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Research report

Independent control of the digits predicts an apparent hierarchy of visuomotor channels in grasping

Jeroen B.J. Smeets *, Eli Brenner, Marianne Biegstraaten

Afdeling Neurowetenschappen, Erasmus MC, Postbus 1738, NL-3000 DR, Rotterdam, The Netherlands

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Abstract

If an object changes position at the onset of a reach-to-grasp movement, both the transport speed and the grip aperture are adjusted. If the object changes in size at the onset, only the grip aperture is adjusted. This combination of results has been interpreted as being the consequence of a hierarchical relationship between visuomotor channels for transport and grip. We argue that our alternative view on grasping can account for the observed behaviour without making new assumptions. In our view, grasping consists of smooth (minimal jerk) movements of each digit to a target position on the object. The digits' target positions change, both when object position and when object size change. A model in which the individual digits move smoothly to these new positions yields the same behaviour as is observed experimentally.

Keywords: Visuomotor; Control; Model; Prehension; Perturbation; Size; Position

1. Introduction

Grasping is a simple task that involves co-ordination of end-effectors. Such co-ordination is a fundamental aspect of motor control. To understand movement co-ordination one needs to know what components of a movement are co-ordinated. Based on the work of Marc Jeannerod et al. (e.g. [11,12,15]), it has widely been assumed that the components of grasping are grip and transport. These components are each controlled within a presumed visuomotor channel: one relating extrinsic object properties (i.e. its location) to the transport component and the other one relating intrinsic object properties (i.e. its shape and size) to the grip component. This view on grasping has been very influential. It forms the basis of many neuropsychological studies. For instance, it forms the basis of the study that showed a differential effect of a brain lesion on perception and action [8].

Our view on grasping (hereafter called the digit-view) is quite different. It is based on the widely accepted notion that 'the final finger position is the controlled variable of prehension' (as formulated on p212 in Ref. [12]). We converted this idea into a model for grasping in which the movements of the digits are controlled [22]. An emerging property of this control of the digits' movements is that the resulting transport and grip appear to be independent of each other. This independence fits well with the conclusions of a large body of experimental work (reviewed in Ref. [22]). However, the results of several experiments (see below) have indicated that transport and grip are not completely independent, but that there is a hierarchy between the transport and grip components: changes in the hand transport influence the grip component, but not the other way around. Is this hierarchy in behaviour a result of a hierarchy of two control mechanisms (thereby refuting the digit-view on grasping), or is it a direct consequence of the control of the digits?

The clearest experimental evidence for the hierarchical co-ordination of transport and grip was given by Paulignan et al. [16,17]. They studied grasping behaviour using two perturbation paradigms. In their experiments, a change of illumination of Perspex dowels was used to

* Corresponding author. Tel.: +31-10-4087565; fax: +31-10-4089457

E-mail address: smeets@fys.fgg.eur.nl (J.B.J. Smeets).

