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Pliers as parts of the body: a kinematic analysis of visuomotor control in tool use

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This thesis is submitted in partial fulfilment of the requirement for the degree of Doctor in Philosophy, completed in the school of Psychology, Bangor University.

Declarations

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

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Abstract

Tool use is a remarkable aspect of human hand function. It is suggested that we used tools ‘as if they were part of our body’. Normal hand movements are efficient partly because they rely on internal models, allowing the brain to predict the sensorimotor consequences of motor commands. Tools alter that relationship between hand movements and their consequences, so this anticipatory control requires the brain to also model the properties of the tool. This thesis aims to examine if the visuomotor system can account for the alteration between hand opening and tool opening when planning and executing movements, and if it does so by developing internal models of tools. This thesis also aims to examine the process of acquisition of those internal models of tools. Using grasping as a main task, our first study examined the learning of pliers-like tools with different ratios of tool opening to hand opening. We probed the learning of the tool models by measuring movement kinematics with motion capture. We found limited evidence that people develop internal tool-models, equivalent to those of the hand. People do compensate for the effects of the tool, but some tool geometry were more difficult to learn than others. Our second study examined whether the visuomotor system learns distinct tool mappings, or whether tool properties are accounted for by adapting the hand representation. The study also examine whether tool geometry was accounted for in perceptual tasks. Our results indicated that adaptation was not the principal mechanism behind the accounting of tool properties and that tool geometry was not accounted for during perceptual tasks. Our last study dissociated the contribution of tool complexity and the requirement to make unusual hand movements, to confirm that tool geometry per se contributes to difficulty learning a novel tool. We used a tool that does not behave qualitatively like the hand. Our results indicated that both factors play a significant role. Overall, our results are not consistent with the idea that tools are ‘used as body parts’, but instead with a visually controlled strategy.

Chapter 1 - General Introduction

1.1 What is a tool?

A defining feature of human behaviour is the ability to use complex tools. Even though humans are not the only species to use tools, they have used tools for millions of years (Panger, Brooks, Richmond, & Wood, 2002), and have developed a vast repertoire of tool use behaviours they employ every day. Tools allow humans to extend their abilities, helping them achieve many tasks that they are unable to perform using their own body.

Humans use a large variety of tools, from a simple stick or hammer, to more complex 'dynamic' tools such as pairs of tongs, right up to hugely complex devices such as musical instruments, or even cars and aeroplanes. Those tools differ vastly in complexity, form and function. They all extend the capability of the body or create new capabilities. A hammer allows someone to drive a nail into an object. A pair of barbecue tongs extends the reach of the user and allows them to pick up objects that are too warm to be picked up by hand. Cars and planes (dramatically) extend the capability of movement of their users.

From a sensorimotor control perspective, all tools—simple or complex—transform or remap hand movements into a different movement in the world. This is the definition of a tool that we use in this thesis: an instrument that when submitted to a certain hand movement results in a different movement of a spatially separate end-effector in the world. Said another way, tools alters the consequences of a given hand movement. Thus, the brain has to understand the nature of this alteration to be able to use tools in the fluid, intuitive manner in which we control our own bodies.

We are interested in the motor system processes underlying the brain's ability to plan and execute movements given the tool transformation of the motor outputs. We used grasping as a model task across our three Chapters. Grasping is a canonical aspect of human hand function, and tools are often used to grasp objects. Moreover, normal grasping has been extensively studied, and so serves as a valuable reference point, or 'baseline'. Our studies used simple pliers-like tools to manipulate and control the transformation of hand movements induced by the tools.

1.2 Overview of thesis

The General Introduction reviews previous research on tool use. The majority of work has been on integration of tools into the brain's internal representation of the body—the so-called 'body schema'. Much less research has focused on the production of movement using tools, and on how the brain is able to take into account the metric aspects of tool transformations when producing movements. To be able to understand how the brain can take into account these tool transformations, we will review how the brain plans and controls normal movements.

The model task chosen for this thesis is grasping. Hence, we will review the existing literature on hand grasping as well as the few studies looking at grasping with tools. The brain is thought to rely on internal models to plan and execute hand movements. We will review this literature to examine how those mechanisms might play a role in tool use. Using a new tool can be interpreted as learning a new task, hence we will review literature on sensorimotor learning to examine if the mechanisms behind sensorimotor learning could be applied to tool learning.

The main aim of this thesis is to investigate how the brain takes into account of the remapping of motor outputs due to the alteration produced by the tool geometry when planning and executing a grasping movement. Particularly, we address this through two main questions. The first question address the whether the visuomotor system is able to account for the tool transformation during grasping movement (Chapter 3, 4 and 5). The second question address the potential mechanisms by which the brain accounts for the tool transformation (Chapter 4).

1.3 Theoretical frameworks in tool use research

1.3.1 Tool use and body representation

Much of the literature has considered human tool use from the perspective of body representation. To be able to interact with objects in space, the brain needs to centralise information about the position and movement of the body parts and also about the position of those objects related to the position of the body. Numerous ways of labelling body representations have been proposed over the last century of research but the idea of a flexible body representation has been described already by Head and Holmes in 1911. The consensus in the literature is that there are at least two body representations, the body image and the body schema (Dijkerman & de Haan, 2007; Gallagher, 1986; Head & Holmes, 1911). The body image is a perceptual, cognitive, or even emotional awareness of the body (Gallagher, 1986). In comparison, the body schema has been seen as a cluster of sensorimotor representations that are action-oriented (de Vignemont, 2010) and can be used to execute or to imagine executing movements accurately (Medina & Coslett, 2010).

From the perspective of body representation, tools are incorporated into the representation of the body schema (Maravita & Iriki, 2004). An influential study in this regard is from Iriki, Tanaka, & Iwamura (1996). They showed that when monkeys had been using a rake to extend the reach of their hand, the receptive fields of some neurons responding to locations around the hand were extended to include the area surrounding the tool. This finding was interpreted as evidence that the body schema was expanded to include the tip of the tool when the monkey intended to use the tool.

Following that study, numerous studies looked at after-effects of tool use, within the framework of tools being incorporated into the body schema (Arbib, Bonaiuto, Jacobs, & Frey, 2009; Canzoneri et al., 2013; Cardinali et al., 2009, 2011, 2012; Martel et al., 2019; Miller, Longo, & Saygin, 2019; Sposito, Bolognini, Vallar, & Maravita, 2012). Cardinali et al. (2009)

looked at the kinematics of a grasping and a pointing movements in humans before and after using a 40 cm-long mechanical grabber (physically extending the arm). Their study was motivated by the idea that the brain does not represent tools separately from the hand/arm, but instead accounts for their properties by altering the representation of the hand and arm. They therefore hypothesised that subjects would move with their hand differently after using their tool, due to changes in the brain's representation of the arm (likely resulting in alteration of the transport component: moving the hand to the desired location). Specifically, they predicted that the after-effect of using their tool would be consistent with an increased length of the arm. Consistent with their predictions, people moved slower after tool use in both the grasping task and the pointing task (smaller peak velocity and longer time to peak velocity, interpreted as an increased perception of arm length; those results were replicated by Martel et al., 2019). The grasping component (opening and closing the hand) was not affected by the use of the tool. They further tested if the kinematic consequences were due to an alteration of the body schema by asking blindfolded participants to point with their (untrained) index finger to the location of tactile stimuli on the (trained) forearm. Their results are consistent with an arm length perceived as longer, suggesting that tool use does alter the representation of the body.

Other studies have looked at the representation of participants' forearm before and after using a tool that extended the reach. The results were also consistent with the idea that tools are integrated in to the body representation, as the forearm was perceived as longer (Canzoneri et al., 2013; Cardinali et al., 2011). Those results are consistent with the idea that tools are represented by altering the representation of the body. Moreover, a study has manipulated the length of the tool in order to see if it resulted in parametric variation in the observed effect (Sposito et al., 2012). They measured forearm length using a bisection task: blindfolded participants had to point to the middle of their upper limb (between the middle finger-tip and elbow) before and after using either a 20 cm or a 60 cm rake. Although using the 60 cm rake led to an increase of the represented arm length, a 20 cm rake was ineffective in altering bisection performance. This suggests that the tool must be a certain length to induce an alteration of the body schema.

Studies in this framework propose limitations on the brain's ability to incorporate tools into the body schema (Tang, Whitwell, & Goodale, 2016). It has been proposed that the body representation is updated selectively, only updating the body-parts whose morphology is functionally modified by the tool (Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Miller, Cawley-Bennett, Longo, & Saygin, 2017; Miller, Longo, & Saygin, 2014). Also, active tool use seems required to produce a change in body representation (Witt, Proffitt, & Epstein, 2005). Furthermore, it might be a requirement to programme the goal of the action with the tool (Bruno et al., 2019) for the tool to be integrated into the body schema.

The body-schema framework is arguably the modal account of tool use. It also seems consistent with the powerful phenomenology of using tools with which we are very familiar. For instance, people often report feeling that tools are a part of their body (Murray, 2004). The body-schema account offers a mechanism for that to occur, by incorporating the representation of the tool into the representation of body parts. There are important limitations to this as an overall account, however, in its current form.

