

REVIEW | *Control of Movement*

A review of grasping as the movements of digits in space

 Jeroen B. J. Smeets, Katinka van der Kooij, and  Eli Brenner

Department of Human Movement Sciences, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

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Smeets JBJ, van der Kooij K, Brenner E. A review of grasping as the movements of digits in space. *J Neurophysiol* 122: 1578–1597, 2019. First published July 24, 2019; doi:10.1152/jn.00123.2019.—It is tempting to describe human reach-to-grasp movements in terms of two, more or less independent visuomotor channels, one relating hand transport to the object's location and the other relating grip aperture to the object's size. Our review of experimental work questions this framework for reasons that go beyond noting the dependence between the two channels. Both the lack of effect of size illusions on grip aperture and the finding that the variability in grip aperture does not depend on the object's size indicate that size information is not used to control grip aperture. An alternative is to describe grip formation as emerging from controlling the movements of the digits in space. Each digit's trajectory when grasping an object is remarkably similar to its trajectory when moving to tap the same position on its own. The similarity is also evident in the fast responses when the object is displaced. This review develops a new description of the speed-accuracy trade-off for multiple effectors that is applied to grasping. The most direct support for the digit-in-space framework is that prism-induced adaptation of each digit's tapping movements transfers to that digit's movements when grasping, leading to changes in grip aperture for adaptation in opposite directions for the two digits. We conclude that although grip aperture and hand transport are convenient variables to describe grasping, treating grasping as movements of the digits in space is a more suitable basis for understanding the neural control of grasping.

coordination; index finger; motor; prehension; thumb

INTRODUCTION: VIEWS ON GRASPING

Picking up a glass of beer or a cup of coffee are regular actions that we perform without many thoughts on how to perform the reach-to-grasp part of the movement. These movements require more coordination than, for instance, switching the light on. Switching the light on is essentially moving one's index finger to a desired position. What is the essence of the reach-to-grasp movement? It definitely involves selecting appropriate positions to put our digits, but what is subsequently coordinated? Since the pioneering work of Marc Jeannerod (1981), grasping is generally regarded as a combination of transporting the hand and adjusting the grip. For the best studied grip, the precision grip, adjusting the grip is reduced to the change in distance between the thumb and index finger. The resulting simple description of grasping has made the precision grip a very popular task to study motor coordination. In this paper, we will review the literature on grasping to

illustrate that this framework for describing grasping does not correspond with the underlying control.

Initially, Marc Jeannerod (1981) proposed that the use of transport and grip was not only a convenient way to describe behavior, but also that the behavior was shaped by an “open-loop control of independent visuomotor channels.” He observed that “the hand assumes movements and postures that are apparently independent of those assumed by the more proximal segments of the limb” (Jeannerod 1988). He interpreted this independence as the posture of the hand being related to intrinsic object properties like size and shape (processed in the temporal lobe of the cerebral cortex) and the movements of the proximal segments being governed by extrinsic properties such as location (processed in the parietal cortex). This led him to propose that there are two specialized input-output modules (visuomotor channels) that are independent of each other, in terms of both anatomy and information processing. He argued that this reduces the problem of visuomotor coordination in grasping to a problem of coordinating these two modules.

This idea to divide tasks into relatively simple modules for which control seems reasonably straightforward is widespread in the study of motor control. For instance, the fact that our body has many more degrees of freedom than are strictly

Address for reprint requests and other correspondence: J. B. J. Smeets, Dept. of Human Movement Sciences, Vrije Univ. Amsterdam, van der Boechorststraat 9, NL-1081 BT Amsterdam, The Netherlands (e-mail: j.b.j.smeets@vu.nl).

required to control the end effector has led several authors to propose solutions for this “degrees-of-freedom problem” (reviewed by Bruton and O’Dwyer 2018; Tresch and Jarc 2009). In doing so, it is assumed that the abundance of possibilities is a problem for the brain. If limitations of the computational power of the brain are relevant, control needs to be simple. Therefore, instead of taking advantage of the abundance of options, the brain restricts itself to a limited set of synergies to construct a whole repertoire of movements (d’Avella et al. 2003; Lee 1984; Soechting and Lacquaniti 1989; Ting and Macpherson 2005; Tresch and Jarc 2009), also for reach-to-grasp movements (Grinyagin et al. 2005; Mason et al. 2001). This description of synergies as a limited set of fixed patterns of muscle activation (i.e., modules) implies that not all theoretically possible movements can actually be performed. This means that the existence of such synergies can be tested (Berger et al. 2013; Lee 1984).

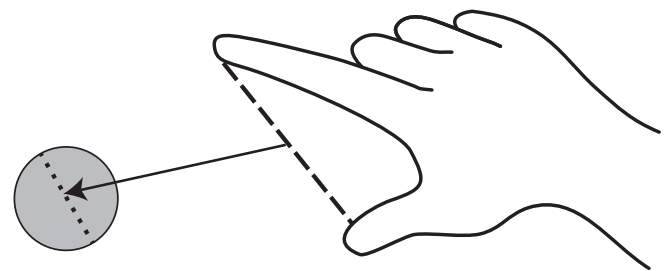
There are also arguments against the assumption that the brain restricts its freedom to choose solutions. A first argument is that if the chosen muscle activation patterns were restricted to a set of general-purpose synergies, it would be remarkable if the optimal solution for various motor tasks would never be excluded by the use of such synergies. There is clear evidence that humans exploit the abundance of possibilities that remain when considering the task constraints (Latash et al. 2001, 2002; van Beers et al. 2013), presumably in search for a better solution. A second, related argument against the choice of movement patterns being restricted is that studies that have explicitly examined the chosen solutions have generally noted that movement strategies are close to optimal in terms of task performance, considering the precision and noise of the motor apparatus (Harris and Wolpert 1998; Trommershäuser et al. 2005; Van Soest et al. 1994). Furthermore, experimental evidence suggests that the spatial characteristics of movements are planned before selecting the muscle activation patterns to produce the desired trajectories (Kistemaker et al. 2014). This hierarchy implies a primacy of the spatial trajectory of the end effector in control. Indeed, visual distortions influence the curvature of movement paths (Smeets and Brenner 2004; Wolpert et al. 1994), whereas force-field perturbations leave curvature unaffected (Kistemaker et al. 2010). A third argument against fixed patterns of muscle activation is that such learned patterns would not transfer across effectors because the anatomic constraints differ, which is in conflict with the phenomenon of motor equivalence: many movement characteristics remain invariant when executed by different effectors in writing (Merton 1972; Wright 1990), pointing (Marteniuk et al. 2000), and grasping while walking (Marteniuk and Bertram 2001). A last argument against fixed patterns of muscle activation as the basis of motor control is that even spinal responses to perturbations are flexible. They can even reverse sign depending on the detailed task constraints (Traub et al. 1980). Taken together, these arguments suggest that movements are controlled in terms of the (spatial) restrictions of the task (e.g., optimal trajectories of the end effector) rather than in terms of restrictions at the anatomic level (e.g., limited sets of muscle activation patterns or changes in joint angles). Therefore, task constraints rather than neuromuscular constraints probably limit behavior.

Not considering human motor behavior to be constrained by the limited capacity of the brain has led to formulations of

grasping in terms of physical task constraints, both by our group (Smeets and Brenner 1999; Verheij et al. 2012) and by others (Rosenbaum et al. 2001). These three papers each described grasping by selecting an existing model for goal-directed pointing movements and extending it to the control of grasping without adding any further constraints. The selected models generated pointing movements in three very different ways: by minimizing jerk (Flash and Hogan 1985), by the dynamics of a damped mass-spring system (e.g., Gribble et al. 1998), and by following posture-based movement plans (Rosenbaum et al. 1995). To apply these models to grasping, the models had to somehow incorporate the fact that grasping consists of making two of these pointing movements at the same time. Two of the three models incorporated a physical coupling between the end effectors (Rosenbaum et al. 2001; Verheij et al. 2012). The third simply postulates that the effectors move simultaneously (Smeets and Brenner 1999). The three resulting models of grasping could all surprisingly easily account for characteristics of grasping that were previously (Hoff and Arbib 1993) thought to be the result of an explicit control strategy within one of the visuomotor channels (e.g., maximum grip aperture is mapped to $4.55 + 0.75 \times$ object diameter) or to be the result of their temporal coordination (a separate mechanism for “time-based coordination” in addition to the controllers).

We, therefore, have two frameworks to describe grasping: a visuomotor-channel framework that describes grasping in terms of constraints on the transport of the hand and constraints on grip aperture and a digit-in-space framework that describes grasping in terms of constraints on the digits’ movements in space (Fig. 1). The aim of the present review of the behavioral literature on grasping is to determine how well these two frameworks can deal with various aspects of grasping. We will start with two sections reviewing our knowledge of how the

Visuomotor channel



Digit-in-space

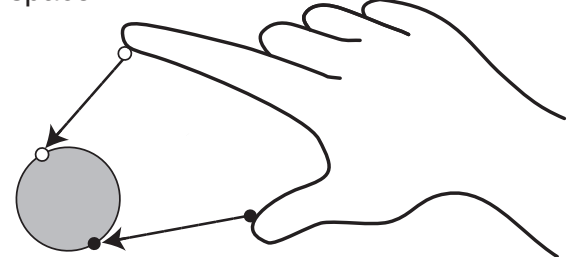


Fig. 1. The two frameworks that are used to describe grasping. In the visuomotor-channel framework (*top*), the grip aperture (dashed line) is scaled to object size (dotted line) and transported to the location of the object (arrow). In the digit-in-space framework (*bottom*), both the thumb (black disk) and index finger (white disk) move to their respective grasping points (arrows).

positions at which digits will contact the object are selected and how the digits generally move toward these positions. We then focus on the control of grasping movements. We will discuss how task constraints affect speed and precision and will also discuss whether grasping movements are preplanned or controlled in real time. The last two sections review how visual information is used in grasping: adaptation to altered visuomotor relations and sensitivity to visual illusions.

SELECTION OF GRASPING CONFIGURATIONS

There are many ways in which one can place one's digits on an object to grasp it. This grasping configuration can be described in terms of grasping points or in terms of a grasping axis, depending on the framework (Fig. 2). The selection of a grasping configuration can be regarded as an optimization of a combination of various factors (Kleinholdermann et al. 2013). A first factor is force closure. As soon as the two digits touch the surface, they start to apply grip force. The forces that they apply to hold the object should be directed along the grasping axis (dashed line in Fig. 2). Forces that are parallel to the object's surface could lead to the digit slipping along the object's surface. How much parallel force can be tolerated without the digit slipping depends on the friction coefficient. This hard physical constraint can be formulated as requiring that the grasping axis should lie within the cones of friction of both digits (Iberall et al. 1986). The only freedom is the choice of a safety margin: the minimal distance to the edges of the cones of friction that are considered safe enough for the grasp. A consequence of this constraint is that cylinders with an elliptical base are grasped with a hand orientation that approximately coincides with one of the principal axes (Cuijpers et al. 2004). Force closure does not appear to be considered to be a very important factor because elliptical cylinders are only approximately grasped along their principal axes and because participants that can choose to grasp an object at a rough or

slippery side only show a very minimal bias to select the rough side (Glowania et al. 2017).

A second factor is the torque around the grasping axis (Lederman and Wing 2003). Large torques can make the object slip if not compensated for by increasing the grip force. A third factor is the visibility of the object: grasping points are chosen such that the grasping hand moves in a way that maximizes the visibility of the object, so the right hand will grasp more to the right than the left hand (Paulun et al. 2014). A fourth factor is the comfort of the configuration, a term used to describe the subjective preference for a certain grip configuration when more grip configurations are possible (Rosenbaum et al. 1990). For picking up cylindrical objects with a precision grip, people clearly have a preferred grip angle (Cuijpers et al. 2004; Lederman and Wing 2003), which depends on the object's position (Schot et al. 2010). A last factor that is considered in the selection are the future forces and movement constraints (Craijé et al. 2011; Lukos et al. 2008; Rosenbaum et al. 2006), even including constraints on a subsequent task after having released the object that is to be grasped (Hesse and Deubel 2010a). The relative importance of each of these factors depends on many details of the task (Paulun et al. 2016).

As both visibility of the object at the time of the grasp and future movement constraints influence the selected grasping points, it seems reasonable to assume that visibility and constraints during the movement to the grasping points are also considered in grasp-point selection. It might be particularly useful to combine searching for an optimal grip configuration with searching for an optimal trajectory. Rosenbaum and colleagues (Elsinger and Rosenbaum 2003; Rosenbaum et al. 2001) have even argued that the choice of grip configuration is based on evaluating the possible movements toward the object. However, the grip configuration hardly depended on how digits approached a cylindrical object when the trajectories were manipulated by having the digits start at very different posi-

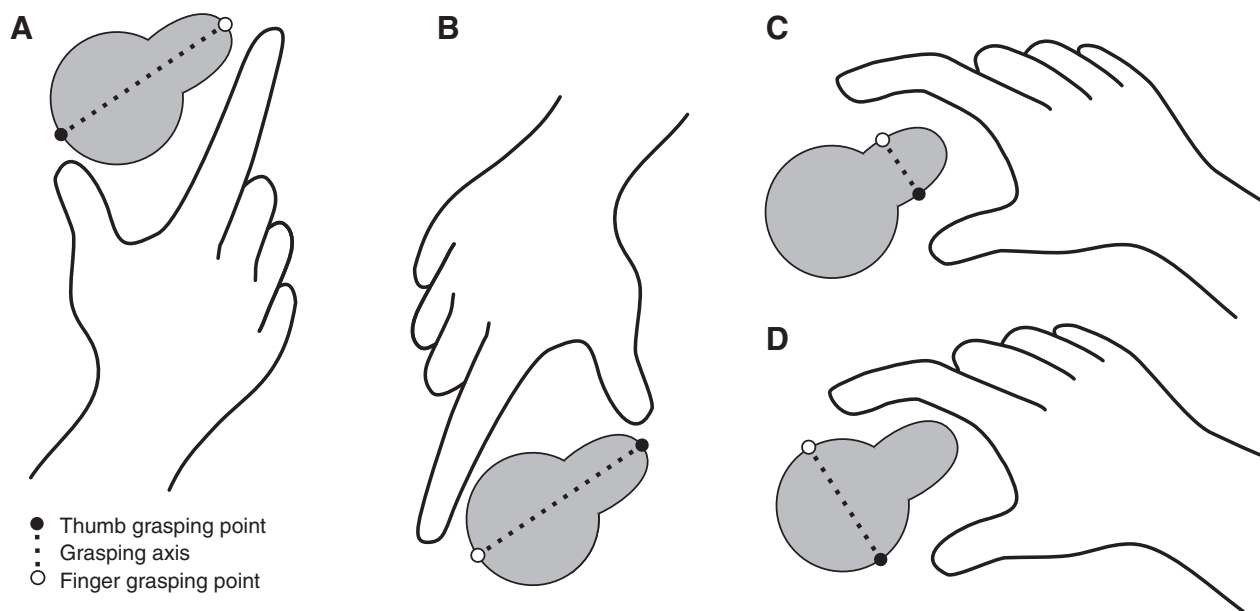


Fig. 2. Selecting the grasping configuration. Hands are indicated with the digits near the selected grasping points. Shown are 4 of the many possible ways to grasp a single object in a given orientation. A and B: 2 configurations with the same grasping axis but grasping points that correspond to a different hand posture and presumably comfort. C and D: 2 configurations with a grasping axis perpendicular to that in A and B. These configurations differ in their final grip size and the required grip force.

tions or when participants themselves chose to move over the object rather than around it to reach the grasping points (Voudouris et al. 2010). Obstacles placed near the trajectories also hardly influenced the grasping points unless they were so close to the otherwise preferred grasping points that they physically constrained the movement (Garzorz et al. 2018; Voudouris et al. 2012) or were on the same side as the arm and so high that the arm could not move over them (Marotta and Graham 2016). Considering how readily grasping points change if the cylinder that is to be grasped is slightly elongated (Cuijpers et al. 2004), the minimal influence of imposing different trajectories suggests that the grasping points are determined by the desired posture at the moment of the grasp rather than by the postures throughout the movement.

Some authors have argued that the information required for grasping must be computed in real time, so all planning must occur just before movement onset (Westwood and Goodale 2003; Westwood et al. 2003). However, there is clear evidence that we take visual information that was obtained up to a few seconds before movement onset into account. For instance, as we discussed above, a cylinder with an elliptical base is best grasped along one of its principal axes. When asked to grasp a cylinder with a circular base 2 s after having viewed a cylinder with an elliptical base, people's grasping orientation was influenced by the previously viewed object. Both the selected grip orientation and the maximum grip aperture were affected (Hesse et al. 2008). Such preview effects on grasping kinematics only occur when the object that is previewed resembles the target (Roche and Chainay 2013) and only when the whole object is previewed (Roche et al. 2015). Expectations can also be set by experience, as has been observed for the effect of object size on grip aperture (Volcic and Domini 2018).

