Synergies in Grasping

Jeroen B.J. Smeets and Eli Brenner

Abstract The reach-to-grasp movement is a prototype of human movement coordination. Since the pioneering work of Jeannerod (Attention and performance, ix. Erlbaum, Hillsdale, NJ, pp 153–169, 1981), this movement is generally considered to be a coordinated combination of hand transport and grip formation. One of the main theoretical reasons for choosing transport and grip as building blocks is that they are anatomically independent: one can determine whether each muscle, joint, or brain area belongs to transport or grip. We have proposed a different view on grasping, in which the coordination problem is formulated as one related to the movements of the digits (Smeets and Brenner in Motor Control 3:237–271, 1999). According to this view, both the transport of the hand and the formation of the grip emerge from the combination of independent digits' movements toward the objects' surface. This independency of the digits resembles the independence of synergies (as discussed in the chapter of d'Avella). Different synergies are activated independently, but a single muscle can be part of several synergies. In this chapter, we will present three types of experiments that were designed to test to what extent the individual digits' movements can be considered as the building blocks of the reach-to-grasp movement.

Keywords Reach-to-grasp · Digits · Finger-thumb asymmetry · Visuomotor · Prehension · Hand transport · Grasp control

Introduction

Marc Jeannerod started the study of the grasping movement by postulating two independent visuomotor channels through which visual input controls the movement (Jeannerod 1981). The argumentation for this postulate was based on the

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observation that grasping can be functionally split into a reach component (bringing the hand to the location of the target) and a grasp component (opening the hand in accordance with the size and shape of the target). A corresponding distinction is present in the nature of visual information: information about intrinsic properties like shape and color ("what") is essentially different from extrinsic properties such as distance and orientation ("where"). Both distinctions are also thought to be present in the neural processing: the neuromuscular system for shaping the hand is to a large extent independent of the system that is used to transport the hand to the object (Brinkman and Kuypers 1973) and it has been argued that there are distinct neural pathways for "what" and "where" (Trevarthen 1968; Ungerleider and Haxby 1994).

An underlying assumption in the above argumentation is that we can understand human sensorimotor control better if we regard it as two (neuro-) anatomically distinct pathways, each serving a distinct function. This assumption that distinct structures are the building blocks of behavior is not specific to the reasoning of the papers cited above, but also underlies some other influential schemes, such as the two visual systems hypothesis (Goodale and Milner 1992; Milner and Goodale 2006, 2008). However, one could also bring order into distributed control systems by the concept of synergies (Lee 1984; Soechting and Lacquaniti 1989; d'Avella et al. 2003; Ting and Macpherson 2005; Latash et al. 2007; Tresch and Jarc 2009; Overduin et al. 2015). The cited studies all define synergy in their own way. For the present purpose, the most important commonality is that a single biomechanical element (e.g., muscle or joint) can be part of several synergies. Importantly, the concept of synergies implies that there is no need to have a strict separation between anatomical aspects of a task. The components could therefore be selected such that they could be combined with other components to perform quite different tasks. This is potentially a more efficient strategy, because it allows any combination of components of movements to be combined in different ways for different tasks. A consequence, however, is that the components might not be optimized for a single task.

We will concentrate on kinematic synergies: movements of joints that are controlled as a single unit. In our earlier work (Smeets and Brenner 1999, 2001, 2008; Verheij et al. 2012), we proposed that the tips of the individual digits are controlled in grasping. In terms of synergies, we thereby assume the existence of two synergies: a thumb synergy and an index finger synergy. Given the fact that the index finger and thumb are part of the same hand, the two synergies' substrates overlap: they both contain the shoulder, elbow, and wrist; they differ in the more distal joints.