First, at the empirical level, it is noteworthy that the after-effects found are typically very small ('arm representations' changed by ~1% of tool length; Cardinali et al., 2009, 2011). It seems difficult to reconcile such small effects (albeit, after-effects) with alteration of the hand/arm representation being the primary mechanism by which tools are controlled. *Second*, by looking only at after-effects, and inferring alterations of body representations following tool use, studies in this framework do not examine the process of planning and executing movements with tools. That is, it can be argued they use tools to probe the body schema, rather than studying the process of tool use per se. A key aim of this thesis is to study tool use directly. *Third*, studies in the body-schema framework have almost exclusively used tools that extend the effective length of the arm. This casts the problem of tool use as dealing with an extended effector. But as noted earlier, we are proficient at using tools that induce more complex transformations to hand movements. It is conceivable that a simple extension could be taken into account by altering the representation of arm length. It is less plausible, however, that transformations involved in riding a bicycle, for example, could be implemented by adapting the representation of the hand/arm, which operate on different geometrical principles (rotating bearings, for example). It is important to note that this does not necessarily imply that the body schema framework does not provide the correct account of how we use devices that extend our arms. It does imply, however, that different mechanisms may be required to use more complex tools, that less closely resemble the hand/arm (see later discussion of 'motor equivalence'; Arbib et al., 2009)

1.3.2 Tool use and peripersonal space

Another class of studies on tool use has examined its effect on the representation of so-called 'peripersonal space'. This is typically defined as the region of space immediately surrounding the body within which objects can be grasped and manipulated (Canzoneri et al., 2013; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). This region of space is specifically represented in the brain (Holmes & Spence, 2004). Many studies have found that the peripersonal space can be altered quickly. Studies of neurological patients using a cross-modal extinction paradigm (Farnè, Iriki, & Làdavas, 2005; Farnè & Làdavas, 2000; Maravita, Husain, Clarke, & Driver, 2001) showed those patients were unable to detect tactile stimulation of the contralesional hand when a visual stimulus was delivered on the ipsilesional hand. However, when the visual stimulation was moved further away from the hand, the extinction decreased (leading to an increase of detection of the contralesional stimulation). After using a tool extending the reach, cross-modal extinction was increased at further distances. Those results have been interpreted as evidence that tool use does expend the peripersonal space (Farnè, Iriki, et al., 2005; Farnè & Làdavas, 2000; Maravita et al., 2001). It has also been suggested that a modification of peripersonal space requires active movement. For example, just holding a tool (Farnè & Làdavas, 2000; Iriki et al., 1996; Maravita et al., 2001), or pointing towards a far object (Canzoneri et al., 2013) was not sufficient to elicit a modification of the peripersonal space. It seems that planning and executing movement with the tool is required to modify the peripersonal space (Anelli, Candini, Cappelletti, Oliveri, & Frassinetti, 2015; Farnè, Bonifazi, & Làdavas, 2005; Maravita, Spence, Kennett, & Driver, 2002). Again, a basic property that should hold here is that a longer tool should result in greater extension of peripersonal space. Consistent with this expectation, longer tools (60 cm) have been shown to induce larger effects on peripersonal space than shorter tools (30 cm; Farnè, Iriki, et al., 2005).

The body schema framework for tool use and ideas around peripersonal space are often thought of as interrelated (Canzoneri et al., 2013). For instance, some authors have proposed that the modification of the peripersonal space after tool use is caused by modification of the body schema (Iriki et al., 1996; Maravita & Iriki, 2004). That is, if the updated body schema includes the tool, then the portion of space represented as reachable would automatically increase as a consequence.

Work on peripersonal space does not directly address sensorimotor control mechanisms, and so cannot be said to provide an account of how we are able to use tools. It does, however, provide strong evidence that tool use causes changes in how we represent the space around us, and our bodies.

1.3.3 Taking into account the geometric properties of tools

As discussed above, while the body schema idea provides a conceptual framework for understanding some classes of tools, it cannot readily account for how the properties of more complex devices can be represented in the brain, which operate in ways that are geometrically different to biological body parts (Grafton, 2010; Johnson-Frey, 2004)—in the words of some researchers, tools that lack 'motor equivalence' (Arbib et al., 2009). Moreover, in order to control a tool effectively, the brain presumably represents the precise, metrical mapping between hand movements and end-effector movements, taking into account the transformations introduced by the tool geometry (Arbib et al., 2009; Frey, 2007). The literature presented above has not investigated the extent to which such transformations are accounted for, and how this process develops with experience of a tool, for instance. This is a primary focus of the studies presented in this thesis.

Normal hand movements are efficient and fluid in part because they are controlled anticipatorily. That is, the brain can plan and control movements online despite sensory and motor noise, and delays in processing sensory feedback, because it can anticipate the consequences of motor commands for the movement of end effectors (McNamee & Wolpert, 2019; Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Kawato, 1998). It has been proposed that the brain uses (accurate) internal models of the motor system—here, of the hand and arm—to achieve this (for more detail see discussion of internal feedforward models etc. in Section 1.5.2). Thus, it seems logical that using tools 'as if they are a body part' requires similarly accurate internal models of the physical properties of tools, so that the visuo-motor system can now anticipate how the end of a tool will move for a given motor command. Such models could in principle also support the planning of tool movements in end-effector units, rather than in terms of specific joint angles etc. (Arbib et al., 2009; Umiltà et al., 2008). They could also allow sensory signals acquired at the hand to be 'reinterpreted', taking into account tool geometry, such that the user perceives the properties of objects felt with the tool, rather than perceiving what the hand is doing (Arbib et al., 2009; Holmes, Sanabria, Calvert, & Spence, 2007; Miller et al., 2018; Takahashi, Diedrichsen, & Watt, 2009; Yamamoto, Shiraki, Uehara, & Kushiro, 2016).

One source of evidence that the brain operates ‘directly’ on the positions of the tool tips, rather than the hand, comes from studies of integration of visual and haptic sensory signals during tool use. In a seminal study, Ernst and Banks (2002) showed that visual and haptic signals about object size are integrated in an optimal manner. Sensory signals are noisy by nature, and different signals are encoded by different sensors, and so must be acquired in unrelated units. When the brain receives multiple signals relating to the same object or event, it combines them to create a combined estimate of the signals that is less noisy than from either signal alone (Ernst & Banks, 2002). In this sensory integration framework, the different signals are also weighted depending on their reliability (the inverse of noise) so that a less noisy signal would be weighted more than a noisier signal.

For integration to be effective, the brain must only combine signals that relate to one another (i.e. that refer to the same object or event; Ernst, 2007; Körding et al., 2007) or the results will be meaningless. This is referred to as solving the sensory ‘correspondence problem’ (Ernst, 2007). The decision of whether to integrate or not can be made on the basis of the similarity of signals, in terms of their spatial (and temporal) coincidence, and whether they indicate a similar magnitude of estimate (Ernst, 2007). For example, if visual and haptic signals originate from different spatial locations, and/or indicate different sizes, they are unlikely to have been caused by the same object, and so should not be combined. Empirical studies indicate that integration is affected by these factors in the manner predicted (Ernst, 2007; Gepshtein, Burge, Ernst, & Banks, 2005; Körding et al., 2007; Takahashi et al., 2009). For example, Gepshtein et al. (2005) showed that spatial separation between hand and visual object abolished visual-haptic integration.

The correspondence problem is complicated in tool use, for the same reason that motor control is complicated. Tools add a spatial offset between haptic signals at the hand and visual signals at the tool-tips. Further, tools often alter the relationship between hand movements and tool-tips movement (Arbib et al., 2009; Frey, 2007; Takahashi & Watt, 2014, 2017). Thus, when using tools the haptic signals—which are necessarily acquired at the hand—and visual signals no longer correspond in space. And when using many tools, the opening of the hand no longer corresponds to the visual (or actual) size. Solving the correspondence problem here therefore requires the brain to recognise that haptic signals on the finger-tips relate to visual signals at the tool-tips (Farnè, Bonifazi, et al., 2005), if they are to be optimally integrated. Takahashi et al. (2009) examined whether the brain takes account of the spatial offset induced by tools, using a size-discrimination task in which subjects felt objects with a simple (virtual) tool, that resembled sticks extending from the fingers. The experimental logic was based closely on studies by Ernst & Banks (2002) and Gepshtein et al. (2005). They showed that when using tools, the decision to integrate or not was based on the proximity of the tool tips to the visual object, not the proximity of the hand per se. That is, the brain correctly took into account the spatial offset created by the tool when deciding whether to integrate signals. This result suggests that the brain can 'relate' haptic signals at the hand with the properties of the world felt with the tool-tips—i.e. it treats haptic signals in terms of their true origin.

In further studies, Takahashi & Watt (2014, 2017) investigated if the brain takes into account changes in the mapping between finger opening and tool-tip opening, using the same sensory-integration paradigm. Here the virtual tools resembled pliers, with different ratios between hand opening and tool-tip opening (the tool ratio was controlled by moving the pivot linking the arms of the pliers-like tool). They found that the brain took the geometrical tool alteration between finger-tips and tool tips into account correctly when deciding to integrate haptic signals at the finger-tips and visual signals at the tool-tips. That is, the haptic signals were in terms of the (distal) object size they referred to, rather than the (proximal) hand opening. Taken together, these results suggest the brain can solve the correspondence problem appropriately when using tools. This finding implies the visuomotor system can correctly account for the remapping of haptic signals induced by the tools' geometries (Takahashi & Watt, 2014, 2017), representing the new relationship between the signals.