All factors in grasp-point selection that were identified by Kleinhodermann et al. (2013) can be regarded as task constraints. When executing a reach-to-grasp movement, one usually has to judge the task constraints based on visual information. If the object is placed in a visual surrounding that shifts the apparent position of the object's center of mass (i.e., the Judd illusion), the choice of grasping points follows this shift (Ellis et al. 1999; Mon-Williams and Bull 2000). This implies that the perceived task constraints are the basis of grasp-point selection rather than the actual constraints (Cuijpers et al. 2006).

TIME COURSE OF GRIP-APERTURE FORMATION

As discussed in the introduction, the basis of the visuomotor-channel framework was the hypothesis of "an open-loop control of independent visuomotor channels" (Jeannerod 1981). This hypothesis was attractive because it conceptually simplified control by separating the control of the digits' positions relative to each other from the control of the wrist's position relative to the trunk and at the same time separated the time-invariant intrinsic object properties such as its size from the time-dependent egocentric properties such as its location. However, this hypothesis had to be rejected. Already in 1990, the laboratory of Jeannerod published a paper with the title "The coupling of arm and finger movements during prehension" (Paulignan et al. 1990). This paper and several others published in the period between 1990 and 1999 showed that various parameters of the wrist movement depend on object

size and many parameters describing grip formation depend on object distance (Jakobson and Goodale 1991; Kudoh et al. 1997; Marteniuk et al. 1990).

A quantitative analysis of experimental findings shows that the coupling between the two visuomotor channels is considerable. The original visuomotor-channel hypothesis predicts that transport parameters such as movement time would only depend on egocentric parameters such as object distance. Movement time is predicted to be independent of intrinsic object properties such as object size. The experimental finding is that movement time increases with object distance (8.5 ms/cm; Kudoh et al. 1997), but it decreases to a similar extent with object size (−6 ms/cm; Marteniuk et al. 1990). The visuomotor-channel hypothesis also predicts that maximum grip aperture would increase with object size but would be independent of object distance. The experimental finding is that the maximum grip aperture increases by 5 mm when object size increases from 20 to 30 mm but also when object distance increases from 20 to 40 cm (Table 1 of Jakobson and Goodale 1991). The experimental findings were thus clearly inconsistent with the original visuomotor-channel hypothesis. To incorporate these results, the hypothesis was amended: instead of assuming two independent visuomotor channels, it was now assumed that the two channels interact.

Within the digit-in-space framework, there is no separate control of transport and grip, as grip formation is described in terms of how the digits move in space. Based on this framework, we originally proposed an independent-digit hypothesis, assuming as radical a separation as in the original visuomotor-channel hypothesis. This independent-digit hypothesis considers the movements of the digits in space during grasping to just be two simultaneous movements of digits to the sides of the object (Smeets and Brenner 1999). Of course, there are limitations to this radical version of the hypothesis because the anatomy of the arm, and in particular the mechanical link between the digits, cannot really be totally ignored. The most obvious example is when there is an obstacle between the two digits' paths. In that case, each digit on its own could move around the obstacle. If the digits were to take the same paths during grasping, the hand would hit the obstacle. There are obvious postural constraints on the independence of the digits' movements. However, if we avoid circumstances in which such constraints become important, we can make several testable predictions on the basis of the independent-digit hypothesis.

The first prediction is that any peculiarity that is observed during grip formation when reaching to grasp symmetric objects should be observed in the movements of both digits because they both have similar constraints. The second is that any peculiarities of the digits' movements during grasping should also be present when reaching to touch the side of the object with a single digit because the constraints are the same. These predictions of the independent-digit hypothesis differ fundamentally from the predictions made by theories that claim that grip aperture is controlled (on the basis of object size). According to such theories, the single-digit reaching movement should resemble the transport component of grasping. This transport component could be the movement of the hand (Jeannerod 1981, 1988). In that case, how grip formation is distributed over the movements of the two digits is not specified, but they could move symmetrically in accordance with the

first of the above-mentioned predictions. However, there is no reason to expect the individual digits' movements when touching the side of the object to resemble their movements when grasping. Alternatively, the transport component could be the movement of the thumb (Haggard and Wing 1997; Mon-Williams and Tresilian 2001), in which case the thumb's movements when touching the side of the object should resemble its movement when grasping, whereas the index finger's movement relative to the thumb should represent specific characteristics of grip formation. We will discuss the experimental findings related to these predictions in the next three paragraphs.

One peculiarity of grip formation is that grip aperture increases with object diameter but that this scaling is incomplete. The scaling factor is ~ 0.8 (Smeets and Brenner 1999). According to the independent-digit hypothesis, this incomplete scaling should be present in the movements of both digits. According to the visuomotor-channel hypothesis, it is less clear what to expect. If one assumes that the thumb is transported (Haggard and Wing 1997; Mon-Williams and Tresilian 2001), one would predict that the incomplete scaling is due to the index finger's movements. To evaluate individual digits' grip scaling, we determined the curvature of the digits' paths. We examined whether the curvature of both digits' paths scaled with object size and found that the maximum deviation from a straight line increased by 0.75 times the object radius for both digits (Smeets and Brenner 2001b). This relation was the same for the dominant and nondominant hand and was also found when grasping with the index fingers of both hands (Fig. 3A). The main difference between the digits was that the thumb's path deviated 0.5 cm more than the index finger's path. We will interpret this difference between the digits in the section ADDITIONAL CONSTRAINTS AND GRIP APERTURE.

It is known that some aspects of motor control differ between participants. A classic example is handwriting: a person's handwriting remains recognizable irrespective of the effector that is used (Merton 1972). In a similar way, the systematic mismatch between the visual and proprioceptive estimation of one's hand's location differs in a consistent way across participants (Kuling et al. 2016; Smeets et al. 2006). Most importantly for the present review, such idiosyncrasies

have been observed in grasping (Bongers et al. 2012). Apparently, every individual has a preferred way to deal with the constraints of a certain task. The second prediction of the independent-digit hypothesis was that all peculiarities of the digits' movements when reaching to grasp an object should be present during single-digit movements with similar constraints for the digit. This prediction of the independent-digit hypothesis might seem unlikely: grasping involves moving the index finger and thumb together, connected by a strong biomechanical constraint that was absent in single-digit movements.

As the movements of the digits when reaching to grasp an object are constrained to have a more or less perpendicular approach to the surface to apply forces in opposite directions with the two digits when grasping (Biegstraaten et al. 2006; Kleinheldermann et al. 2007; Smeets and Brenner 1999), tasks that involve reaching to touch or to push an object can be designed to impose similar constraints on each digit to those during grasping. Such tasks can be used to test the second prediction (Smeets et al. 2010). To compare the idiosyncrasies, each participant in each of the three tasks (reach to touch, push, or grasp) was characterized by a curve representing the average deviation of the two digits from a straight line. In accordance with the prediction that peculiarities of the digits' movements when reaching to grasp an object should be present during single-digit movements, the trajectories in pushing and touching resembled those for grasping for each participant. They did so much more closely than did the trajectories of different participants performing the same task (Fig. 3B). Similar results were found in a study on interceptive movements (Schot et al. 2011). In that study, a sphere was either rolling along a track or presented stationary on that track and participants were asked to either pick it up with a precision grip or hit it with a single digit. We compared the movements of the digits between those combinations of task and sphere motion and found that the movement paths were more similar across tasks (hitting vs. grasping) than across sphere motion (rolling vs. stationary), supporting the notion that grasping is not controlled fundamentally differently from single-digit movements.

We have argued that approaching an object's surface perpendicularly helps reach the selected positions on the target object's surface in the presence of perceptual and motor noise

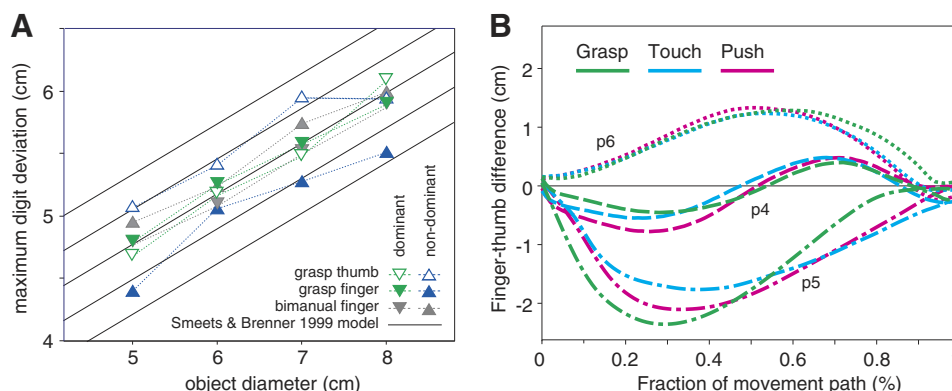


Fig. 3. Deviation of the digits' paths from a straight line in grasping. A: maximum deviation from a straight line to the center of the target object for the 2 digits in 3 grasping tasks: grasping with the dominant hand, grasping with the nondominant hand, and bimanual grasping with the index fingers of both hand. [Data replotted from Smeets and Brenner (2001b).] In line with the model prediction (plotted for 5 different values of the approach parameter), all deviations scale in a similar way with object diameter. B: difference in deviation from a straight line between the index finger and the thumb for grasping compared with that in single-digit tasks. [Data of participants (p) 4–6 replotted from Smeets et al. (2010).] Finger-thumb difference is for each participant very similar for the 3 tasks but differs considerably between participants.

(Smeets and Brenner 1999). Based on this assumption, we were able to account for several characteristics of grip formation, including the incomplete grip scaling. The shape of the trajectories does not provide evidence that people aim for a perpendicular approach, as closing one's grip also gives an approximately perpendicular approach when grasping a cylinder or a cube. To test whether people aim for a perpendicular approach, one should grasp objects for which closing one's grip does not lead to movements that approach the surface perpendicularly, such as trapezoids. Experiments with such objects showed that the digits' trajectories when closing the grip tend to approach the surface perpendicularly (Kleinholdermann et al. 2007). Thus the digits were moving along suitable paths for the orientation of the surfaces that they were heading for, rather than just moving toward each other.

In the above reasoning, we assume that the orientation and the location of the target object are perceived veridical. It is known that this is not always the case. For instance, people have biases that depend on gaze direction. When they shift their gaze while remembering a target's location, the biases are remapped with the gaze shift (Henriques et al. 1998). Within the visuomotor-channel framework, one might expect such a remapping for the transport component to leave the grip component unaffected because only the transport component is assumed to be based on egocentric properties. This prediction has been tested and found to be false: an intervening saccade also influenced grip orientation (Selen and Medendorp 2011). This suggests that grip orientation might be part of the transport component, but in that case transport and grip must largely be controlled together because the grip aperture depends strongly on grip orientation unless the object is completely symmetric. Within the digit-in-space framework, an intervening saccade can be expected to lead to remapping of the target positions for the two digits and thus to cause a change in the emerging grip orientation. Since the digit-in-space framework specifies that the digits will approach the object perpendicularly, viewing-geometry-dependent biases in perceived orientation (Doumen et al. 2005) might explain why Selen and Medendorp (2011) even found a larger remapping effect on grip-aperture orientation than on the average position of the digits.

Overall, the results in this section are very easy to describe using the digit-in-space framework, where each digit's trajectory is a direct consequence of constraints on that digit. To describe these results in terms of the visuomotor-channel framework, one needs to make many ad hoc extensions to the framework. However, as described above, both frameworks require some mechanism for coordinating the two assumed components of grasping. Either the timing of the movements of the two digits or the timing of grip formation and transport of the hand has to be coordinated.

ONLINE CONTROL

Contrary to the initial proposal of "open-loop control of independent visuomotor channels" (Jeannerod 1981), it is now generally accepted that ongoing reach-to-grasp movements can be adjusted to changing circumstances. The ability to adjust ongoing movements has mainly been studied by perturbing the target object in some manner. Kinematic responses to perturbations of a target object's position are already observed ~100

ms after the perturbation. These adjustments presumably update an ongoing (and thus already planned) movement on the basis of the latest sensory evidence about target location (Brenner and Smeets 2018; Scott 2016; Smeets et al. 2016). This notion of online control can be open-loop (based purely on information from the environment) or closed-loop (based on information about the ongoing movement as well).

Online control is especially interesting to study because concentrating on responses with the shortest latency isolates the most direct pathways guiding actions and thus only the most direct control mechanisms. More elaborate considerations, possibly involving interactions between the controlled channels, take more time so they will not influence the initial response to a perturbation. Thus studying the initial responses to a perturbation can reveal the most basic elements of control. What these basic elements are expected to be depends on the framework. According to the visuomotor-channel framework, the two channels controlling the transport and the grip component are presumed to be the basic elements. According to the digit-in-space framework, the positions of the thumb and index finger in space are presumed to be the basic elements. Irrespective of the framework, one would expect that perturbations of one basic element (grip aperture or finger position) would only affect that channel. Is this the case?

A first set of studies that aimed at understanding the online control of grasping was performed in the laboratory of Marc Jeannerod (Paulignan et al. 1991a, 1991b). In these studies, real objects of various sizes were located at different positions in a dark environment. One object was illuminated from within, indicating that this was the target. In a fraction of the trials, the illumination changed once the participant started to move, to indicate that a different object was the target. The authors designed this experiment to test the visuomotor-channel hypothesis and expected only the transport component of the movement to be perturbed when the second object had the same size as the first. The results proved this hypothesis to be incorrect: the authors found that the perturbation induced not only a double-peaked velocity profile, but also a double-peaked grip-aperture profile (Paulignan et al. 1991b). Both the velocity and the grip-aperture profile also changed if the second object was at the same position but had a different size (Paulignan et al. 1991a). Within the digit-in-space framework, both types of perturbations involve a change in the location of the contact points of both digits. If one models the digits' movements as maximally smooth movements toward the new positions of the contact points, one obtains responses that resemble those experimentally observed (Smeets et al. 2002). However, the latencies of the adjustments were >300 ms, so one might question whether the double-peaked profiles for grip aperture and velocity are a direct adjustment to the changed target or planning a new movement that considers the presence of the nonilluminated objects that might have acted as obstacles (Paulignan and Jeannerod 1996; Smeets et al. 2016).

The experiments of Paulignan et al. (1991a, 1991b) that we discussed above provided a critical test that showed a large deviation from the predictions of the visuomotor channel theory. In a similar way, one could test whether the two digits are controlled independently in accordance with the digit-in-space framework. By constructing objects that can quickly be enlarged on one side without the other side changing, one can selectively perturb the contact position for one digit. If the two

digits are completely independent, the responses should be independent. van de Kamp and Zaal (2007) developed such an object and found that perturbing one digit's contact position affected some aspect of the kinematics of the other digit in two of the four cases that were tested. However, the effects were only visible in a combination of five measures, rather than in a specific measure. We conclude that the coupling between the digits that was observed in the study of van de Kamp and Zaal (2007) is much weaker than the coupling between the visuomotor channels that was observed by Paulignan et al. (1991a, 1991b).

If the online control of grasping behaves in the same way as the online control of goal-directed pointing movement, the vigor of the response will be larger for later changes (Liu and Todorov 2007; Oostwoud Wijdenes et al. 2011). We are not aware of any experiment directly testing this prediction, but we have found some indirect evidence. If you use a fixed displacement threshold to determine the onset of movement correction, the latency is overestimated by ≤ 100 ms (Oostwoud Wijdenes et al. 2014). The overestimation is smaller for more vigorous responses, so a shorter latency can be an indication of a more vigorous response. Thus, if the digits' responses to a change in target size are more vigorous later in the movement, we expect the latency to decrease. This is what was observed for responses to changes in object size (Hesse and Franz 2009; van de Kamp et al. 2009): the reported latencies for changes near the end of the movement are ~ 100 ms shorter than those for perturbations near movement onset.

If grasping consists of moving the digits independently to selected positions on an object, then one would expect to see online adjustments when those positions displace, even if there is no need to make any adjustments to successfully grasp the object. In a study that examined this, participants were asked to grasp a cube or a sphere that could rotate during the grasping movement (Voudouris et al. 2013). In both cases, the digits responded in accordance with the changes in the positions of the grasping points. For the cube, it is logical, and in agreement with earlier experiments (Desmurget et al. 1996), that the hand would follow the rotation at short latency (115 ms). For the sphere, neither the size nor the position changed so that there was no reason to adjust the grasping movement in terms of grip aperture or orientation. In the terminology of the digit-in-space framework, the digits should follow the selected grasping points. They did so for ~ 50 ms, after which the grip orientation returned (almost) to the orientation that it would have had if there had been no rotation. This is consistent with the digits' movements being the basic elements that are controlled.