At the level of muscles, synergies have been defined as coherent time-varying patterns of muscle activations (d'Avella et al. 2003; Tresch and Jarc 2009). It has been shown for force control that the directional tuning of the synergies that are determined on the basis of the forces exerted at the end effector closely resemble the tuning of synergies that are based on an analysis of the EMG of more than ten muscles that are involved (Ting and Macpherson 2005). Therefore, we limit our analysis to the movements of the end effectors: the index finger and thumb. The

essence of the concept of synergies is that the same synergies are used in many tasks to simplify control. In other words, specific characteristics of synergies should be visible in more than a single task. If the thumb and finger synergies are indeed the building blocks of grasping movements, we should be able to see the signature of the same two synergies in other tasks like pointing (we use this term for pointing to an object by moving to touch it with a single digit). In this chapter, we will describe three ways to study the signature of synergies in kinematics. The first way is to study idiosyncratic differences in the kinematics of the end effector: if synergies vary between individuals, the same differences should be visible in all tasks that involve these synergies. The second way is to adapt the synergies: if a synergy is adapted in pointing, this adaptation should transfer to grasping. The third way is to observe fast responses: if a target changes during a goal-directed movements, the fastest responses should be a direct manifestation of the synergies, neglecting higher coordination.

Idiosyncratic Kinematics

If the movements of the digits are the synergies in grasping movements, the characteristics of the movements of the digits during grasping movements should be similar to those of movements of a single digit. The typical grasping movement starts with both digits at a staring position, then moving the hand toward the object while at the same time moving the digits apart to open the hand to be able to grasp the object (Jeannerod 1981). At about 75 % of the movement time (at 95 % of the distance; Cuijpers et al. 2004), the digits start closing to contact the object (Jeannerod 1984). How can we compare the movements of the digits in this task with a movement of a single digit with similar constrains?

We argued that we could do so by looking at the difference in shape of the trajectory between finger and thumb. If a separate finger synergy and thumb synergy exist in grasping, the resulting trajectory formation is likely to be slightly different for the two digits. Of course, finding a difference does not prove that they are separate synergies. It might be that the trajectory of the thumb is less curved than that of the index finger because the thumb is transported during grasping, and the finger moves relative to the thumb, as has been proposed on the basis of such findings (Haggard and Wing 1997; Mon-Williams and McIntosh 2000; Galea et al. 2001). If this were the case, one would not expect to find the same difference between finger and thumb if one were to compare the trajectories of pointing movements with these digits. On the other hand, if the difference between finger and thumb are completely due to differences in the synergies, one would expect the same differences to be present in other tasks involving the same synergies. To test these predictions one could use a task that is expected to recruit the same synergies as in the reach-to-grasp movement, but while independently performing different movements at different times with the two digits.

We decided to compare the reach-to-grasp movement with the reach-to push movement: move a single digit toward an object's surface in order to push that object away. This comparison is a reanalysis of the data of two of the three tasks in an earlier study (Smeets et al. 2010). We evaluated how much the trajectories of the two digits deviated from each other's mirror image, both when moving together during the reach-to-grasp movement, and when moving independently during a reach-to-push movement. We did this by dividing each path of an active digit into 100 segments of equal length, and subsequently averaging the paths of all trials for each of the 101 ends of the segments. We subsequently mirrored the average trajectory of one of the digits, and aligned the start and end position with that of the other digit, and determined the difference between the two (Fig. 1). We refer to this difference as the finger-thumb asymmetry.

We have two hypotheses for this finger-thumb asymmetry. The first hypothesis is based on the view that this asymmetry is based on the specificities of the control of grasping (Haggard and Wing 1997; Mon-Williams and McIntosh 2000; Galea et al. 2001). If this "grasp control" hypothesis were correct, one would expect the finger-thumb asymmetry in grasping to be consistent across subjects, and one would not expect the asymmetry in grasping to be very consistent with the asymmetry in pushing. In both cases, a slight asymmetry might be caused by the underlying anatomy (reducing the similarity between subjects with different physique or introducing some similarity between tasks performed with the same arm, respectively). On the other hand, if the asymmetry were caused by the difference between the thumb synergy and the finger synergy ("digit control" hypothesis), one would expect little consistent asymmetry across subjects, but one would expect each subject to show a consistent finger-thumb asymmetry across the two tasks. Finding such idiosyncratic asymmetries would not tell us anything about the underlying reason for the asymmetry. It might be that small anatomical differences between subjects are responsible. However, finding similar asymmetries, even if due to anatomical differences, in both pushing and grasping would support the idea that the two tasks are based on similar control mechanisms.

