omega = 10$; $\gamma = 10$; $\beta = 90$; $\sigma = 0.75$; $r_{crit} = 0$) except the parameter c_{vision}, which was allowed to vary across participants and tasks (as discussed later). The parameter c_{vision} represents the strength of the contribution of the first-order time-to-contact variable (see Appendix; cf. Schöner, 1994; Zaal & Bootsma, 2004; Zaal et al., 1998). We optimized the values of the c_{vision} parameter to have a best fit between the average model predictions and the average observed initiation moments by finding the c_{vision} parameter setting that resulted in a minimum sum of squared prediction errors. In a first pass, we allowed c_{vision} to vary only across participants (see Table 1 for the values of c_{vision}). In a subsequent analysis, c_{vision} was allowed to vary across participants but also between tasks (prehension *vs.* catching; see Table 1).

Model accuracy was evaluated in terms of a *temporal prediction error*, which was defined as the time difference of the experimentally observed moment of hand-closure initiation and the moment of hand-closure initiation as predicted by the dynamic timing model; a positive difference meant that the model prediction preceded the observed moment of initiation of hand closure.

A problem for the comparison of the four dependent variables that we identified before (closing distance, closing time, first-order time-to-contact, and dynamic-timing-model prediction error) is that they are defined along different dimensions. To arrive at dependent measures that are defined along the same dimension for each dependent variable, we computed temporal prediction errors, analogous to the dynamic-timing-model prediction error, for each variable that we considered in our comparison. To this end, we assumed that these variables (closing time, closing distance, or first-order time-to-contact) were to be kept constant at a specific value in the control of grasping. We took this value (which was allowed to vary across participants) to be the value at which the sum of squared prediction errors was minimal, just as we had done for the dynamic-timing-model error. Next we inspected for each trial when this value was reached, and computed the difference in time between the latter moment and the moment of hand-closure initiation. We did so for the variables of closing time, closing distance, and first-order time-to-contact. The resulting dependent variables were all along the dimension of real time, just as the prediction error of the dynamic timing model. Thus, a fair comparison among all four of the temporal prediction errors was possible.

Each dependent variable (temporal prediction errors of closing distance, closing time, first-order time-to-contact, and the dynamic timing model) was

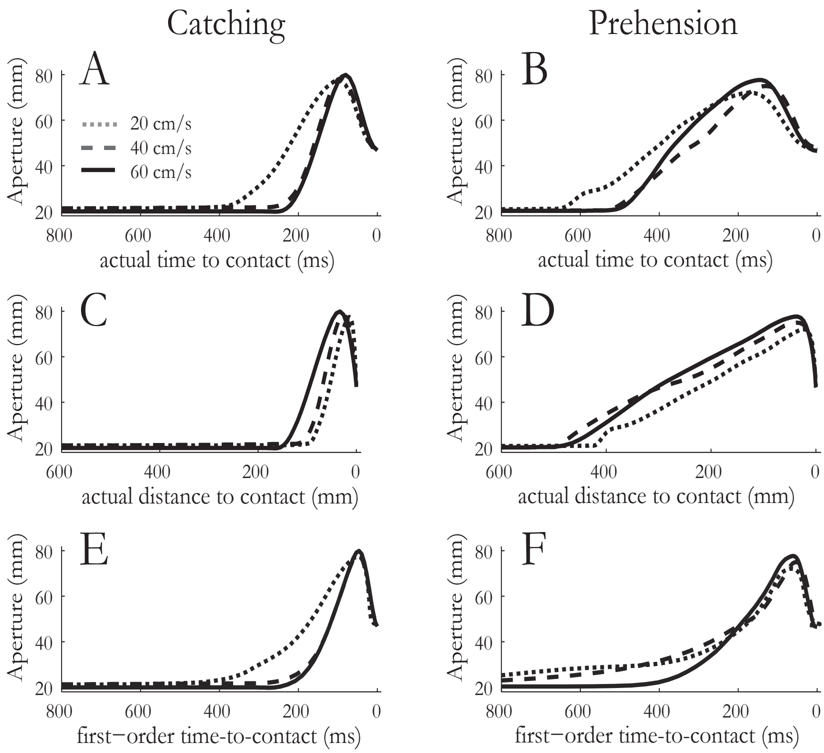

Figure 1. Typical examples of hand-aperture profiles of six different trials of one and the same participant, of the catching task (left column) and of the prehension task (right column). The dotted, dashed, and solid lines represent the 20, 40, and 60 cm/s levels of object velocity, respectively. The hand-aperture profiles are plotted as a function of the actual time-to-contact (top row), the actual distance to contact (middle row), and the first-order time-to-contact (bottom row).

analyzed with a separate repeated-measures analysis of variance (ANOVAs) with task (catching *vs.* prehension), object velocity (20, 40, or 60 cm/s), and initial distance (75 *vs.* 100 cm) as within-participant factors. Greenhouse-Geisser corrections of degrees of freedom were used when sphericity assumptions were violated. For every statistically significant effect, we calculated effect sizes using generalized *eta*-squared values (cf. Bakeman, 2005). These effect sizes were interpreted according to Cohen's (1988) recommendation of .02 for a small effect, .13 for a medium effect, and .26 for a large effect. In post-hoc analyses, we applied Bonferroni corrections to control Type-I errors.

Results

Figure 1 shows typical examples of hand-aperture profiles. Figures 1A and B present the hand aperture as a function of actual time-to-contact (i.e., the time until the end of the grasping movement), equivalent to the most familiar representation of hand apertures in prehension, and given in the majority of the studies of grasping and catching (e.g., in the context of prehension: Castiello, 2005; Jeannerod, 1984, 1988; Marteniuk, Leavitt, MacKenzie, & Athènes, 1990; Zaal et al., 1998; but see Bongers, Zaal, & Jeannerod, submitted for publication; and in the context of catching: Mazyn, Savelsbergh, Montagne, & Lenoir, 2007; Savelsbergh, Whiting, Pijpers, & van Santvoord, 1993; Savelsbergh et al., 1991). In Figures 1C and D, hand aperture is plotted as a function of actual distance to contact (i.e., hand-object distance), a less familiar representation, although given in a subset of prehension studies that stress the role of distance rather than time (e.g., see Haggard & Wing, 1998; Rand et al., 2006; Wallace, Stevenson, Spear, & Weeks, 1994; Wing & Fraser, 1983; Zaal & Bootsma, 2000). Finally, Figures 1E and F give hand aperture as a function of first-order time-to-contact ($TC_1(D)$; cf. Lee, 1976).

Closing time, closing distance, and first-order time-to-contact

Although we will perform our inferential statistics on the temporal prediction errors that we defined before, for the sake of comparison of the present data with results of previous papers, Table 2 gives the values of the three variables of closing time, closing distance, and $TC_1(D)$, at the moment of the initiation of hand closure. Table 2 presents the averages and average standard deviations of these three variables, for the three object-velocity conditions. As we explained before, we did not analyze these averages per se, but inspected temporal prediction errors, to allow a proper comparison among the variables (see Section 2 for details).

We found a large effect of object velocity on the closing-time prediction error, $F(1.40, 19.59) = 28.77, p < .0001, \eta^2_G = .269$ (see Table 3). Post-hoc tests learned that all means were different from each other ($p < .05$). In addition, the ANOVA showed a large task effect, $F(1, 14) = 19.51, p < .0005, \eta^2_G = .432$, M (SD) = 12.1 (22.0) and -11.6 (29.7) ms for catching and prehension, respectively.

Table 2. Means and average within-participant standard deviations (between brackets) of closing time, closing distance, and first-order time-to-contact $TC_1(D)$, at the moment of initiation of hand closure, as a function of object velocity.

	Object velocity (cm/s)		
	20	40	60
Closing time (ms)	122.4 (32.0)	107.9 (24.8)	100.1 (20.7)
Closing distance (mm)	12.5 (6.6)	18.0 (6.7)	23.3 (8.2)
$TC_1(D)$ (ms)	54.8 (16.0)	47.9 (11.5)	46.3 (10.5)

Table 3. Means and average within-participant standard deviations (between brackets) of the model prediction errors (ms) as a function of object velocity.

	Object velocity (cm/s)		
	20	40	60
Constant closing time	-11.0 (32.0)	3.5 (24.8)	3.3 (20.7)
Constant closing distance	12.1 (22.0)	-7.7 (14.4)	-18.4 (12.9)
Constant $TC_1(D)$	-2.7 (25.8)	6.1 (16.1)	7.7 (14.3)
Dynamic timing			
Same c_{vision}	-10.8 (35.2)	0.7 (21.6)	-0.5 (22.4)
Different c_{vision}	-8.4 (34.9)	3.0 (21.7)	2.2 (22.1)

Table 4. The significant Object-Velocity x Task interaction effect of the dynamic-timing-model prediction errors (ms). Means and average within-participant standard deviations (between brackets).

	Object velocity (cm/s)		
	20	40	60
Prehension	-3.2 (36.3)	3.6 (26.2)	2.8 (26.1)
Catching	-13.7 (33.5)	2.4 (17.2)	1.5 (18.1)

The ANOVA on the closing-distance prediction error revealed a large effect of object velocity, $F(1.13, 15.77) = 119.42, p < .001, \eta^2_G = .503$ (see Table 3). The post-hoc tests showed that all levels of object velocity differed from each other ($p < .01$). Furthermore, the ANOVA showed a small to medium Task x Object-Velocity interaction, $F(1.32, 18.49) = 7.67, p < .05, \eta^2_G = .068$.

Finally, we found a small to medium effect of object velocity on the prediction error of first-order time-to-contact at the moment of hand-closure initiation, $F(1.21, 16.91) = 13.33, p < .005, \eta^2_G = .125$ (see Table 3). Post-hoc tests indicated that all differences between the means, except for the difference between the two highest object velocities, were statistically significant ($p < .05$).

Dynamic timing model

As we mentioned in Section 2, we first evaluated the model predictions using the same c_{vision} parameter setting for the prehension and the catching tasks. Inspection of the average prediction errors learned that in the catching task, the model, on average, was some 15.5 (*SD* = 23.4) ms too late, whereas in the prehension task, it was some 8.5 (*SD* = 29.4) ms too early. Although these differences were rather small, a large task effect was found, $F(1, 14) = 50.34, p < .001, \eta^2_G = .418$. Furthermore, we found a small to medium effect of object velocity, $F(1.25, 17.53) = 7.95, p < .01, \eta^2_G = .117$ (see Table 3). Post-hoc tests showed that the average prediction error of the lowest object-velocity condition differed from the other object-velocity conditions ($p < .05$). Finally, the ANOVA revealed a small to medium Task x Object-Velocity interaction, $F(1.19, 16.67) = 9.59, p < .01, \eta^2_G = .039$.

Given the two effects that include the factor of task, we were interested to see if allowing the c_{vision} parameter to vary, not only across participants, but also across tasks, would result in a situation in which the model would predict the initiation of hand closure in both tasks accurately, albeit with different strengths of the optical information on the intrinsic dynamics of hand opening and closing. The ANOVA on the prediction errors revealed a same pattern of effects as we had found when we used the same values of the c_{vision} parameter for both tasks, although with smaller effect sizes. The analysis showed a medium to large effect of object velocity, $F(1.23, 17.28) = 7.89, p < .01, \eta^2_G = .142$ (see Table 3). Again, the prediction errors in the slowest object-velocity condition differed from those in the two other object-velocity conditions ($p < .05$). Furthermore, we found a small effect of task, $F(1, 14) = 7.55, p < .05$, $\eta^2_G = .028$, M (SD) = -3.6 (22.9) and 1.1 (29.5) ms for catching and prehension, respectively. Finally, the ANOVA revealed a small Task x Object-Velocity interaction effect, $F(1.24, 17.42) = 6.11, p < .05, \eta^2_G = .028$ (see Table 4). To unpack this interaction effect, we performed two ANOVAs, with factors of object velocity and initial distance, for the prehension task and catching task separately. Whereas we found no statistically significant effects of any of both factors for the prehension task, the analysis of the catching data revealed a large object-velocity effect, $F(1.22, 17.13) = 9.53, p < .010, \eta^2_G = .248$, due to different prediction errors when catching the objects that approached at the lowest velocity ($p < .05$).