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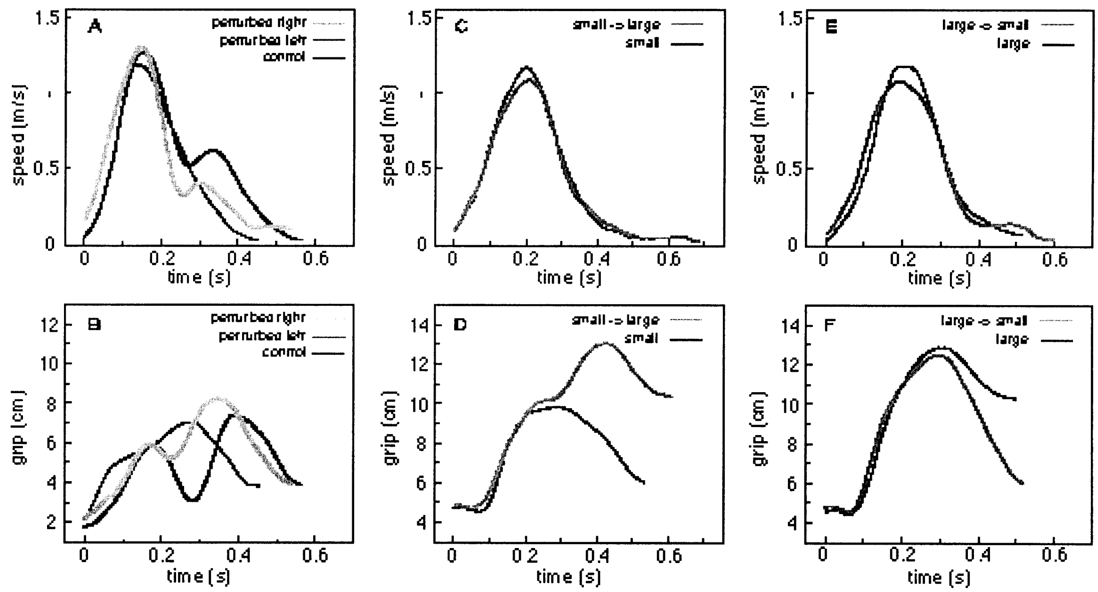

Fig. 1. The typical examples of the experiments of Paulignan et al. [16,17] replotted in the format we will use for our model results. Thin curves represent unperturbed (control) trials; thicker curves perturbed trials. A change of target position affects both the transport speed (A) and the grip aperture (B). A change of target size affects the grip aperture (D and F), but leaves the speed profiles unaffected (C and E).

change target size or location in some trials. When object size was perturbed [16], one might have expected a reorganisation of the grip, without a concomitant change of the transport component, because this manipulation only involved the putative intrinsic visuomotor channel. That is indeed what is found (Fig. 1C–F). When object position was perturbed [17], one might have only expected a change in the transport component, because this manipulation only involved the information in the putative extrinsic visuomotor channel. However, the profiles of both the transport component and the grip component showed a double peak in trials in which the target location was perturbed (Fig. 1A and B). Paulignan et al. concluded from the asymmetry in the results of these experiments [16,17] that there is a hierarchy between these components, whereby the reduction of transport speed triggers the onset of grip closure.

These results have been modelled by Hoff and Arbib using three hypothesised controllers: one for transport, one for preshape and one for enclosure [10]. In order to successfully incorporate all experimental findings, the model had to include many parameters and became rather complicated. We wanted to investigate whether the independent control of the digits can explain the asymmetric coupling between the transport and grip components. We therefore modelled both the above mentioned experiments by adapting our simple model for grasping [22] so that it could also deal with target-perturbation experiments. We did so using the approach outlined by Henis and Flash in Ref. [9]. This modelling was not aimed at explaining the experiments in detail. We therefore did not tailor the parameters to the specific experiment. We used the same set of parameters, based on values from the literature, to describe both experiments.

2. Target perturbations in a minimum jerk model

There are two ways to implement a change in target position in a minimum jerk description [6,9]. In the first one, the superposition scheme, the modified trajectories result from the vectorial addition of two movements: one for moving between the initial position of the hand and the initial target position, and a second one for moving from the initial to the final target position. These two movements each have their own timing. In the second implementation, the abort–replan scheme, the initial movement is aborted at an intermediate location and smoothly replaced by a new movement from that intermediate location to the final target position.

Although the superposition scheme has proven to be successful in some cases [9], it will not always provide acceptable results. This depends on the boundary conditions at the target. If the boundary conditions are zero speed and acceleration (as in Ref. [9]) the scheme works fine. However, if the first movement ends with a non-zero speed [20] or acceleration [22], this scheme works less well. This is especially the case if the correction continues after the first movement: the superposition movement will show a discontinuity in speed or acceleration at the time that the first movement ends. Since prolonged movement times are typical for the modified movement trajectories that we want to describe [16,17], and our implementation has non-zero end-point accelerations [22], we chose to implement the abort–replan scheme.