Fig. 1 Determining the finger-thumb asymmetry from the (*average*) movement paths of the digits (*top*). The ends of the paths were aligned and one was mirrored (*middle*), after which the separation between the two was determined (shown magnified by two at the *bottom*)
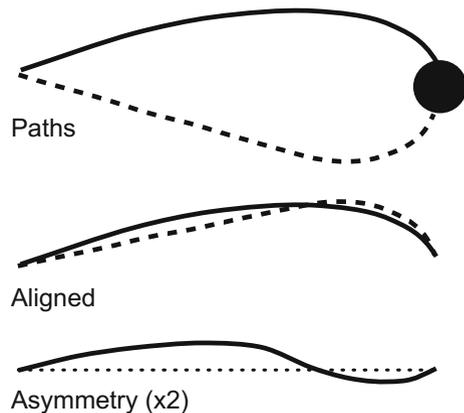
We assessed the asymmetry by the Pearson's correlation coefficient between the asymmetry values across segments of the path (based on the average of 20 trials for a subject in a task). We did this both across tasks (within a subject), and across subjects (within a task). We chose this method because the two digits move independently (on different trials) in the pushing experiments, while they were physically connected when grasping. As this physical connection limits the possible curvature of the digits' paths, it might change the overall size of the asymmetry. We therefore chose to use the correlation along the path, rather than some measure of the distance itself (such as the sum of the squared differences) as our measure of the asymmetry. The predictions for the two hypotheses are plotted schematically, together with the experimentally obtained values in Fig. 2.

In line with both hypotheses, the asymmetries found when pushing are not highly correlated across subjects. This means that the differences between the shapes of the trajectories of finger and thumb are idiosyncratic, and thus not determined by the differences in anatomy between the two digits (which are common to all subjects). For the other two correlations, the hypotheses made opposite predictions. In line with the digit control hypothesis, we found that the asymmetries when grasping are not highly correlated across subjects, just as in pushing. So, also here, the differences in the trajectories are idiosyncratic, rather than being determined by a control mechanism or anatomic difference that is shared by all participants. The finding that the asymmetry in grasping is highly correlated with that in pushing is obviously also in line with the digit control hypothesis. This correlation means that if a certain difference between the trajectories of finger and thumb is found when moving together while grasping, a similar difference is found when comparing pushing with the thumb with pushing with the index finger.

The results are in line with the predictions made by assuming separate synergies for the control of finger and thumb that are used for both pushing and grasping. The overall correlation between subjects in the asymmetry is about 0.25 in both tasks. This means that the consistency in the difference between finger and thumb across subjects is not negligible, which is probably not surprising given the anatomical
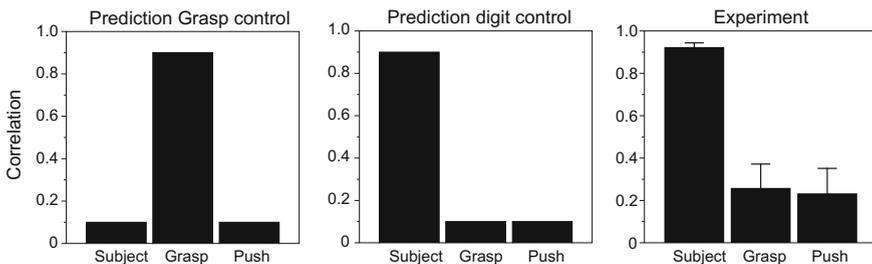

Fig. 2 Predictions for two hypotheses and the actual experimental values for the correlation between asymmetries. The correlation is calculated between the two tasks within each *subject*, or between subjects within the grasp or push task. For the predictions, we plotted "strong correlation" as 0.9, and "weak correlation" as 0.1. For the experimental data (reanalysed from Smeets et al. 2010), the *error bars* show the standard error of the mean across subjects and pairs of subjects

differences between the digits. Most importantly for the present discussion is that the consistency in the asymmetry across subjects is the same for both tasks. In terms of the digit control hypothesis: apparently, despite the anatomical similarities between subjects, the finger synergy and the thumb synergy differ in a consistent way between subjects.

Visuomotor Adaptation of Synergies

Pointing

A second line of research that supports the existence of separate synergies for the thumb and index finger is that of visuomotor adaptation. We performed an experiment in which subjects were pointing alternatingly to the left and right side of a cube, using the thumb and the index finger, respectively (Schot et al. 2014). The cube could be placed at one of three positions at the far end of a wooden board. Subjects made their (curved) movements under the board, so the hand was invisible during most of the movement. Only the digit that made contact with the cube became visible when it was near the cube. We used the last position of the digit before it became visible to measure adaptation.