Although interesting, there are limitations to what can be concluded from these studies for the control of actions with tools. *First*, the experiments took place in a virtual visual-haptic environment (using a stereoscope and force-feedback robots). As such, the tools and objects were rendered virtually, and participants did not pick up real pliers to judge the size of real objects. It is then possible that the brain did not invoke the same visuomotor processes that are involved in real-world movements. Tactile feedback was not accurate, for example, and the movement of the tools was constrained in unnatural ways. *Second*, these studies were explicitly about perception, and investigating how flexible sensory integration processes are. As such, they do not directly examine how movements are controlled in tool use. In this thesis, we investigated the production of movements with real tools and objects. Our goal is to understand how the motor system can account for the altered relationship between hand opening and tool-tip opening, to produce the appropriate finger movements required to produce the desired tool-tip movements.

Compelling evidence that the brain can take into account the mechanical/geometrical properties of tools also comes from single-unit physiology work in macaques. Specifically, there is evidence that the movement of tool tips is encoded in pre-motor (and even motor) regions in the macaque brain, independent of the hand movement required to achieve this. Umiltà et al. (2008) investigated the cortical coding of grasping movements made with normal pliers and ‘reverse-pliers’, wherein the hand was opened to close the tool. They measured from neurons in area F1 (primary motor cortex) and F5 (premotor cortex) and identified neurons that discharged in association with different phases of normal grasping movements. Some fired maximally during opening of the hand, while others coded for the hand closure phase. Following a prolonged training period (carried out over 6 months) recordings were then made during use of the two tool types. A subset of neurons in area F5 of the monkey brain was found to fire for opening and closure of the ‘grasp’, independent of the tool used. That is, some encoded opening of the tool-tips, whether it required opening of the hand (normal pliers) or closure of the hand (reverse pliers). The presence of neurons firing for the movement of the tool-tips is consistent with the idea that the brain can plan and execute movements in end-effector units, taking into account a dramatic remapping of the relationship between hand and end-effector movement. Moreover, this finding reinforces the idea that tools can be controlled ‘as part of the body’, in that premotor neurons (and even some primary motor neurons) were found to encode end-effector movements, not the hand per se.

1.4 Reaching and grasping

An emergent idea from the above theoretical approaches to tool use is that of tools being ‘controlled as body parts’. That is, it is proposed that mechanisms are co-opted, or employed, such that the brain can control tools using similar control principles, and using the same neural substrates, as for normal movements with the hands. In this thesis we are studying tool use using a model task of grasping. It is therefore useful to consider key features and the motor system needs to be able to make predictions about, or anticipate the consequences of motor commands. This is non-trivial because it requires understanding principles of normal grasping movements made with the hand. If tools are indeed ‘used as body parts’, we would expect similar features to be evident in tool use. Moreover, differences between grasping movements made with the hand and pliers-like tools may reveal insights into tool use-specific processes and features.

1.4.1 Fundamentals of goal-directed movements

There are several fundamental aspects of goal-directed movements that have important implications for grasping movements, and therefore for movements to control tools. At its simplest, and assuming a target has been identified, the brain must first select an appropriate movement to achieve the intended goal. It should then execute this movement appropriately, correcting for any errors that result.

This process is highly non-trivial. Successful movements must balance the probability (and value) of a successful outcome against factors such as energetic costs, timing constraints, comfort and so on. Because all stages of the process are corrupted by noise—from sensory estimates of the target, through to motor output (Schlicht & Schrater, 2007; Takemura, Fukui, & Inui, 2015; Trommershäuser, Maloney, & Landy, 2003)—the problem is rendered probabilistic in nature. Planning and controlling movements can therefore be thought of as decision-making under uncertainty, or as optimisation problems (Harris & Wolpert, 1998; Flash & Hogan, 1985; Shadmehr, Huang, & Ahmed, 2016; Todorov & Jordan, 2002; Trommershäuser et al., 2003; Wolpert & Landy, 2012)

Because the feedback given by the nervous system is too slow to allow, on its own, for rapid, dexterous movements (Flanagan, Bowman, & Johansson, 2006), normal movements are typically controlled via a combination of planning and online control (Elliott, Chua, & Helsen, 2001; Meyer, Abrams, Kornblum, Wright, & et al, 1988). In both cases (producing the appropriate movement, or updating it) the system needs to be able to predict, or anticipate, the consequences of a given motor output in order to know what to do. A fundamental challenge here is that the motor system is highly redundant, in that even for simple movements the same end state can typically be reached via a vast number of different movements (the so-called 'degrees-of-freedom problem' in motor control). Thus, selecting which movement to make is not straightforward (Körding & Wolpert, 2006; Shadmehr et al., 2016). Moreover, it does not seem plausible for movements to be planned and controlled directly at the level of the massively complex patterns of coordinated muscle groups, and changing joint-angles involved in specifying movements (Diedrichsen, Shadmehr, & Ivry, 2010; Todorov, 2004; Todorov & Jordan, 2002). Instead, some form of dimension reduction is required, to make decision-making tractable. This has given rise to the related ideas of motor primitives, and motor synergies—stereotypical spatiotemporal patterns of control signals at multiple levels (activation of groups of muscles, up to higher-level co-ordination)—which could be used as 'building blocks' for complex movements (Santello et al., 2016; Thoroughman & Shadmehr, 2000; Wolpert & Ghahramani, 2000). Taken together, this reasoning highlights how normal motor control relies on efficient and accurate 'models', or mappings, of the relationships between desired movements of end effectors in the world, and the specific muscle activations needed to produce them. This information is presumably acquired over a lifetime of experience, though must also be constantly calibrated to deal with changing conditions such as fatigue (Kording, Tenenbaum, & Shadmehr, 2007; Monjo, Terrier, & Forestier, 2015). Logically, then, controlling tools as a body part requires similar relationships to be established for how tool movements are related to motor output (either by piggy-backing on 'models' used for normal hand function, or by creating new models and control processes/motor synergies).

A closely related problem exists for interpreting proprioceptive signals. Proprioception is important in-the-moment for establishing the initial configuration of body parts for planning movements, and for providing online feedback (integrated with information from vision; van Beers, Sittig, & van der Gon, 1999; van Beers, Wolpert, & Haggard, 2002; Proske & Gandevia, 2012; Sarlegna & Sainburg, 2009). It is also important over longer timescales for maintaining calibration of the models used for motor control. Here, the pattern of joint angles, muscle extension etc. sensed by the proprioceptive afferents must be converted into meaningful positions of end-effectors in space (for example, to know how large an object is that one is feeling; Berryman, Yau, & Hsiao, 2006). This requires solving a very similar mapping problem to that for producing motor output. Thus, again, for normal movements (and perception) to make use of proprioception, some kind of internal model, or mapping, of the relationship between end effector and low-level signals is required. And this would need to be established for the new relationships introduced by tools for them to be 'used as a body part' (Arbib et al., 2009).

1.4.2 Key features of grasping movements

Grasping is a complex movement, that involves a preshaping of the hand as it approaches the target object, characterised by a progressive opening of the digits, followed by a closing phase until the object is grasped (Jeannerod, 1984; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). There is still a debate on how grasping movements are controlled, with accounts falling into two main frameworks. The first framework suggests that grasping is achieved by controlling two somewhat independent, though coordinated components——the reach (or transport) component, and the grasp component (Jeannerod, 1981, 1999; Jeannerod et al., 1995). These map onto the biomechanically independent actions of moving the hand to the object/target location (reach), and shaping the opening of the digits to enclose the object (grasp), respectively. The second framework considers grasping as the combination of two pointing movements, one each for the thumb and finger(s), towards selected positions on the surface of the object, and obviously constrained by their biomechanical connection (Smeets & Brenner, 1999).

Grasping has been heavily investigated throughout the years. Motion capture data have commonly been used to characterise movement 'velocity profiles' (of the wrist or thumb), and hand opening or ‘grip aperture profiles’, describing how each property varies with time (see Section 2.5). Various kinematic ‘landmarks’ have been identified which occur ‘in-flight’, and vary systematically with object properties, indicating the anticipatory nature of grasping movements.

Grasping velocity profiles show a stereotypically bell-shaped pattern, with a slightly extended ‘tail’ as the hand slows down in final approach to the object. A principal landmark of this velocity profile is that the maximum velocity reached reliably scales with object distance, such that grasping movements to farther objects elicit higher movement velocities (Jeannerod, 1981, 1984).

The grasping profile shows how the hand gradually opens before closing on the target object. A key landmark here is the peak/maximum grip aperture reached, before the object is grasped, which scales reliably with object size (along the grasped dimension), such that larger objects elicit larger peak grip apertures (Jeannerod, 1981, 1984; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990; Smeets & Brenner, 1999; Wing, Turton, & Fraser, 1986). Peak grip aperture occurs at around 60-70% of the duration of the reach (Gentilucci et al., 1991; Jakobson & Goodale, 1991; Jeannerod, 1981, 1984; Wing et al., 1986), indicating that it, too, is an anticipatory feature (Jeannerod, 1984).

Both velocity and grasp profiles exhibit these in-flight ‘scaling’ relationships not only when the hand and object is visible during the movement, but also when vision is prevented at movement onset, indicating that movement plans reflect estimates of object properties are anticipatory (Jakobson & Goodale, 1991), and that the visuomotor system can generate appropriate commands given these estimates (Jeannerod, 1997; Santello, Flanders, & Soechting, 2002; Winges, Weber, & Santello, 2003).