The initial movement follows the model described in [22]. Most parameters are based on the experimental data in [16,17]: the movement time is 500 ms, the object is at 35 cm distance and is 1.5 cm in diameter (6 cm for simulating the movements towards the large dowels in [16]). When simulating the change in object position [17] we used a displacement of 10 cm. The only free parameter in the model is the approach parameter a_p, for which we chose 1.5 m (the average value used to describe the experiments reviewed in Ref. [22]).

Aborting and re-planning a (correction) movement is something that one expects to take the same time as planning a movement in response to the appearance of a target. This is indeed what has been found for pointing movements, provided that the second stimulus appears more than 50 ms after the first [6,9,24]. We chose to abort the movement towards the initial target position at 350 ms after the target perturbation. This is a reasonable value for the reaction time, corresponding to the RT for grasping in randomised conditions [5]. Thus in our model, the correction movement starts 350 ms after the perturbation. The initial conditions of this second movement are the position, speed and acceleration of the initial movement at that instant. The correction movement lasts 250 ms, so that it ends 100 ms after the end of unperturbed movements, mimicking the experimentally found difference in movement time [16,17]. At the end of the correction movement, the digits contact the perturbed object with the same a_p as they would have had if the initial movement had not been perturbed. As the accuracy constraints on the movements remain the same, and a_p is thought to reflect those constraints, there is no reason to expect the a_p to change.

The above reasoning will be formalised in the remainder of this section. We model the movements of the digits in only two (horizontal) dimensions. Each dimension of a minimum jerk movement can be expressed as a function of time (t_u for the unperturbed movement; t_c for the correction movement) by:

$$x(t) = c_0 + c_1 t + c_2 t^2 + c_3 t^3 + c_4 t^4 + c_5 t^5 \tag{1}$$

The values for the six constants c_i can be found by applying six boundary conditions. We use the values for position x, speed $\dot{x}$ and acceleration $\ddot{x}$ at the onset and end of the movement:

$$c_0 = x(0)$$

$$\mathrm{MT}c_1 = \mathrm{MT}\dot{x}(0)$$

$$\mathrm{MT}^2 c_2 = \tfrac{1}{2}\mathrm{MT}^2\ddot{x}(0)$$

$$\begin{aligned}\mathrm{MT}^3 c_3 = \tfrac{1}{2}(&\mathrm{MT}^2(\ddot{x}(\mathrm{MT}) - 3\ddot{x}(0)) \\ &- 4\mathrm{MT}(2\dot{x}(\mathrm{MT}) + 3\dot{x}(0)) + 20(x(\mathrm{MT}) - x(0)))\end{aligned}$$

$$\begin{aligned}\mathrm{MT}^4 c_4 = \tfrac{1}{2}(&-\mathrm{MT}^2(2\ddot{x}(\mathrm{MT}) - 3\ddot{x}(0)) \\ &+ 2\mathrm{MT}(7\dot{x}(\mathrm{MT}) + 8\dot{x}(0)) - 30(x(\mathrm{MT}) - x(0)))\end{aligned}$$

$$\begin{aligned}\mathrm{MT}^5 c_5 = \tfrac{1}{2}(&\mathrm{MT}^2(\ddot{x}(\mathrm{MT}) - \ddot{x}(0)) - 6\mathrm{MT}(\dot{x}(MT) + \dot{x}(0)) \\ &+ 12(x(\mathrm{MT}) - x(0)))\end{aligned} \tag{2}$$

These equations have been written in a manner that shows that equation Eq. (1) can very easily be scaled with MT. The right side of the equations Eq. (2) are the constants one would get if equation Eq. (1) would be expressed as a function of the relative time t/MT. By writing it in this way it can be seen that the path becomes completely independent of MT if we scale the boundary values for speed $\dot{x}(0)$, $\dot{x}(\mathrm{MT})$ by 1/MT (if the MT is doubled, the initial and final speed are halved), and those for acceleration $\ddot{x}(0)$, $\ddot{x}(\mathrm{MT})$ by $1/\mathrm{MT}^2$. This scaled final acceleration is what we have defined as the approach parameter a_p [22]. For each unperturbed movement component x_u in our study, these boundary conditions are:

$$x_u(0) = 0; \quad x_u(MT_u) = l_u;$$

$$\dot{x}_u(0) = 0; \quad \dot{x}_u(MT_u) = 0;$$

$$\ddot{x}_u(0) = 0; \quad \ddot{x}_u(MT_u) = a_p/MT_u^2 \tag{3}$$

where l_u and a_p are the appropriate components of the movement amplitude and approach parameter vector. These values determine the course of the whole unperturbed movements (until $t_u = \mathrm{MT}_u = 0.5$ s), and also determine the course of the perturbed movement until the onset of the correction movement (at $t_u = 0.35$ s). The correction movement $x_c(t_c)$ starts at $t_c = 0$ and lasts until $t_c = \mathrm{MT}_c = 0.25$ s when l_c is reached. This corresponds to the interval $t_u = 0.35$–0.6 s relative to the start of the unperturbed movement. The speed and acceleration at the start of the correction movement are equal to those of unperturbed movement at $t_u = 0.35$. The boundary conditions of the correction movement $x_c(t_c)$ are thus:

$$x_c(0) = x_u(0.35); \quad x_c(MT_c) = l_c;$$

$$\dot{x}_c(0) = \dot{x}_u(0.35); \quad \dot{x}_c(MT_c) = 0; \tag{4}$$

$$\ddot{x}_c(0) = \ddot{x}_u(0.35); \quad \ddot{x}_c(MT_c) = a_p/MT_c^2$$

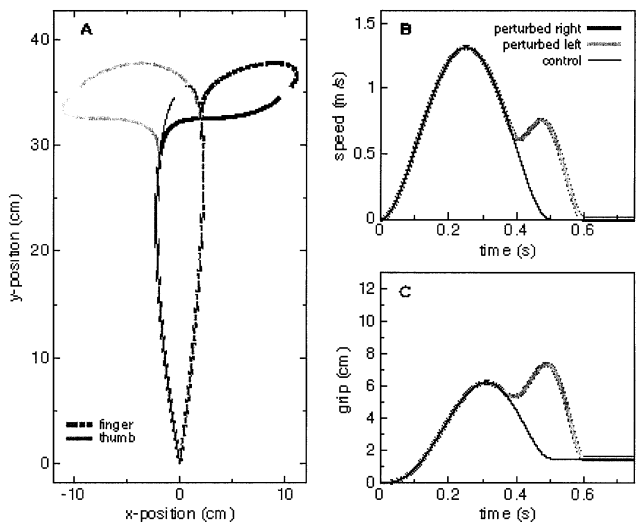

Fig. 2. Model calculations for the responses to position perturbations. Thin curves indicate the predictions for an unperturbed (control) trial, thicker curves those for perturbed trials. A: the minimum jerk path of the digits. B: the resulting profile for the transport speed. C: the resulting profile for the grip aperture. Panels B and C show the predictions for the experimental results shown in Fig. 1A and B.

3. Results

In Fig. 2 we present the model predictions for 10 cm perturbations of object position to the left and to the right. Fig. 2A shows the digits' movement paths. Fig. 2B the speed of the average of the digits' positions (transport speed) and Fig. 2C shows the distance between the digits (grip aperture), both as a function of time. The transport speed profile shows a clear second peak after correction onset, as is found experimentally (Fig. 1A). The main result is that the model predicts a double peak in the grip aperture, the remarkable experimental result of the experiments of Paulignan et al. ([17], replotted in Fig. 1B). In terms of the visuomotor channel hypothesis: a perturbation in the extrinsic channel influences the grip component, which is not part of that channel. Note that although the predicted adjustments of the digits' paths are quite different for the two directions of perturbation, the model predicts that both the transport speed and the grip aperture are exactly the same for both directions.