Discussion

The main purpose of the current study was to see if the timing of closure of the hand was controlled similarly in prehension and catching, both with approaching objects. Given the earlier successes (Zaal & Bootsma, 2004; Zaal et al., 1998) of modeling the initiation of hand closure in prehension with Schöner's (1994) dynamic timing model, with the hand-closure initiation timed on the basis of first-order time-to-contact information, we took this model as our starting point of the study. Zaal and Bootsma (2004) reported, for prehension of stationary objects, effects of distance, size, and width on the $TC_1(D)$ values in their experiment but that the dynamic timing model accommodated all these variations: they found no significant effects on the average prediction errors. The present study showed that this was not the case in all the conditions that we tested, in which we asked our participants to either reach for and grasp an object approaching at a constant velocity or catch it (with a stationary hand). We found effects of both object velocity and task on the quality of the dynamic timing model's prediction of the moment of hand-closure initiation. Importantly, we also found an interaction effect of these two factors. It turned out that the dynamic timing model had difficulty fitting particularly the condition of catching the object approaching at its lowest velocity. In the other conditions, the prediction errors were less than 5 ms, on average.

In line with previous studies, which had shown that closing time (Laurent et al., 1994; Rand & Stelmach, 2005; Rand et al., 2006, 2008; Zaal & Bootsma, 2004) and closing distance (e.g., Carnahan & McFadyen, 1996; Rand & Stelmach, 2005; Rand et al., 2006; Wang & Stelmach, 2001; Watson & Jakobson, 1997; Zaal & Bootsma, 2004; Zaal et al., 1998) varied with factors such as object velocity, object orientation, object width, object size, reaching amplitude, and reaching velocity, we found a large effect of the velocity with which the object approached on these two variables. The effects of object velocity on these two factors that came out of our experiment corroborated the conclusion that closing time or distance are not being kept constant, and, thus, do not act as control variables in the coordination of reaching and grasping or in the timing of catching in the situation that the hand is not moving.

Our results showed that the dynamic timing model did not perform well for the current catching task of a stationary hand and an object approaching at constant velocity, especially when the target arrived at a low speed. From this, one might conclude that the model was not appropriate to explain the timing of hand-closure initiation in catching. An alternative conclusion might be that our choice of designing the catching task in such a constrained way might have brought our participants in a rather unnatural situation, in which they were invited to show behavior that they would not show in natural catching. We have planned experiments to explore this possibility. In these experiments, objects arrive at non-constant velocities or we allow the hand to move when objects do arrive at constant velocities.

When we looked at the different object-velocity effects in our data, we found that the dynamic timing model most closely fit the patterns of results of the current experiment. Except for the condition of catching approaching objects at the lowest speed used in the current study, temporal prediction errors were less than 5 ms (cf. Table 4). The dynamic timing model did explain the results just a little better than a model with the timing of the initiation of hand closure at a critical value of first-order time-to-contact, and much better than models in which closure distance or time were to be kept constant. Temporal prediction errors of the constant-time-to-contact account were roughly twice as big as those of the dynamic timing model, except for the prediction errors of the lowest object velocity (see Table 3). This lowest object velocity proved to be problematic, particularly for the current catching task (we did not find a significant object-velocity effect when we considered the data of the prehension task separately). Taken together, the dynamic timing model accounted for much of the variability seen in closing time and closing distance, and a small amount of the variability seen in first-order time-to-contact. For now, we conclude that the dynamic timing model does a fine, albeit not a perfect, job in predicting the moment of the initiation of hand closure on the basis of first-order time-to-contact, at least for the task of prehension. As to the task of catching, the jury is still out.

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Appendix Model equations

The dynamic timing model is a set of differential equations, originally formulated by Schöner (1994), and adopted for the situation of the grasping of prehension by Zaal and colleagues (Zaal & Bootsma, 2004; Zaal et al., 1998). In the model, a state variable x is mapped onto the hand-opening and hand-closing regimes of prehension. The model equations combine the so-called intrinsic dynamics -the dynamics that give the state variable x its stability properties- and the contribution of the visual information:

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = f_{grasp} + f_{vision} \qquad (1)$$

In the model three attractors in state space are defined. That is to say, there are two fixed-point attractors, for the hand-opening regime (x_{open}) and the hand-closing regime (x_{close}), respectively, and a limit-cycle attractor passing through these two fixed-point attractors:

$$f_{grasp} = f_{osc} + f_{open} + f_{close} \tag{2a}$$

$$f_{osc}(x, y) = \begin{pmatrix} \alpha & \omega \\ -\omega & \alpha \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} - \gamma \begin{pmatrix} (x^2 + y^2)x \\ (x^2 + y^2)y \end{pmatrix} \tag{2b}$$

$$f_{open}(x, y) = -\beta_{\text{int}} f_{range} \begin{pmatrix} x - x_{open} \\ y - y_{open} \end{pmatrix} \tag{2c}$$

$$f_{close}(x, y) = -\beta_{\text{int}} f_{range} \begin{pmatrix} x - x_{close} \\ y - y_{close} \end{pmatrix} \tag{2d}$$

$$f_{range}(x, y, x_i, y_i) = \exp\left[-\frac{(x - x_i)^2 + (y - y_i)^2}{2\sigma} \right] \tag{2e}$$

The contribution of the visual variable r(D), which is the inverse of $TC_1(D)$ in our case, is defined:

$$f_{vision}(x, y, x_{open}, y_{open}, x_{close}, y_{close}) =$$
$$\beta_{vision}(D) \left[+ f_{range}(x, y, x_{open}, y_{open}) \begin{pmatrix} x - x_{open} \\ y - y_{open} \end{pmatrix} - f_{range}(x, y, x_{close}, y_{close}) \begin{pmatrix} x - x_{close} \\ y - y_{close} \end{pmatrix} \right] \tag{3a}$$

$$\beta_{vision}(D) = c_{vision}(r(D) - r_{crit}) \tag{3b}$$

A closer inspection of Eq. (3a) shows large similarities with Eqs. (2c) and (2d). A growing value of the visual variable r(D) leads to an increase of the variable β_{vision}, resulting in a decrease in the strength of attraction of the point attractor at X_{open} and an increase in the strength of attraction of the point attractor at X_{close}. For a more detailed introduction to the model and its equations, we refer the reader to Schöner (1994).

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5

A common first-order time-to-contact based control of hand-closure initiation in catching and grasping

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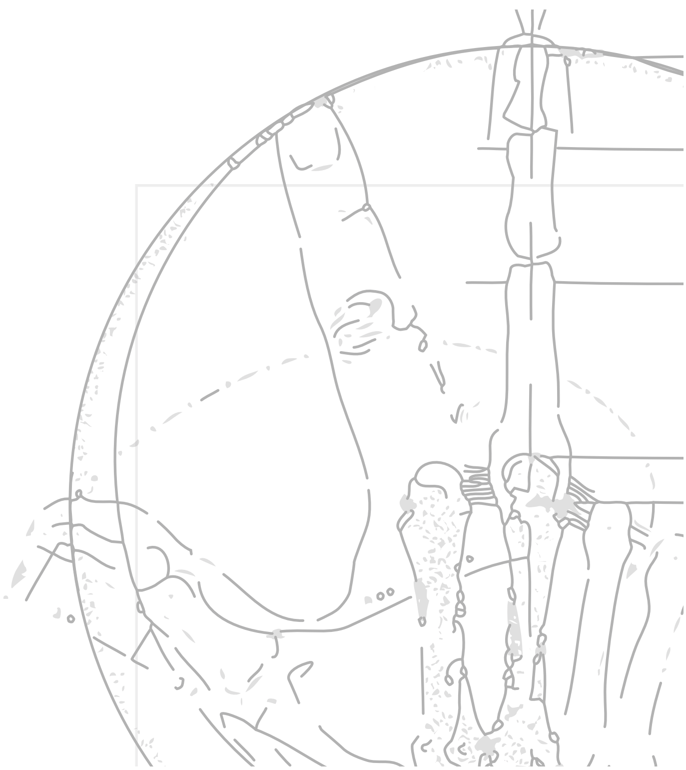
submitted for publication



Abstract

To catch or grasp an object, the initiation of hand closure has to be coordinated with the relative movement between hand and object. In a previous study (van de Kamp et al., 2010), the authors studied two tasks, catching while keeping the hand stationary and prehension, in search of a common control of the initiation of hand closure for both tasks. They showed that the initiation of hand closure could well be based on first-order time-to-contact in the prehension task but not in the catching task they had studied. The current study tested if the fact that the hand-object gap closed at a linear rate made that the initiation of hand closure could not be explained on the basis that same first-order time-to-contact in the catching task. In Experiment 1, the participants had to catch targets that approached at nonlinear rates while keeping the hand stationary. In Experiment 2, the participants were free to move their hand in catching the approaching objects, allowing the closure of the hand-object gap to happen at an nonlinear rate as it would in natural movements. The results showed that the first-order time-to-contact based control of the initiation of hand closure did apply in Experiment 2 whereas it did not in Experiment 1. It was concluded that constraining the catching task such that it became unnatural led to a hampered timing, thus obstructing the finding of the common control in the previous study, and in Experiment 1 of the current study.

Introduction

When reaching out to grasp a pencil rolling off our desk or when we catch a pitch in baseball, the opening- and closing movements of our grasping hand need to be coordinated with the closure of the gap between our grasping hand and the target object. It has been suggested that the timing of hand-closure initiation -that is, the transition from hand opening to hand closing- is based on first-order time-to-contact information, the information about the time needed to close the current gap between the grasping hand and the target object when the speed of gap closure would remain unchanged (e.g., Bootsma & Peper, 1992; Lee, 1976; Savelsbergh, Whiting, & Bootsma, 1991). Given that this first-order time-to-contact is a property of the relative hand-object movement, it does not matter whether the hand moves towards the object, the object moves towards the hand, or the hand and the object move towards each other. This makes that the same first-order time-to-contact based initiation of hand closure could apply in all three conditions.

In a previous study (van de Kamp, Bongers, & Zaal, 2010), in which we compared catching and prehension, we tested the hypothesis of a first-order time-to-contact based generic control of the initiation of hand closure in both tasks. In the prehension task, participants were asked to reach for and grasp an object approaching at a constant velocity. For this task, we concluded that the timing of hand-closure initiation could be well understood on the basis of first-order time-to-contact information. However, for the catching task, in which participants were asked to keep the grasping hand stationary while catching the approaching object, the results were less convincing. Why would this be the case?

One obvious difference between van de Kamp et al.'s (2010) prehension and grasping tasks was the way that the hand-object gap was closed: In the prehension task the grasping hand moved towards the object in order to grasp it, whereas in the catching task the hand was kept stationary. This difference in how the hand contributes to the closure of the hand-object gap might be responsible for the differences between prehension and catching that we found in our earlier study (van de Kamp et al., 2010). Because reaching movements are characterized by a bell-shaped velocity profile, the hand-object gap is closed at a typical, nonlinear rate in prehension. In contrast, given the constant object velocity and the stationary hand, the hand-object gap was closed at a linear rate in the catching task. Is it the (non)linearity of the gap closure speed that caused the observed differences, we asked. And if so, does it matter what the shape of nonlinearity is exactly? Does the nonlinearity need to be the same as in natural reaching? In the current study we tried to answer these questions by manipulating the hand-object relation in two different ways. In a first experiment, we had the object close the hand-object gap at a nonlinear rate while instructing our participants to keep the catching hand stationary. In a second experiment, we did not give instructions as to how to pick up the target object, participants were free to move their catching hand, thereby leaving the rate of change in hand-object closure up to the person performing the task.

As mentioned before, in our earlier study (van de Kamp et al., 2010), we found that first-order time-to-contact could explain the moment of initiation of hand closure in prehension but not in catching. To understand how the differences in hand-object gap closure affect control of grasping, we used two models that relate the gap closing between hand and object with information controlling the grasp. Before turning to the experiments, we will briefly discuss these two accounts of how first-order time-to-contact information is related to the initiation of hand closure. Both accounts use the same information but differ in the way that the information is being used (i.e., the control law; Bootsma, Fayt, Zaal, & Laurent, 1997; Warren, 1988). The most straightforward way of relating the initiation of a movement response to first-order time-to-contact is to trigger the movement upon reaching a threshold value of tau, the optical variable specifying first-order time-to-contact (Bootsma & Oudejans, 1993; Lee, 1976; Lee, Young, Reddish, Lough, & Clayton, 1983; Lee & Reddish, 1981; Michaels, Zeinstra, & Oudejans, 2001; Savelsbergh, Whiting, & Bootsma, 1991, Savelsbergh, Whiting, Pijpers, & Van Santvoord, 1993; Tresilian, 1991). We will refer to this way of using first-order time-to-contact information as the critical-tau model.