Goal-directed movements are also adjusted to other changes in the constraints than a change in target position. For instance, an obstacle that moves near the path is avoided at a short latency (Aivar et al. 2008; Nashed et al. 2012). According to the digit-in-space framework, this characteristic of the fast adjustment is expected to be present in the movements of the digits in grasping. As we will discuss later in the section ADDITIONAL CONSTRAINTS AND GRIP APERTURE, the movements of the digits depend on object shape in a manner that is consistent with some parts of the object other than the contact points being treated as obstacles. More generally, the digits' paths, and thus maximum grip aperture, depend on object shape. Maximum grip aperture is larger for grasping a thin bar with a length of 4.1 cm than for grasping a disk with a diameter of 4.1

cm (Eloka and Franz 2011). Therefore, if a bar were to suddenly change into a disk, one might expect to see a fast response in grip aperture, even if the object dimension along the opposition axis remains constant. This is indeed what has been reported: a fast adjustment in grip aperture is observed when the bar is replaced by a disk during the reach-to-grasp movement (Eloka and Franz 2011).

Not only visual information about the target and environment are used in the online control of movement, but also visual feedback about the hand (Brenner and Smeets 2003; Dimitriou et al. 2013). This information is used to complement haptic information in continuously updating the estimate of the location of the end effector throughout the movement, just as visual information is continuously used to update the estimate of the target's location. One might have expected that instead of comparing an estimate of the target with an estimate of the effector, direct visual information about the relative positions of the hand and target is used. However, this is not the case, even when haptic position information is not directly coupled to the position of the end effector, for instance, when using a computer mouse to bring a cursor to a target (Brenner and Smeets 2003, 2006). The two frameworks each suggest that a certain kind of visual feedback is used to guide grasping: the locations of the digits (digit-in-space framework) or the grip aperture and hand position (visuomotor-channel framework). To evaluate which of the two kinds of information is used, we will interpret the findings of an experiment that manipulated the reliability of visual information (Volcic and Domini 2016).

When you are reaching to grasp a ball with your index finger aiming to touch an invisible point on the far side of the ball, the visual information about the contact point of the finger is much less reliable than that of the thumb. Whether this difference in reliability is relevant for feedback control depends on the information that is used in the control of grasping. If information about the distance between the digits is used to control grip aperture, the difference in reliability between the digits is irrelevant. However, if feedback about the individual digits' positions is used to control the individual digits' movements, less reliable information for one digit should lead to corrections with a lower gain for that digit. Therefore, one can expect a lower gain of online adjustments for the index finger than for the thumb. This prediction was tested experimentally by Volcic and Domini (2016) by scaling the visual feedback about the distance between the digits (i.e., about grip aperture). When grasping in the frontal plane with both digits continuously in view, both digits responded equally to the manipulated feedback. However, when using a horizontal grip with the index finger partly occluded, the thumb responded much more strongly than the index finger. This is consistent with the individual digits being controlled on the basis of visual feedback, rather than grip aperture being controlled, which is incompatible with the visuomotor-channel hypothesis. In this context, it is important to realize that knowing whether one will have visual information for online control, for instance, because one can see that some parts of the digits' trajectories will be occluded, influences details of the digits' trajectories (Bozzacchi et al. 2018).

The perturbation studies that we discussed above examined the responses to changes in the visual input. Mechanical perturbations can be used to answer the same questions. For instance, if there were independent visuomotor channels for the

control of transport and grip, perturbing the transport would leave the grip unaffected. However, what is found is that when mechanically blocking the movement of the wrist during a reach-to-grasp movement, the opening of the grip stops as well (Yang and Feldman 2010). This result is logical if you assume that the aim is to bring digits to a contact point on the object. Blocking the wrist blocks the movement of the digits along their planned trajectories in space. If the digits would move relative to the wrist, this would move the digits away from the planned trajectories. In a similar fashion, perturbing the grip might be expected leave the transport component unaffected. However, this is not the case (Schettino et al. 2017).

Thus the fastest responses show a strong coupling between the two channels in the visuomotor-channel framework while showing a very modest coupling between the digits in the digit-in-space framework. Moreover, the gain of the digits' responses depends on the reliability of the information about the individual digits. This supports the digit-in-space framework, complementing the observation that the hand follows selected grasping points rather than relying on grip aperture and object position.

TRANSFER OF ADAPTATION

Thus far, we have described how the influence of constraints on grasping behavior can reveal the underlying control structure. Another popular method for studying visuomotor architecture is through adaptation. Humans can adapt rather quickly to a change in the relation between sensory input and the corresponding motor behavior. This adaptation can be interpreted as updating an internal forward model of the sensorimotor mapping (Krakauer and Mazzoni 2011). Transfer of adaptation from one task to another suggests that the tasks use the same internal model of sensorimotor mapping. A very interesting phenomenon is that adapting to a task does not always generalize to tasks that seem almost identical. For instance, adapting a slicing movement back and forth through a target does not lead to any effects on a movement that has to stop at the same target location (Scheidt and Ghez 2007). This finding implies that a movement's specific constraints are critical for generalization. Investigating how adaptation generalizes across tasks can reveal the nature of such constraints and

thereby help identify the scope of the underlying internal model.

An example of visuomotor adaptation in grasping is grasping objects for which the haptically experienced size or orientation differs from the visually experienced values. After repeated grasping, the maximum grip aperture and its orientation adapt toward the haptically experienced values (Säfström and Edin 2004; Weigelt and Bock 2007). These findings can be explained in terms of the visuomotor-channel framework: the channel relating visual information about object size to grip-aperture control is adapted as well as the one relating object orientation to the orientation of grip aperture. Within the digit-in-space framework, the explanation of adaptation in grasping with distorted visual size information is less straightforward. Adaptation to a visuohaptic size mismatch can be explained within the digit-in-space framework by assuming that two internal models are adapted: models relating visual information about the location of each of the two contact positions to the movements of the corresponding digit in space. To adapt to a different size, the adaptation of the index finger would have to be in the opposite direction than that of the thumb. This might sound unlikely, as movements of the index finger and the thumb share the arm that moves them through space, but the index finger and thumb can be adapted in opposite directions (Schot et al. 2014), resulting in an aftereffect of the thumb aiming to the left of the target while the index finger aims to the right (blue dashed curves in Fig. 4) or vice versa (red dotted curves). Therefore, the fact that one can adapt grip aperture to object size is not an argument against either of the frameworks.

The example of adapting individual digits illustrates that adaptation can be quite specific rather than generalizing across any similar goal-directed arm movement. Besides being specific to the digit that is moved, prism adaptation is also specific to the location in the workspace (i.e., to the posture of the adapting arm): learning to deal with visual effects of prisms with the hand in a certain posture does not transfer to the same movement starting from another arm posture (Redding and Wallace 2006). Within the digit-in-space framework, adaptation to object size involves adapting index finger and thumb in opposite directions. As both of these adaptations are posture-specific, this size adaptation should be specific to a certain arm

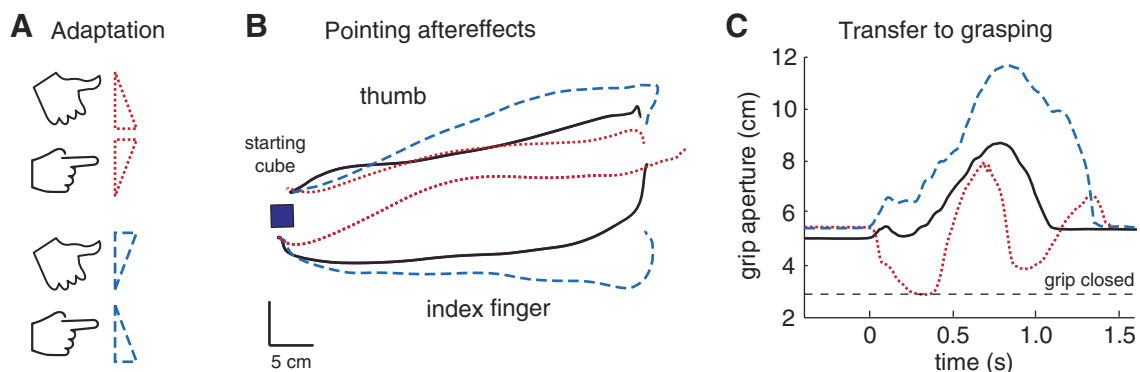


Fig. 4. Adaptation of pointing and transfer to grasping. *A*: adaptation to prisms in opposite directions when pointing with the 2 digits. *B*: top view of 3 trials in which the participant tapped the left side of a cube with the thumb and 3 trials in which the participants tapped the right side of the cube with the index finger. Continuous black curves: last trial of each digit before adaptation. Dashed blue and dotted red curves: 1st pointing trial of each digit after removing the prisms. Target cube is on the right. [Adapted from Fig. 2A in Schot et al. (2014).] *C*: transfer to grasping: in the 1st trial after adaptation, grip initially closes until the digits touch (instead of opening; dotted red curve) or opens much wider (dashed blue curve) than it did in the last trial before adaptation (solid black curve). [Adapted from Schot et al. (2017).]

posture. This prediction is clearly the opposite of what one would predict according to the visuomotor-channel framework. According to that framework, adaptation would occur completely in the grip channel, which only involves the distal musculature and intrinsic object properties, so grip adaptation should be independent of the arm posture. The experimental results are in line with the digit-in-space framework: the adaptation of grip aperture is specific for the hand's location in the workspace (Cesaneck and Domini 2017).

As argued in the first paragraph of this section, transfer of adaptation to related tasks depends on the similarity between the task constraints. Following this reasoning, the digit-in-space framework predicts rather unexpected transfer of adaptation. Within this framework, grip formation emerges from movements of the digits to positions on the target's surface. Therefore, adaptation of grip aperture in grasping should transfer to deviations in pointing and vice versa. Such transfer is not expected within the visuomotor-channel framework, as pointing movements involve the musculature that is used in the transport channel rather than that used in the grip channel. Is there evidence for transfer between pointing and grip formation? A first finding that is in line with the digit-in-space framework is that the adaptation of grip orientation in grasping transfers to pointing with the index finger to the side of the object when the pointing movement resembled the movement of the index finger in the adaptation phase (Weigelt and Bock 2010).

A second finding on transfer of adaptation that is in line with the digit-in-space framework is based on the hypothesis that grip adaptation to object size is based on opposite adaption of the two digits. If so, adaptation of the digits in opposite directions should lead to aftereffects in the grip aperture during grasping. This prediction makes no sense within the visuomotor-channel framework, as grip aperture depends on size within this framework and size information is never perturbed in adaptation of the individual digits. To test this prediction, an experiment was conducted in which participants alternated between tapping the left side of an object with their thumb and tapping the right side of the object with the index finger, with the direction of the prism being coupled with the digit that was used so that the digits adapted in opposite directions. After such adaptation, the prisms were removed and participants were asked to grasp the object. The grip aperture showed a clear aftereffect (Schot et al. 2017; Smeets and Brenner 2016). A very interesting phenomenon was observed in the case that the adaptation made the index finger move more leftward and the thumb more rightward (red dotted curves in Fig. 4). When subsequently grasping without prisms, the consequence of the index finger moving more leftward and the thumb more rightward was that instead of starting by opening their grip, the participants started by closing their grip (Schot et al. 2017).

All examples of (lack of) transfer of adaptation that we described in this section make sense within the digit-in-space framework. They are unforeseen from the viewpoint of the visuomotor-channel framework.

INFLUENCE OF ILLUSIONS ON GRASPING

Visual illusions can be used as a tool to study the coding of goal-directed movements (de Grave et al. 2004). Aglioti et al. (1995) were the first to use grasping to test the two-visual-

systems hypothesis. According to this hypothesis, all visual attributes are processed twice: in the ventral pathway for recognizing objects (perception) and in the dorsal pathway for guiding one's hand toward them (Goodale and Milner 1992). Aglioti et al. (1995) and most other authors interpret the findings in grasping experiments in terms of the visuomotor-channel framework and discuss whether visual size illusions affect maximum grip aperture to the same extent as their perceptual effect. This is not a correct comparison in the digit-in-space framework because maximum grip aperture is an emergent property of movements of the digits toward positions rather than a variable that is controlled directly on the basis of an estimate of object size (Fig. 1). If grip aperture does not rely on estimating object size, there is no reason to expect size illusions to influence grasping movements. Instead, illusions affecting perceived positions should do so (Smeets and Brenner 2006; Smeets et al. 2009). We are, therefore, not surprised to see that many studies find little effect of size illusions on grasping (e.g., Whitwell et al. 2018), although we do not regard studies that report otherwise (e.g., Kopiske et al. 2016) as evidence against the two-visual-systems hypothesis either. We will not discuss the two-visual-systems hypothesis itself here (see for recent reviews: de Haan et al. 2018; Goodale and Milner 2018; Medendorp et al. 2018; Schenk and Hesse 2018) but will discuss what some grasping studies that were designed to test the validity of the two-visual-systems hypothesis can tell us about the control of grasping.

The most frequently studied illusion in grasping experiments concerned with the two-visual-systems hypothesis is the Ebbinghaus illusion. In such experiments, a thin disk that is to be grasped is surrounded by flankers. If the disk is surrounded by large flankers, it appears to be smaller than if it is surrounded by small flankers. According to the visuomotor-channel framework, this size illusion affects the input of the grasping channel and should, therefore, influence grip aperture. According to the digit-in-space framework, the illusion should only affect grasping if it influences the perceived position of grasping points. Many studies have reported that this illusion influences peak grip aperture (Aglioti et al. 1995; de Grave et al. 2005; Franz et al. 2000; Haffenden and Goodale 2000; Haffenden et al. 2001; Kopiske et al. 2016; Pavani et al. 1999). The most intensively discussed concern about this illusion is that the flankers that surround the disk might act as obstacles and thereby have an effect on peak grip aperture that is unrelated to their effect on perceived size (Haffenden and Goodale 2000; Haffenden et al. 2001). The fact that the exact location of the flankers influences the selected grasping points (de Grave et al. 2005) supports this idea. However, an extensive preregistered study with 144 participants showed that obstacle-like effects cannot explain the effect of the Ebbinghaus illusion on peak grip aperture (Kopiske et al. 2016). How does the choice of a framework affect the interpretation of these results?

When interpreted within the visuomotor-channel framework, the results of Kopiske et al. (2016) imply that this size illusion affects grasping, which is inconsistent with the basic version of the two-visual-systems hypothesis. Interpretation of the results of Kopiske et al. (2016) within the digit-in-space framework is less straightforward, as size information (and thus a size illusion) is not relevant in the control of grasping. One could explain the finding that the Ebbinghaus illusion influences peak grip aperture within the digit-in-space frame-

work by assuming that the Ebbinghaus illusion influences perceived locations. In a simple pencil-and-paper experiment, we examined whether this could be the case. We found that the perceived positions of potential grasping points are indeed influenced by the Ebbinghaus illusion (Smeets and Brenner 2019). In line with the reported lack of effect on grip aperture of the empty space illusion (Stöttinger et al. 2012) and diagonal illusion (Stöttinger et al. 2009), we found that a combination of these illusions did not affect perceived positions.

A second very popular illusion is the Müller-Lyer illusion or the Brentano version of it. In this illusion, a line segment appears to be longer when outward-pointing fins are attached to its ends than when inward-pointing fins are attached to its ends. How this illusion affects pointing movements depends on the starting position. When asked to point at one of the vertices, there is a clear effect of the fins on the movement end points when starting from another vertex (de Grave et al. 2004; Mendoza et al. 2006). The effect of the fins is much smaller when starting from other positions and even completely disappears when starting at a position that results in a movement perpendicular to the illusion (de Grave et al. 2004, 2009). A similar pattern has been reported for saccades (de Grave et al. 2006a, 2006b). To study grasping with this illusion, a physical bar is placed on a printed or projected version of the illusion. The many studies using this paradigm have been reviewed by Bruno et al. (2010). Do the results fit one of the frameworks?

According to the digit-in-space framework, the starting-position dependence of the effects of the Müller-Lyer illusion on pointing should be reflected in the susceptibility of grip aperture to this illusion. Therefore, one would expect that the starting position would matter, with a reduced effect of the illusion when starting from the side compared with a movement along the illusion. Unfortunately, the exact configuration is not provided in many studies, which makes this prediction rather difficult to evaluate for this review. Moreover, the fins can also act as obstacles, which would also result in a larger maximum grip aperture for outward-pointing fins. Experimental evidence that such obstacle-like aspects of the Müller-Lyer figure influence the grasping behavior is provided by a study from our group (Biegstraaten et al. 2007). In this study, participants started on the side. We found that grip aperture was larger for the fins-out than for the fins-in configuration, but the movement times were also longer, which suggests that the difference was not only one of size, but also mainly caused by the fins acting as obstacles.