In Fig. 3 we present the model predictions for the transport speed and grip aperture for the changes in object-size. Fig. 3A and B shows the predictions for the increase in size, and in Fig. 3C and D for the decrease in size. The responses to both perturbations have essentially the same characteristics: the grip aperture is clearly reorganised, whereas the transport speed remains largely unaffected. The transport speed is very low in the 100 ms that the perturbed movements last longer than the unperturbed ones. In terms of the visuomotor channel hypothesis: the prediction of our model is that a

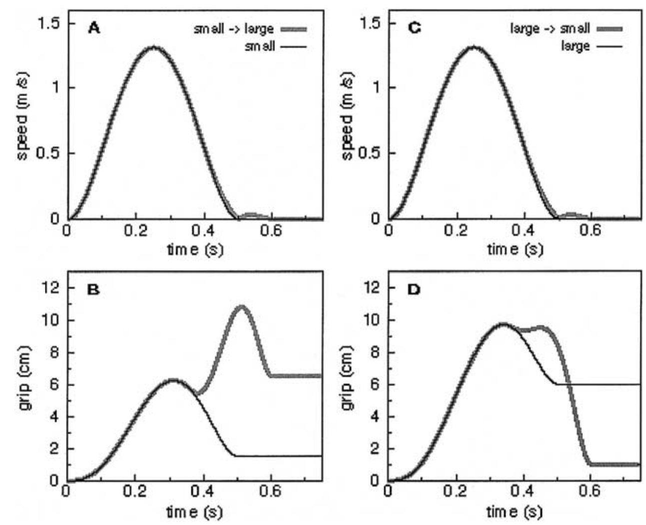

Fig. 3. Model calculations for the responses to size perturbations. Thin curves indicate the predictions for an unperturbed (control) trial, thick curves those for a perturbed trial. The direct outcome of the model (the individual digit's trajectories) is not plotted, only the resulting profiles of transport speed (A and C) and grip aperture (B and D). B: the predicted response to an increase in size (compare with Fig. 1C and D). C and D: the predicted response to a decrease in size (compare with Fig. 1E and F).

perturbation of the intrinsic channel (object size) does not influence the transport component.

In summary, the model trajectories reproduce the asymmetric interaction between the two visuomotor channels that Paulignan et al. [16,17] found experimentally.

4. Discussion

The basis for our model predictions is that the individual digits are controlled in grasping, rather than that a transport and grip component are controlled. Using a rather simple model to generate smooth movements of the digits, we predicted how they would respond to a change in the object's properties. We treated the perturbation of object size and object position in exactly the same way. We implemented them both as changes in the individual digits' target positions. For both digits, we implemented the correction according to the abort-and replan scheme of Henis and Flash [9], with the timing of the correction movements being the same for both perturbations.

Although the same scheme always governed the formation of the digit's response trajectory, its shape depended on the direction in which the digit's target shifted. As the target positions for the two digits moved either in the same direction (object position perturbation) or in opposite directions (object size perturbation), the transport and grip components looked quite different in the two object perturbation conditions. This result resembles closely the intriguing experimental results of Paulignan et al. [16,17]. Thus our simulation of the individual digits' movements predicts the asymmetric behaviour of the transport and grip components that has been observed.

Our model results resemble the experimental results even better than may appear from the typical examples in Fig. 1. For instance, our model predicts a second peak in the grip aperture for both kinds of size-perturbations. This feature is not visible in the typical example for the decrease in object size shown in Fig. 1F. However, table 3 in Paulignan et al. [16] mentions the timing of the second peak, which suggests that there was also a second peak in the aperture in most trials in which the size of the object changed from large to small. The model by Hoff and Arbib [10] also predicts this second peak.

There are some clear differences between the trajectories predicted by the model and the ones found experimentally. These differences are inherent to the limitations of the minimum jerk model. A first limitation is that a minimum jerk pointing movement (with zero derivatives at its boundaries) always has its peak speed at 50% of the movement time [7], whereas it is experimentally found at a time that depends on the movement speed [14]. The transport speed of an unperturbed grasping movement in our model has the same profile as a pointing movement, with its peak at 50% of the movement time. In the experiments that we discuss here, the peak speed was found before 40% of the movement, as was found for slow pointing movements [14]. A second limitation is that our model doesn't take obstacles into account. In the experimental set-up for the position perturbation experiments [17], there were obstacles (non-lit dowels) at all possible locations of the objects. If the subjects had chosen the model trajectories that are shown in Fig. 2 for the perturbed trials, they would have bumped into the dowels.