Instead of using a threshold approach to explain how first-order time-to-contact information is related to hand-closure initiation, Zaal and colleagues (Zaal, Bootsma, & Van Wieringen, 1998; Zaal & Bootsma, 2004) took a nonlinear-dynamics approach (e.g., Kelso, 1995). Therefore, they elaborated a version of Schöner's (1994) model, consisting of a set of differential equations that describe the two possible states of the system (see van de Kamp et al., 2010). One is the hand-opening state, the other is the hand-closing state. The optical variable tau affects the stability of the hand-opening state and the hand-closing state of the grasping system. Note that the way the gap between the hand and the object closes determines the evolution of tau, and thus, the stability of the hand-opening or hand-closing state. This dynamic model, which we will refer to as the dynamic-tau model, should, in essence, make the control system more robust to perturbations in the hand-object relation. As compared to the critical-tau model, the dynamic-tau model, therefore, is expected to explain more of the variability seen in different grasping conditions.

In our previous study (van de Kamp et al., 2010), we asked the question whether the critical-tau model or the dynamic-tau model would be best in explaining the timing of hand-closure in both catching and prehension. As had been reported before (Zaal et al., 1998; Zaal & Bootsma, 2004), the dynamic-tau model seemed most promising in explaining the timing of hand-closure initiation in prehension. Unfortunately, as we pointed out before, neither the dynamic-tau model nor the critical-tau model was found completely successful in explaining the initiation of hand-closure when participants were instructed to keep the hand stationary while catching the approaching object. For this reason, in the current study, we focused on the nature of the hand-object relation in catching and asked whether introducing nonlinearities into this relation would result in grasping behavior that could be accounted for by either of the two models. If this were the case, a generic understanding of the control of hand-closure initiation in catching and prehension might come into reach.

EXPERIMENT 1

Method

Participants

Ten men and ten women, with an average age of 20.3 years (ranging from 18 to 23 years) participated in the experiment. All were right-handed and had normal or corrected to normal vision. The participants were naive to the exact purpose of the experiment, gave their informed consent, and were paid a small fee for participating.

Apparatus

We used the same apparatus as van de Kamp and colleagues (2010). A cylindrical target object (diameter: 3 cm, height: 1.5 cm) was placed on top of a magnet embedded object carrier, which was made to move along a plain white tabletop (2 m x 2 m) by means of a magnetic coupling to a servo-motor-driven mechanism underneath. The exact path of the target object's movement was computer-controlled through a user interface that was developed for this purpose (LabView, National Instruments, Austin, TX, USA). Using an Optotrak system (NDI, Waterloo, Ontario, Canada), the positions of four infrared light emitting diodes (IREDs) were captured at a rate of 200 Hz. The IREDs were placed on the center of the target object, the lateral lower corner of the index-finger nail, the medial lower corner of the thumb nail, and the skin immediately proximal tot the styloid process of the radius at the wrist.

Procedure and design

Participants were asked to catch the target object that approached with one of five constant object accelerations (-50, -20, 0, 20, and 50 cm/s^2) arriving at the catching hand at one of two velocities (40 and 60 cm/s). Participants sat along the side of the table, with their right side touching the table edge and their sagittal plane parallel to the table edge. The object approached along the participants' sagittal plane, some 30 cm away from the edge of the table. At the start of each trial, with the tips of the thumb and index finger touching, these were placed on the table top on a marked interception position. As illustrated by the dashed line in Figure 1, the approaching movement of the target object was realized in three phases. First, the object covered a 3 cm distance by quickly accelerating until reaching one of four constant velocities (20, 40, 60, 80 cm/s). In the second phase, this object velocity was maintained until the beginning of the third phase in which the object was made to decelerate or accelerate again (-50, -20, 0, 20, and 50 cm/s^2). The initiation of phase three was timed such that the object arrived at the pick-up location with an object velocity of either 40 cm/s or 60 cm/s. In all conditions the total distance covered was 103 cm. Participants were to catch the approaching object between the pads of the thumb and index finger while keeping the position of their hand fixed. After liftoff, the object was to be placed on the table top somewhere near the pickup location. During the object approach, headphone delivered white noise was played. The 10 randomized conditions (5 accelerations x 2 end velocities) were presented in 10 blocks, resulting in a total of 100 trials per participant.

Data analysis

In total, we used 1965 trials for the data analyses. In 35 trials, we encountered problems with controlling the object carrier or some IRED data was missing. Position data was smoothed using a low-pass recursive second-order Butterworth filter with a cut-off frequency of 10 Hz. Hand position was defined as the average position of the thumb and the index-finger IRED. Hand aperture was defined as the three-dimensional distance between the thumb and the index finger IREDs. The rate of change of hand aperture was computed using a three point finite difference algorithm. The initiation of hand closure was determined by looking back from the moment of peak closing velocity to detect the first moment that the hand closing speed dropped below a threshold of 2 cm/s. The start and end of the grasping movement were defined as the moment when hand opening and closing speed rose above or dropped below a threshold of 2 cm/s, respectively. The interception location was defined as the hand position at the end of the grasping movement.

First-order time-to-contact $TC_1(D)$ at the moment of hand-closure initiation was computed by dividing the distance (projected along the line of the object approach) between the object and the interception location by the momentary speed at which this distance was closed.

To evaluate the accuracy of the critical-tau model and the dynamic-tau model we computed temporal prediction errors for both models (cf. van de Kamp et al., 2010). Within each trial this temporal prediction error was defined as the time difference between the experimentally observed moment of hand-closure initiation and the moment of hand-closure initiation as predicted by the model. To determine the temporal prediction errors of the critical-tau model, we assumed that first-order time-to-contact was to be kept constant at a specific value in the control of grasping. This value (which was allowed to vary across participants) was taken to be the value at which the sum of squared prediction errors was minimal (cf. van de Kamp et al., 2010; Zaal & Bootsma, 2004). Next, we inspected for each trial when this value was reached, and computed the difference in time between the latter moment and the moment of hand-closure initiation. Analogously, we determined the temporal dynamic-tau model error by computing the difference between the predicted moment of hand-closure initiation and the experimentally observed moment of hand-closure. To arrive at the model prediction, we numerically simulated the model's set of differential equations (see van de Kamp et al., 2010; Zaal et al., 2004) using a Runge-Kutta algorithm with a fixed time step equal to the time step of the kinematic data. Following previous model simulations (van de Kamp et al., 2010; Zaal et al., 2004) all parameters were set at a fixed value ($\alpha = 10$; $\omega = 10$; $\gamma = 10$; $\beta = 90$; $\sigma = 0.75$; $r_{crit} = 0$) except the parameter c_{vision}, which was allowed to vary across participants. Within each participant, the c_{vision}, parameter setting was optimized by finding the minimum sum of the squared temporal prediction errors between the model predictions and the observed initiation moments (see Table 1 for the values of c_{vision}).

Table 1. Values of the c_{vision} parameter that were used in the simulations of Experiment 1.

Participant	1	2	3	4	5	6	7	8	9	10
c_{vision}	6.83	5.82	6.56	4.94	5.74	6.11	6.40	5.05	5.82	5.42
Participant	11	12	13	14	15	16	17	18	19	20
c_{vision}	4.83	5.74	5.05	5.43	5.95	5.26	7.67	5.10	5.37	5.69

These mean prediction errors were analyzed with a repeated-measures analyses of variance (ANOVA) with: model (critical-tau *vs*. dynamic-tau), object acceleration (-50, -20, 0, 20, and 50 cm/s^2), and object velocity (40, 60 cm/s) as within-participant factors. In case the assumption of sphericity was violated, the degrees of freedom were adjusted using Greenhouse-Geisser corrections. The corresponding effect sizes (η^2_G) were calculated based on generalized *eta*-squared values (cf. Bakeman, 2005) and interpreted according to Cohen's (1988) recommendation of .02 for small effects, .13 for medium effects, and .26 for large effects. In post-hoc analyses, we applied the Bonferroni correction procedure.

Results

Figure 1 shows an example of a trial in which the target object aproached the participant at a constant object acceleration of 20 cm/s^2 arriving at the catching hand with an object velocity of 60 cm/s. The Figure shows that during this object acceleration, the catching hand was opened to subsequently enclose the target object. In all conditions, the grasping movement started during the phase in which the object accelerated/decelerated (3rd phase, see Method section). The average prediction errors of both the critical-tau model, $M(SD) = 1.1$ (16.6) ms, and the dynamic-tau model, $M(SD) = 0.6$ (14.4) ms, were rather small and did not differ significantly from each other. We did find a large main effect of object acceleration, $F(2.82, 53.65) = 13.33$, $p < .0001$, $\eta^2_G = .272$. A small Model x Acceleration interaction effect, $F(1.38, 26.18) = 180.14$, $p < .0001$, $\eta^2_G = .043$, indicated that the mean prediction errors for object accelerations -50 cm/s^2 through 50 cm/s^2 of the critical-tau model: -8.7, -0.5, 2.6, 5.3, and 6.6 ms (21.0, 17.8, 15.7, 16.0, and 12.4 ms, respectively) seemed to represent a slightly different effect of object acceleration than those of the dynamic-timing model: -4.7, 0.5, 1.9, 3.1, and 2.2 ms (20.7, 17.7, 15.5, 15.8, and 12.5 ms, respectively). Furthermore, we found a large effect of object velocity, $F(1, 19) = 154.25$, $p < .0001$, $\eta^2_G = .317$, showing that on average the two models were 3.7 (18.2) ms too late with low velocities (40 cm/s), whereas with high velocities (60 cm/s) they were 5.4 (14.8) ms too early. Finally, we found a Model x Acceleration x Velocity interaction effect, $F(2.46, 46.76) = 17.61$, $p < .0001$, $\eta^2_G = .001$, the size of which was so small that we did not further consider this effect.

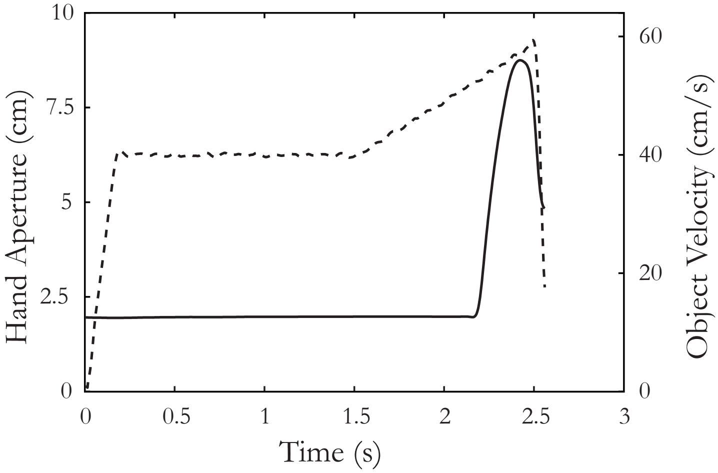


Figure 1. An exemplary trial showing Object Velocity (dashed line) and Hand Aperture (solid line) as a function of time.

Discussion

The rationale for this first experiment was to see if explicitly introducing nonlinearities in the closure of the hand-object gap of a catching task would result in grasping behavior that could be explained on the basis of first-order time-to-contact information. This nonlinear hand-object gap closure was achieved by manipulating the target object's speed of approach (having it accelerate or decelerate) while having the participants keep their catching hand stationary. We found a number of significant effects on the prediction errors, which meant that neither the critical-tau nor the dynamic-tau model proved successful in relating the timing of hand-closure initiation to first-order time-to-contact. These current findings regarding a catching task of a stationary hand and accelerating objects are congruent with our previous results with a catching task of a stationary hand and an object approaching at constant velocity (van de Kamp et al., 2010). Consequently, one might conclude that the adopted time-to-contact models are just 'no good' in explaining the timing of hand-closure initiation in catching and thus, that we have to conclude that our search for a common control of hand-closure initiation in both catching and prehension turns out to be fruitless. Alternatively, one could say that by designing our catching tasks in a rather constrained way, we might have brought our participants in an unnatural catching situation. That is, by manipulating the movement of the approaching object while instructing the participants to keep the catching hand stationary we, possibly, invited our participants to show behavior they would not show in natural catching. This would clarify why we had such a hard time explaining this (unnatural) grasping behavior on the basis of first-order time-to-contact information.