1.4.3 Other factors affecting grasping movements

The kinematics of grasping movements are driven not only by object properties, but also by other factors, that demonstrate a remarkable degree of refinement in grasp control. As noted above, perceptual processes and planning and execution of actions, are inherently noisy, and in that context, control of grasping can be viewed as selecting the appropriate movement to meet a desired goal under uncertainty. A key aspect of this is that grasping movements are 'adjusted' to take account of the degree of uncertainty in knowledge of the properties of target objects, and of movements of the hand.

For example, increased noise in visual estimates of object properties such as size used to plan the movement, and in vision of the object and hand during the movement, has been shown to result in the motor system adding a precisely calibrated margin-for-error to grip apertures, in order to manage the otherwise increased risk of failing to grasp, while preserving the scaling of hand preshaping to object sizes (Hesse & Franz, 2009a; Keefe, Suray, & Watt, 2019; Schlicht & Schrater, 2007). These findings imply that the degree of uncertainty in visual information is known, and appropriate adjustments to movements are made to compensate, indicating a highly refined control process.

Studies have shown that larger peak grip apertures are also observed when visual feedback is removed at movement onset, and slower movements are also sometimes programmed (Gentilucci, Daprati, Toni, Chieffi, & Saetti, 1995; Hesse & Franz, 2009b; Jakobson & Goodale, 1991; Tang et al., 2016; Wing et al., 1986), again resembling a strategy to ensure a successful grasp under uncertainty.

Overall, the grasping system appears able to make (non-trivial) calculations required to precisely adjust movements in a manner that compensates for the degree of uncertainty/noise in various aspects (Keefe et al., 2019; Schlicht & Schrater, 2007; Trommershäuser et al., 2003; Wolpert & Landy, 2012). Achieving this requires knowledge of how making different possible movements affects the likelihood of errors (Keefe et al., 2019). This behaviour therefore suggests a highly refined ability to anticipate the consequences of different hand movements. Thus, using a tool 'as a body part' would imply that the brain can anticipate how likely different tool movements are to be successful, despite having different physical properties than the hand.

1.4.4 The role of visual and proprioceptive information in the online control of grasping

Another key feature of normal grasping movements is that rapid and largely automatic fine-tuning occurs during the movement. This online control relies on vision and proprioception for its efficiency.

As mentioned previously, due to the inherent noise in the nervous system, perception and execution of action are noisy. The system is thought to weight visual and proprioceptive signals to hand position and optimally integrates them into a less noisy estimate that can be used during motor planning and execution (van Beers et al., 1999, 2002). It has been suggested that while vision is mainly used in the first stage of motor planning (more weight given to visual signals), to define the movement plan in an extrinsic coordinate system, proprioception contributes in particular to localising the hand (more weight is given to proprioceptive signals) and transforming the 'visual plan' into motor commands (Proske & Gandevia, 2012; Sarlegna & Sainburg, 2009). There has been little if any work on the role of proprioception in control of grip aperture, specifically (as opposed to hand position), but it seems reasonable to assume that proprioceptive signals play a role here too.

Research has shown that changes to the position or size of an object during movements triggers fast corrections (Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, McKenzie, Marteniuk, & Jeannerod, 1990), indicating that online control of grasping is continuous, rapid and efficient. Indeed, vision of the hand is not necessary for the system to adapt to perturbations (Goodale, Pelisson, & Prablanc, 1986; Hesse & Franz, 2009a; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc, Pélisson, & Goodale, 1986), with visual feedback being particularly important during the closure phase of grasping movements (Rand, Lemay, Squire, Shimansky, & Stelmach, 2007; Santello et al., 2002; Winges et al., 2003). In fact, we do not always look at the hand, especially during the early phase of grasping movements. The gaze often does not follow the movement but is instead anticipatory, directed towards the object target, and particularly to potential contact positions (Brouwer, Franz, & Gegenfurtner, 2009; Roland S. Johansson, Westling, Bäckström, & Randall Flanagan, 2001; Land, 2006). Thus, overall, in normal grasping, the motor system's ability to respond quickly to changes in the properties of the target seems to rely on proprioception, and feedforward or anticipatory processes (Hesse & Franz, 2009a).

Evidence for the role of proprioception in grasp control also comes from studies of neurological patients. Impaired proprioception, caused by peripheral nerve damage, results in alterations of temporal features of the grasping movement, marked by a lengthening of the time to maximum opening of the grip (Gentilucci, Toni, Chieffi, & Pavesi, 1994). Patients with impairment in proprioception also show a lengthening of the closing phase of the grip (Gentilucci et al., 1994) suggesting a greater visual control is needed in the closing phase, to compensate for the lack of proprioceptive signals (Gentilucci, Toni, Daprati, & Gangitano, 1997; Jeannerod, 1997).

Taken together, these studies provide compelling evidence that proprioception plays an important role in normal online control of grasping, alongside information from vision. For tools to be controlled similarly, as discussed earlier, it would therefore be necessary for the brain to be able to interpret not only visual signals about their movements, but also (and more challengingly) what proprioceptive signals at the hand mean for tool tip opening and movement.

1.4.5 Grasping with tools: what we know

As discussed above, in the framework of movements as decision-making, tools present various challenges to the visuomotor system. Because the tool does not itself possess sensory afferents, the brain cannot directly sense the tool position in space, or the tool-tips' opening, from non-visual signals. These properties must instead be inferred from the hand, using an understanding of the mapping between the two (a 'model' of the tool's properties). Thus, any noise in the model, which is seemingly unavoidable, must propagate into non-visual estimates of tool movements, and motor plans, making them less reliable.

Using pliers-like tools further challenges the system by reducing the availability of tactile signals. In normal grasping, contact between the hand and object is conveyed by tactile signals (Flanagan et al., 2006). Those 'contact events' are essential for skilful movement (Johansson & Westling, 1984; Nowak & Hermsdörfer, 2006), offering the system salient sensory events that it can anticipate and use. Indeed, the timing, and the location of those contact events, can inform on the success of the movement (Flanagan et al., 2006). Many tools render these tactile sensations substantially less salient, partly because the digits are constantly in contact with the tool handles (i.e. there is always 'contact') and partly because signals are attenuated by the physical structure of the tool. Recent evidence suggests that humans can sense more detailed information from tactile signals acquired with tools than previously thought. For instance, it has been found that the location of a touch on a tool can be reliably identified from signals acquired at the handle, indicating that complex physical properties of tools can be accounted for in this regard (Miller et al., 2018). Nonetheless, compared to directly sensed normal tactile signals, attenuation of tactile signals in tool use would be expected to affect the automatically issued corrections made in response to slip signals, for instance, after the object is grasped (Johansson & Flanagan, 2009; Johansson et al., 2001) , as well as how grasping movements are planned (finger-tip anaesthetised has been found to result in larger peak grip aperture and in alteration of the temporal course of finger opening for example; Gentilucci et al., 1997).

Thus, even if tools are 'used as body parts', using the same neural processes and control principles, we should nonetheless expect some differences in quantitative parameters of movements made with tools vs. the hand, due to differences in the quality of the signals available, and the noise induced by models of the tool mapping.

This thesis aims to address the question of whether pliers-like tools are 'used as body parts' by examining whether various canonical features of normal grasping movements are similarly present in grasps with tools. There is an existing literature on kinematics of grasping with tools that provides some insight into this. Gentilucci, Roy & Stefanini (2004) measured grasping movements made with a tool composed of a handle and two mechanical fingers. To open the tool, participants were required to press the handle (thus, the end-effector movement was reversed with respect to the opening of the hand). They reported qualitative similarities between hand and tool grasping, in that the tool-tips were opened gradually to reach a peak, before being closed on the object. Compared to grasping with the hand, grasping with a tool resulted in a flattening of the grasp profile (less pronounced peak), with a greater proportion of time spent with the tool tips wide open. This 'plateau' seems to be a feature of tool grasping, having also been observed by others (Bongers, 2010; Golenia, Schoemaker, Mouton, & Bongers, 2014; Itaguchi & Fukuzawa, 2014). Gentilucci et al. (2004) found that the peak effector aperture was attained sooner, and that the closing phase of the tool-tips was longer, compared to normal grasping. It has been suggested that the plateau phase was a sign of the increased reliance on visual feedback (Golenia et al., 2014) due to lack of proprioceptive signal coming from the tool. As visual signals are processed slower than proprioceptive signals, the 'plateau' would be the consequence of that 'extra' time needed to process the visual signals required for movement control. The plateau could also be the result of widely opening the tool-tips, as a default strategy, resulting from having a poor understanding of the tool properties, to increase the chances of grasping the target object successfully. The emerging idea is that a better understanding of the altered relationship between finger-tips movement and tool-tips movement could allow the system to plan a more finely-tuned movement. Despite the presence of these plateaus, however, peak effector apertures still scaled with object size, indicating the presence of a degree of anticipatory control of tools in these studies (Gentilucci et al., 2004; Itaguchi & Fukuzawa, 2014).