After a baseline phase with an unperturbed (binocular) view of the target, we gave the subjects a special pair of prism spectacles. These spectacles contained one leftward and one rightward deviating prism, combined with shutters. The shutters ensured that the subjects only looked through one of the prisms; which one depended on the movement they were asked to make. They experienced a leftward deviated view when pointing with their thumb and a rightward deviated view when pointing with their index finger. As subjects saw the target cube displaced 5 cm to the left of its actual position when moving the thumb, subjects initially moved their thumb to a position 5 cm more to the left than without a prism. In a next trial (with the index finger), subjects saw the cube 5 cm to the right, leading to an error in the opposite direction. After 45 trials with each digit, we removed the prisms, and let the subjects view binocularly again. Comparing the behavior in the post-adaptation phase with the baseline is a clean measure of the effect of adaptation of the digits' movements. In a second session, we reversed the pairing (Schot et al. 2014). What do we expect to happen to the arm movements?

Visuomotor adaptation can be divided in a visual and a motor (proprioceptive) component (Redding and Wallace 1988). As human vision combines the images of the two eyes from early vision on, the visual part of the adaptation will be common for the movements of both digits, and thus cancel each other. If one does not assume that separate synergies for the control of the digits' movements adapt independently, but assumes that each of the joints adapts independently, one would predict that adaptation will be distributed over the joints that are involved in the movement (depending on how much each joint contributes to the movement). As

the shoulder, elbow, and wrist are responsible for most of the transport of the digits in space, this would mean that most of the adaptation would occur in these joints. The consequence would be that the effect of the two opposite perturbations would cancel each other. We would therefore expect very little adaptation. Only information about the orientation of the eyes and of some joints in the hand would adapt. If the synergies underlying the finger and thumb movements adapt, one would expect considerable adaptation of both synergies in opposite directions.

What we found is that both digits adapted to the visual displacement that was associated with their own movement (Fig. 3b, c). The adaptation that was obtained was about 60 % for both digits (asymptotes in Fig. 3). Each digit's adaptation resembled the conventional result for viewing through prisms (Martin et al. 1996) or moving through force fields (Shadmehr and BrashersKrug 1997). Such adaptation can be described by various models of (sensori-)motor learning (Smeets et al. 2006; Smith et al. 2006). The results are therefore consistent with the predictions based on independent synergies for the index finger and thumb.

The adaptation was incomplete. This could be interpreted as evidence that the adaptation of the two digits was not independent. However, it has been shown that in conditions with terminal feedback continuous forgetting can lead to incomplete adaptation (van der Kooij et al. 2015). If forgetting were the cause of the incomplete adaptation in Fig. 3, a similar incomplete adaptation would be obtained for blocks of trials with only movements of the thumb (or of the index finger), although the adaptation would probably be less incomplete because the trials with the same digit
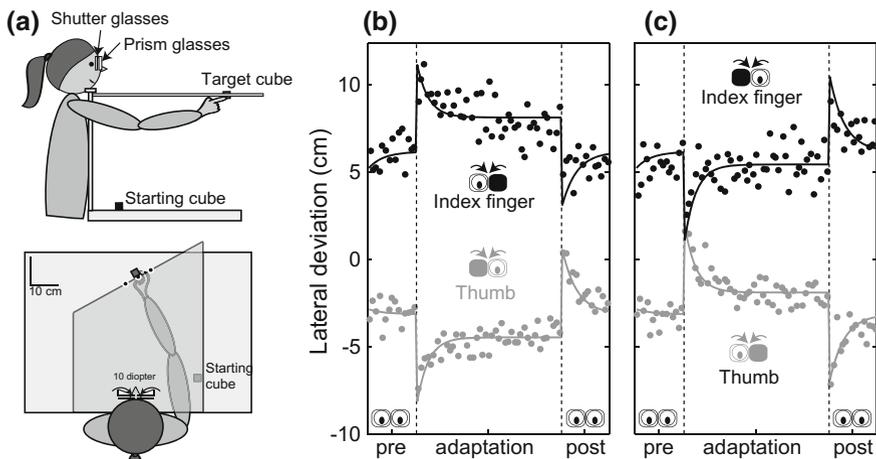