So, what would a more natural catching task look like? What, for instance, would happen if we left the hand free? How would the closure of the hand-object gap evolve if we kept the movement of the target object under experimental control (we chose a constant velocity of approach), but this time, the movement of the grasping hand was left up to the person performing the catching task? In the next experiment, in which participants were free to move their hand while catching the target object approaching at constant velocities, we studied the possibility that if the movement of the hand turns out to be of any significance in catching, we might find grasping behavior that can be explained on the basis of first-order time-to-contact information.

EXPERIMENT 2

Method

Participants

A new set of participants (nine female and six male), all right-handed and with an average age of 29 years (range 25 to 35) took part in the experiment. All participants had normal or corrected-to-normal vision, were naive to the exact purpose of the experiment, gave their informed consent, and were paid a small fee for their participation.

Apparatus, procedure, and design

The main difference between Experiment 1 and 2 was in the procedure and design. The apparatus was identical to that of Experiment 1. Again, we sampled the positions of the IREDS, now at a 100 Hz, and had the participants catch the target object approaching with one of five constant velocities (10, 20, 30, 40, and 50 cm/s) starting from one of two different distances (55 and 65 cm). In the same way as in the first experiment, the right hand, with the tips of the thumb and index finger touching, was positioned on a starting position indicated on the table. Yet, this time, participants received no explicit instructions as to how they were to grasp the approaching object (i.e., keeping their hand at a fixed position or not). Instead, at the start of each trial, they received one of three headphone delivered instructions that were followed by white noise. The instructions: 'forward', 'middle', or 'backward' corresponded to three goal positions that were indicated on a line parallel to the object's line of approach (10 cm to the left). The middle goal was drawn directly left to the hand's starting position. The forward and backward goal positions were drawn 20 cm in front of or behind the middle goal position. Participants were asked to place the approaching object at the instructed goal position. Importantly, this meant that participants were free to either keep their hand at a fixed location catch the object and bring it to the instructed goal position, or alternatively, reach for and grasp the object to bring it to the goal position. Presenting all 30 randomized conditions (3 goal x 5 object velocity x 2 initial hand object distance) in 6 blocks resulted in a total of 180 trials for each participant.

Data analysis

All 2700 trials were used for the data analyses. In addition to the dependent variables of Experiment 1, we analyzed the reaching amplitude of the catching hand which was defined as the distance (projected along the dimension of the object approach) between the initial hand location and the interception location. In all other respects, the data analysis and numerical simulations (see Table 2 for the values of c_{vision}) were identical to those of Experiment 1.

Table 2. Values of the c_{vision} parameter that were used in the simulations of Experiment 2.

Participant	1	2	3	4	5	6	7	8	9	10
c_{vision}	3.94	3.78	3.89	3.9	3.71	3.82	3.96	4.02	3.62	3.37
Participant	10	11	12	13	14	15				
c_{vision}	3.37	3.71	3.53	3.41	4.11	4.23				

Results

Figure 2 shows for each level of object velocity an exemplary trial in which the rate of change in the closure of the hand-object gap is plotted against time. The Figure illustrates that by reaching out their hand to grasp the approaching object, participants, indeed, generated a nonlinear closure of the hand-object gap.

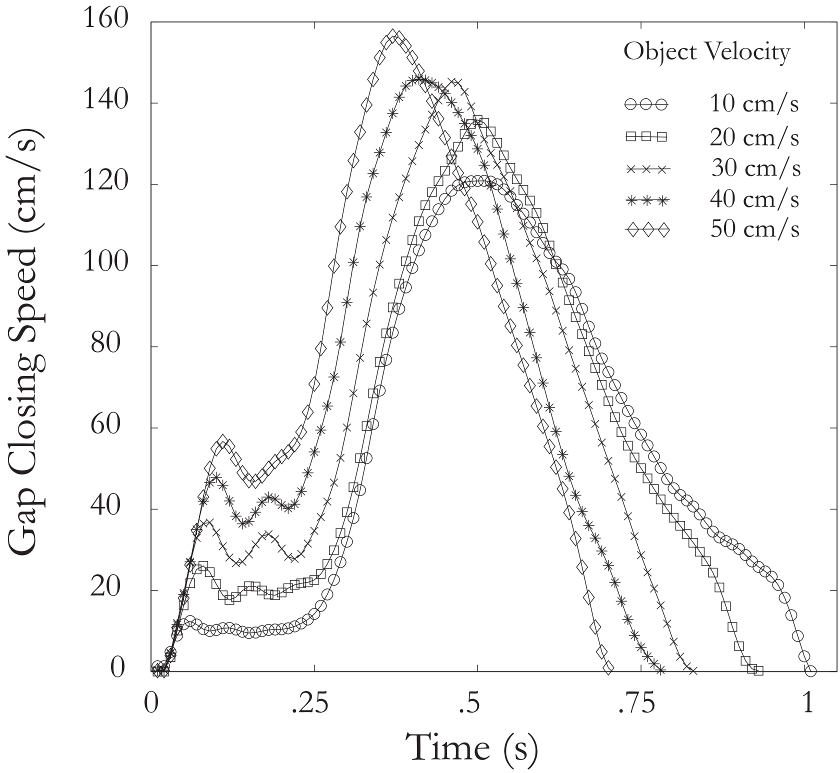


Figure 2. Five exemplary trials showing a participant's rate of change in the decrease of the distance between the target object and the caching hand for object velocities 10, 20, 30, 40, and 50 cm/s.

Reaching amplitude

The two lines in Figure 3 represent the average reaching amplitudes for the two distances plotted against the five levels of object velocity. The ANOVA showed a large effect of object velocity, $F(1.46, 20.41) = 860.24$, $p < .0001$, $\eta^2_G = .874$ on reaching amplitude. Means for velocities 10 cm/s through 50 cm/s were: 382.4, 289.1, 210.7, 149.7, and 101.7 (16.7, 21.6, 24.3, 26.3, and 28.3 respectively) mm. Post-hoc comparisons revealed that these mean values were different among all levels of object velocity ($p < .0001$). We also found a difference in reaching amplitudes between the near 192.6 (22.6) mm and the far 260.9 (24.2) mm levels of distance. The ANOVA revealed that this effect was also large, $F(1, 14) = 827.00$, $p < .0001$, $\eta^2_G = .448$. Furthermore, a small interaction effect, $F(4, 56) = 43.53$, $p < .0001$, $\eta^2_G = .021$, was found between object velocity and distance (see Figure 3).

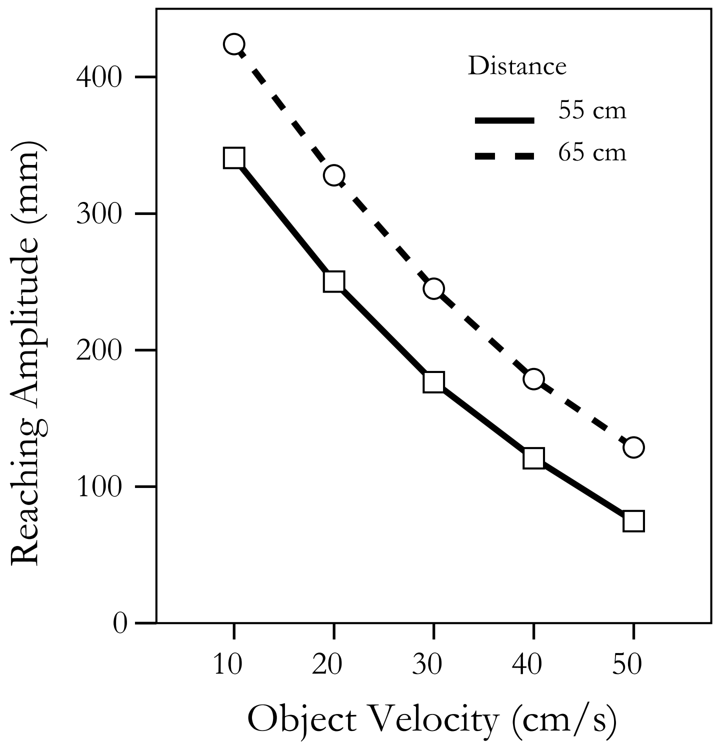


Figure 3. Average reaching amplitudes for the two distances (55 cm and 65 cm) plotted against the five levels of object velocity (10, 20, 30, 40, and 50 cm/s).

Temporal prediction errors

The critical-tau model and the dynamic-tau model seemed to do equally well in explaining the variability seen in the different conditions of a catching task in which participants were free to move their hand in order to catch objects approaching at five different constant velocities and from two different distances. The average prediction errors for object velocity 10 cm/s through 50 cm/s were: -0.3, 0.9, 3.4, 3.6, and 2.8 (34.2, 33.1, 27.7, 20.8, and 19.0) ms for the critical-tau model and: 4.0, 5.4, 2.2, -1.0, and -4.6 (31.8, 28.9, 21.7, 18.1, and 16.7) ms for the dynamic-tau model. The small Model x Velocity interaction effect, $F(2.08, 29.15) = 51.20, p < .001, \eta^2_G = .027$, indicates that the average prediction errors for the critical-tau model seem to represent a different effect than those for the dynamic-tau model, but given the small effect size this effect will not be further interpreted. Also, the significant Velocity x Distance effect, $F(4, 56) = 4.15, p < .01, \eta^2_G = .030$, and the Model x Velocity x Distance effect, $F(1.87, 26.15) = 3.95, p < .05, \eta^2_G = .002$, had such small effect sizes that they were not interpreted. Finally, we found a medium to small effect of goal position, $F(2, 28) = 10.61, p < .0001, \eta^2_G = .075$. Post-hoc tests learned that the effect could be attributed to a difference between the 'forward' goal position, *M*(*SD*) = 7.2 (23.6) ms, as compared to the 'backward' position, *M*(*SD*) = -1.9 (26.5) ms, and the 'middle' position, *M*(*SD*) = -0.3 (24.6) ms.

Discussion

In this second experiment we aimed to find out what participants would do when they were given no instructions as to how they were to pick up the approaching objects. Figure 3 clearly shows that, in contrast to what we instructed our participants to do in our previous catching tasks (see Experiment 1; but also van de Kamp et al., 2010), participants did not keep their hand stationary while catching the approaching objects. Quite on the opposite, participants in the current experiment reached out for the object in order to grasp it, and the amplitude of the reach varied with object speed. This supports the idea that our previous design of a catching task in which the hand was to be kept stationary while the object's speed of approach was controlled experimentally might have resulted in unnatural catching behavior. It seems defendable that in our earlier studies we could not understand the timing on the basis of first-order time-to-contact because of the unnatural situation in which we brought the participants, as we did in Experiment 1 of this study and in van de Kamp et al. (2010).

We found that when participants were left free to move their catching hand, the amount of reaching was scaled to the object's velocity of approach and the initial hand-object distance (Figure 3). So, when the object approached at low speed and from a far distance, participants showed considerable reaching amplitudes. When, on the other hand, the object approached at high speed and from nearby participants hardly reached out to grasp it. Bearing in mind our previous instruction to keep the catching hand stationary at all conditions (think of a horizontal line in Figure 3, representing zero reaching amplitudes for all levels of object velocity) it becomes clear that this instructed behavior is indeed quite different from what we just found in unconstrained catching. Furthermore, Figure 3 shows that this difference in behavior seems to increase with decreasing levels of object velocity. This means that we might probably keep our catching hand close to stationary with fast approaching objects. However, when objects approach real slowly, we will probably not sit and wait for the object to arrive. All this implies that fitting a model to the timing of hand-closure initiation as observed in a catching task with a stationary hand and an object approaching at a constant velocity would be most problematic at the lowest level(s) of object velocity. This is exactly what the prediction errors in our previous study were telling (van de Kamp et al., 2010). In that study we found a velocity effect on the prediction errors of both the critical-tau and the dynamic-tau model that, according to the ANOVAs' post-hoc tests (as well as Table 3 in van de Kamp et al., 2010), could be fully attributed to the slowest object-velocity condition that we used there (20 cm/s).

Now that we know that allowing the hand to move plays an important role in catching, the next question is whether the timing of hand-closure initiation could be understood on the basis of first-order time-to-contact when the hand is not kept stationary. Our results showed that, when the movement of the grasping hand is up to the person performing the catching task, we no longer find a main effect (or interaction effect of considerable size) of object velocity on the models' prediction errors. In terms of effect sizes, the only effect on the models' prediction errors worth discussing was the effect of goal position. Since this factor was simply a dummy factor which turned out to be unrelated to the participants' reaching behavior we, for now, accept it as it is and turn to our conclusion that the variability observed in the different conditions of unconstrained catching can be well explained on the basis of first-order time-to-contact.