The above studies reveal clear similarities, and some differences, between grasping movements with the hand and with pliers-like tools. The conclusions that can be drawn for our purposes are limited, however, for several reasons. *First*, any successful grasp seemingly requires opening of an effector to enclose the object, before closure of that effector. Thus, qualitative similarities in grasp profiles could reflect these physical requirements, and so cannot be unambiguously interpreted as indicating the presence of common control processes or mechanisms (cf. Gentilucci et al., 2004). *Conversely*, while the quantitative differences observed between hand and tool grasping could result from differences in control processes, as noted above they could also result from differences in the various signals available, and uncertainty in the tool mapping, rather than different control processes per se (in this regard, it is notable that Gentilucci et al., 2004, used a complex tool that reversed the action of hand opening). *Furthermore*, differences in the mechanical properties of tools vs. hands (the spatial offset between handles and tool tips, for instance) mean that movement kinematics may differ for purely physical/mechanical reasons, rather than due to different control processes being employed.

For the above reasons, our experiments emphasise less the quantitative comparison between grasping movements made with tools vs. without, but instead examine primarily the ability to take account of changes to the properties of tools, holding the global factors involved in using a tool constant. To our knowledge, the only study to compare movements made with different tools (Golenia et al., 2014) asked participants to grasp only one object with one tool, at a fixed distance, leading to the possibility that participants behaviour relied on learning a specific movement rather than a model of how to use the tool that was transferable to other situations. In our studies we therefore used a relatively large number of object sizes (five) and several object distances (three) to vary the task demand, and encourage more general learning of tool properties. Since we have construed the problem of tool use as one of knowing the mapping between hand/finger movements and movements of the tool tips, our main manipulation was to vary the precise nature of this relationship. To do this, we varied the ratio between finger-tip opening and tool-tip opening (which we refer to as tool 'gain') by moving the pivot point of simple pliers-like tools. In each study, we used one tool that preserved the normal relationship between tool-tip and finger-tip opening (1:1 tool), providing a condition relatively close to normal grasping. We also used tools that opened wider than the hand (1.4:1 tool) and less wide than the hand (0.7:1 tool), allowing us to examine how the different tool geometries were taken into account, while holding the degree of mechanical complexity constant. As will be seen in later chapters, this 'tool geometry approach' also allows us to make some (tentative) quantitative predictions about the expected movements with tools under different possible scenarios.

1.5 Overview of internal models literature

The above discussion invokes non-specific ideas of 'internal models' that, for instance, encode relationships between muscle and joint postures and end-effector movements in the world. The general idea is that such models could allow prediction of the consequences of motor commands, and the interpretation of proprioceptive signals, in high-level terms enabling, for instance, movement planning in end-effector units, and understanding properties of objects that we feel. Within the framework of Optimal Control Theory, researchers have proposed various more specific (and sometimes overlapping) ideas about the nature and purpose of internal models for motor control, which offer insights for our purposes. We briefly review the principal ideas here.

The literature in this area suggests that dexterous and smooth movements are the results of the use of internal models that allowing the brain to anticipate motor and sensory consequences. Moreover, these predictions (derived from a copy of the efferent signal, or motor command) are then thought to be compared to actual outcome (from sensory feedback), in order to continuously calibrate and refine the internal model. Optimal control of movement is defined similarly to earlier, as optimising a cost-function (or loss function) that considers the probability and value of success, while minimising some specified costs, such as energy, time, discomfort, jerk, muscle activation, etc. (Todorov & Jordan, 2002; Wolpert et al., 1995). Given the large number of possible combinations of objects and environments for which the motor system must provide appropriate motor commands, Optimal Control Theory provides a quantitative framework for calculating the ideal movement in a system (including non-biological systems such as robots). Implementations of the idea for human motor control assume internal models in the brain that encode how parts of the system function, including their noise properties (McNamee & Wolpert, 2019; Scott, 2004; Todorov & Jordan, 2002; Wolpert et al., 1995).

If tools are ‘used as body parts’, we would expect tool movements to be planned and executed using the same mechanisms. This would support the idea that the system can plan movements in ‘tool-units’, despite the mechanical constraints, and geometrical transformations induced by tools.

1.5.1 Definition of an internal model

In the sensorimotor context, an internal model has been defined as a system that mimics the behaviour of a natural process (McNamee & Wolpert, 2019; Wolpert et al., 1995; Wolpert & Kawato, 1998). Two kinds of model have been defined. First, a forward model that allows the prediction of future states based on the current state and on the upcoming motor control signals (via a copy of the efferent signals; McNamee & Wolpert, 2019; Mehta & Schaal, 2002; Miall & Wolpert, 1996; Wolpert et al., 1995; Wolpert & Kawato, 1998). A key feature of this idea is that it allows a degree of feedback control based on predicted movements in the near future. This helps overcome the inherent delays in sensory feedback, thus supporting smoother, more fluid movements. Furthermore, forward models have been proposed as a key mechanism in filtering the sensory inputs we receive from the consequences of our own actions, allowing the brain to successfully 'cancel' sensory reafferences and be more attuned to external events (McNamee & Wolpert, 2019).

Second, an inverse model is proposed, which estimates the motor command that will cause a particular desired state (McNamee & Wolpert, 2019; Wolpert et al., 1995; Wolpert & Kawato, 1998). This can be used functionally to transform a goal into the motor commands required to achieve it (Telgen, Parvin, & Diedrichsen, 2014). The acquisition of an inverse model seems to be slower than that of a forward model (Wolpert & Kawato, 1998). Inverse model are not providing internal representations of processes, but instead it may be more accurate to consider them as 'control policies' (Haith & Krakauer, 2013).

In this framework, both types of model are in constant interaction. Each efference-copy signal produced by an inverse model is used by a forward model to anticipate the future states, and their sensory consequences, in that particular movement. This interactive process makes the movement less prone to errors introduced by delays in the sensory feedback (as mentioned previously). This also allows the system, by receiving sensory and motor feedback, to adjust the movement to reach the desired goal (Wolpert & Kawato, 1998), by optimally combining the output of the internal model to the various feedback signals (McNamee & Wolpert, 2019). The separation of different processes also allows, in principle, determination of where changes should be made to minimise errors in future movements (Wolpert et al., 1995; see section 1.6.4).

By nature, those models are highly adaptable. Indeed, they capture information about the properties of the sensorimotor system. These properties tend to change throughout life (e.g. due to growth) but also in each interaction with the environment in different context (Wolpert & Ghahramani, 2000; Wolpert & Kawato, 1998).

1.5.2 Internal models and tool use

One of the potential benefits of using those models is they could allow the motor system to deal with a world in which relationships between motor commands and resulting outcomes readily changes (Wolpert & Kawato, 1998). As tools alter the relationship between hand movements and what happens in the world (Arbib et al., 2009), internal models could encode the new relationship between the different signals. This has been proposed as the mechanism by which haptic signals at the hand were 'remapped' to the location of an object felt with a tool, and to take tool geometry into account, in integration of visual and haptic signals to object size (Takahashi et al., 2009; Takahashi & Watt, 2014, 2017).

Conceptually, there are several distinct possibilities for how these new relationships could be implemented within the internal model framework. One possibility is that the existing models (and control policies) for the hand/arm are altered to reflect, or incorporate the properties of tools. This is closely analogous to the body schema idea, and implies that the representation of the hand would be altered, to accommodate the tool properties. Here, presumably, accurate information about the hand per se is no longer accessible. As mentioned earlier, this seems plausible for tools that behave in a manner that is mechanically similar to the hand (Arbib et al., 2009), and where relatively simple parameters of the hand model could be adjusted to accommodate the tool properties (spatial position, grasp opening gain etc.). This process seems conceptually similar to that of classical adaptation (e.g. to prism-induced distortions). It seems less plausible, however, for more complex devices that include biologically impossible transformations.

A second, alternative possibility is that components representing the tool geometry could be added to those for the hand/arm. These would relate hand posture (specified by the existing hand model) to tool-tip movement, but the brain could still access information about the state of the hand per se. In principle, such a mechanism might more easily accommodate tools that are mechanically dissimilar to the hand, but implies the capability to separately represent devices that are external to the body.

Third, a completely new model could be created that includes the transformations due to the arm/hand and those of the tool. Such a model might, again, accommodate transformations that are very dissimilar to those of the hand more easily than by altering the hand model per se. It can potentially also account for the fact that the hand itself may move differently when ‘attached to’ a mechanical device that imposes its own constraints (i.e. the required hand model may change).

The second and third possibilities, above, would both seem to require the ability to rapidly switch between different models, as required by the current task. And in all cases, it will likely be insightful to examine the flexibility of these models in accommodating transformations that differ qualitatively from the hand/arm. Given appropriate computational mechanisms— in engineering terms, the right set of basis functions (Donchin, Francis, & Shadmehr, 2003; Santello et al., 2016) —the brain may, under any of the possibilities above, be able to represent mappings induced by a wide range of non-biological devices. If, however, the computational mechanisms are less general, and reflect their development to control hands and arms, specifically, they may place constraints on what types of mappings can be taken account of, even in the case of distinct tool models.

It is also possible that how the new mapping is implemented depends on what suits the properties of the tool to be used. For example, it is conceivable that a tool that is mechanically similar to the hand may result in adaptation of the hand model, whereas a tool that differs more fundamentally may require a distinct model.

1.6 Overview of sensorimotor learning literature

Inherent in the above arguments is the idea that when using a new tool, the tool user has to learn its properties, and the new mapping that comes from using it. This section will focus on how those alterations might be learned, and accounted for, from the perspective of sensorimotor learning. This might help us understand, or at least give us a framework to think about, how people learn to use new tools.