Fig. 3 Simultaneous adaptation of index finger and thumb to opposite prism displacement; data are reanalysed from (Schot et al. 2014). **a** *Side* and *top* views of the subject performing a finger pointing movement. The hand remains invisible until just before the end of the movement. **b**, **c** behavior for the two sessions with opposite pairing between the digit that was moving and the viewing eye (and therefore the direction of the displacement). *Points* average response of the eight subjects. *Curves* exponential fit to the data points (constrained to have a change in deviation equal to the size of the prism-induced displacement at the time of addition/removal of the prism)

Fig. 4 Adaptation with
alternating prism-digit
association compared with a
blocked association. In the
latter case there is complete
adaptation
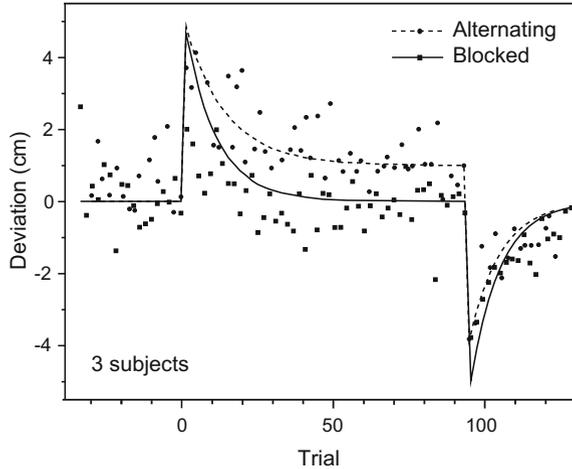
will be closer to each other in time (or number of movements). We tested this with a
small number of subjects (3), and found *complete* adaptation (Fig. 4). Apparently,
the present paradigm (involving real prisms and goal-directed movements that
contact the targets) does not lead to trial-to-trial forgetting. We do not know why,
but perhaps the presence of haptic feedback in the present experiments is important
(Cuijpers et al. 2008; Schenk 2012). Thus, the adaptation that we found on its own
does not provide conclusive evidence for adaptation within synergies related to the
digits.

Transfer to Grasping

In the previous section, we argued that we could adapt the synergies for the thumb
and index finger separately. The main claim in this chapter is that the same syn-
ergies that are used in pointing are used in the reach-to-grasp movement. If this
claim is correct, adaptation of the synergies during pointing should result in an
aftereffect in the reach-to-grasp movement. As the adaptation is in opposite
directions for the two digits, we predict that the aftereffect of adapting pointing
movements will be an increase or decrease of grip aperture (depending on the
direction of adaptation).

The best way to test a prediction for the transfer of an aftereffect from pointing to
grasping would be to make it quantitative. However, based on Fig. 3b, we realized
that such a prediction would be unrealistic. After removal of the prisms, the pre-
dicted deviation of each digit has changed by about 3 cm. For grasping, this would
imply that the grip aperture would be either increased or reduced by 6 cm,
depending on the pairing between prism and digit during the adaptation phase. As
our objects' widths are less than 5 cm, the planned positions for the digits in the

aftereffect of the thumb-left pairing would correspond to a crossed configuration of the thumb and the index finger. And the planned positions for the digits in the thumb-right pairing would correspond to the grip aperture for an extremely large object, bigger than any object used in research on the precision grip (Smeets and Brenner 1999). In both cases, the planned end configuration is outside the normal range (left part of Fig. 5), inevitably leading to limited transfer. Therefore, we cannot expect to have full transfer of the aftereffect of adaptation from pointing to grasping, so we limit our prediction to a qualitative one: there will be clear transfer from pointing to grasping.

To test this prediction, we repeated the adaptation experiment, and made one change relative to the experiment described above: we not only varied the position of the block, but also its size. In this way, we ensured that all parameters of grasping that might be controlled vary between trials: both the contact positions (our theory) and the position and size of the target (classical theory). Note that the visual perturbation that we applied in the adaptation phase only shifted positions, leaving the size of the objects unaltered.