Some aspects of the model's predictions are the result of our deliberate choice to use the same parameters for both kinds of perturbations. Only in this way is it possible to show that control of the digit's movements leads to the observed asymmetry between the transport and grip components. That such control could be sufficient is evident from our model results. Nevertheless, it is insightful to discuss the sensitivity of the model for changes in timing. If the correction movement starts earlier, the second peak in the profiles of both transport speed and grip aperture fuse with the first peak. If the adjustment starts before peak transport speed, no second peak is visible. Delaying the response first introduces a second peak in the speed profile (for object position perturbation) and with a bit more delay also one in the grip profile (both peaks are completely separated if the response starts after 320 ms). In the typical example of Fig. 1F, the perturbed movement ends quite early. This might be an indication of an early response in this trial, which could explain the absence of a double peak in this example.

Short latency ($\approx$ 100 ms) goal-directed responses to a perturbation of an object's position have been found in pointing movements [2,18,25], as well in grasping [4]. In their grasping movements, Paulignan et al. [17] also found a first response to a change in target position after about 100 ms. However, this response was not goal-directed, but consisted only of a deceleration of the hand. No fast responses were observed for perturbations of object size [16] or for combined changes of position and size [3]. This lack of a short latency goal-directed response in these grasping experiments seems to be at odds with our assumption that grasping is controlled in the same way as pointing. However, short latency goal-directed responses have been found in grasping. Desmurget et al. [4] found such fast responses to a change in the orientation of a bar. Presumably, fast responses in grasping are only possible if no new set of suitable grasping positions for the digits need to be determined. In Desmurget et al.'s experiment [4], the bar really rotated, so that the same positions on the bar remained suitable for grasping. In the other experiments [3,16,17] various objects were continuously present, with a change of light indicating that the target object for grasping had changed. When another object becomes the target, a new set of suitable grasping positions for the digits needs to be determined, probably making short latency goal-directed responses impossible.

As already mentioned, we assume in our model that the accuracy constraints at the object are the same for perturbed and unperturbed movements. This was achieved by keeping the approach parameter a_p constant. Our definition of this parameter was specifically chosen to make the movement path independent of the movement time, so that this parameter corresponds to the required accuracy. In this way, we could predict how accuracy constraints would affect grasping behaviour [22]. A consequence is that the acceleration at contact decreases with increasing movement time (Eqs. (3) and (4)). This is in line with experimental results showing that impact force and deceleration at impact decrease with increasing movement time for pointing [1,23]. In the calculations presented here, the movement time for the correction movement (MT_c) is smaller than for the unperturbed movement (MT_u), so the same value for a_p corresponds to a larger final acceleration for the correction movement.

Our model is very simple: it has only one parameter, which we did not vary in the present study. The model treats grasping as independent (but simultaneous) pointing movements of the digits. We have previously shown that this model could describe a wide range of experimental results on the transport and grip component of prehension very well [22]. Moreover, it could also describe the movements of the individual digits [21]. In the present study, we extended the model predictions to perturbation experiments. This showed that the experimentally observed asymmetric coupling between the hand transport and grip opening follows directly from the symmetric control of the digits.

These results add to the attractiveness of the digit-view on grasping. They do not prove that this view is right. The wealth of studies interpreted using the grip-control view on grasping do not prove that that view is right either, as those studies can also be interpreted using the digit-view [19,20,22]. For instance, Goodale, Milner et al. [8,13] reported that some patients are able to preshape their hand to object size, while not being able to indicate that size with her hand. Our interpretation is that these patients are able to process positions (needed for grasping) but not sizes (needed for indicating size).

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