1.6.1 What is sensorimotor learning?

Sensorimotor learning has been defined as improvement, through practice, in the performance of sensory-guided behaviour (Krakauer & Mazzoni, 2011). That improvement requires learning how to gather task-relevant sensory information to choose the appropriate motor response (Telgen et al., 2014; Wolpert, Diedrichsen, & Flanagan, 2011), leading to the implementation of new predictive (forward model) and reactive (inverse model) control mechanisms. When developing a new control mechanism, the system does not necessarily start from a blank slate, but can rely instead on previously acquired sensorimotor models (Gentilucci et al., 1995; Roland S. Johansson, 1998; Kluzik, Diedrichsen, Shadmehr, & Bastian, 2008), if such sensorimotor models exist (e.g. absence of existing model when learning to ride a bike).

Sensorimotor learning implies a change in the mechanisms transforming goals into motor commands.

Sensorimotor learning is learning how to better perform a task, faster and with more accuracy. Under this framework, it has been proposed that learning can happen in different components. One component has to be learned is a *forward model*, as described in the previous section. The forward model relies on prior information to predict future states and consequences of motor commands (Wolpert et al., 1995; Wolpert & Kawato, 1998). Another component is a *reactive control-feedback loop*. As the Optimal Feedback Control (Todorov, 2004) framework suggests, the system can use moment-by-moment feedback to update the motor commands. An emergent property of that framework is the 'minimal intervention principle' (Todorov, 2004; Todorov & Jordan, 2002), that is variability is ignored in dimensions irrelevant to the goal of the task. This account could explain how the motor system can deal with the inherent noise during movement execution, and not be overwhelmed by the computational complexity. A last component is the *biomechanical properties* of the body, or the tools used (Wolpert et al., 2011; Wolpert & Flanagan, 2010). A combination of the three components is necessary to learn most tasks. The weight given to each component will depend on the task to learn.

Applied to learning tools, this framework implies that people would have to learn the mechanical properties of the tool, how the tool alters the relationship between signals, between motor commands and their outcomes in the world in order to link motor goals with the tool to the appropriate hand motor commands. It also implies that difficulties (failures to learn) may emerge in particular components of this process.

1.6.2 Learning the task structure

The previous section considers learning the models relevant to a new behaviour. Another aspect of sensorimotor learning that has been identified is learning the task structure.

For a task such as grasping, the overall movement is at one level highly similar across many different objects, but requires fine-tuning to particular circumstance. Thus, when facing varying movements with the same structure, the brain can extract a set of general principles about the task structure (Braun, Aertsen, Wolpert, & Mehring, 2009) as well as some abstract motor strategies applicable in other environments (Braun, Mehring, & Wolpert, 2010). Once a structure has been learned, parameters tuned to a specific situation can be applied to the motor strategies to plan the most appropriate movement for that particular situation. Existing task structures can provide those existing motor strategies so the motor system does not start from a blank slate when facing a new task. When deciding which specific motor commands to choose, it has been proposed that the visuomotor system uses a Bayesian strategy, relying on prior knowledge about the structure, and parameters relevant to the task (Krakauer & Mazzoni, 2011).

In a variable environment, in which the alteration/transformation faced by the motor system is not constant, the rate of learning the structure of the task, as well as the learning of the altered relationship between the signals, is slow (Gonzalez Castro, Hadjiosif, Hemphill, & Smith, 2014). This appears consistent with the Contextual Interference Effect (Battig, 1966; Shea & Morgan, 1979). That is, a high level of interference (e.g. randomisation of trials vs. low level of interference: blocked trials) during motor learning would lead to poorer performance, but would improve retention (performance on later performance test) and an adaptability to novel situation (Brady, 1998; Magill & Hall, 1990; Merbah & Meulemans, 2011; Shea & Morgan, 1979). It has been suggested that high interference would lead improved ‘long-term’ learning, by inducing more flexibility in the structural neuronal organisation of the motor response (Brady, 1998; Merbah & Meulemans, 2011). This effect has been found in a large variety of motor learning tasks (for reviews: Brady, 1998; Magill & Hall, 1990). This effect could be driven by an increased cognitive activity during high interference context (Brady, 1998, 2008; Merbah & Meulemans, 2011). Taken together, it seems that a more ‘consistent’ environment would improve the rate of ‘learning’, while a less ‘consistent’ environment would lead to a deeper learning.

When facing the task of grasping objects using a pliers-like tool, the motor system may therefore be able to rely on (or build on) an existing hand grasping task structure (or on an existing tool grasping task structure, depending on prior experience). Those programmes could then be optimally tuned to the use of our pliers-like tools.

1.6.3 Motor primitives

As mentioned earlier, motor primitives (and the related idea of motor synergies) have been proposed as solutions to the requirement for dimension reduction in motor control, providing ‘building blocks’ for complex movements (Santello et al., 2016; Thoroughman & Shadmehr, 2000; Wolpert & Ghahramani, 2000)

In the specific terms of Optimal Control Theory framework for motor control, motor primitives can be seen as an element of computation in the internal inverse model transforming desired limb trajectories into motor commands (Thoroughman & Shadmehr, 2000). Those elements can be flexibly combined to generate more complex movements (McNamee & Wolpert, 2019; Wolpert et al., 2011), rendering highly flexible movement control tractable. Already possessing some motor primitives would facilitate the learning of new movements requiring the use of those primitives.

The presence or absence of existing primitives might then determine what constraints are imposed on learning (Wolpert et al., 2011). Motor primitives could also help localise the origin of an error when performing a movement, allowing the system to correct only a subpart of the movement (Thoroughman & Shadmehr, 2000; Wolpert & Ghahramani, 2000).

Grasping with a pliers-like tool is a complex movement, but is at least superficially similar to normal grasping if, for instance, the tool-tips open when the hand opens. Thus, the motor system may well be able to rely on existing motor primitives for grasping that it can assemble to carry out the tool grasping movement. Alternatively, the differences in feedback available, the mechanical properties of the tool (which in turn affect grasping forces, and constrain movements to certain dimensions) may mean that the existing grasping synergies cannot be applied without alteration. Furthermore, for tools that behave differently than the hand—reverse-pliers, for example, where the hand must be opened to exert grasping forces—existing motor primitives (and task structures) may not be useful. This idea will be explored in Chapter 5.

1.6.4 Credit assignment problem

When learning a new task, a new movement, or to use a new tool, the motor system will face errors. Efficient learning requires correctly assigning the error to its underlying cause, so that the correction can be made to the correct aspect. That problem has been called the ‘credit assignment problem’ (Wolpert et al., 2011).

Movement planning requires the motor system to account for different movement properties, such as trajectory, movement speed, endpoint, etc. When errors arise, the motor system first needs to identify their source (forward model, motor programme, noise in the motor system, task, external events, …). Unfortunately, the information obtained during a single error is often not conclusive (for instance it may be too noisy to clearly identify the source of the error). The system would use the predictions generated by a forward model to weight the different signals and locate the most likely source of the error (Wolpert & Flanagan, 2010; Wolpert et al., 1995; Wolpert & Landy, 2012) That process would update the internal models and allow for future planning and execution of that movement to be more efficient, by reducing the prediction errors (Albert & Shadmehr, 2016; Krakauer & Mazzoni, 2011).

When facing an error, the motor system can also link that error to contextual cues, such as task, tool or environment. For example, when executing a reaching movement in a new environment, a large error signal could be attributed to the motor program used, but also to the new environment disrupting the movement (Wolpert & Landy, 2012). In this situation, the magnitude of the error signal can be used by the system to attribute the error to the correct internal (movement or model) or external (environment) factors (Kluzik et al., 2008). Indeed, small errors would probably be attributed to the movement itself, while larger errors would probably be attributed to the new environment in which the movement is not appropriate. If the system is unable to attribute the error to the control mechanisms used, or to the inherent noise in the nervous system, it could lead to the creation of a new internal representation, mapping the new relationship between the sensory and motor signals (Ingram, Howard, Flanagan, & Wolpert, 2010; Sadeghi, Ingram, & Wolpert, 2018).

When using a pliers-like tool, one possibility (albeit naïve) is that the motor system behaves initially as if it is grasping with the hand. Then participants will generate errors, directly related to the tool-induced alterations in the relationship between a given motor command and its consequences (the movement of the tool-tips). Assuming the motor system (correctly) attributes the errors to this tool mapping, it would stimulate component to be developed/updated, leaving other aspects intact. Similarly, if motor programmes need to be altered to produce the appropriate movements with tools, this could be identified specifically, and adjustments made.

1.6.5 Adaptation versus skill learning

In several places we have discussed ideas of tool use piggybacking on existing control policies and internal models, vs. developing new ones. This relates closely to ideas from studies of hand movements of the distinction between adaptation and skill learning. Specifically, two distinct modes of sensorimotor learning have been proposed for developing a new mapping between hand movements and the movement of a cursor or other end-effector (Wolpert &

Flanagan, 2016). The first mode is referred to as *adaptation*. Adaptation can be interpreted as a *recalibration* and a correction of biases to maintain an optimal level of performance of the system. When performing a movement, the motor system is comparing the actual state of the movement to the state predicted by the forward model. If error signals arise, and are attributed to the internal model, then that model is updated.