General Discussion

In this study we continued our search for a common control of hand-closure initiation in both catching and prehension. We presented two experiments following up van de Kamp et al. (2010). Whereas, for the task of prehension, modeling the initiation of hand closure on the basis of first-order time-to-contact information had been successful with Schöner's (1994) dynamic-tau model (van de Kamp et al., 2010; Zaal & Bootsma, 2004; Zaal et al., 1998), in catching this had not yet been the case (van de Kamp et al., 2010). In the current study we asked the question whether the grasping hand's contribution to the closure of the hand-object gap might be responsible for this difference in our findings. Was it the linearity in gap closure that obstructed the natural timing of hand-closure initiation in the previous catching task, or is the typical, natural pattern in the closure of the hand-object gap essential in the natural timing of hand-closure initiation?

In the first experiment we showed that simply introducing nonlinearities to the task of catching did not result in grasping behavior that (like in prehension) could be explained on the basis of first-order time-to-contact information. In the second experiment we showed that when participants were left free to move their catching hand, *a*) the hand-object gap was closed at a typical, nonlinear rate and *b*) both the critical-tau and the dynamic-tau model proved successful in relating the timing of hand-closure initiation to first-order time-to-contact. This implies that it was not just the nonlinearity in the gap closure between object and hand that was responsible for the hampered timing of the initiation of hand closing, but that there is something special in the trajectory of gap closure invoked by the moving hand in natural prehension.

Now that both models have been found to be successful in the context of catching, the next question, of course, is which approach account is most promising in our search for a common control in both catching and prehension? Is the initiation of hand closure simply triggered at a critical value of first-order time-to-contact (Bootsma & Oudejans, 1993; Lee, 1976; Lee et al., 1983; Lee & Reddish, 1981; Michaels et al., 2001; Savelsbergh et al., 1991, Savelsbergh et al., 1993; Tresilian, 1991) or might this information be used in a more dynamic way (van de Kamp et al., 2010; Zaal et al., 1998; Zaal & Bootsma, 2004)? It is not easy to make an empirical judgment based on the variety of dependent variables that have been reported previously. One complication is that these different measures have been defined along different dimensions. This means that we cannot quantitatively compare the outcome measures of the dynamic-tau model (van de Kamp et al., 2010; Zaal & Bootsma, 2004; Zaal et al., 1998) with the values of first-order time-to-contact that have been reported in the many studies on catching and prehension (Bennett, van der Kamp, Savelsbergh, & Davids, 1999; Caljouw, van der Kamp, & Savelsbergh, 2004; van de Kamp et al., 2010; Wallace, Stevenson, Weeks, & Kelso, 1992; Zaal & Bootsma, 2004; Zaal et al., 1998). To arrive at dependent measures that are defined along the same dimension for each dependent variable (i.e., model prediction), we computed temporal prediction errors (van de Kamp et al., 2010). In our perspective, a fair comparison between the predictions of the critical-tau model and the predictions of the dynamic-tau model can only be made on the basis of these prediction errors, which, unfortunately, feature only in our latest studies (i.e., the current study and that of van de Kamp et al., 2010). All in all, these two studies showed that the dynamic-tau model has been successful in predicting hand closing initiation in prehension (cf. van de Kamp et al., 2010) and also in catching (Experiment 2). The critical-tau model, on the other hand, has only proved adequate in our last catching task (Experiment 2). Therefore, we think it is fair to conclude that the dynamic approach seems most promising as a vehicle to understand the generic control of hand-closure initiation in catching and prehension.

Another conclusion drawn from our results is that if one cares to study natural catching behavior, one should be careful when using instructions to constrain the participants' behavior. We showed for instance that a simple instruction like keeping the grasping hand stationary might already have resulted in unnatural grasping behavior. The reason for keeping the catching hand stationary was that this makes it easier to experimentally perturb the time-to-contact information (e.g., Savelsbergh et al., 1991). Given the finding that it does actually make a difference whether the hand is kept stationary or not, when interested in natural behavior one might want to consider an alternative setup in which the movement of the target object is still under experimenter control, but the movement of the grasping hand is left to the person performing the catching task. Please note that the problems we encountered at the lowest level of object velocity (i.e., the 20 cm/s condition in van de Kamp et al.'s, 2010, experiment), might not have occurred in other catching studies since these studies employed much higher levels of object velocity (50 - 150 cm/s; e.g., Caljouw et al., 2004; Savelsbergh et al., 1991; Mazyn, Savelsbergh, Montagne, & Lenoir, 2007).

In the end, the dynamic-tau model was found successful in predicting the initiation of hand closing not only in prehension but also in unconstrained catching. One might, however, ask the question: to what extent are these catching and prehension tasks still different behaviors? This problem seems to hinge on the definitions of the tasks of 'prehension' and 'catching'. Should we be strict and, as soon as a target moves, consider the task to be that of catching, for which the model would not apply if participants were instructed to keep the grasping hand stationary (especially with low object velocities)? In that case, the task of prehension would only imply stationary targets. However, a number of studies have referred to the task they studied as a task of prehension also when participants had to seize objects moving along a tabletop (e.g., Carnahan & McFadyen, 1996; Carnahan, Vandervoort, & Swanson, 1998; Chieffi, Fogassi, Gallese, & Gentilucci, 1992; Mason & Carnahan, 1999; Majsak, Kaminski, Gentile, & Gordon, 2008; Zaal et al., 1998; Zaal, Bootsma, & van Wieringen, 1999). A redefinition of what the task of prehension entails would imply that these studies were not on prehension but some other task, and that, therefore, their results cannot be generalized to the task of prehension. Importantly, this line of reasoning is the complete opposite of what we think should be the take-home massage of this study. In contrast to the idea that the human movement repertoire consists of a set of well-defined, mutually exclusive, actions (e.g., catching exclusively refers to the act of grasping approaching objects whilst prehension exclusively refers to the act of picking up stationary objects) we like to think that the human movement repertoire reflects a spectrum of actions and task domains covering a wide range of such actions. In our second experiment we showed that behavior traditionally defined as prehension (i.e., the picking up of stationary objects), when object speed increased, seemed to gradually blend into behavior traditionally defined as catching (grasping fast approaching objects). We, however, did not find a clear delineation point between these behaviors. Therefore, in terms of control, catching and prehension could just as well come under the same umbrella. This finding nicely fits the concept of a generic control mechanism for the timing of hand-closure initiation in both catching and grasping. In the current study we showed that one and the same first-order time-to-contact based initiation of hand closure could apply in both catching and prehension. As to which approach (the dynamic-tau or the critical-tau) best explains the timing in hand-closure initiation, the jury is still out, however, a generic understanding of the visual guidance of grasping is certainly possible.

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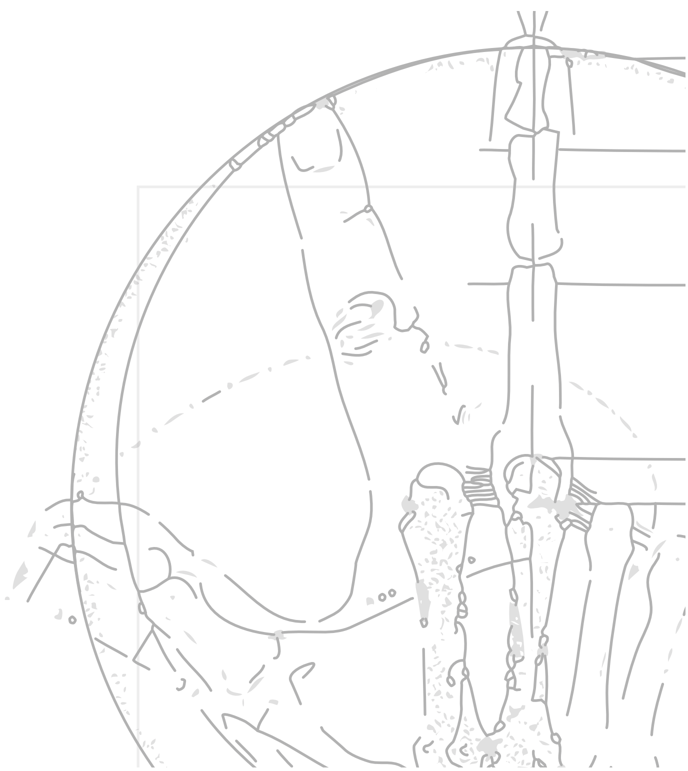
6

General Discussion



This thesis is concerned with how human grasping is controlled. The aim of the studies presented in this thesis was to contribute to the development of a broader understanding of catching and prehension movements. The chosen approach to describe the control of grasping movements was to identify 1) the controlled variables, 2) the information and 3) the control law. Below, the studies addressing each of these items will be discussed in general.

The controlled variables in prehension

Chapter 2 covers the question of what are the controlled variables in prehension. Whereas traditionally prehension has been seen as the act of coordinated reaching and grasping, Smeets and Brenner (1999) proposed an alternative view in which prehension is considered to be the combination of two independently moving digits. Basically, the issue boils down to the question whether humans control the aperture between their thumb and index finger or whether this hand aperture is really an emergent property related to the time course of the positions of the two digits moving to their respective end points. The latter hypothesis was tested by perturbing the end position of one of the digits while leaving the end position of the opposing digit unchanged. In the experiment reported in *Chapter 2* participants reached for and grasped an object of which the side surfaces could be made to slide in and out just after the reaching movement had started. In conflict with Smeets and Brenner's double-pointing hypothesis, it was found that in some cases perturbing the end position of one digit also affected the kinematics of the opposing digit. This finding clearly disagrees with the double-pointing account. It was concluded that since there is no real other alternative than prehension being either reaching and grasping or being pointing and pointing, rejecting the latter hypothesis logically leads to accepting the reaching and grasping hypothesis.

In a re-examination of the support for their 'new view on grasping', Smeets and Brenner (2001) reflected on the findings reported in *Chapter 2* and acknowledged that the double pointing hypothesis is not always correct in predicting that the index finger and thumb move completely independent. Indeed, their own data (Smeets, Brenner, & Martin, 2009) already showed a small correlation between the two digits. The authors, however, did not interpret this as a rejection of their hypothesis. Instead, they argued that the correlations they presented as well as the perturbation effect on the kinematics of the opposing (non-perturbed) digit, presented in *Chapter 2*, would be the outcome of an anatomical coupling between the two digits. Since the correlations were rather small, and did not occur in a bimanual grasping task (Smeets et al., 2009), the authors concluded that extending their model with a coupling between the digits was unnecessary (Smeets & Brenner, 2001).

First off all, the results reported in *Chapter 2* showed that the perturbation effect was not present in each and every condition. Therefore, it seems unlikely that the observed effects were the consequence of a biomechanical linkage between the digits through a shared hand. Assuming that the tests reported in *Chapter 2* have sufficient statistical power (i.e., controlling the type II error rate) I think it is fair to argue that if the biomechanical link would be responsible for effects of the perturbations showing up in the opposing digit, these effects should have been observed always in both digits. The results in *Chapter 2* showed that this is not the case. Second, the concluding suggestion of *Chapter 2* was not that a coupling between the digits should be added to the double-pointing model; the concluding suggestion was that the double-pointing hypothesis should be rejected.

In a more recent paper Smeets and colleagues (Smeets, Martin, & Brenner, 2010), again, stated that the findings reported in *Chapter 2* (i.e., that the two digits do not always move independent from each other) should be considered a correlation between the digits caused by anatomical factors. The ultimate test in this matter seems to involve a bimanual grasping task in which the anatomical linkage between thumb and index finger is minimal. Whereas, in an earlier non-perturbation study on bimanual grasping (Smeets et al., 2009) the authors had not found a correlation between the index fingers of the left and the right hand, an unpublished perturbation experiment carried out in our lab seemed to hint at a different result. That is to say, perturbing the kinematics of the digit of one hand (using the apparatus described in *Chapters 2* and *3*) showed a nearly significant effect ($p = .064$) on the kinematics of the digit of the opposing hand. This suggests that if one uses a perturbation paradigm to study bimanual grasping, one could show that the digits of either hand do not move independently from each other, also when the anatomical linkage between thumb and index finger is minimal. Strictly speaking (i.e., when choosing an alpha of .05), the perturbation effect is not significant. An explanation for the fact that in bimanual grasping the perturbation effect was less strong than in unimanual grasping might be that in bimanual grasping the variability in the digit's trajectories is much higher than in unimanual grasping. To reduce this variability, Smeets and colleagues (Smeets et al., 2009) had participants clasp their hands and stick out their index fingers to grasp the target object. In hindsight, it would have been a good idea if I had instructed the participants to clasp their hands as well, because the perturbation effect that I found would than probably have reached significance. This finding would have shown that, in line with the results from *Chapter 2*, also in bimanual grasping the Smeets and Brenner's (1999) hypothesis that prehension should be seen as the combination of independent digit's movements rather than the combination of reaching and grasping will be problematic.