The right panel of Fig. 5 shows that in all three conditions, grip aperture scales in a normal way with object size. Importantly, apertures are larger after adaptation of pointing with the thumb-right pairing than after adaptation with the opposite pairing. In this figure, we see a slightly smaller effect for the large object in the thumb-right pairing, presumably due to the ceiling effect that we predicted for this pairing. For the opposite pairing, we frequently observed that subjects' digits touched each other once or twice in the first few trials of grasping, in line with the prediction of the bottom-left of Fig. 1. The transfer from pointing to grip aperture
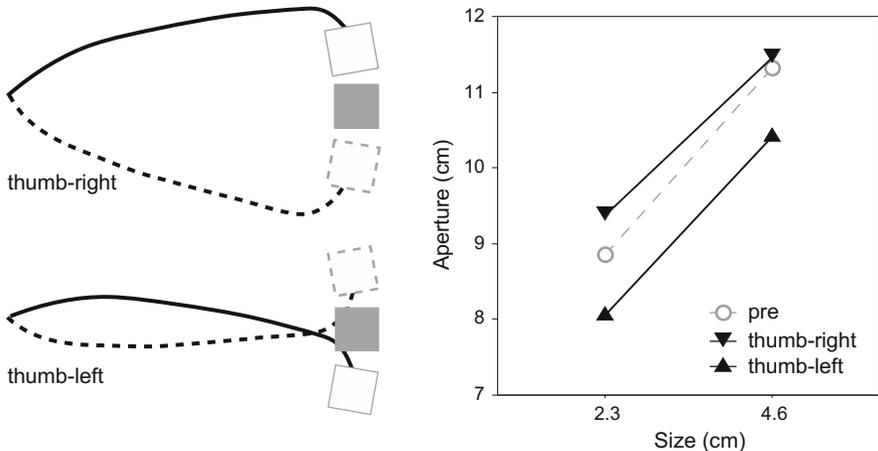

Fig. 5 Transfer from pointing to grasping. *Left panel* the paths corresponding to 100 % transfer for both pairings. The *solid squares* represent the target; the *open squares* and *curves* represent the situation corresponding with a full aftereffect. These paths are impossible to produce. *Right panel* the actual grip apertures when the digits were approaching the border of the board (for the two target sizes). There is a clear transfer of the aftereffect

shows that grasping is not controlled fundamentally differently from moving the individual digits during pointing. Assuming that synergies regulate movements of the thumb and index finger separately, irrespective of the task, provides a parsimonious explanation for these findings. Assuming that grip aperture is regulated by a separate synergy involved in grasping cannot account for the transfer.

Fast Responses to Perturbations

Humans are known to be able to adjust their movements to changes in the position of a target with a very short (∼110 ms) latency (reviewed by Cluff et al. 2015; Smeets et al. 2016). Such fast responses are very interesting, as they must be based on the least amount of information processing possible: a fast link between visual information and the fundamental elements of control. As these fast responses do not take into account all information, the responses can sometimes be counterproductive. We showed this for a situation in which an obstacle is initially positioned to the left of the line connecting the hand to the target. In unperturbed trials, subject then veer slightly rightward. If this obstacle jumps to the right of the line, the optimal response would be to veer slightly leftward. This is however not what happens: subjects follow the target, and veer more to the right, and therefore hit the obstacle (Aivar et al. 2008). The reason is probably that the movement was planned to pass the obstacle on the right, and the first response to a change in position was a direct response to the change in the obstacle's position, without reconsidering one's options.

As fast responses link low-level elements of perception to those of motor control, they can be used to reveal the synergies that underlie grasping behavior. This has been done in paradigms that involved changes in the position and/or size of an object (Paulignan et al. 1991a, b; Smeets et al. 2002; van de Kamp and Zaal 2007; Hesse and Franz 2009; van de Kamp et al. 2009). For instance, the fact that a perturbation of the contact position for one digit sometimes has a small effect on the trajectory of the other digit (van de Kamp and Zaal 2007) has been used to argue that they cannot be controlled independently. However, the coupling between the digits can also be mechanical. We therefore present data on responses to object rotation.

There are relatively few studies on responses to object rotation when grasping (Desmurget et al. 1996; Voudouris et al. 2013). The oldest experiment showed that you can adjust the orientation of your hand during a whole-hand-grip grasping movement to a change in object orientation with a short latency (Desmurget et al. 1996). In our experiment (Voudouris et al. 2013), we let subjects grasp lightweight objects (a cube or a sphere) with a precision grip. The objects were magnetically connected to a motor that could rotate them very quickly over 12° (clockwise or counterclockwise) as soon as the subject initiated their grasping movement. For grasping the cube, it is clear that subjects should respond to the perturbation, otherwise their grip orientation will not coincide with the surfaces of the cube. For

grasping the ball, rotating the hand in response to the ball's rotation does not provide any advantage. What would we expect for various direct couplings between visual information and controlled synergies?