The adaptation of an existing forward model leads to reduced occurrences of similar errors in the future (Shadmehr, Smith, & Krakauer, 2010; Wolpert et al., 2011). The motor system does not learn by simply seeing the error, but by the process of correcting it (Shadmehr et al., 2016). This process allows for trial-to-trial learning, and so there is a gradual improvement in performance (Krakauer & Mazzoni, 2011).

Unlearning the adaptation can be rapid (Davidson & Wolpert, 2004). A key idea from Smith, Ghazizadeh, & Shadmehr (2006) is that there are two processes acting in parallel during adaptation, a fast process, correcting any error quickly but with poor information retention and a slow learning process that retains information longer (Smith et al., 2006). This echoes the fast acquisition of a forward model versus the slow acquisition of an inverse model (Wolpert & Kawato, 1998).

A similar mode of learning has been defined as use-dependent learning. That learning happens by pure repetition of a movement, without perturbation, or the need to know the outcome of the movement (Diedrichsen et al., 2010; Wolpert et al., 2011). The repetition of movements to a specific target reduces variability and induces a bias towards the trained target. In Bayesian term, the motor system seems to update the prior with the sensory consequences of the previous movement (Verstynen & Sabes, 2011). The use-depending learning seem to be task sensitive (Diedrichsen et al., 2010) and a decrease of accuracy can observed for other task (Verstynen & Sabes, 2011). Use-depending learning and adaptation can work together.

In summary, adaptation relates to recalibration of an existing motor control policy to a new situation (Telgen et al., 2014). A second mode of sensorimotor learning has been defined as *skill learning*. The goal here is to reduce variability, without any existing performance limit. In situations where the motor system cannot use existing motor control mechanisms or internal models, new ones have to be developed. This is the process of skill learning.

A diminution in variability is an important feature of skill-learning (Reis et al., 2009; Shmuelof, Krakauer, & Mazzoni, 2012). Skill learning has also been defined as an improvement in the speed-accuracy trade-off in a task that does not involve a perturbation (Reis et al., 2009; Shmuelof et al., 2012). Performance improvement in skill learning is relatively slow, and requires practice to improve from baseline (Shmuelof et al., 2012). Skill learning has been also characterised by an offline improvement of performance (e.g. improved performance following sleep, referred to as consolidation; Abe et al., 2011; Telgen et al., 2014; Wright, Rhee, & Vaculin, 2010) and long-term retention (Abe et al., 2011; Reis et al., 2009). In contrast, learning due to adaptation typically results in 'forgetting'—reduced performance following removal from the learning setting (e.g. following sleep; Telgen et al., 2014). Other mechanisms, such as reward and motivation, have been found to promote consolidation of skill learning (Shmuelof et al., 2012; Wolpert et al., 2011).

In skill learning, at early stages of practice, variability can represent an exploration strategy. Indeed, more task-relevant variability at baseline may even lead to faster learning (Wu, Miyamoto, Castro, Ölveczky, & Smith, 2014); though these results are yet to be replicated (Sternad, 2018). Thus, the changes in performance due to skill learning can be quite different than the progressive reduction in error seen in adaptation.

As defined above, adaptation and skill learning have been distinguished experimentally by several signatures (Telgen et al., 2014). The first is the effect of the speed of the task. As adaptation relies on an existing motor control mechanism, increasing the speed of the task does not lead to a marked increase in errors. When learning a new motor control mechanism, however, increasing the speed of the task leads to increased errors, because the control mechanism used by the system is not correct, and more (corrective) control is required (Telgen et al., 2014). A second signature is the time required to respond to an unexpected perturbation. If the system is adapting, it can react rapidly using existing motor control mechanisms. However, because skill learning requires the development new control mechanisms, it initially leads to slow responses, because a suitable control process is not available (Telgen et al., 2014). A third signature, as mentioned above, is retention in memory. Skill learning shows signs of offline improvement of performance (Abe et al., 2011; Telgen et al., 2014; Wright et al., 2010) while adaptation does not (Telgen et al., 2014). Skill learning has been characterised by slow learning curve and a long term retention (Abe et al., 2011; Reis et al., 2009) while adaptation has been characterised by a rapid 'learning' curve and a rapid deadaptation (Davidson & Wolpert, 2004; Smith et al., 2006).

The implications of the distinction between adaptation and skill learning essentially mirror the emergent points from considering motor primitives, task structure, internal models etc. It may be possible to use some tools by recalibrating (adapting) existing motor models, whereas others may require new models (skill learning). Again, this seems likely to depend on how similar the actions of the tools are to those of the hand, and how similar the movements required to operate them are to grasping.

1.6.6 Summary and overview of experiments

Tools alter the relationship between hand movements and the movements of the relevant end-effector in the world (i.e. the tool-tips). It is often speculated that we use tools 'as if they are a part of our body' (e.g. Cardinali et al., 2009), and the phenomenology of tool use is highly suggestive of this. This idea implies that at some level the brain incorporates, or takes account of, the specific, metrical properties of tools in a way that allows normal motor control processes to be invoked, resulting in fluid, dextrous, anticipatory use of tools.

How this might be achieved has been described in various terms, including via internal representations of the body (the body schema account) and through the frameworks of sensorimotor learning and optimal control. In many ways, these very different levels of description make similar predictions. Tools that are more like hands may be easier to use ‘like a body part’ than tools that are more different. But regardless of this the pervasive underlying idea is that the properties of the tool are represented in the visuomotor system—implicitly or explicitly—in a way that allows rapid, highly optimised motor control processes to operate on them.

Experimental investigation of this is sparse, however. There are very few studies of movement dynamics during tool use, for example. And while humans are clearly highly adept tool users, the constraints on how we learn to use tools, whether tool use does indeed show the remarkably refined features evident in behaviours such as grasping, and the mechanisms underlying this, remain to be determined.

This thesis represents preliminary steps towards doing this. Our primary aim is to examine how participants plan and execute movements with tools, using grasping as a model task (and normal grasping as a baseline for ‘optimised’ performance). Specifically, we explore the process of accounting for alterations in the mapping between hand opening and tool opening, and look for evidence that this is achieved by creating internal models that reflect the properties of tools. Our secondary aim is therefore to examine the process of acquisition of these internal models, or altered mappings.

More generally, most of the literature on adaptation, skill learning etc. has used experimental paradigms such as prism adaptation, or force-field adaptation, with simple reaching or pointing movements. These tasks allow researchers to constrain movements and highly control all the parameters of the experiments (Sternad, 2018), but at the cost of real-world complexity. Our work allows us to gain insights into whether these principles can be applied to more complex movements, such as tool grasping.

Our first study (Chapter 3) examined movements made with pliers-like tools that had different ratios of tool opening to hand opening. We probed the presence of anticipatory behaviour by looking for the presence of typical relationships between end-effector (here tool-tip, rather than digit) kinematics and variations in object properties. Specifically, we examined whether grasping behaviour differed ‘appropriately’ with different tools, in a way that indicated the geometrical properties of each tools were appropriately taken into account. We probed for the existence of accurate and reliable internal models of tools by, in some conditions, examining how tool movements were made when visual feedback was presented, and so online control must rely on non-visual signals (e.g. proprioception). We also examined performance over several days, with a view to gaining insights into how people learned to use the tools.

Our second experimental (Chapter 4) probes acquisition of internal models of tools in more detail. Specifically, we examined whether tool use leads to alteration of the felt opening of the hand (as per body-schema account predictions) or was more consistent with a separate or independent process of modelling the tool mapping. We also examined whether tool geometry was taken into account similarly in perception and motor control.

Our third experimental chapter (Chapter 5) explored use of a tool that behaves differently to the hand, requiring the grasp to be opened in order to close it. We again looked for evidence for anticipatory behaviour, such as relationships between in-flight tool kinematics and object properties, to determine whether performance was impaired in this situation. We also attempted to dissociate the hand movement required to perform the task from the tool geometry—using a reverse grasping task—to better understand whether difficulty using this tool came from making an unusual hand movement per se, or from the acquisition of an internal model of an ‘unusual’ tool.