The finding that prehension is really the coordinated act of reaching and grasping, does not necessarily support Jeannerod's 'visuo-motor channels hypothesis' (Jeannerod, 1981, 1984, 1999) which states that the two components are independent and operate exclusively on channel-specific information (i.e., one operating on the basis of intrinsic object properties and the other operating on extrinsic object properties). In this respect, I agree with Smeets and Brenner that the distinction between intrinsic and extrinsic object properties is problematic and that therefore the independence of the two components can be questioned.

However, with two components making up one act, reaching and grasping, somehow, need to be coordinated. Based on the work of Jeannerod (1981, 1999), the traditional view on this issue has been that the grasping is temporally ordered on the time scale provided by reaching. Empirical evidence for a hierarchy of reaching over grasping (cf. Gentilucci, Chieffii, Scarpa, & Castiello, 1992; Jeannerod, 1981, 1999) seemed to come from experiments showing that when object location or size were changed at movement onset, adjustments in the reach component were much faster than adjustments in the grasp component. In *Chapter 3* this account is challenged by the finding that the grasp component can be just as rapid in responding to a change in object size as the reach component is reported to respond to a change in object position. By perturbing object size at different instances during the movement, it was shown that grasp adjustments came in many different forms and that these adjustments could well be within approximately 120 ms, especially when the perturbations came late in the movement. This number compares with the adjustment times that have been reported previously for reaching movements (e.g., Paulignan, et al., 1991) and pointing movements (e.g., Brenner & Smeets, 1997; Liu & Todorov, 2007; Soechting & Lacquaniti, 1983). The finding that adjustments to the grasp component can be as fast as the adjustments to the reach component implies that the time scale on which an adjustment in the grasp component is ordered is not necessarily provided by reaching. This means that, empirically, the control model of a hierarchy of reaching over grasping lost one of its fundamental underpinnings.

As put forward in *Chapter 3*, an alternative means to consider the way the grasp component might adjust to size perturbations would be to view the response to such perturbations as resulting from the online control of the hand aperture (cf. Zaal, Bootsma, & van Wieringen, 1999). In this control model of grasping, the long response times that were found when object size was perturbed at movement onset (see *Chapter 3*, but also, Hesse & Franz, 2009; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1990; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991) would not necessarily reflect the minimal time that the grasp component would need to adjust to the perturbations. That is to say, these response times might be long because the grasping system was just not in a hurry to respond. Indeed, when late perturbations put pressure on the system, rapid adjustments were administered.

The conclusion that the kinematic details of the grasping movement are continuously regulated online rather than ordered in a predefined hierarchical fashion, received instant approval by a study of Hesse & Franz (2009) who reported the exact same findings in the exact same issue of the exact same journal (what are the odds). The authors used a slightly different experimental setup in which object size was perturbed by projecting a virtual object overlaying the real object to be grasped. In line with the results presented in *Chapter 3*, Hesse & Franz (2009) showed that 1) grasping adaptations to the new object size were achieved by smooth changes of the hand aperture over time, 2) the moment of grasp adjustment in response to early perturbations occurred later in time (300 ms) than the grasp adjustment in response to late perturbations (160 ms). Interestingly, the authors replicated these findings in a second experiment in which participants could not see their moving hand. The finding that the effects of changing object size during prehension with vision of the hand were similar to those without such vision made the authors conclude that visual feedback about the moving hand is not necessary for the control of grasping. Before discussing what this means in terms the online visual control of the hand aperture, let me first recall that in order to study a control law, one should, in chorus, consider the information that is used for the control.

The information used for the control of grasping

In *Chapter 4*, both the control law and the information that might be used for the control of hand closure initiation in grasping are addressed. In line with previous research (e.g., Zaal & Bootsma, 2004) it was shown that in comparison to accounts that use, for instance, closing time and closing distance information, an account for the use of first-order time-to-contact information was the most promising. What these three variables have in common is that they all describe a relation between the target object and the grasping hand. Closing distance and closing time, however, can only be known *a posteriori*. First-order time-to-contact, on the other hand, is a prospective variable (also referred to as tau) which is directly available and, therefore, can be used for the online control of grasping movements.

As laid out in earlier chapters, first-order time-to-contact equals the current distance between hand and target divided by the rate of change of that distance. Although my thesis does not really cover the 'perceptual side of the story' and it is simply assumed that time-to-contact information is available, I would like to discuss two issues regarding the information used for the control of grasping. With respect to the first issue let me recall the finding of Hesse & Franz (2009) that visual feedback about the moving hand is not necessary for the control of grasping. One could ask the question how we manage to pick up time-to-contact information between a target object and our hand if we cannot see our hand. One answer to this question would be that the perceptual system for picking up the information is more than just the retina. It might for instance just as well involve hand proprioception.

A second issue that I would like to address in this discussion concerns the inconsistency between the first-order time-to-contact (that is referred to in this thesis) and the actual time-to-contact. According to its definition (current) first-order time-to-contact equals to the actual time-to-contact if the hand-object speed does not change. However, in reality hand and object almost never move at constant speed, therefore, in prehension the relative hand-object speed changes all the time. So, for most of the time the first-order time-to-contact does not correspond to the actual time-to-contact. A number of studies (e.g., Benguigui, Ripoll, & Broderick, 2003; Senot, Prevost, & McIntyre, 2003) have indeed reported that when the distance between the actor and the object of interception is closed at a non-linear rate (like in prehension or catching accelerating objects), the current and actual time-to-contact diverge (cf. Tresilian, 1995). Therefore, it has been suggested that other, higher-order, sources of information might be used for the timing of interceptive actions (McIntyre et al., 2001; Michaels et al., 2001; Tresilian, 1995, 1999; see for a review: Zago et al., 2009). Many studies have formulized a second-order time-to-contact variable and evaluated its use for the timing of interceptive actions. Whereas some studies suggested that threshold values of higher-order time-to-contact can not be ruled out [1] (Lacquaniti et al., 1989; Tresilian, 1999; Michaels et al., 2001), most studies did not find them (Benguigui et al., 2003; Bootsma & Oudejans, 1993; Bootsma & Peper, 1992; Lee et al., 1983; Michaels & de Vries, 1998; Michaels et al., 2001; Port et al., 1997; Senot et al., 2003; Tresilian, 1990; 1994). Because the hypothesized critical (threshold) value of first-order time-to-contact would be generally small, it was agreed that the mismatch between the current first-order time-to-contact and the actual time-to-contact would be tolerable for the magnitudes of acceleration that receivers normally encounter (Tresilian, 1999) and that, therefore, motor

[1] Lacquanity and colleagues found that in catching falling objects, the initiation of hand closure was too precise to be based on first-order time-to-contact information alone. They hypothesized that for the guidance of these interceptive actions humans rely on a second-order time-to-contact variable that takes the force of gravity into account. Based on the finding that -under micro gravity conditions (0g)- motor responses seemed to be time-locked to the 1g arrival of objects, the authors proposed a model in which gravitational acceleration is internalized in the brain (cf. McIntyre et al., 2001; Zago et al., 2009).

responses might just as well be based on first-order time-to-contact ignoring acceleration information (but see: Wann, 1996).

Essential in this matter is to grasp the notion that the mismatch between the current first-order time-to-contact and the actual time-to-contact is not due to an over- or underestimation of time to contact. That is to say, first-order time-to-contact is not an estimate of actual time to contact (which we do not know during our reaching) but a continuous specification of when hand and object would meet if the speed of approach would not change (i.e., the definition of first-order time-to-contact). This implies that a one-to-one relation exists between the current first-order time-to-contact and the time that it would take the hand to reach the target. The fact that the speed of approach does often change is irrelevant to that one-to-one relation. Therefore, one could argue that the fact that the current first-order time-to-contact does not equal the actual time to contact, a conclusion that can only be drawn *a posteriori*, does not rule against the use of that variable in the on-line visual control of grasping (cf. Zaal & Bootsma, 2004).

The important next question addressed in *Chapters 4* and *5* is whether the threshold type of control adopted by the above mentioned studies is the right way to relate the first-order time-to-contact information to the initiation of hand closure in catching and/or prehension?

The control law in grasping

Bootsma and colleagues (Bootsma, Fayt, Zaal, & Laurent, 1997) stated that a lack of evidence for the use of a 'threshold' type of control (i.e., the critical-tau model relating time-to-contact information to the moment of hand closure) should not lead to the conclusion that this information is not used in the regulation of movement, yet, the way in which it is used (i.e., the control law cf. Warren, 1988) should be reconsidered as well. In *Chapters 4* and *5* the timing of hand closure in grasping was studied from a dynamical systems perspective (i.e., the dynamic-tau model).

The idea is that grasping behavior is best understood from a dynamical system approach endowing the opening and closing states with stability-related features. Elaborating on the work of Schöner (1994), Zaal and colleagues (1998, 2004) proposed a formulation of how the stability of the hand opening state and the stability of the hand closing state are coupled to time-to-contact information. At the beginning of the movement, when time-to-contact between the grasping hand and the target object is long, the opening state is most stable, whilst the hand closing state is unstable. During the movement the inverse of the time-to-contact grows exponentially resulting in a loss of stability in the hand opening state and a gain of stability in the hand closing state. At a certain point in time (i.e., the initiation of hand closure), the model's hand closing state has become more stable than the hand opening state and a swift transition -which has stability features of its own- from the hand opening state into the hand closing state takes place (for more details see Schöner, 1994; Zaal, 1998, 2004). A consequence of this 'non-linear dynamics' alternative for the use of first-order time-to-contact over the 'threshold type of control' is that hand closure does not have to occur at a constant value of first-order time-to-contact. This means that when the hand-object gap is closed in a second order fashion (think for example of the decelerative phase in reaching) model predictions are still accurate. Furthermore, the dynamical regulation of the initiation of hand closure makes the system resistant to perturbations. Because grasping behavior is continuously geared to visual information, it can be adjusted to changes in the environment-actor relation at any time. The advantage of continuously adjusting the opening and closing of the grasping hand is lacking in the 'threshold type of control' for which the initiation of hand closure at a critical time-to-contact is irreversible.

Two tasks sharing the same information and the same control law

In a control scenario that involves first-order time-to-contact information, it does not really matter whether the hand moves toward the object, the object moves towards the hand or a combination of both takes place. This is because the first-order time-to-contact information is about the relative hand-object movement. In *Chapter 4* it was tested which models were suited to explain the timing of grasping irrespective of whether this grasping pertains to prehension (that involved reaching) or catching (in which the hand hardly moved). In comparison with other accounts, the dynamic timing model performed best in explaining the data. In *Chapter 4* it was shown that whereas the dynamic timing model proved successful in the context of prehension (see also Zaal & Bootsma, 2004; Zaal et al., 1998) it did not equally well predict the timing of the grasping in the catching task of a stationary hand and an object approaching at constant velocity, especially when the target arrived at a low speed. It might have been that the predictions were poor because in this catching task the hand-object gap was closed at a linear rate. *Chapter 5* describes two catching experiments in which the relative hand-object movement decreased at a non-linear rate. In the first experiment participants were to catch the targets approaching at nonlinear rates while keeping the hand stationary. In the second experiment participants were free to move their hand in catching the approaching objects, allowing the closure of the hand-object gap to happen at a nonlinear rate as it would in natural movements. The results reported in *Chapter 5* showed that whereas the first-order time-to-contact based control of the initiation of hand closure could not explain the data from Experiment 1, it could explain the data from Experiment 2. It was concluded that constraining the catching task such that it became unnatural led to a hampered timing, thus (in *Chapter 4* and in the first experiment presented in *Chapter 5*) obstructing the finding of a common control. It seems defendable that, previously, the timing of grasping could not be explained on the basis of first-order time-to-contact, because the instruction to keep the catching hand stationary brought the participants in an unnatural grasping situation. Yet, in unconstrained catching and prehension the variability observed in the different conditions could be well explained on the basis of first-order time-to-contact.