An additional reason to suspect that the misperceived size is not responsible for the effects of the Müller-Lyer illusion on grip aperture is that if the bar would appear to be shorter than it really is, the digits should aim at positions that are closer together than the size of the bar. If so, they would unexpectedly contact the bar before they expected to do so, with a strong impact as a consequence. On the other hand, for a bar that appears longer than it is, the contact will not occur at the planned moment, at which the digits' speeds are low, so the digits should reaccelerate. Contrary to those expectations, we did not observe any difference in the digits' velocities during the last 50 ms before contact (Biegstraaten et al. 2007). The effect of the illusion on maximum grip aperture is, therefore, probably mainly due to the fins acting as obstacles. As we cannot rule out a small effect of an illusory difference in size as well, the experiments on grasping the Müller-Lyer illusion

do not provide specific support for either of the two frameworks.

If one misjudges the size of an object that one is reaching to grasp, one will have a peculiar velocity profile just before contact (as discussed in the previous paragraph), but one will also use this error to update one's movement plan for the next movement toward the same object (Cesaneek and Domini 2017; Kopiske et al. 2017). Such updating illustrates the effect of errors in previous trials on reaching to grasp, in line with the literature on pointing (van Beers 2009), interception (de Lussanet et al. 2001), and the control of grip force (Westling and Johansson 1984). In the previous section, we already presented support for the digit-in-space framework based on the transfer of such updating from reaching with individual digits to grasping with both digits (Schot et al. 2017). Considering such updating in the context of the visuomotor-channel framework, with grip aperture being based on size perception, one might consider that updating based on feedback near the time of contact could be responsible for the resistance of grip aperture to size illusions. A carefully designed preregistered study showed that visuomotor adaptation of grasping is not the primary source of the immunity to illusions in closed-loop grasping (Cesaneek et al. 2018). The lack of adaptation found in that study is easily explained in the digit-in-space framework: the illusion does not induce errors in perceiving the contact positions, so there were no errors to adapt to.

Interpretation of the effects of size illusions on grasping depends on many assumptions that are not easy to test. Therefore, these studies do not provide strong support for or against either of the frameworks.

ADDITIONAL CONSTRAINTS AND GRIP APERTURE

We started this review by discussing how various constraints on achieving a stable grip could guide the selection of grasping points and of the trajectories of reach-to-grasp movements. Subsequently, we discussed several paradigms (perturbations, adaptation, and illusions) in which the constraints were manipulated to try to reveal the mechanisms of the control of grasping. In the present section, we will turn to experiments that studied how other constraints, such as positions that should be avoided, influence the shaping of human reach-to-grasp movements. Can these experiments shed light on how the grasping movement is controlled? We will start by discussing the constraints imposed by the object itself and then move to constraints that are imposed by other objects.

A first constraint is related to the tolerance of the selection of grasping points: the contact surface area. For a given object size, it has been found that a larger contact surface results in a larger maximum grip aperture (Bootsma et al. 1994; McIntosh et al. 2018). Why does the size of the contact surface affect grip aperture? One way to explain this is to consider all of the object's surface except for the selected grasping points as an obstacle that is to be avoided (Verheij et al. 2012). Making sure to avoid the rest of the surface can be achieved by following movement paths that are further from the object's surface, which corresponds to a larger grip aperture, with an approach of the surface that is closer to perpendicular (Smeets and Brenner 1999).

Considering parts of the target object as obstacles can explain many other reported phenomena of grip aperture that

have hitherto been explained in terms of the visuomotor-channel hypothesis. When grasping a 5-cm-diameter circular cylinder, people select grasping points along a preferred orientation, and the digits move toward them in a manner that ensures that they are never close to the rest of the cylinder's surface. When grasping an elliptically shaped cylinder with axes of 5 and 8 cm with its minor axis at this preferred orientation, the same trajectories of the digits would make them pass quite close to the surface, making the elongated surface of the cylinder a potential obstacle (Fig. 5A). Indeed, the maximum grip aperture is larger when the cylinder is elongated in the direction orthogonal to the grasping axis (Cuijpers et al. 2004). A similar reasoning explains why the maximum grip aperture is >1 cm larger when grasping a 6-cm cube along its sides than when grasping a smaller cube along its 6-cm diagonal (Verheij et al. 2014a).

Considering most of the surface of a target object as an obstacle implies that if the digits travel a longer distance along the surface on their way to the grasping points, the maximum grip aperture may be larger and the movement time longer (Fig. 5B). This was indeed found to be the case in a recent experiment (Verheij and Smeets 2018). The increases with distance traveled along the surface are considerable: 0.4-mm-larger maximum grip aperture and 7-ms-longer movement time for each additional centimeter along the object (Fig. 5 of Verheij and Smeets 2018). The effects of the size of the contact surface on the speed and grip aperture, therefore, depend on the digits' paths relative to the object. It is, therefore, not surprising that the effect of an increase of the contact surface in height has an effect on maximum grip aperture different from a

similar increase of the contact surface in the horizontal direction (Borchers et al. 2014).

According to the model that implements independent-digit control by minimum-jerk movements (Smeets and Brenner 1999), a larger maximum grip aperture to obtain better precision should occur earlier in the movement. This effect of precision on the timing of maximum grip aperture has indeed been reported (McIntosh et al. 2018; Zaal and Bootsma 1993). In the experiments on the contribution of both digits to grip formation, it was observed that the movements of the thumb were $\sim 30\%$ more variable than those of the index finger (Smeets and Brenner 2001b). A larger variability constrains the approach to be more perpendicular, which corresponds with a larger deviation earlier in the movement (Smeets and Brenner 1999). Indeed, the deviation from a straight line was $\sim 10\%$ larger and occurred earlier in the movement (after covering 60% rather than 75% of the distance) for the thumb than for the index finger (Smeets and Brenner 2001b). Moreover, the timing of the two maxima varied independently, suggesting that the moment of peak grip aperture might be better regarded as an emergent property of the timing of the two digits' movements, rather than a property that is controlled in itself.

In addition to the relation between the precision of grasping movements and peak grip aperture, the precision of the peak grip aperture itself is also relevant. If peak grip aperture were a controlled variable (as it is assumed to be within the visuomotor-channel framework), one might expect it to obey the basic psychophysical law that the variability of a quantity is a fixed fraction of its magnitude (Weber's law). However, the variability of maximum grip aperture is independent of the maximum grip aperture itself (Ganel et al. 2008). Within

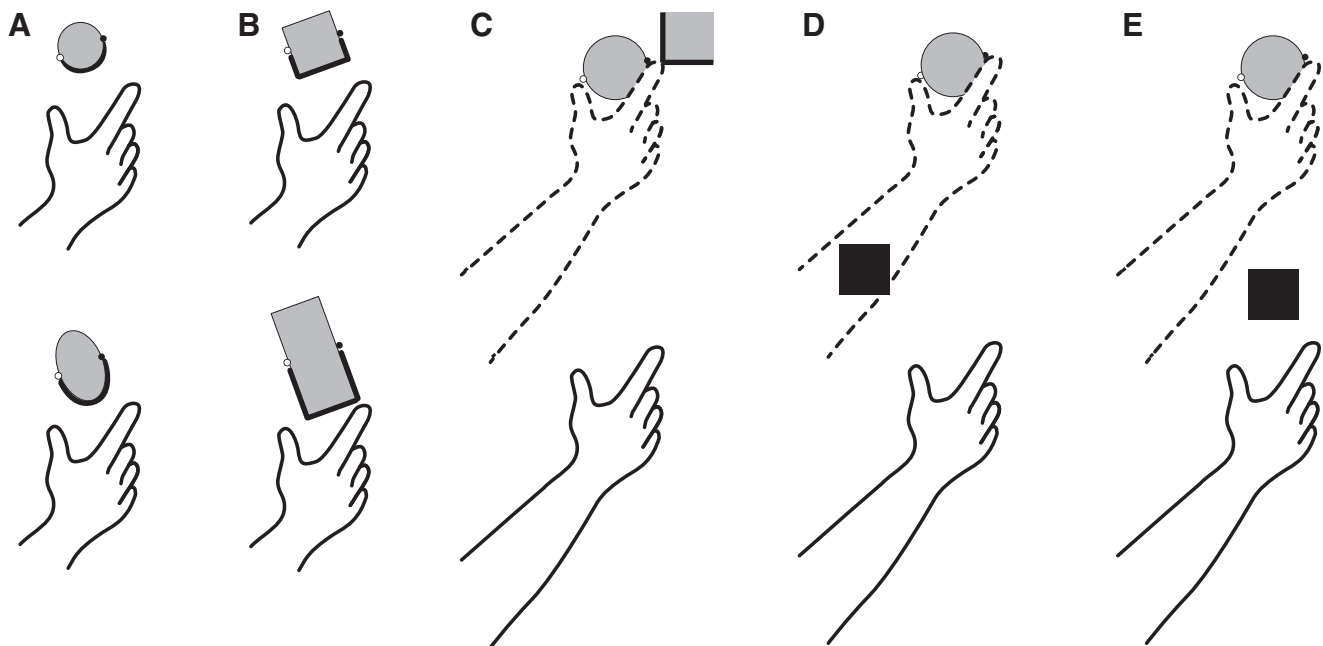


Fig. 5. Role of obstacles in grasping (top view). Open and filled circles indicate the intended grasping points. Black indicates an object or part of an object that can interfere with the reach-to-grasp movement. Dashed arms indicate the preferred grasping configuration without the presence of obstacles. A: when grasping a circular object, the grasping points can be anywhere on the object's surface, and half of the surface needs to be avoided. If the object is elongated and grasped close to the smaller axis, the grip aperture will be larger than for the circular object because the digits move along parts of the object with which they must be sure not to collide. B: when grasping a cube, the centers of 2 opposite sides provide a stable grasp. For bars of the same width, the part that one has to make certain to avoid hitting is larger. C: if there is an obstacle (cube) close to the target object (ball), it will influence the choice of grasping points. D: objects can interfere with the posture of the forearm when the digits contact the object. E: if an object is on (or close to) a digit's usual path, it will influence the digit's trajectory (and the maximum grip aperture).

the visuomotor-channel framework, the absence of Weber's law requires an explanation. These have been provided in terms of biomechanical constraints (Manzone et al. 2017; Schenk et al. 2017; Utz et al. 2015) and in terms of the two-visual-systems hypothesis (Bruno et al. 2016; Ganel et al. 2008; Heath et al. 2017; Manzone et al. 2017). Within the digit-in-space framework, no additional explanation is required. According to this framework, the maximum grip aperture emerges from the independent movements of the individual digits, each toward its own contact position, rather than being controlled on the basis of size. There is no reason to assume that the variability in each individual digit's movement depends on hand opening, except for extreme hand postures. Thus, if grip aperture is not controlled on the basis of an estimate of size, there is no reason to expect Weber's law-like behavior for peak grip aperture (Smeets and Brenner 2008).

A last group of studies that have manipulated the constraints of the object that is to be grasped are studies that involve pantomimed grasping. In pantomimed grasping, the object is not present at the position at which it is seen but is only visible through a mirror (Bingham et al. 2007; Schenk 2012), is presented at a different location (Rinsma et al. 2017), is presented as a two-dimensional image (Ozana and Ganel 2019), or has to be remembered (Goodale et al. 1994). Crucially, the participants know in advance that there will be no contact at the end of the grasping movement (Bingham et al. 2007; Schenk 2012). The important consequence (not mentioned in the cited studies) is that in such a situation the participant knows that there will be no contact, so there are no constraints on the direction of approach. These studies report that removing the object induces consistent changes in several aspects of grasping behavior. A first consistent change that has been reported is a reduction of peak grip aperture to a value that is barely larger than the grip aperture at the end of the movement (Ansuini et al. 2016; Bartelt and Darling 2002; Goodale et al. 1994; Holmes et al. 2013; Ozana and Ganel 2018, 2019; Rinsma et al. 2017). A second consistent finding is a larger effect of contextual illusions (Chan and Heath 2017; Ozana and Ganel 2018; Rinsma et al. 2017; Westwood et al. 2000). A third consistent finding is that for pantomimed grasping, variability in peak grip aperture scales with peak grip aperture (Davarpanah Jazi et al. 2015; Holmes et al. 2013; Manzone et al. 2017), unlike the lack of scaling in normal grasping that was discussed in the previous paragraph. A last finding is that an individual without a functional ventral stream (DF) does not scale her grip aperture with object size in pantomimed grasping (Goodale et al. 1994; Schenk 2012), whereas she does when grasping actual objects. How can we explain these characteristics of pantomimed grasping?

Many authors have tried to explain the characteristics of pantomimed grasping within the visuomotor-channel framework in terms of a lack of calibration (Bingham et al. 2007; Chan and Heath 2017; Davarpanah Jazi and Heath 2017; Schenk 2012). However, this explanation has been questioned because the effects remain if the object contact (and thus feedback) is provided after the digit's movements have stopped without contact (Davarpanah Jazi and Heath 2017). Given the importance of knowing that contact will occur, the distinct characteristics of pantomimed grasping are likely to be related to the lack of risk of unwanted contact with the object. All of the above-mentioned findings can be understood by assuming

that when grasping actual objects, one guides the digits to contact locations in space with an approach perpendicular to the surface, whereas for pantomimed grasping, one scales grip aperture to match the perceived size of the target object while moving to the object's location. Therefore, the visuomotor-channel framework is better suited to describe pantomimed grasping, whereas the digit-in-space framework is better suited to describe grasping an actual object.

Now that we have discussed constraints imposed by the object that is to be grasped, it is time to consider constraints imposed by objects other than the target. For instance, grasping trajectories change when an obstacle prevents the digits from moving to their usual positions (Fig. 5C; Voudouris et al. 2012) or the hand from moving along a straight path to the target (Fig. 5E; Alberts et al. 2002; Saling et al. 1998; Voudouris et al. 2012). In the latter situation, the hand can curve over the obstacle that is placed on its path and is likely to move more slowly than without the presence of such an obstacle. The configuration used in the three last-mentioned studies (a horizontal grip and a movement that curves over the obstacle) ensured that (in terms of the visuomotor-channel framework) the obstacle did not interfere with grip formation. It only interfered with hand transport. Nevertheless, the obstacle reduced maximum grip aperture (Alberts et al. 2002; Saling et al. 1998; Voudouris et al. 2012). A similar reduction of maximum grip aperture was found when the hand's path was curved due to explicit instructions (Hesse and Deubel 2010b). In terms of the visuomotor-channel framework, these findings require an explicit coupling between the two channels. For the digit-in-space framework, both digits slow down as a result of curving over the obstacle in accordance with the well-known relation between speed and curvature for single-effector movements (Viviani and Terzuolo 1982). Since slower movements have less risk of hitting the target object accidentally, the approach can pass closer to the object's surface, so maximum grip aperture can be smaller (Smeets and Brenner 1999; Verheij et al. 2012). No effect on maximum grip aperture is observed if a vertical curvature is induced without slowing down the movement (Verheij et al. 2014b).

This section showed that when reaching to grasp an object, the spatial properties of the grasping movement are affected by constraints imposed by the properties of that object and of any obstacles. The effects of constraints on (peak) grip aperture can be understood within the digit-in-space framework without additional assumptions. In the visuomotor-channel framework, ad hoc explanations are needed to explain the results.

CONSTRAINTS AND MOVEMENT TIMING: THE SPEED-ACCURACY TRADE-OFF

In the previous section, we mainly discussed how constraints influence maximum grip aperture. In the present section, we will turn to experiments that studied how the constraints on the precision of grasping influence the timing of human reach-to-grasp movements. The relation between movement speed and the precision of movement has been studied since the late 19th century (Woodworth 1899). The attention for this theme increased after Paul Fitts provided a theoretical explanation in terms of information theory. He defined the information present in a movement as the binary logarithm of the ratio between amplitude and precision. He furthermore argued that move-

ment duration of repetitive movements should be proportional to the resolution in terms of such information (Fitts 1954). Given the fact that this simple theory does not hold very well for discrete movements (Fitts and Peterson 1964), we do not expect Fitts' law to hold for grasping. Instead, we developed for this review a new approach to the speed-accuracy trade-off in grasping that generates testable predictions. This new approach is inspired by the digit-in-space framework. As we have no equivalent new approach for the visuomotor-channel framework, we cannot compare the two frameworks with respect to the speed-accuracy trade-off.