According to the grasp control hypothesis, the presumed synergies are the transport and grip: the transport synergy, that includes the orientation (Jeannerod 1981; Desmurget et al. 1996), is coupled to the extrinsic object properties position and orientation, whereas the grip synergy is coupled to the intrinsic object property size. As none of these properties changes when a ball rotates, this hypothesis predicts no response (which is indeed optimal). According to the digit control hypothesis, the presumed synergies are the digit's movements. These movements are directed to suitable contact positions on the surface of the object. So, if the object rotates, the intended contact positions move, which will lead to fast adjustment of the digits' movements.

In line with the prediction of the digit control hypothesis, we always see a fast response to object rotations (Fig. 6). The sign of the response depends on the direction of the rotation: the digits follow the object's surface. The response is initially the same for the cube and the ball, but continues for more than 200 ms for the cube (left panel), whereas it disappears within 50 ms for the ball (central panel).

To test whether the short duration of the response for the ball is due to a reselection of grasping points, we performed an experiment in which the cube was placed in an ambiguous orientation that allowed for two grasping orientations (right panel of Fig. 6). We restrict our analysis to the subjects who changed their grip orientation in response to the perturbation. We see an initial following response that stops after about 50 ms and reverses its direction. This response is very similar to the response to the rotation of the ball. Thus the fastest response consists of digits following the local position on the surface, whereas only the later parts of the
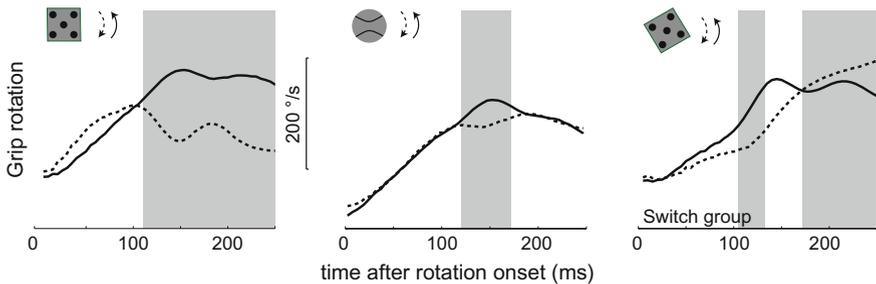

Fig. 6 The velocity of rotation of the grip in response to target rotations in opposite directions. Data replotted from Voudouris et al. (2013). The *gray* area indicates times at which the rotation speed differed for the two directions. Three conditions are displayed: grasping a cube for which it is clear by which surfaces it can best be grasped (*left*), grasping a ball (*center*), and grasping a cube that is oriented so that it is not evident how best to grasp it (*right*). In the latter case, subjects sometimes switch their choice of surfaces in response to the perturbation. In all conditions we see an initial fast response in the direction of the rotation of the target (*solid curves* above *dashed* ones). For the ball and the cube with the ambiguous orientation, subjects chose new contact points within 50 ms of their initial response

response consider the object's shape (for the ball) and orientation (for the cube). The results of the fast responses thus suggest that the synergies are therefore related to the positions on the surface of the object (i.e., digit control), rather than to the object as a whole (grasp control).

Take Home Message

We used three totally different paradigms to study whether the classical grip control (with synergies *transport* and *grip*) or digit control (with synergies for the individual digits) yield the most comprehensive description of the reach-to-grasp movement. We found that the peculiarities of the digits' movements varied considerably between subjects, but were (within a subject) remarkably consistent across grasping with two digits and pushing with a single digit. Second, we showed that by using prisms, we can adapt the pointing movements of finger and thumb in opposite directions, and that the aftereffect of these adaptations transfers to grasping. Third, we show that when grasping a ball with a precision grip, the digits show a fast following response to a (task-irrelevant) rotation of the ball. All these findings suggest that the elements that are controlled in grasping are synergies for the individual digits, rather than synergies for transport and grip.

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