A common control in catching and prehension

The second half of this thesis was dedicated to the search for a common control of hand-closure initiation in both catching and prehension. *Chapters 4* and *5* showed that the dynamic-timing model was most successful in predicting hand closing initiation in prehension and also in catching. The critical-tau model, on the other hand, was found less successful as it proved adequate only for the catching task in the second experiment described in *Chapter 5*. For this reason I think it is fair to conclude that the dynamic approach seems most promising as a model for understanding the generic control of hand-closure initiation in catching and prehension.

This conclusion might raise two related questions that will be discussed in the concluding piece of this thesis. The first question is, why bother about a generic understanding of the control of grasping in catching and in prehension, and the second question would be to what extent are the catching and prehension tasks studied in this thesis still different behaviors? Starting with the latter one could, based on the last two chapters of this thesis, argue that the difference between the two behaviors is, indeed, rather arbitrary. As Figure 3 in *Chapter 5* shows, it is hard to say when the observed grasping behavior is best characterized as catching and when it should be characterized as prehension. What we do know is that participants scaled their reaching amplitudes to the object's velocity of approach (see again Figure 3, *Chapter 5*). This illustrates that, as a function of object speed, behavior that is traditionally referred to as prehension (i.e., reaching to grasp stationary objects) gradually blended into behavior that is traditionally referred to as catching (grasping fast approaching objects by keeping the hand stationary). My interpretation of these results is that catching and prehension are basically the same thing, and that the blend of different behaviors (including catching and prehension) that I have observed in the experiments composing this thesis form a spectrum of actions covering the task domain of grasping.

The suggestion that the human movement repertoire does not consist of a set of predefined actions, but that it represents the gradual transition from one behavior into another fits the idea that, in terms of control, our actions are not predefined, they could just as well emerge from the actor-environment interaction (Warren, 2006). Take for example the observations described in this thesis. If an object does not move, we reach for it to grasp it. The amount of reaching, however, is reduced as a function of the approaching object's speed. So, the first-order time-to-contact that participants perceived was -in part- subject to the participant's reaching action which, then again, was scaled to the velocity of the (approaching) object, which can be perceived by picking up information about time-to-contact between hand and object, etcetera, etcetera.

The theory that the grasping behavior which we saw in catching and in prehension emerged from the ongoing action-environment interaction might offer an answer to the questions as to what is the actual difference between catching and prehension, and why we should bother about a generic control? Maybe the answer should be that to get a better understanding of how our grasping movements are controlled in catching and prehension, we should not focus on the discriminating aspects of the movement, but instead, try to understand what, in terms of control, these behaviors have in common.

So where do we stand when it comes to understanding how human grasping is controlled? The ultimate test to verify if one understands a control system would be to see if one could artificially replicate human behavior. In other words, would it be possible to, based on the knowledge gathered in this thesis, make a robot behave like our participants? Whereas the dynamic timing model, studied in this thesis would definitely improve a robot's grasping abilities in terms of timing the initiation of its hand closure, more research is needed to develop a full blown model for the control of catching and prehension movements. One important aspect that needs to be addressed is the modeling of the actual grasp formation. That is, this thesis dealt with the timing of hand closure, but it did not cover the shaping of the digits over time (forming the well-known grip aperture). Another line of research would be to make a coupling between the dynamic-timing model, that featured so prominently in this thesis, and the existing models on how our reaching and pointing movement are controlled (e.g., Schöner, 1990; Zaal et al., 1999). All in all, there is a great deal of work left to be done in this field. Still, I like to think that this thesis added valuable material for a convincing case of a generic understanding for the control of grasping which, in my opinion, is a powerful vehicle for revealing motor control in a much broader sense.

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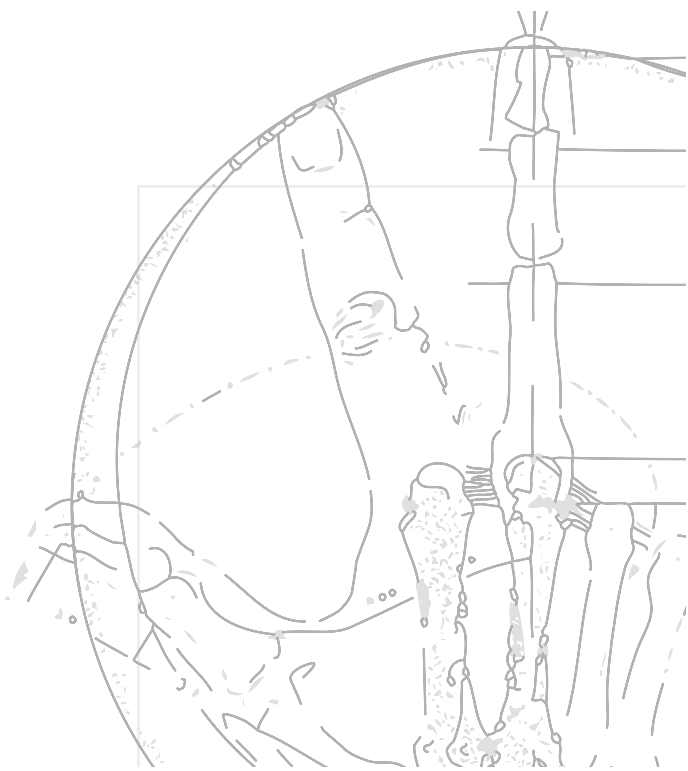
Summary



Getting a grip on grasping

Grasping enables humans to get a grip on a variety of surrounding things. This thesis describes a number of experiments studying grasping behavior. The aim of this thesis is to get a better understanding of how grasping movements are controlled in catching and prehension movements.

Chapter 1, is meant to provide some background on the experimental work reported in this thesis. The framework for the studies presented in this thesis is provided by a vast body of research on the visual guidance of goal-directed movements like hitting, catching, and prehension. A major research question that has been referred to in these studies concerned the timing of these movements. For instance, how do we, before raising our glass, manage to close our grasping hand around it in just the right time and place? In order to answer this question, this thesis focused on 1) the controlled variables, 2) the information, and 3) the control law. Previous studies paved the way in the development of these fundamental underpinnings of motor control. Zaal and colleagues (e.g. Zaal & Bootsma, 2004; Zaal, Bootsma, & Van Wieringen, 1998), for example, provided a model that based on time-to-contact information (tau) predicts the moment of hand closure in prehension. This 'dynamic-tau model', central to this thesis, combines elements of the theories of direct-perception and dynamical systems.

Before focusing on the information and the control law involved in grasping, the question: 'what are the controlled variables in prehension?' is addressed in *Chapter 2*. After 20 years of prehension research that had been based mainly on Jeannerod's (1981, 1984) hypothesis that prehension should be considered as the coordinated act of a reaching and a grasping movement, Smeets & Brenner (1999) proposed 'a new view on grasping'. Their alternative explanation was that prehension might just as well be seen as the simultaneous pointing movements of the thumb and the index finger. Whereas, traditionally, the hand aperture (i.e. the distance between thumb and index finger) had always been considered to be one of the controlled variables in grasping, according to Smeets and Brenner's 'double pointing hypothesis', this hand aperture is really an emergent property related to the time course of the positions of the two digits moving to their respective end points. In *Chapter 2* the latter hypothesis

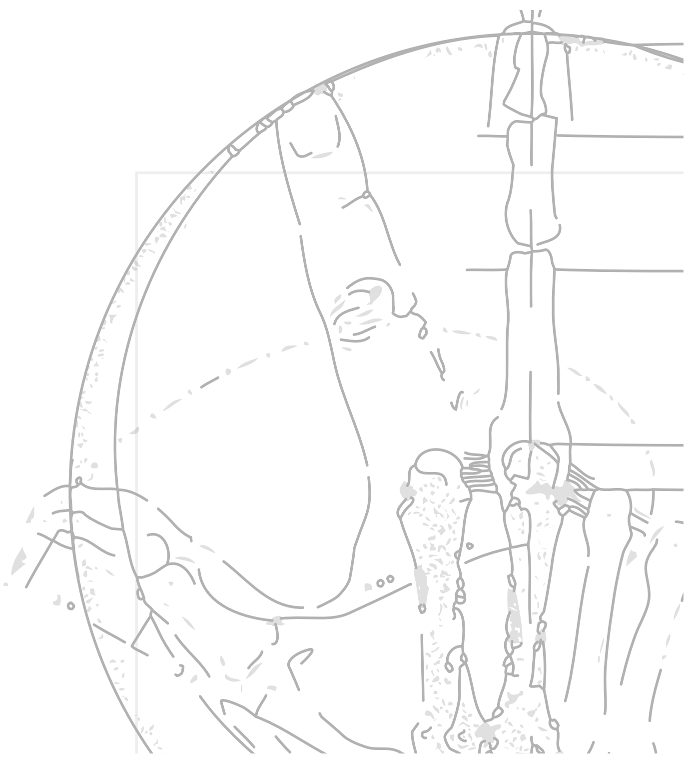
was tested by perturbing the end position of one of the digits while leaving the end position of the opposing digit unchanged. In the experiment reported in *Chapter 2* participants reached for and grasped an object of which the side surfaces could be made to slide in and out just after the reaching movement had started. In conflict with Smeets and Brenner's double-pointing hypothesis, it was found that in some cases, perturbing the end position of one digit also affected the kinematics of the opposing digit. This finding clearly disagrees with the double-pointing account. Therefore, it was concluded that rejecting the latter hypothesis logically leads to accepting the reaching and grasping hypothesis.

With two components making up one act, reaching and grasping, somehow, need to be coordinated. The traditional view on this issue has been that the grasping is temporally ordered on the time scale provided by reaching. Empirical evidence for a hierarchy of reaching over grasping seemed to come from experiments showing that when object location or size were changed at movement onset, adjustments in the reach component were much faster than adjustments in the grasp component. In *Chapter 3* of this thesis, this account is challenged by the finding that the grasp component can be just as rapid in responding to a change in object size (within 120 ms) as the reach component is reported to respond to a change in object position. These findings imply that the time scale on which an adjustment in the grasp component is ordered is not necessarily provided by reaching. This means that, empirically, the control model of a hierarchy of reaching over grasping lost one of its fundamental underpinnings.

This thesis studies an alternative means to consider the way the grasp component might adjust to size perturbations proposing that the responses to such perturbations result from the online control of the hand aperture. Instead of being ordered in a predefined hierarchical fashion the kinematic details of a grasping movement are believed to be continuously regulated, online, based on time-to-contact information. In *Chapters 4* and *5*, both the control law and the information that might be used for the control of hand closure initiation in grasping have been addressed. The idea tested in these chapters is that grasping behavior is best understood from an approach combining elements of the theories of direct-perception and dynamical systems. In a control scenario that involves first-order time-to-contact information, it does not really matter whether the hand moves toward the object, the object moves towards the hand or a combination of both takes place. This is because the first-order time-to contact information is about the relative hand-object movement. *Chapters 4* and *5* describe a number of experiments that provide evidence for a generic model for understanding the control of hand-closure initiation in both catching and prehension.

Chapter 6 reviews the impact of the results presented in this thesis. In this last chapter the implications, contributions, deficits, and practical application of the knowledge gained by this thesis are being discussed.

Samenvatting



Grip krijgen op hoe wij grijpen

Het grijpen van voorwerpen is een handigheid die het zijn van de mens heeft medebepaald. Dit proefschrift beschrijft een aantal experimentele studies naar het oppakken en vangen van objecten. Studies die tot doel hebben ons begrip met betrekking tot de bewegingssturing van het grijpen te vergroten.

De introductie, beschreven in *Hoofdstuk 1*, schetst het kader waarbinnen dit promotieonderzoek is uitgevoerd. De oorsprong van dit experimentele werk ligt in eerdere studies naar de visuele sturing van doelgerichte bewegingen zoals het vangen, oppakken en slaan van voorwerpen. Een van de vragen die binnen dit onderzoeksveld wordt gesteld betreft de 'timing' van dit soort bewegingen. Hoe wordt bijvoorbeeld de opening tussen duim en wijsvinger gecontroleerd zodat, alvorens het glas te heffen, de hand zich sluit rond het glas op precies de juiste plaats en op precies het juiste moment? Om deze vraag te kunnen beantwoorden worden in dit proefschrift zowel 1) de gecontroleerde variabelen, als wel 2) de informatie en 3) de controlewetten die hierop van toepassing zijn bestudeerd. Eerder onderzoek heeft op deze terreinen al vooruitgang geboekt. Zo biedt het werk van Zaal en collega's (e.g. Zaal & Bootsma, 2004; Zaal, Bootsma, & van Wieringen, 1998) een model voor het reiken en grijpen van de mens dat op basis van tijd-tot-contact informatie (tau) het moment van handsluiten voorspelt. Dit 'dynamisch-tau model' dat elementen uit de perceptie-actie theorie en de dynamische systeemtheorie combineert speelt een centrale rol in dit proefschrift.