According to the digit-in-space framework, any adequate description of the speed-accuracy trade-off in two-digit pointing should also be applicable to the speed-accuracy trade-off in grasping. To develop such a description of the speed-accuracy trade-off in two-digit pointing, we turn to a classic experimental paper (Kelso et al. 1979). Kelso and colleagues investigated the speed-accuracy trade-off in making bimanual goal-directed movements. The participants' task was to move their index finger as fast as possible to either an easy target (large and near) or a difficult target (small and far). This task could be performed by the right index finger (toward a target on the right), the left index finger (toward a target on the left), or both fingers simultaneously. The main conclusion of Kelso et al. (1979) was that if the two targets differed in difficulty for the two hands, the two digits nevertheless had very similar movement times, close to that of the single digit moving to the more difficult of the two targets. This result is sometimes interpreted as showing that the digit with the most difficult movement determines the overall movement time. However, closer inspection of the data shows that the movement times toward the more difficult target are slightly longer when there is a second digit making a goal-directed movement than when a single digit moves to this target. How much longer depends on how difficult the other digit's movement is (Marteniuk et al. 1984). Given the fact that we want to develop a model that is applicable to grasping, and grasping studies generally report a single movement time for both digits, we develop a model that makes predictions for the average movement time based on the constraints for the individual digits.

To predict how the average movement time of the two digits in the task of Kelso et al. (1979) depends on the difficulties for the individual digits, we start with *Eq. 4* of Welford et al. (1969), an equation that was developed to describe the deviations from Fitts' law in discrete movements. This equation splits the index of difficulty in two terms, one for the distance and one for the tolerance, in such a way that the resulting digit difficulty is proportional to the movement time. To apply this model to two digits, we assume that the measures for the two digits can be added quadratically as in Pythagoras' theorem. This yields the following equation for the digit difficulty D :

$$D = \log_2 \sqrt{A_1^2 + A_2^2} - 0.6 \log_2 \sqrt{W_1^2 + W_2^2}. \quad (1)$$

For pointing movements, the indices 1 and 2 indicate the left and right index finger. For grasping, they refer to the index finger and thumb. The value of 0.6 was obtained experimentally for single-digit movements (Welford et al. 1969). We used an effective value for width and amplitude rather than the corresponding stimulus values in all calculations. The effective width W takes the width of the digit into account (Hoffmann

and Sheikh 1991) and equals the size of the target (in centimeters) plus the width of the index finger (estimated to be 1.5 cm). The effective amplitude A is the distance to the center of the target (in centimeters; Welford 1960).

The digit difficulty measure given by *Eq. 1* and the data of Kelso et al. (1979) correlate very well (Fig. 6A). Both the digit difficulty and the observed movement time were larger when combining two movements to targets of the same difficulty than for single movements to targets of the same difficulty (compare filled and open symbols of the same color in Fig. 6A). When an easy and a difficult movement are combined, the overall digit difficulty and observed movement time are slightly lower than that of the most difficult target (bicolored disks in Fig. 6A). Although a linear fit of the measured movement time as a function of the model difficulty fits the data very well ($R^2 = 0.99$), the slope is very steep, corresponding to information transfer at a rate of 24 bits/s. We are not sure how to interpret this value, which is more than two times as high as the 10 bits/s reported for the classic task (Fitts 1954). Given the fact that the reported movement times are unusually short (78 ms, averaged across participants for the easiest condition), it might be that all movement times reported by Kelso et al. (1979) are underestimated, for instance, by the use of a switch as a measure for movement onset (Brenner and Smeets 2019). As such underestimation increases with movement time (as it takes more time to reach a fixed threshold for slower movements), this leads to an overestimation of the rate of information transfer.

Now that we have obtained an adequate description of how the speed of two-digit pointing depends on the movement amplitude and target size, the next question is whether the same measure of difficulty (*Eq. 1*) can predict the speed-accuracy relationship in grasping. Recently, Coats et al. (2018) performed an experiment that is very well-suited to test whether this is the case. They varied the size of the contact surface that was available for the thumb independently of that for the index finger (both 1, 2, or 3 cm wide) and also varied movement distance (10, 30, and 50 cm in their Experiment 1a and 10, 20, and 30 cm in their Experiments 2 and 3). According to the digit-in-space framework, grasping can be regarded as two digits of the same hand moving to targets that are on a single object. We, therefore, plotted the results of the three experiments of Coats et al. (2018) as a function of the digit difficulty (Fig. 6B). The fit is again quite good: $R^2 = 0.92$, with a slope corresponding to 5.5 bits/s information transfer. This slightly lower rate of information transfer than in the 10 bits/s of the original experiment (Fitts 1954) is not surprising, as the instructions were not to maximize speed but both speed and precision. This means that the actual variability will be less than assumed in our calculations based on contact surface size.

The next step is to expand *Eq. 1* to also describe how the movement time of the digits is affected by constraints imposed by obstacles. Many studies have shown that the presence of an obstacle results in prolongation of most time parameters of grasping, including movement time, grip opening time, and grip closure time (Biegstraaten et al. 2003; Mon-Williams and Tresilian 2001; Saling et al. 1998). If there are obstacles present while one is reaching to grasp an object, we add a term describing the effect of the obstacles (following the equation on page 533 in Biegstraaten et al. 2003) to obtain a difficulty D :

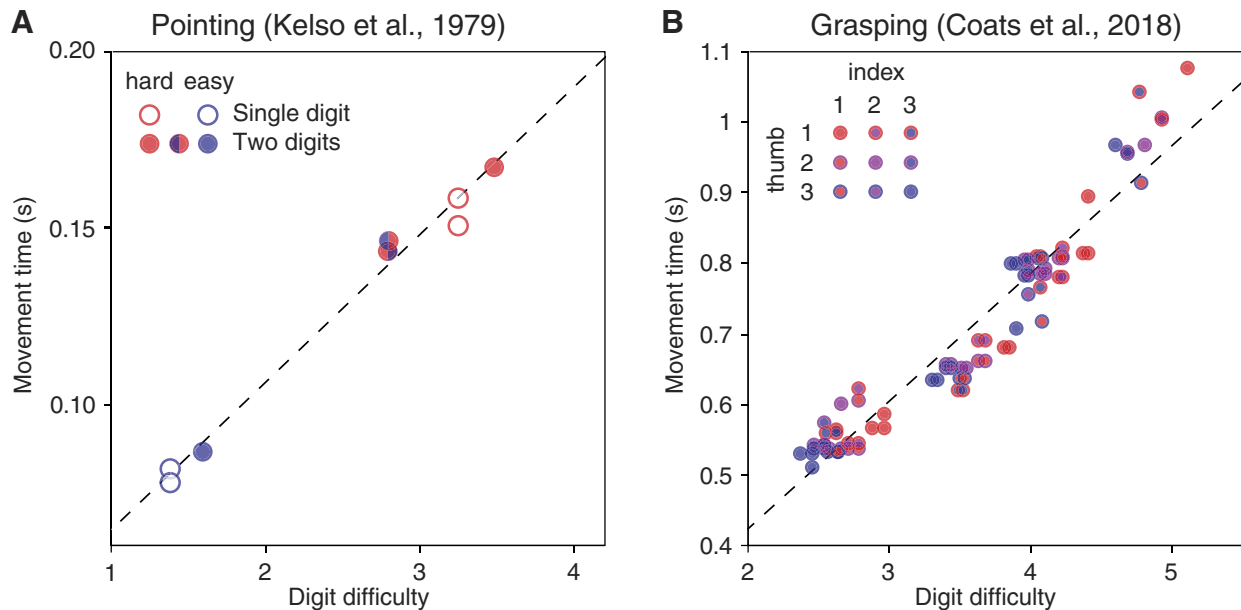


Fig. 6. Speed-accuracy trade-off for 2 digits moving to targets that differ in difficulty. As a measure for speed, we use the average movement time of the 2 digits. As a measure of accuracy, we use the digit difficulty as defined in Eq. 1. *A*: combining goal-directed movements of the index fingers of the left and the right hand (Kelso et al. 1979). For each digit, the target is either easy (blue) or difficult (red). Participants moved either with the index finger of 1 hand (open circles) or with the index fingers of both hands (filled circles). Bicolored disks are for combinations of an easy and a difficult target. Dashed line indicates the best linear fit. *B*: combining movements of finger and thumb in grasping an asymmetric object (Experiments 1a, 2, and 3 from Coats et al. 2018). Four different distances were used (not indicated; longer distances have higher difficulty). For each distance, 9 combinations of contact surface areas for the index finger and thumb were used (color coded).

$$D = \log_2 \sqrt{A_1^2 + A_2^2} - 0.6 \left(\log_2 \sqrt{W_1^2 + W_2^2} - \log_2 \sqrt{\frac{1}{S_1^2} + \frac{1}{S_2^2}} \right). \quad (2)$$

The separations S_i are the effective minimal separations between the digits and the obstacle (in centimeters), again considering the 1.5-cm widths of the index finger and thumb. We used the ratio of 0.6 between precision and amplitude for both aspects of precision (target width and obstacle separation) because Biegstraaten et al. (2003) found a ratio of 0.59 between the effects of the obstacle separation and amplitude in grasping, which is very similar to the value of 0.6 that Welford et al. (1969) reported for the ratio between the effects of target width and amplitude in pointing.

We used Eq. 2 to relate the task constraints (expressed as digit difficulty) to the movement time in various studies (Fig. 7). We plotted the results of three experiments involving obstacles, one with symmetric obstacle placement (Hoffmann et al. 2019) and two in which the separation for thumb and index finger varied independently (Biegstraaten et al. 2003; Mon-Williams and McIntosh 2000). We found good fits ($R^2 = 0.94, 0.83$, and 0.93) with slopes corresponding to an information transfer of 6.9, 5, and 10.3 bits/s. As a comparison, we plotted the data of several studies without obstacles (disks in Fig. 7). We replotted the results of Fig. 6B (Coats et al. 2018) and added the results of two other recent studies on the effect of contact surface size on the movement time in grasping (Hoffmann et al. 2019; McIntosh et al. 2018) as well as adding the results of two classic studies (Bootsma et al. 1994; Marteniuk et al. 1990). The fits were again reasonably good ($R^2 = 0.92, 0.93, 0.90, 0.81$, and 0.68), with quite a large

variation in the rate of information transfer (5.5, 10.0, 11.2, 8.8, and 18.5 bits/s). The differences in slope and intercept might be related to differences in instruction (e.g., the role of accuracy) or differences in the data analysis (e.g., how the movement time was determined). Equation 2 can, therefore, summarize the difficulty of grasping that is constrained by object size as well as obstacles, even in cases in which the constraints differ between the two digits.

In this section, we have developed a description of the difficulty of pointing with two digits to two targets (Eq. 1) that can also be applied to grasping. The difficulty of the task according to this equation captures the speed-accuracy trade-off for the overall movement time of these tasks in situations in which the difficulty for the two digits differs from each other (Fig. 6). This model of difficulty can be extended to situations with obstacles as well (Eq. 2; Fig. 7). The digit-in-space framework predicted that this should be possible.

DISCUSSION

We start the discussion by considering what we have presented in terms of the visuomotor-channel framework. The overall summary of the experimental results discussed in this review is that task constraints influence grasping behavior in a manner that shows a strong interrelation between the transport and grip component. This is inconsistent with the original visuomotor-channel hypothesis as formulated by Jeannerod (1981). The independent timing of the two channels was already questioned by work of his own laboratory (as discussed in Jeannerod 1999). The results presented in this review also question the information processing underlying the visuomotor-channel framework and, therefore, the more recent interpretations of grasping within this framework. In particular, the

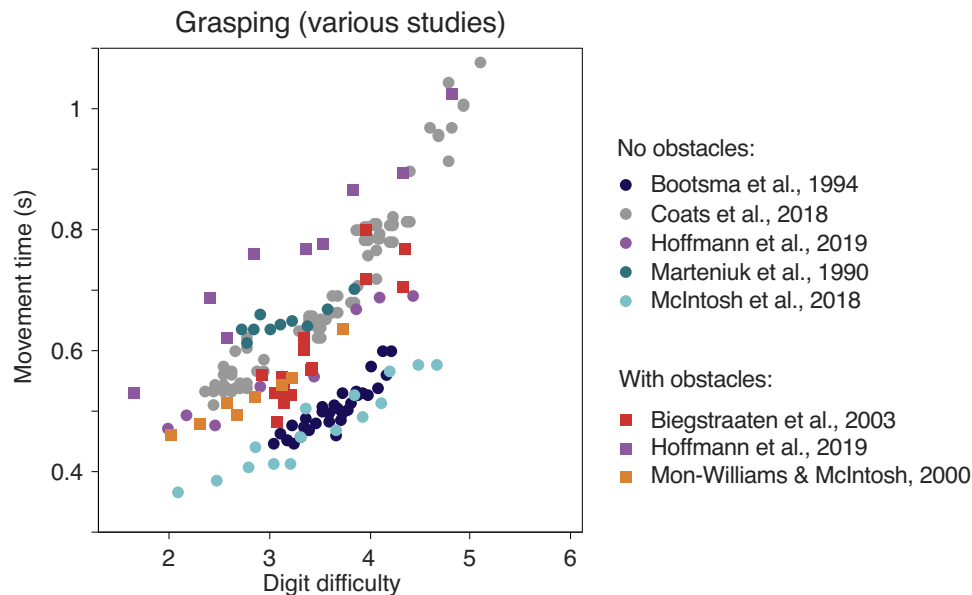


Fig. 7. In line with the digit-in-space framework, the speed-accuracy trade-off in various grasping studies increases more or less linearly with the digit difficulty. Digit difficulty (*Eq. 2*) is a weighted combination of the difficulties for each of the digits, based on size, movement distance, and distance to obstacles. Squares represent results of experiments involving obstacles (Biegstraaten et al. 2003; Hoffmann et al. 2019; Mon-Williams and McIntosh 2000). Disks represent experiments without obstacles. In addition to the data of Fig. 6B involving unequal contact surfaces (Coats et al. 2018), we included 4 studies on speed-accuracy trade-off in grasping in which the constraints for both digits were the same: 2 classic ones (Bootsma et al. 1994; Marteniuk et al. 1990) and 2 recent ones (Hoffmann et al. 2019; McIntosh et al. 2018).

results question whether grip formation is based on intrinsic object properties such as size.

Two lines of evidence show that perceived size is not used to control grip aperture. The first line consists of experiments that show that many size illusions do not affect grip aperture (Aglioti et al. 1995; Smeets and Brenner 2006; Whitwell et al. 2018). The second line of evidence is that grip variability appears to be independent of object size (Ganel et al. 2008; Smeets and Brenner 2008). These two lines of evidence are far from conclusive, as they can be interpreted within the visuomotor-channel framework by making one additional assumption: the existence of two visual systems (Goodale 2014). Studies that use other designs than relating maximum grip aperture in grasping with size perception, however, show very little evidence for separate processing for perception and action (Smeets and Brenner 2001a). Examples are motion perception and interception (de la Malla et al. 2018), size illusions and goal-directed hand movements (de Grave et al. 2009), and size illusions and saccades (Medendorp et al. 2018).

Within the digit-in-space framework, the interpretation of the two findings discussed in the previous paragraph is that the control of grip aperture is based on information on grasping points for the digits rather than on information on object size. Based on this digit-in-space framework, we developed a minimum-jerk model that made quantitative predictions for the dependence of maximum grip aperture and its timing on various experimental parameters (Smeets and Brenner 1999). Those predictions were confirmed by a review of the literature at that time (Figs. 6–8 in Smeets and Brenner 1999). However, there are some examples of experimental findings that are clearly not in line with the model proposed in the original paper. The most obvious is that the model predicts that maximum grip aperture in unperturbed grasping is independent of object distance, which is clearly not the case (see section TIME

COURSE OF GRIP-APERTURE FORMATION). As the visuomotor-channel framework predicts exactly the same independence, this failure does not favor either framework.

In the present review, we have discussed five additional predictions based on the digit-in-space framework. None of these predictions is easy to understand in terms of the visuomotor-channel framework. They are all confirmed experimentally. In chronological order, the predictions are as follows. 1) Digits in grasping should approach their contact surfaces perpendicularly. They do so (Kleinholdermann et al. 2007). 2) Digits' trajectories should be similar in grasping and pushing. They are very similar (Smeets et al. 2010). 3) Digits should respond quickly to position perturbations, even when there is no need to adjust grip. The digits respond to the rotation of a ball that is to be grasped (Voudouris et al. 2013). 4) Adaptation of tapping should transfer to grasping. Tapping with thumb and index finger can adapt in opposite directions (Schot et al. 2014), and this transfers to grip aperture in grasping (Schot et al. 2017). 5) A description of the speed-accuracy trade-off for two-digit pointing should also hold for grasping. It does (Fig. 6 in this review).

In addition to these explicit predictions, we reviewed various other experimental results that are easy to describe within the digit-in-space framework. Based on the digit-in-space framework, one could develop other models for trajectory generation than the minimum-jerk model we originally proposed. It is, for instance, possible to implement the framework in a more elaborate way, including a springlike coupling between the digits (Verheij et al. 2012). In this way, the model behavior shows some dependencies between the digits despite independent control. However, the aim of modeling is not to build a model that behaves exactly as humans do. The essence of using modeling to help understand human behavior is finding an optimal trade-off between easily understanding the working of

the model and finding a good correspondence with the real world (Smeets and Brenner 2002) in such a way that allows one to easily make predictions.

This review provides compelling evidence that the use of the digit-in-space framework is the most promising for understanding reach-to-grasp behavior. This has important implications for the study of the neurophysiological basis of grip formation. For instance, this review suggests that the control of grasping relies on the control of the kinematics of the digits in space rather than on the control of variables that are intrinsic to the muscles. We, for instance, discussed the gaze-dependent biases in reaching and grasping (Henriques et al. 1998; Selen and Medendorp 2011). For reaching, the neural correlate of the gaze dependency has been studied in detail in the posterior parietal cortex (reviewed by Crawford et al. 2011; Medendorp et al. 2008). For grasping, such a neural correlate has only been studied to a very limited extent (Leoné et al. 2015). One could try to determine whether the posterior parietal cortex codes positions for finger and thumb rather than object position by applying the paradigm of Medendorp et al. (2003) to grasping. In this paradigm, a saccade is made between planning and executing a pointing movement. If this saccade brings the remembered goal of the pointing movement from one hemisphere to the other, the brain activity switches hemispheres as well. By varying which part(s) of the object (finger contact, thumb contact, and center) switch hemispheres, one could test whether grasping relies on the memory of two separate grasping positions (one for the thumb and one for the index finger) or the memory of one object position.

One consequence of the view that we propose is that the same neural networks should be involved in reaching and grasping. More specifically, regions that are involved in the control of goal-directed single-digit movements should also be involved in grasping, provided that the constraints for the digits are comparable. This applies to all of the methods that have been used to study the involvement of various (networks of) brain areas in the control of grasping (for reviews, see, for instance, Fattori et al. 2017; Gallivan and Culham 2015; Janssen and Scherberger 2015). Thus it should apply to perturbations of brain activity by stimulating such brain areas (Davare et al. 2006; Schettino et al. 2015) as well as to relating the activity in such areas to variations in object properties and locations (Cavina-Pratesi et al. 2010, 2018; Fabbri et al. 2014; Grol et al. 2007; Króliczak et al. 2008; Michaels and Scherberger 2018; Overduin et al. 2015; Rouse and Schieber 2016; Takahashi et al. 2017; Verhagen et al. 2008). Some of the above-mentioned studies included reaching movements toward the same objects or locations as were used for grasping, to better understand the variations with location (Cavina-Pratesi et al. 2010, 2018; Fabbri et al. 2014), but the digits in the two kinds of movements were never confronted with comparable constraints. Using the proper constraints is extremely important: removing the contact constraints (in pantomimed grasping) not only leads to different behavior as we discussed, but also to a totally different pattern of brain activity (Króliczak et al. 2007). To test the critical prediction of the digit-in-space framework that regions that are involved in the control of goal-directed single-digit movement are similarly involved in grasping, experiments should compare the role of these areas in grasping with their role in carefully matched single-digit pointing tasks (such as the pushing and touching tasks in Smeets et

al. 2010). In this way, one can investigate the neurophysiological basis of grasping as coordinating the two digits' movements in space.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.B.J.S. analyzed data; J.B.J.S., K.v.d.K., and E.B. interpreted results of experiments; J.B.J.S. prepared figures; J.B.J.S. drafted manuscript; J.B.J.S., K.v.d.K., and E.B. edited and revised manuscript; J.B.J.S., K.v.d.K., and E.B. approved final version of manuscript.

REFERENCES

- Aglioti S, DeSouza JF, Goodale MA. Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5: 679–685, 1995. doi:10.1016/S0960-9822(95)00133-3.
- Aivar MP, Brenner E, Smeets JBJ. Avoiding moving obstacles. *Exp Brain Res* 190: 251–264, 2008. doi:10.1007/s00221-008-1475-9.
- Alberts JL, Saling M, Stelmach GE. Alterations in transport path differentially affect temporal and spatial movement parameters. *Exp Brain Res* 143: 417–425, 2002. doi:10.1007/s00221-002-1005-0.
- Ansuini C, Cavallo A, Campus C, Quarona D, Koul A, Becchio C. Are we real when we fake? Attunement to object weight in natural and pantomimed grasping movements. *Front Hum Neurosci* 10: 471, 2016. doi:10.3389/fnhum.2016.00471.
- Bartelt R, Darling WG. Opposite effects on perception and action induced by the Ponzo illusion. *Exp Brain Res* 146: 433–440, 2002. doi:10.1007/s00221-002-1198-2.
- Berger DJ, Gentner R, Edmunds T, Pai DK, d'Avella A. Differences in adaptation rates after virtual surgeries provide direct evidence for modularity. *J Neurosci* 33: 12384–12394, 2013. doi:10.1523/JNEUROSCI.0122-13.2013.
- Biegstraaten M, de Grave DDJ, Brenner E, Smeets JBJ. Grasping the Müller-Lyer illusion: not a change in perceived length. *Exp Brain Res* 176: 497–503, 2007. doi:10.1007/s00221-006-0744-8.
- Biegstraaten M, Smeets JBJ, Brenner E. The influence of obstacles on the speed of grasping. *Exp Brain Res* 149: 530–534, 2003. doi:10.1007/s00221-003-1374-z.
- Biegstraaten M, Smeets JBJ, Brenner E. The relation between force and movement when grasping an object with a precision grip. *Exp Brain Res* 171: 347–357, 2006. doi:10.1007/s00221-005-0271-z.
- Bingham G, Coats R, Mon-Williams M. Natural prehension in trials without haptic feedback but only when calibration is allowed. *Neuropsychologia* 45: 288–294, 2007. doi:10.1016/j.neuropsychologia.2006.07.011.
- Bongers RM, Zaal FTJM, Jeannerod M. Hand aperture patterns in prehension. *Hum Mov Sci* 31: 487–501, 2012. doi:10.1016/j.humov.2011.07.014.
- Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaal FTJM. The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. *Exp Brain Res* 98: 535–541, 1994. doi:10.1007/BF00233990.
- Borchers S, Verheij R, Smeets JBJ, Himmelbach M. The influence of object height on maximum grip aperture in empirical and modeled data. *J Exp Psychol Hum Percept Perform* 40: 889–896, 2014. doi:10.1037/a0035061.
- Bozzacchi C, Brenner E, Smeets JBJ, Volcic R, Domini F. How removing visual information affects grasping movements. *Exp Brain Res* 236: 985–995, 2018. doi:10.1007/s00221-018-5186-6.
- Brenner E, Smeets JBJ. Continuously updating one's predictions underlies successful interception. *J Neurophysiol* 120: 3257–3274, 2018. doi:10.1152/jn.00517.2018.
- Brenner E, Smeets JBJ. Fast corrections of movements with a computer mouse. *Spat Vis* 16: 365–376, 2003. doi:10.1163/156856803322467581.

- Brenner E, Smeets JBJ. How can you best measure reaction times? *J Mot Behav* 51: 486–495, 2019. doi:10.1080/00222895.2018.1518311.
- Brenner E, Smeets JBJ. Two eyes in action. *Exp Brain Res* 170: 302–311, 2006. doi:10.1007/s00221-005-0213-9.
- Bruno N, Knox PC, de Grave DDJ. A metaanalysis of the effect of the Müller-Lyer illusion on saccadic eye movements: no general support for a dissociation of perception and oculomotor action. *Vision Res* 50: 2671–2682, 2010. doi:10.1016/j.visres.2010.09.016.
- Bruno N, Uccelli S, Viviani E, de'Sperati C. Both vision-for-perception and vision-for-action follow Weber's law at small object sizes, but violate it at larger sizes. *Neuropsychologia* 91: 327–334, 2016. doi:10.1016/j.neuropsychologia.2016.08.022.
- Bruton M, O'Dwyer N. Synergies in coordination: a comprehensive overview of neural, computational, and behavioral approaches. *J Neurophysiol* 120: 2761–2774, 2018. doi:10.1152/jn.00052.2018.
- Cavina-Pratesi C, Connolly JD, Monaco S, Figley TD, Milner AD, Schenk T, Culham JC. Human neuroimaging reveals the subcomponents of grasping, reaching and pointing actions. *Cortex* 98: 128–148, 2018. doi:10.1016/j.cortex.2017.05.018.
- Cavina-Pratesi C, Monaco S, Fattori P, Galletti C, McAdam TD, Quinlan DJ, Goodale MA, Culham JC. Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *J Neurosci* 30: 10306–10323, 2010. doi:10.1523/JNEUROSCI.2023-10.2010.
- Cesane E, Campagnoli C, Taylor JA, Domini F. Does visuomotor adaptation contribute to illusion-resistant grasping? *Psychon Bull Rev* 25: 827–845, 2018. doi:10.3758/s13423-017-1368-7.
- Cesane E, Domini F. Error correction and spatial generalization in human grasp control. *Neuropsychologia* 106: 112–122, 2017. doi:10.1016/j.neuropsychologia.2017.09.026.
- Chan J, Heath M. Haptic feedback attenuates illusory bias in pantomime-grasping: evidence for a visuo-haptic calibration. *Exp Brain Res* 235: 1041–1051, 2017. doi:10.1007/s00221-016-4860-9.
- Coats RO, Holt RJ, Bingham GP, Mon-Williams MA. Predicting the duration of reach-to-grasp movements to objects with asymmetric contact surfaces. *PLoS One* 13: e0193185, 2018. doi:10.1371/journal.pone.0193185.
- Craje C, Lukos JR, Ansuini C, Gordon AM, Santello M. The effects of task and content on digit placement on a bottle. *Exp Brain Res* 212: 119–124, 2011. doi:10.1007/s00221-011-2704-1.
- Crawford JD, Henriques DY, Medendorp WP. Three-dimensional transformations for goal-directed action. *Annu Rev Neurosci* 34: 309–331, 2011. doi:10.1146/annurev-neuro-061010-113749.
- Cuijpers RH, Brenner E, Smeets JBJ. Grasping reveals visual misjudgements of shape. *Exp Brain Res* 175: 32–44, 2006. doi:10.1007/s00221-006-0531-6.
- Cuijpers RH, Smeets JBJ, Brenner E. On the relation between object shape and grasping kinematics. *J Neurophysiol* 91: 2598–2606, 2004. doi:10.1152/jn.00644.2003.
- d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci* 6: 300–308, 2003. doi:10.1038/nn1010.
- Davare M, Andres M, Cosnard G, Thonnard JL, Olivier E. Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *J Neurosci* 26: 2260–2268, 2006. doi:10.1523/JNEUROSCI.3386-05.2006.
- Davarpanah Jazi S, Heath M. The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. *Brain Cogn* 114: 29–39, 2017. doi:10.1016/j.bandc.2017.03.002.
- Davarpanah Jazi S, Yau M, Westwood DA, Heath M. Pantomime-grasping: the 'return' of haptic feedback supports the absolute specification of object size. *Exp Brain Res* 233: 2029–2040, 2015. doi:10.1007/s00221-015-4274-0.
- de Grave DDJ, Biegstraaten M, Smeets JBJ, Brenner E. Effects of the Ebbinghaus figure on grasping are not only due to misjudged size. *Exp Brain Res* 163: 58–64, 2005. doi:10.1007/s00221-004-2138-0.
- de Grave DDJ, Brenner E, Smeets JBJ. Illusions as a tool to study the coding of pointing movements. *Exp Brain Res* 155: 56–62, 2004. doi:10.1007/s00221-003-1708-x.
- de Grave DDJ, Brenner E, Smeets JBJ. The Brentano illusion influences goal-directed movements of the left and right hand to the same extent. *Exp Brain Res* 193: 421–427, 2009. doi:10.1007/s00221-008-1638-8.
- de Grave DDJ, Franz VH, Gegenfurtner KR. The influence of the Brentano illusion on eye and hand movements. *J Vis* 6: 5, 2006a. doi:10.1167/6.7.5.
- de Grave DDJ, Smeets JBJ, Brenner E. Why are saccades influenced by the Brentano illusion? *Exp Brain Res* 175: 177–182, 2006b. doi:10.1007/s00221-006-0536-1.
- de Haan EHF, Jackson SR, Schenk T. Where are we now with 'what' and 'how'? *Cortex* 98: 1–7, 2018. doi:10.1016/j.cortex.2017.12.001.
- de la Malla C, Smeets JBJ, Brenner E. Errors in interception can be predicted from errors in perception. *Cortex* 98: 49–59, 2018. doi:10.1016/j.cortex.2017.03.006.
- de Lussanet MH, Smeets JBJ, Brenner E. The effect of expectations on hitting moving targets: influence of the preceding target's speed. *Exp Brain Res* 137: 246–248, 2001. doi:10.1007/s002210000607.
- Desmurget M, Prablanc C, Arzi M, Rossetti Y, Paulignan Y, Urquizar C. Integrated control of hand transport and orientation during prehension movements. *Exp Brain Res* 110: 265–278, 1996. doi:10.1007/BF00228557.
- Dimitriou M, Wolpert DM, Franklin DW. The temporal evolution of feedback gains rapidly update to task demands. *J Neurosci* 33: 10898–10909, 2013. doi:10.1523/JNEUROSCI.5669-12.2013.
- Doemen MJ, Kappers AM, Koenderink JJ. Visual space under free viewing conditions. *Percept Psychophys* 67: 1177–1189, 2005. doi:10.3758/BF03193551.
- Ellis RR, Flanagan JR, Lederman SJ. The influence of visual illusions on grasp position. *Exp Brain Res* 125: 109–114, 1999. doi:10.1007/s002210050665.
- Eloka O, Franz VH. Effects of object shape on the visual guidance of action. *Vision Res* 51: 925–931, 2011. doi:10.1016/j.visres.2011.02.002.
- Elsinger CL, Rosenbaum DA. End posture selection in manual positioning: evidence for feedforward modeling based on a movement choice method. *Exp Brain Res* 152: 499–509, 2003. doi:10.1007/s00221-003-1573-7.
- Fabbri S, Strnad L, Caramazza A, Lingnau A. Overlapping representations for grip type and reach direction. *Neuroimage* 94: 138–146, 2014. doi:10.1016/j.neuroimage.2014.03.017.
- Fattori P, Breveglieri R, Bosco A, Gamberini M, Galletti C. Vision for prehension in the medial parietal cortex. *Cereb Cortex* 27: 1149–1163, 2017. doi:10.1093/cercor/bhv302.
- Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47: 381–391, 1954. doi:10.1037/h0055392.
- Fitts PM, Peterson JR. Information capacity of discrete motor responses. *J Exp Psychol* 67: 103–112, 1964. doi:10.1037/h0045689.
- Flash T, Hogan N. The coordination of arm movements: an experimentally confirmed mathematical model. *J Neurosci* 5: 1688–1703, 1985. doi:10.1523/JNEUROSCI.05-07-01688.1985.
- Franz VH, Gegenfurtner KR, Bühlhoff HH, Fehle M. Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychol Sci* 11: 20–25, 2000. doi:10.1111/1467-9280.00209.
- Gallivan JP, Culham JC. Neural coding within human brain areas involved in actions. *Curr Opin Neurobiol* 33: 141–149, 2015. doi:10.1016/j.conb.2015.03.012.
- Ganel T, Chajut E, Algom D. Visual coding for action violates fundamental psychophysical principles. *Curr Biol* 18: R599–R601, 2008. doi:10.1016/j.cub.2008.04.052.
- Garzorz IT, Knorr AG, Gilster R, Deubel H. The influence of obstacles on grasp planning. *Exp Brain Res* 236: 2639–2648, 2018. doi:10.1007/s00221-018-5321-4.
- Glowania C, van Dam LCJ, Brenner E, Plaisier MA. Smooth at one end and rough at the other: influence of object texture on grasping behaviour. *Exp Brain Res* 235: 2821–2827, 2017. doi:10.1007/s00221-017-5016-2.
- Goodale MA. How (and why) the visual control of action differs from visual perception. *Proc Biol Sci* 281: 20140337, 2014. doi:10.1098/rspb.2014.0337.
- Goodale MA, Jakobson LS, Keillor JM. Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia* 32: 1159–1178, 1994. doi:10.1016/0028-3932(94)90100-7.
- Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends Neurosci* 15: 20–25, 1992. doi:10.1016/0166-2236(92)90344-8.
- Goodale MA, Milner AD. Two visual pathways – where have they taken us and where will they lead in future? *Cortex* 98: 283–292, 2018. doi:10.1016/j.cortex.2017.12.002.
- Gribble PL, Ostry DJ, Sanguineti V, Laboisière R. Are complex control signals required for human arm movement? *J Neurophysiol* 79: 1409–1424, 1998. doi:10.1152/jn.1998.79.3.1409.
- Grinyagin IV, Biryukova EV, Maier MA. Kinematic and dynamic synergies of human precision-grip movements. *J Neurophysiol* 94: 2284–2294, 2005. doi:10.1152/jn.01310.2004.