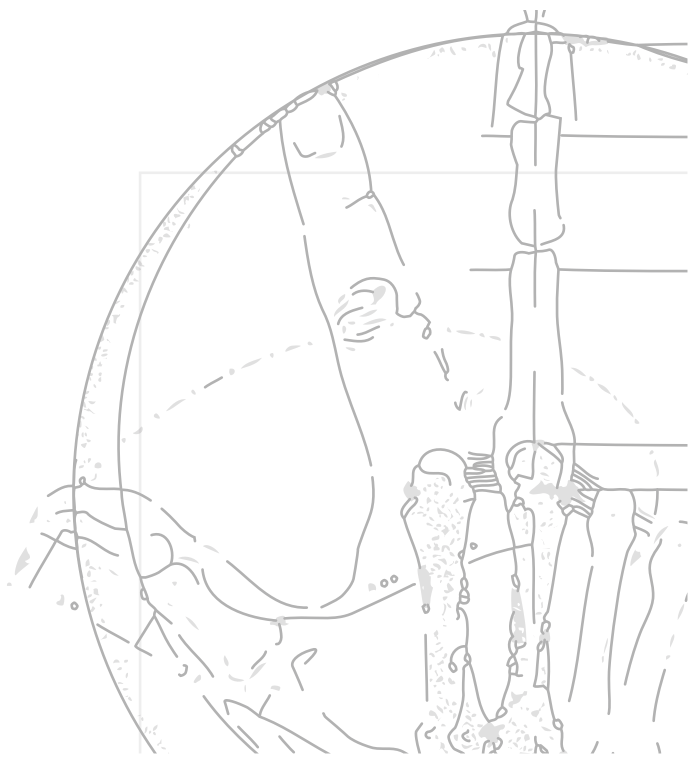
Alvorens de informatie en controlewetten die betrekking hebben op de sturing van onze grijpbewegingen te bestuderen wordt in *Hoofdstuk 2* van dit proefschrift stilgestaan bij de vraag wat de gecontroleerde variabelen zijn bij het oppakken van voorwerpen. Sinds het invloedrijke werk van Jeannerod (1981, 1984) wordt aangenomen dat een dergelijke beweging kan worden opgevat als een gecoördineerde actie van reiken en grijpen. Echter, tien jaar geleden stelden Smeets & Brenner (1999) dat een reik- en grijpbeweging ook kon worden opgevat als een gelijktijdig uitgevoerde wijsbeweging van duim en wijsvinger. De consequentie van deze 'double pointing hypothesis' is dat de grijpcomponent als zodanig niet bestaat, maar een emergerende eigenschap is, die voortkomt uit de gelijktijdig uitgevoerde duim- en wijsvingerbeweging. Uiteraard staat deze hypothese een model dat het reiken en grijpen van de mens beschrijft in de weg. Dat wil zeggen, het heeft geen zin om de timing van een grijpbeweging te bestuderen wanneer deze beweging, in feite, geen gecontroleerde variabele is. Zodoende is in *Hoofdstuk 2* van dit proefschrift gestart met een experiment dat is ontworpen om een antwoord te vinden op de vraag welke van deze twee hypothesen de meest aannemelijke is. Door gebruikmaking van een geavanceerd object, waarvan de grootte plotseling kan worden veranderd, wordt in *Hoofdstuk 2* aangetoond dat er geen empirische grond lijkt te bestaan voor het aannemen van de 'double pointing hypothesis'. Derhalve wordt in dit hoofdstuk geconcludeerd dat het oppakken van voorwerpen, als vanouds, kan worden opgevat als een gecoördineerde actie van reiken en grijpen.

Wanneer een actie als het oppakken van een voorwerp bestaat uit twee componenten, rijst de vraag hoe deze componenten onderling gecoördineerd worden. De traditionele opvatting was dat de grijpbeweging wordt aangeroepen op geleide van de reikbeweging. Empirisch bewijs voor deze hiërarchie van het reiken over het grijpen kwam van experimenten, die hadden aangetoond dat de mens zich sneller aan weet te passen aan een verstoring van de reikcomponent, dan aan een verstoring van de grijpcomponent. In *Hoofdstuk 3* van dit proefschrift worden vraagtekens geplaatst bij deze traditionele opvatting en wordt aangetoond dat wanneer tijdens een grijpbeweging een object plotseling verandert van grootte, het grijpen zich binnen 120 ms weet aan te passen. Deze responstijd is vergelijkbaar met de responstijden die zijn gerapporteerd voor reikbewegingen die zich aanpasten aan een verandering in object locatie. De bevinding dat aanpassingen aan het grijpen net zo snel kunnen verlopen als aanpassingen aan het reiken impliceert dat het tijdschema, waarop het grijpen wordt aangeroepen, niet per se bepaald wordt door de reikbeweging. Dit betekent dat, empirisch gesproken, het idee van een hiërarchie van het reiken over het grijpen een van zijn fundamentele onderbouwingen lijkt te zijn kwijtgeraakt.

In dit proefschrift is studie gedaan naar een alternatieve zienswijze voor hoe de grijpcomponent gecontroleerd wordt. Het idee is dat de kinematische details van de grijpbeweging niet van te voren zijn bepaald, maar dat zij continu, online, gereguleerd worden op basis van tijd-tot-contact informatie. In *Hoofdstukken 4* en *5* van dit proefschrift komen zowel de controlewet als de informatie die mogelijk gebruikt wordt voor het sturen van een grijpbeweging aan de orde. Het idee dat in deze hoofdstukken wordt getoetst is dat grijpgedrag het best kan worden beschreven door middel van een model dat elementen uit de perceptie-actie theorie en de dynamische systeemtheorie combineert. Een fascinerend gegeven is dat het voor een dergelijk model niet uitmaakt of de hand naar het object beweegt, het object naar de hand, of dat zowel hand als object in beweging zijn. *Hoofdstukken 4* en *5* van dit proefschrift beschrijven een aantal experimenten waarmee wordt aangetoond dat een enkel model kan volstaan voor de sturing van ons grijpen tijdens het vangen alsook het oppakken van al dan niet bewegende voorwerpen.

In *Hoofdstuk 6* worden de uitkomsten van de in dit proefschrift beschreven experimenten in onderlinge samenhang besproken. Er wordt in dit hoofdstuk stilgestaan bij de implicaties van dit proefschrift. Bediscussieerd wordt wat dit proefschrift heeft bijgedragen aan ons begrip van hoe wij grijpen, wat er is blijven liggen voor vervolgonderzoek en op welke gebieden de verworven kennis van toepassing zou kunnen zijn.

DANKWOORD



"*Niemand kan alleen. Ik schreef dit proefschrift met velen om mij heen. Enkelvoud beperkt, maar samen staan wij sterk*." (vrij naar Stef Bos). Hier wil ik dankzeggen aan iedereen die op welke manier dan ook heeft bijgedragen aan de totstandkoming van dit proefschrift.

Frank Zaal, zonder jou was dit proefschrift er niet gekomen. Bedankt dat je me de kans gaf te promoveren op het door jou opgezette project: 'The continuous visual control in goal-directed movements'. Ik bewonder je talent voor de wetenschap en ben je dankbaar voor wat je mij hebt geleerd, je altijd kritische oog en je doorzettingsvermogen. Van kaft tot inhoud verwijst mijn proefschrift naar het jouwe. Ik hoop dat je er trots op zult zijn.

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Bert Otten, inhoudelijk heb je ons alle vrijheid gegeven dit proefschrift te schrijven, maar ik ben blij dat je ceremonieel een hoofdrol speelt. Jij hebt me lang geleden laten zien dat wetenschap net als kunst een uiting is om je verwondering vast te leggen. Waar de wetenschapper woorden en formules gebruikt, gebruikt de kunstenaar schilderingen, foto's, gedichten en muziek. Te bewonderen verwondering.

Voor het onderzoek beschreven in dit proefschrift hebben we de meest fantastische opstellingen gebouwd. Een blokje dat van grootte verandert en een tafel, waarover objecten in twee dimensies kunnen worden bewogen. Henry van de Crommert, Wim Kaan, Wolter de Goede en Hans Thole bedankt, jullie hebben hierin een belangrijke rol gespeeld.

Ik bewaar goede herinneringen aan de tijd aan de Bloemsingel, A. Deusinglaan en Oostersingel. Door de jaren heen heb ik lief en leed mogen delen met collega BW'ers. Zonder iemand te zijn vergeten wil ik de volgende personen in het bijzonder noemen. Joost, buddy, dankzij jou werd onze kamer/bezemkast al snel 'the comedy corner'. Ik bewonder je humor en de keuzes die je hebt gemaakt. Helco, altijd enthousiast, in voor een chat en een helpende hand. Joanne, thanks for reading, listening and our kroketten-breaks. Rob B., Arjan, Esther, Pieter-Jelle, Harjo, Riemer, Linda (jouw rechterhand stond model voor de figuren in dit proefschrift), Wouter, Michel, Berdien, Rob W. en Gert-Jan, allemaal bedankt!

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Na Groningen kwam Manchester. Langs deze weg wil ik Frederik en Linda bedanken voor de warme ontvangst. Also thanks to Ian Loram (and everyone at the IRM) for offering me a new challenge and allowing me 'room' to finish this thesis.

Gelukkig bestaat er nog een leven naast het schrijven van een proefschrift.

Op sportief gebied kon ik de nodige energie kwijt bij GD/ULteam. Het was een mooie tijd en ik denk met veel plezier terug aan al die trainingen, wedstrijddagen en toernooien.

Ate, Sjouke, Marjan, Juha en Janneke. Geworteld in Groningen groeit onze vriendschap verder, waar ook ter wereld (al mis ik de vrijdagmiddagborrels in de Minnaar wel).

Ook wil ik hier graag 'de Kajuiten' noemen. Berry en Marieke, Caroline, Debby en Mark, Erik en Marlies, Evert en Jelmer, Frederik en Mirjam, Jeanine. Bedankt voor de jarenlange vriendschap en de onvergetelijke weekendjes weg. Nu is het tijd voor het lang beloofde feestje!

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Lieve moeder, Jannemieke en pa. Bedankt voor alles, 'een enkel opbeurend woord', de creativiteit en de werklust, die ik van jullie heb meegekregen.

Henri, Christien, Corine en Marcel, bedankt voor de interesse en steun.

Lieve Nienke, het is de eenvoud van de tweevoud, samen zijn we meer. You make me feel like flying!

STELLINGEN

behorende bij het proefschrift
Getting a grip on grasping
Cornelis van de Kamp
16 maart 2011

1. Prehension is really reaching and grasping (dit proefschrift).

2. Hoe meer wij het als onderzoekers ergens over oneens zijn, hoe moeilijker het zal zijn onze onenigheden bij te leggen. Dit is goed want, de dynamiek van onenigheid is de motor van de wetenschap.

3. De bevinding dat aanpassingen aan het grijpen net zo snel kunnen verlopen als eerder gerapporteerde aanpassingen aan het reiken, impliceert dat het argument, dat het grijpen hiërarchisch gezien onder het reiken valt, niet langer houdbaar is. (dit proefschrift).

4. Eén enkel model volstaat voor de sturing van ons grijpen tijdens het vangen en het oppakken van al dan niet bewegende voorwerpen (dit proefschrift).

5. Het menselijk bewegingsrepertoire lijkt niet te bestaan uit een set van voorgeprogrammeerde acties, maar weerspiegelt de graduele overgang van de ene gedraging in de andere. Wanneer dit als denkraam wordt toegepast in de robotica, zal de geloofwaardigheid van ‘humanoids’ toenemen.

6. Na het indienen van een artikel, ondervind je als promovendus aan den lijve dat de bewoording ‘submission’ niet treffender had kunnen zijn.

7. De stelling van Harry Mulisch “Sommige vragen zijn zo goed dat het jammer zou zijn ze met een antwoord te verknoeien” wijst erop dat de wetenschapper enige bescheidenheid past.