- Grol MJ, Majdandžić J, Stephan KE, Verhagen L, Dijkerman HC, Bekkering H, Verstraten FAJ, Toni I. Parieto-frontal connectivity during visually guided grasping. *J Neurosci* 27: 11877–11887, 2007. doi:10.1523/JNEUROSCI.3923-07.2007.
- Haffenden AM, Goodale MA. Independent effects of pictorial displays on perception and action. *Vision Res* 40: 1597–1607, 2000. doi:10.1016/S0042-6989(00)00056-0.
- Haffenden AM, Schiff KC, Goodale MA. The dissociation between perception and action in the Ebbinghaus illusion: nonillusory effects of pictorial cues on grasp. *Curr Biol* 11: 177–181, 2001. doi:10.1016/S0960-9822(01)00023-9.
- Haggard P, Wing A. On the hand transport component of prehensile movements. *J Mot Behav* 29: 282–287, 1997. doi:10.1080/00222899709600842.
- Harris CM, Wolpert DM. Signal-dependent noise determines motor planning. *Nature* 394: 780–784, 1998. doi:10.1038/29528.
- Heath M, Manzone J, Khan M, Davarpanah Jazi S. Vision for action and perception elicit dissociable adherence to Weber's law across a range of 'graspable' target objects. *Exp Brain Res* 235: 3003–3012, 2017. doi:10.1007/s00221-017-5025-1.
- Henriques DY, Klier EM, Smith MA, Lowy D, Crawford JD. Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 18: 1583–1594, 1998. doi:10.1523/JNEUROSCI.18-04-01583.1998.
- Hesse C, de Grave DDJ, Franz VH, Brenner E, Smeets JBJ. Planning movements well in advance. *Cogn Neuropsychol* 25: 985–995, 2008. doi:10.1080/02643290701862399.
- Hesse C, Deubel H. Advance planning in sequential pick-and-place tasks. *J Neurophysiol* 104: 508–516, 2010a. doi:10.1152/jn.00097.2010.
- Hesse C, Deubel H. Effects of altered transport paths and intermediate movement goals on human grasp kinematics. *Exp Brain Res* 201: 93–109, 2010b. doi:10.1007/s00221-009-2070-4.
- Hesse C, Franz VH. Corrective processes in grasping after perturbations of object size. *J Mot Behav* 41: 253–273, 2009. doi:10.3200/JMBR.41.3.253-273.
- Hoff B, Arbib MA. Models of trajectory formation and temporal interaction of reach and grasp. *J Mot Behav* 25: 175–192, 1993. doi:10.1080/00222895.1993.9942048.
- Hoffmann ER, Chan AH, Lam CK. Reach/grasp times with lateral reach obstructions. *J Mot Behav* 51: 351–361, 2019. doi:10.1080/00222895.2018.1485008.
- Hoffmann ER, Sheikh IH. Finger width corrections in Fitts' law: implications for speed-accuracy research. *J Mot Behav* 23: 259–262, 1991. doi:10.1080/00222895.1991.9942037.
- Holmes SA, Lohmus J, McKinnon S, Mulla A, Heath M. Distinct visual cues mediate aperture shaping for grasping and pantomime-grasping tasks. *J Mot Behav* 45: 431–439, 2013. doi:10.1080/00222895.2013.818930.
- Iberall T, Bingham G, Arbib MA. Opposition space as a structuring concept for the analysis of skilled hand movements. In: *Generation and Modulation of Action Patterns*, edited by Heuer H, Fromm C. Berlin: Springer-Verlag, 1986, p. 158–173.
- Jakobson LS, Goodale MA. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res* 86: 199–208, 1991. doi:10.1007/BF00231054.
- Janssen P, Scherberger H. Visual guidance in control of grasping. *Annu Rev Neurosci* 38: 69–86, 2015. doi:10.1146/annurev-neuro-071714-034028.
- Jeannerod M. Intersegmental coordination during reaching at natural visual objects. In: *Attention and Performance IX*, edited by Long J, Baddeley A. Hillsdale, NJ: Erlbaum, 1981, p. 153–169.
- Jeannerod M. *The Neural and Behavioural Organization of Goal-Directed Movements*. Oxford, UK: Clarendon, 1988.
- Jeannerod M. Visuomotor channels: their integration in goal-directed prehension. *Hum Mov Sci* 18: 201–218, 1999. doi:10.1016/S0167-9457(99)00008-1.
- Kelso JA, Southard DL, Goodman D. On the nature of human interlimb coordination. *Science* 203: 1029–1031, 1979. doi:10.1126/science.424729.
- Kistemaker DA, Wong JD, Gribble PL. The central nervous system does not minimize energy cost in arm movements. *J Neurophysiol* 104: 2985–2994, 2010. doi:10.1152/jn.00483.2010.
- Kistemaker DA, Wong JD, Gribble PL. The cost of moving optimally: kinematic path selection. *J Neurophysiol* 112: 1815–1824, 2014. doi:10.1152/jn.00291.2014.
- Kleinholdermann U, Brenner E, Franz VH, Smeets JBJ. Grasping trapezoidal objects. *Exp Brain Res* 180: 415–420, 2007. doi:10.1007/s00221-007-0867-6.
- Kleinholdermann U, Franz VH, Gegenfurtner KR. Human grasp point selection. *J Vis* 13: 23, 2013. doi:10.1167/13.8.23.
- Kopiske KK, Bruno N, Hesse C, Schenk T, Franz VH. The functional subdivision of the visual brain: is there a real illusion effect on action? A multi-lab replication study. *Cortex* 79: 130–152, 2016. doi:10.1016/j.cortex.2016.03.020.
- Kopiske KK, Cesanek E, Campagnoli C, Domini F. Adaptation effects in grasping the Müller-Lyer illusion. *Vision Res* 136: 21–31, 2017. doi:10.1016/j.visres.2017.05.004.
- Krakauer JW, Mazzoni P. Human sensorimotor learning: adaptation, skill, and beyond. *Curr Opin Neurobiol* 21: 636–644, 2011. doi:10.1016/j.conb.2011.06.012.
- Króliczak G, Cavina-Pratesi C, Goodman DA, Culham JC. What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. *J Neurophysiol* 97: 2410–2422, 2007. doi:10.1152/jn.00778.2006.
- Króliczak G, McAdam TD, Quinlan DJ, Culham JC. The human dorsal stream adapts to real actions and 3D shape processing: a functional magnetic resonance imaging study. *J Neurophysiol* 100: 2627–2639, 2008. doi:10.1152/jn.01376.2007.
- Kudoh N, Hattori M, Numata N, Maruyama K. An analysis of spatiotemporal variability during prehension movements: effects of object size and distance. *Exp Brain Res* 117: 457–464, 1997. doi:10.1007/s002210050241.
- Kuling IA, Brenner E, Smeets JBJ. Errors in visuo-haptic and haptic-haptic location matching are stable over long periods of time. *Acta Psychol (Amst)* 166: 31–36, 2016. doi:10.1016/j.actpsy.2016.03.011.
- Latash ML, Scholz JF, Danion F, Schöner G. Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res* 141: 153–165, 2001. doi:10.1007/s002210100861.
- Latash ML, Scholz JP, Schöner G. Motor control strategies revealed in the structure of motor variability. *Exerc Sport Sci Rev* 30: 26–31, 2002. doi:10.1097/00003677-200201000-00006.
- Lederman SJ, Wing AM. Perceptual judgement, grasp point selection and object symmetry. *Exp Brain Res* 152: 156–165, 2003. doi:10.1007/s00221-003-1522-5.
- Lee WA. Neuromotor synergies as a basis for coordinated intentional action. *J Mot Behav* 16: 135–170, 1984. doi:10.1080/00222895.1984.10735316.
- Leoné FT, Monaco S, Henriques DY, Toni I, Medendorp WP. Flexible reference frames for grasp planning in human parietofrontal cortex. *eNeuro* 2: ENEURO.0008-15.2015, 2015. doi:10.1523/ENEURO.0008-15.2015.
- Liu D, Todorov E. Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci* 27: 9354–9368, 2007. doi:10.1523/JNEUROSCI.1110-06.2007.
- Lukos JR, Ansuini C, Santello M. Anticipatory control of grasping: independence of sensorimotor memories for kinematics and kinetics. *J Neurosci* 28: 12765–12774, 2008. doi:10.1523/JNEUROSCI.4335-08.2008.
- Manzone J, Davarpanah Jazi S, Whitwell RL, Heath M. Biomechanical constraints do not influence pantomime-grasping adherence to Weber's law: a reply to Utz et al. (2015). *Vision Res* 130: 31–35, 2017. doi:10.1016/j.visres.2016.09.018.
- Marotta JJ, Graham TJ. Cluttered environments: differential effects of obstacle position on grasp and gaze locations. *Can J Exp Psychol* 70: 242–247, 2016. doi:10.1037/cep0000079.
- Marteniuk RG, Bertram CP. Contributions of gait and trunk movements to prehension: perspectives from world- and body-centered coordinates. *Mot Contr* 5: 151–165, 2001. doi:10.1123/mcj.5.2.151.
- Marteniuk RG, Ivens CJ, Bertram CP. Evidence of motor equivalence in a pointing task involving locomotion. *Mot Contr* 4: 165–184, 2000. doi:10.1123/mcj.4.2.165.
- Marteniuk RG, Leavitt JL, MacKenzie CL, Athenes S. Functional relationships between grasp and transport components in a prehension task. *Hum Mov Sci* 9: 149–176, 1990. doi:10.1016/0167-9457(90)90025-9.
- Marteniuk RG, MacKenzie CL, Baba DM. Bimanual movement control: information processing and interaction effects. *Q J Exp Psychol A* 36: 335–365, 1984. doi:10.1080/14640748408402163.
- Mason CR, Gomez JE, Ebner TJ. Hand synergies during reach-to-grasp. *J Neurophysiol* 86: 2896–2910, 2001. doi:10.1152/jn.2001.86.6.2896.
- McIntosh RD, Mon-Williams M, Tresilian JR. Grasping at laws: speed-accuracy trade-offs in manual prehension. *J Exp Psychol Hum Percept Perform* 44: 1022–1037, 2018. doi:10.1037/xhp0000512.
- Medendorp WP, Beurze SM, Van Pelt S, Van Der Werf J. Behavioral and cortical mechanisms for spatial coding and action planning. *Cortex* 44: 587–597, 2008. doi:10.1016/j.cortex.2007.06.001.

- Medendorp WP, de Brouwer AJ, Smeets JBJ. Dynamic representations of visual space for perception and action. *Cortex* 98: 194–202, 2018. doi:10.1016/j.cortex.2016.11.013.
- Medendorp WP, Goltz HC, Vilis T, Crawford JD. Gaze-centered updating of visual space in human parietal cortex. *J Neurosci* 23: 6209–6214, 2003. doi:10.1523/JNEUROSCI.23-15-06209.2003.
- Mendoza JE, Elliott D, Meegan DV, Lyons JL, Welsh TN. The effect of the Müller-Lyer illusion on the planning and control of manual aiming movements. *J Exp Psychol Hum Percept Perform* 32: 413–422, 2006. doi:10.1037/0096-1523.32.2.413.
- Merton PA. How we control the contraction of our muscles. *Sci Am* 226: 30–37, 1972. doi:10.1038/scientificamerican0572-30.
- Michaels JA, Scherberger H. Population coding of grasp and laterality-related information in the macaque fronto-parietal network. *Sci Rep* 8: 1710, 2018. doi:10.1038/s41598-018-20051-7.
- Mon-Williams M, Bull R. The Judd illusion: evidence for two visual streams or two experimental conditions? *Exp Brain Res* 130: 273–276, 2000. doi:10.1007/s002219900258.
- Mon-Williams M, McIntosh RD. A test between two hypotheses and a possible third way for the control of prehension. *Exp Brain Res* 134: 268–273, 2000. doi:10.1007/s002210000479.
- Mon-Williams M, Tresilian JR. A simple rule of thumb for elegant prehension. *Curr Biol* 11: 1058–1061, 2001. doi:10.1016/S0960-9822(01)00293-7.
- Nashed JY, Crevecoeur F, Scott SH. Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J Neurophysiol* 108: 999–1009, 2012. doi:10.1152/jn.01089.2011.
- Oostwoud Wijdenes L, Brenner E, Smeets JBJ. Analysis of methods to determine the latency of online movement adjustments. *Behav Res Methods* 46: 131–139, 2014. doi:10.3758/s13428-013-0349-7.
- Oostwoud Wijdenes L, Brenner E, Smeets JBJ. Fast and fine-tuned corrections when the target of a hand movement is displaced. *Exp Brain Res* 214: 453–462, 2011. doi:10.1007/s00221-011-2843-4.
- Overduin SA, d'Avella A, Roh J, Carmana JM, Bizzi E. Representation of muscle synergies in the primate brain. *J Neurosci* 35: 12615–12624, 2015. doi:10.1523/JNEUROSCI.4302-14.2015.
- Ozana A, Ganel T. Dissociable effects of irrelevant context on 2D and 3D grasping. *Atten Percept Psychophys* 80: 564–575, 2018. doi:10.3758/s13414-017-1443-1.
- Ozana A, Ganel T. Weber's law in 2D and 3D grasping. *Psychol Res* 83: 977–988, 2019. doi:10.1007/s00426-017-0913-3.
- Paulignan Y, Jeannerod M. Prehension movements: the visuomotor channels hypothesis revisited. In: *Hand and Brain: Neurophysiology and Psychology of Hand Movements*, edited by Wing AM, Haggard P, Flanagan R. Orlando, FL: Academic, 1996, p. 265–282.
- Paulignan Y, Jeannerod M, MacKenzie C, Marteniuk R. Selective perturbation of visual input during prehension movements. 2. The effects of changing object size. *Exp Brain Res* 87: 407–420, 1991a. doi:10.1007/BF00231858.
- Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M. Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Exp Brain Res* 83: 502–512, 1991b. doi:10.1007/BF00229827.
- Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M. The coupling of arm and finger movements during prehension. *Exp Brain Res* 79: 431–435, 1990. doi:10.1007/BF00608255.
- Paulun VC, Gegenfurtner KR, Goodale MA, Fleming RW. Effects of material properties and object orientation on precision grip kinematics. *Exp Brain Res* 234: 2253–2265, 2016. doi:10.1007/s00221-016-4631-7.
- Paulun VC, Kleinhoddermann U, Gegenfurtner KR, Smeets JBJ, Brenner E. Center or side: biases in selecting grasp points on small bars. *Exp Brain Res* 232: 2061–2072, 2014. doi:10.1007/s00221-014-3895-z.
- Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farnè A. Are perception and action affected differently by the Titchener circles illusion? *Exp Brain Res* 127: 95–101, 1999. doi:10.1007/s002210050777.
- Redding GM, Wallace B. Generalization of prism adaptation. *J Exp Psychol Hum Percept Perform* 32: 1006–1022, 2006. doi:10.1037/0096-1523.32.4.1006.
- Rinsma T, van der Kamp J, Dicks M, Cañal-Bruland R. Nothing magical: pantomimed grasping is controlled by the ventral system. *Exp Brain Res* 235: 1823–1833, 2017. doi:10.1007/s00221-016-4868-1.
- Roche K, Chainay H. Visually guided grasping of common objects: effects of priming. *Vis Cogn* 21: 1010–1032, 2013. doi:10.1080/13506285.2013.851136.
- Roche K, Verheij R, Voudouris D, Chainay H, Smeets JBJ. Grasping an object comfortably: orientation information is held in memory. *Exp Brain Res* 233: 2663–2672, 2015. doi:10.1007/s00221-015-4360-3.
- Rosenbaum DA, Halloran ES, Cohen RG. Grasping movement plans. *Psychon Bull Rev* 13: 918–922, 2006. doi:10.3758/BF03194019.
- Rosenbaum DA, Loukopoulos LD, Meulenbroek RGJ, Vaughan J, Engelbrecht SE. Planning reaches by evaluating stored postures. *Psychol Rev* 102: 28–67, 1995. doi:10.1037/0033-295X.102.1.28.
- Rosenbaum DA, Marchak F, Barnes HJ, Vaughan J, Slotta J, Jorgensen M. Constraints for action selection: overhand versus underhand grips. In: *Attention and Performance XIII: Motor Representation and Control*, edited by Jeannerod M. Hillsdale, NJ: Erlbaum, 1990, p. 321–342.
- Rosenbaum DA, Meulenbroek RJ, Vaughan J, Jansen C. Posture-based motion planning: applications to grasping. *Psychol Rev* 108: 709–734, 2001. doi:10.1037/0033-295X.108.4.709.
- Rouse AG, Schieber MH. Spatiotemporal distribution of location and object effects in primary motor cortex neurons during reach-to-grasp. *J Neurosci* 36: 10640–10653, 2016. doi:10.1523/JNEUROSCI.1716-16.2016.
- Säfstöm D, Edin BB. Task requirements influence sensory integration during grasping in humans. *Learn Mem* 11: 356–363, 2004. doi:10.1101/lm.71804.
- Saling M, Alberts J, Stelmach GE, Bloedel JR. Reach-to-grasp movements during obstacle avoidance. *Exp Brain Res* 118: 251–258, 1998. doi:10.1007/s002210050279.
- Scheidt RA, Ghez C. Separate adaptive mechanisms for controlling trajectory and final position in reaching. *J Neurophysiol* 98: 3600–3613, 2007. doi:10.1152/jn.00121.2007.
- Schenk T. No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *J Neurosci* 32: 2013–2017, 2012. doi:10.1523/JNEUROSCI.3413-11.2012.
- Schenk T, Hesse C. Do we have distinct systems for immediate and delayed actions? A selective review on the role of visual memory in action. *Cortex* 98: 228–248, 2018. doi:10.1016/j.cortex.2017.05.014.
- Schenk T, Utz KS, Hesse C. Violations of Weber's law tell us more about methodological challenges in sensorimotor research than about the neural correlates of visual behaviour. *Vision Res* 140: 140–143, 2017. doi:10.1016/j.visres.2017.05.017.
- Schettino LF, Adamovich SV, Bagce H, Yarossi M, Tunik E. Disruption of activity in the ventral premotor but not the anterior intraparietal area interferes with on-line correction to a haptic perturbation during grasping. *J Neurosci* 35: 2112–2117, 2015. doi:10.1523/JNEUROSCI.3000-14.2015.
- Schettino LF, Adamovich SV, Tunik E. Coordination of pincer grasp and transport after mechanical perturbation of the index finger. *J Neurophysiol* 117: 2292–2297, 2017. doi:10.1152/jn.00642.2016.
- Schot WD, Brenner E, Smeets JBJ. Grasping and hitting moving objects. *Exp Brain Res* 212: 487–496, 2011. doi:10.1007/s00221-011-2756-2.
- Schot WD, Brenner E, Smeets JBJ. Posture of the arm when grasping spheres to place them elsewhere. *Exp Brain Res* 204: 163–171, 2010. doi:10.1007/s00221-010-2261-z.
- Schot WD, Brenner E, Smeets JBJ. Simultaneous adaptation of the thumb and index finger of the same hand to opposite prism displacements. *J Neurophysiol* 111: 2554–2559, 2014. doi:10.1152/jn.00326.2013.
- Schot WD, Brenner E, Smeets JBJ. Unusual prism adaptation reveals how grasping is controlled. *eLife* 6: e21440, 2017. doi:10.7554/eLife.21440.
- Scott SH. A functional taxonomy of bottom-up sensory feedback processing for motor actions. *Trends Neurosci* 39: 512–526, 2016. doi:10.1016/j.tins.2016.06.001.
- Selen LP, Medendorp WP. Saccadic updating of object orientation for grasping movements. *Vision Res* 51: 898–907, 2011. doi:10.1016/j.visres.2011.01.004.
- Smeets JBJ, Brenner E. 10 years of illusions. *J Exp Psychol Hum Percept Perform* 32: 1501–1504, 2006. doi:10.1037/0096-1523.32.6.1501.
- Smeets JBJ, Brenner E. A new view on grasping. *Mot Contr* 3: 237–271, 1999. doi:10.1123/mcj.3.3.237.
- Smeets JBJ, Brenner E. Action beyond our grasp. *Trends Cogn Sci* 5: 287, 2001a. doi:10.1016/S1364-6613(00)01684-3.
- Smeets JBJ, Brenner E. Curved movement paths and the Hering illusion: positions or directions? *Vis Cogn* 11: 255–274, 2004. doi:10.1080/13506280344000356.
- Smeets JBJ, Brenner E. Does a complex model help to understand grasping? *Exp Brain Res* 144: 132–135, 2002. doi:10.1007/s00221-002-1056-2.
- Smeets JBJ, Brenner E. Grasping Weber's law. *Curr Biol* 18: R1089–R1090, 2008. doi:10.1016/j.cub.2008.10.008.
- Smeets JBJ, Brenner E. Independent movements of the digits in grasping. *Exp Brain Res* 139: 92–100, 2001b. doi:10.1007/s002210100748.

- Smeets JBJ, Brenner E.** Some illusions are more inconsistent than others. *Perception* 48: 638–641, 2019. doi:[10.1177/0301006619853147](https://doi.org/10.1177/0301006619853147).
- Smeets JBJ, Brenner E.** Synergies in grasping. In: *Progress in Motor Control: Theories and Translations*, edited by Latash ML, Laczko J. Berlin; Heidelberg, Germany: Springer, 2016, p. 21–34.
- Smeets JBJ, Brenner E, Biegelstraaten M.** Independent control of the digits predicts an apparent hierarchy of visuomotor channels in grasping. *Behav Brain Res* 136: 427–432, 2002. doi:[10.1016/S0166-4328\(02\)00189-4](https://doi.org/10.1016/S0166-4328(02)00189-4).
- Smeets JBJ, Brenner E, Martin J.** Grasping Occam's razor. In: *Progress in Motor Control V: A Multidisciplinary Perspective*, edited by Sternad D. Berlin: Springer-Verlag, 2009, p. 499–522.
- Smeets JBJ, Martin J, Brenner E.** Similarities between digits' movements in grasping, touching and pushing. *Exp Brain Res* 203: 339–346, 2010. doi:[10.1007/s00221-010-2236-0](https://doi.org/10.1007/s00221-010-2236-0).
- Smeets JBJ, Oostwoud Wijdenes L, Brenner E.** Movement adjustments have short latencies because there is no need to detect anything. *Mot Contr* 20: 137–148, 2016. doi:[10.1123/mc.2014-0064](https://doi.org/10.1123/mc.2014-0064).
- Smeets JBJ, van den Dobbelaert JJ, de Grave DDJ, van Beers RJ, Brenner E.** Sensory integration does not lead to sensory calibration. *Proc Natl Acad Sci USA* 103: 18781–18786, 2006. doi:[10.1073/pnas.0607687103](https://doi.org/10.1073/pnas.0607687103).
- Soechting JF, Lacquaniti F.** An assessment of the existence of muscle synergies during load perturbations and intentional movements of the human arm. *Exp Brain Res* 74: 535–548, 1989. doi:[10.1007/BF00247355](https://doi.org/10.1007/BF00247355).
- Stöttinger E, Aigner S, Hanstein K, Perner J.** Grasping the diagonal: controlling attention to illusory stimuli for action and perception. *Conscious Cogn* 18: 223–228, 2009. doi:[10.1016/j.concog.2008.04.003](https://doi.org/10.1016/j.concog.2008.04.003).
- Stöttinger E, Pfusterschmied J, Wagner H, Danckert J, Anderson B, Perner J.** Getting a grip on illusions: replicating Stöttinger et al [Exp Brain Res (2010) 202:79–88] results with 3-D objects. *Exp Brain Res* 216: 155–157, 2012. doi:[10.1007/s00221-011-2912-8](https://doi.org/10.1007/s00221-011-2912-8).
- Takahashi K, Best MD, Huh N, Brown KA, Tobaa AA, Hatsopoulos NG.** Encoding of both reaching and grasping kinematics in dorsal and ventral premotor cortices. *J Neurosci* 37: 1733–1746, 2017. doi:[10.1523/JNEUROSCI.1537-16.2016](https://doi.org/10.1523/JNEUROSCI.1537-16.2016).
- Ting LH, Macpherson JM.** A limited set of muscle synergies for force control during a postural task. *J Neurophysiol* 93: 609–613, 2005. doi:[10.1152/jn.00681.2004](https://doi.org/10.1152/jn.00681.2004).
- Traub MM, Rothwell JC, Marsden CD.** A grab reflex in the human hand. *Brain* 103: 869–884, 1980. doi:[10.1093/brain/103.4.869](https://doi.org/10.1093/brain/103.4.869).
- Tresch MC, Jarc A.** The case for and against muscle synergies. *Curr Opin Neurobiol* 19: 601–607, 2009. doi:[10.1016/j.conb.2009.09.002](https://doi.org/10.1016/j.conb.2009.09.002).
- Trommershäuser J, Gepshtein S, Maloney LT, Landy MS, Banks MS.** Optimal compensation for changes in task-relevant movement variability. *J Neurosci* 25: 7169–7178, 2005. doi:[10.1523/JNEUROSCI.1906-05.2005](https://doi.org/10.1523/JNEUROSCI.1906-05.2005).
- Utz KS, Hesse C, Aschenneller N, Schenk T.** Biomechanical factors may explain why grasping violates Weber's law. *Vision Res* 111: 22–30, 2015. doi:[10.1016/j.visres.2015.03.021](https://doi.org/10.1016/j.visres.2015.03.021).
- van Beers RJ.** Motor learning is optimally tuned to the properties of motor noise. *Neuron* 63: 406–417, 2009. doi:[10.1016/j.neuron.2009.06.025](https://doi.org/10.1016/j.neuron.2009.06.025).
- van Beers RJ, Brenner E, Smeets JBJ.** Random walk of motor planning in task-irrelevant dimensions. *J Neurophysiol* 109: 969–977, 2013. doi:[10.1152/jn.00706.2012](https://doi.org/10.1152/jn.00706.2012).
- van de Kamp C, Bongers RM, Zaal FTJM.** Effects of changing object size during prehension. *J Mot Behav* 41: 427–435, 2009. doi:[10.3200/35-08-033](https://doi.org/10.3200/35-08-033).
- van de Kamp C, Zaal FTJM.** Prehension is really reaching and grasping. *Exp Brain Res* 182: 27–34, 2007. doi:[10.1007/s00221-007-0968-2](https://doi.org/10.1007/s00221-007-0968-2).
- Van Soest AJ, Bobbert MF, Van Ingen Schenau GJ.** A control strategy for the execution of explosive movements from varying starting positions. *J Neurophysiol* 71: 1390–1402, 1994. doi:[10.1152/jn.1994.71.4.1390](https://doi.org/10.1152/jn.1994.71.4.1390).
- Verhagen L, Dijkerman HC, Grol MJ, Toni I.** Perceptuo-motor interactions during prehension movements. *J Neurosci* 28: 4726–4735, 2008. doi:[10.1523/JNEUROSCI.0057-08.2008](https://doi.org/10.1523/JNEUROSCI.0057-08.2008).
- Verheij R, Brenner E, Smeets JBJ.** Grasping kinematics from the perspective of the individual digits: a modelling study. *PLoS One* 7: e33150, 2012. doi:[10.1371/journal.pone.0033150](https://doi.org/10.1371/journal.pone.0033150).
- Verheij R, Brenner E, Smeets JBJ.** The influence of target object shape on maximum grip aperture in human grasping movements. *Exp Brain Res* 232: 3569–3578, 2014a. doi:[10.1007/s00221-014-4046-2](https://doi.org/10.1007/s00221-014-4046-2).
- Verheij R, Brenner E, Smeets JBJ.** Why does an obstacle just below the digits' paths not influence a grasping movement while an obstacle to the side of their paths does? *Exp Brain Res* 232: 103–112, 2014b. doi:[10.1007/s00221-013-3723-x](https://doi.org/10.1007/s00221-013-3723-x).
- Verheij R, Smeets JBJ.** The target as an obstacle: grasping an object at different heights. *Hum Mov Sci* 61: 189–196, 2018. doi:[10.1016/j.humov.2018.08.005](https://doi.org/10.1016/j.humov.2018.08.005).
- Viviani P, Terzuolo C.** Trajectory determines movement dynamics. *Neuroscience* 7: 431–437, 1982. doi:[10.1016/0306-4522\(82\)90277-9](https://doi.org/10.1016/0306-4522(82)90277-9).
- Volcic R, Domini F.** On-line visual control of grasping movements. *Exp Brain Res* 234: 2165–2177, 2016. doi:[10.1007/s00221-016-4620-x](https://doi.org/10.1007/s00221-016-4620-x).
- Volcic R, Domini F.** The endless visuomotor calibration of reach-to-grasp actions. *Sci Rep* 8: 14803, 2018. doi:[10.1038/s41598-018-33009-6](https://doi.org/10.1038/s41598-018-33009-6).
- Voudouris D, Brenner E, Schot WD, Smeets JBJ.** Does planning a different trajectory influence the choice of grasping points? *Exp Brain Res* 206: 15–24, 2010. doi:[10.1007/s00221-010-2382-4](https://doi.org/10.1007/s00221-010-2382-4).
- Voudouris D, Smeets JBJ, Brenner E.** Do obstacles affect the selection of grasping points? *Hum Mov Sci* 31: 1090–1102, 2012. doi:[10.1016/j.humov.2012.01.005](https://doi.org/10.1016/j.humov.2012.01.005).
- Voudouris D, Smeets JBJ, Brenner E.** Ultra-fast selection of grasping points. *J Neurophysiol* 110: 1484–1489, 2013. doi:[10.1152/jn.00066.2013](https://doi.org/10.1152/jn.00066.2013).
- Weigelt C, Bock O.** Adaptation of grasping responses to distorted object size and orientation. *Exp Brain Res* 181: 139–146, 2007. doi:[10.1007/s00221-007-0911-6](https://doi.org/10.1007/s00221-007-0911-6).
- Weigelt C, Bock O.** Adaptation of the precision grip orientation to a visual-haptic mismatch. *Exp Brain Res* 201: 621–630, 2010. doi:[10.1007/s00221-009-2076-y](https://doi.org/10.1007/s00221-009-2076-y).
- Welford AT.** The measurement of sensory-motor performance: survey and reappraisal of twelve years' progress. *Ergonomics* 3: 189–230, 1960. doi:[10.1080/00140136008930484](https://doi.org/10.1080/00140136008930484).
- Welford AT, Norris AH, Shock NW.** Speed and accuracy of movement and their changes with age. *Acta Psychol (Amst)* 30: 3–15, 1969. doi:[10.1016/0001-6918\(69\)90034-1](https://doi.org/10.1016/0001-6918(69)90034-1).
- Westling G, Johansson RS.** Factors influencing the force control during precision grip. *Exp Brain Res* 53: 277–284, 1984. doi:[10.1007/BF00238156](https://doi.org/10.1007/BF00238156).
- Westwood DA, Chapman CD, Roy EA.** Pantomimed actions may be controlled by the ventral visual stream. *Exp Brain Res* 130: 545–548, 2000. doi:[10.1007/s002219900287](https://doi.org/10.1007/s002219900287).
- Westwood DA, Goodale MA.** Perceptual illusion and the real-time control of action. *Spat Vis* 16: 243–254, 2003. doi:[10.1163/15685680322467518](https://doi.org/10.1163/15685680322467518).
- Westwood DA, Heath M, Roy EA.** No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. *J Mot Behav* 35: 127–133, 2003. doi:[10.1080/00222890309602128](https://doi.org/10.1080/00222890309602128).
- Whitwell RL, Goodale MA, Merritt KE, Enns JT.** The Sander parallelogram illusion dissociates action and perception despite control for the litany of past confounds. *Cortex* 98: 163–176, 2018. doi:[10.1016/j.cortex.2017.09.013](https://doi.org/10.1016/j.cortex.2017.09.013).
- Wolpert DM, Ghahramani Z, Jordan MI.** Perceptual distortion contributes to the curvature of human reaching movements. *Exp Brain Res* 98: 153–156, 1994. doi:[10.1007/BF00229120](https://doi.org/10.1007/BF00229120).
- Woodworth RS.** Accuracy of voluntary movement. *Psychol Rev Monogr Suppl* 3: 1–114, 1899. doi:[10.1037/h0092992](https://doi.org/10.1037/h0092992).
- Wright CE.** Generalized motor programs: reexamining claims of effector independence in writing. In: *Attention and Performance XIII: Motor Representation and Control*, edited by Jeannerod M. Hillsdale, NJ: Erlbaum, 1990, p. 294–320.
- Yang F, Feldman AG.** Reach-to-grasp movement as a minimization process. *Exp Brain Res* 201: 75–92, 2010. doi:[10.1007/s00221-009-2012-1](https://doi.org/10.1007/s00221-009-2012-1).
- Zaal FTJM, Bootsma RJ.** Accuracy demands in natural prehension. *Hum Mov Sci* 12: 339–345, 1993. doi:[10.1016/0167-9457\(93\)90023-1](https://doi.org/10.1016/0167-9457(93)90023-1).