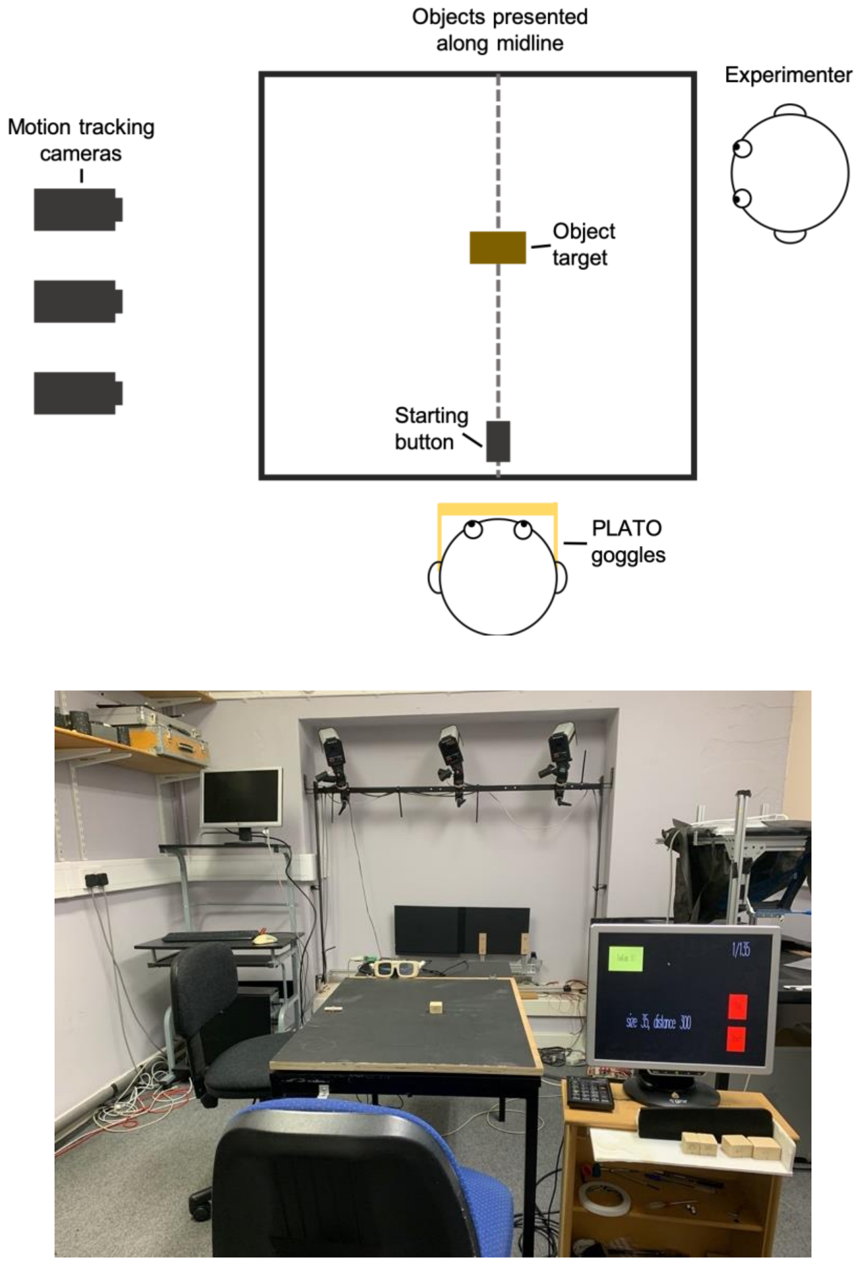
Chapter 2 – General Methods

In this thesis, we examine participants movements when using tools. As mentioned previously, we used grasping as a model task, and we used pliers-like tools to vary the relationship between hand opening and tool-tip opening, allowing us to observe qualitative and also quantitative differences between grasping movements made with the hand, and with the different tools.

The main dependent measures in all three empirical chapters are kinematic indices of grasping movements (with and without tools). Here, we describe the principal methods used during the grasping tasks, including the techniques for capturing and analysing kinematic data, the pliers-like tools used, and the various other generic details of the tasks and apparatus.

2.1 Apparatus

The main setup is shown in Fig. 2.1. Participants were seated at a ~60 x ~60cm table, with their body midline aligned on a 1.5 x 2 cm starting button. The table surface was covered in matt black cardboard. A starting button allowed us to ensure participants started from the same spatial location on all trials, in all conditions. Fig. 2.1b shows the motion-capture cameras (far wall; see Section 2.3. on movement recording), and the console monitor (bottom-right) used to convey instructions to the experimenter for each trial.



(a)

(b)

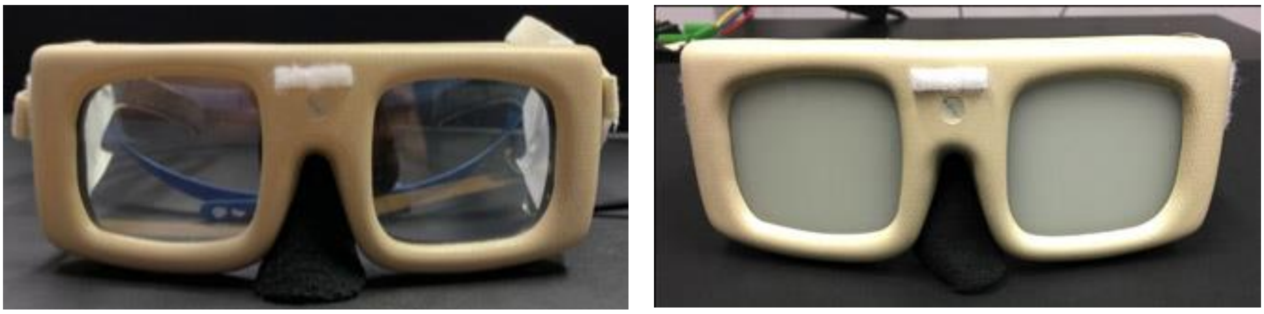
Figure 2.1. The experimental setup. (a) Schematic of the experiment apparatus. (b) Photo from behind the position of the experimenter (participants' chair is on the left).

The grasped objects were five small balsa wooden blocks, shown in Fig. 2.2. Their sizes in the grasped dimension (front to back) were: 25, 30, 35, 40, & 45 mm. They were all 35 mm wide and 25 mm high. Balsa wood was chosen because its light weight made it easier to lift the objects with the tools. The objects weighted from approximately 10g (25 mm object) to 20g (45 mm object).

(a) **(b)**

Figure 2.2. Objects grasped in main experiments. (a) The 35 mm object from the participants' point of view. The motion-capture marker can be seen on the left side of the object. (b) The 5 object sizes.

Participants' vision of the scene was controlled using a pair of rapid-switching ferro-electric shutter-glasses (PLATO Vision Occlusion Spectacles, Translucent Technologies Inc., Canada) operated by the experiment computer. These are shown in Fig. 2.3.



(a) **(b)**

Figure 2.3. Ferro-electric shutter glasses used to control participants' vision. (a) The glasses in their opened (transparent) state, and (b) in their translucent state.

2.2 Tools

The goals of this thesis involve studying movements made with tools with different relationships between index finger and thumb opening, and the opening of the tool-tips. This allowed us to control the different physical transformation that participants had to take into account when using the tools, while keeping other factors essentially constant.

In most cases we used three lightweight (~23g) 3-D printed tongs, or pliers-like tools. The tools are shown in Fig. 2.4. They were 15 cm long, and had a single pivot, the position of which was varied in order to vary the ratio between tool-tips opening and handle opening. The three ratios were 0.7:1 (tool-tips opening less than the fingertips; the yellow tool in Fig. 2.4), 1:1 (tool-tips opening the same amount as the fingertips; the blue tool in Fig. 2.4, and 1.4:1 (tool-tips opening more than the fingertips; red in Fig. 2.4). Black rubber balls attached to the tool-tips ensured there was adequate friction between tools and objects to pick the latter up without excessive grip force. The friction between the two arms was kept minimal, allowing the tools to be opened and closed with little force. The three tools shown in Fig. 2.4 were used in Chapter 3 and Chapter 4. The 1:1 tool was also used in Chapter 5 (along with a reversing tool, which is described in that chapter). Two motion-capture markers were attached to each tool (one to each arm, permanently attached to ensure reliable measurements). Participants were instructed to use the tools by using only their thumb and index finger, one in each handle. This ensured that movements were as comparable as possible to the precision grasps (using thumb and index finger) employed in the normal (hand) grasping conditions. Throughout the thesis, the colours of the tools (red, blue yellow) will be used to denote data from the respective conditions (with hand data presented in green).

Figure 2.4. The three tools used in most experiments. The handles are on the right side. The motion capture markers can be seen near the black balls.

2.3 Movement recording

On hand grasping trials, we recorded the x, y and z positions of markers attached to the wrist, the medial tip of the thumb nail, and the lateral tip of the index fingernail. During tool grasping trials, we recorded from markers on the wrist, and the two markers on the tool arms, just next to the rubber balls (Fig. 2.4). Marker positions were recorded at a sampling rate of 240 Hz, using a ProReflex motion capture system (Qualisys AB; Fig. 2.1b). Prior to analysis. the 3-D coordinates were low-pass filtered (Butterworth filter, 12Hz cut-off). In hand conditions each trial recorded a fixed period of 3 secs (720 frames) following the go signal. In tool conditions, recordings lasted 4 secs (960 frames), to account for the possibility that longer movement time could be needed to successfully grasp the objects.

When analysing the hand grip aperture, or tool tip aperture, the ‘raw’ 3-D marker separation was corrected for the marker positions, such that it reflected the actual separation between the pulpar surfaces of the digits (hand conditions) or the insides of the rubber balls on the tools (tool conditions).

2.4 Kinematics of grasping

In this thesis, we aim to better understand how people use tools, by analysing grasping movements made with our various pliers-like tools. Hand grasping movements are typically analysed by extracting the value of various kinematic indices—specific, easy-to-identify dependent measures—that have been found to vary reliably with variations in experimental conditions, and so are thought to reflect underlying movement programmes (Jeannerod, 1981, 1984; Smeets & Brenner, 1999; Wing et al., 1986). Grasping movements are highly stereotypical. Fig. 2.5 shows typical examples of velocity and grip aperture profiles, as a function of time. The velocity profile of the movement (Fig. 2.5a) usually follows a bell-shaped profile, with an asymmetrically extended final phase as the hand closes on the object. The grip aperture profile (Fig. 2.5b) also forms a stereotypical profile, whereby the grasp aperture is gradually opened until reaching a peak, before closure of the hand to enclose and grasp the object. The most commonly identified kinematic indices are peak velocity, representing the highest velocity observed on the velocity profile, and peak grip aperture, representing the largest opening observed on the grip aperture profile.

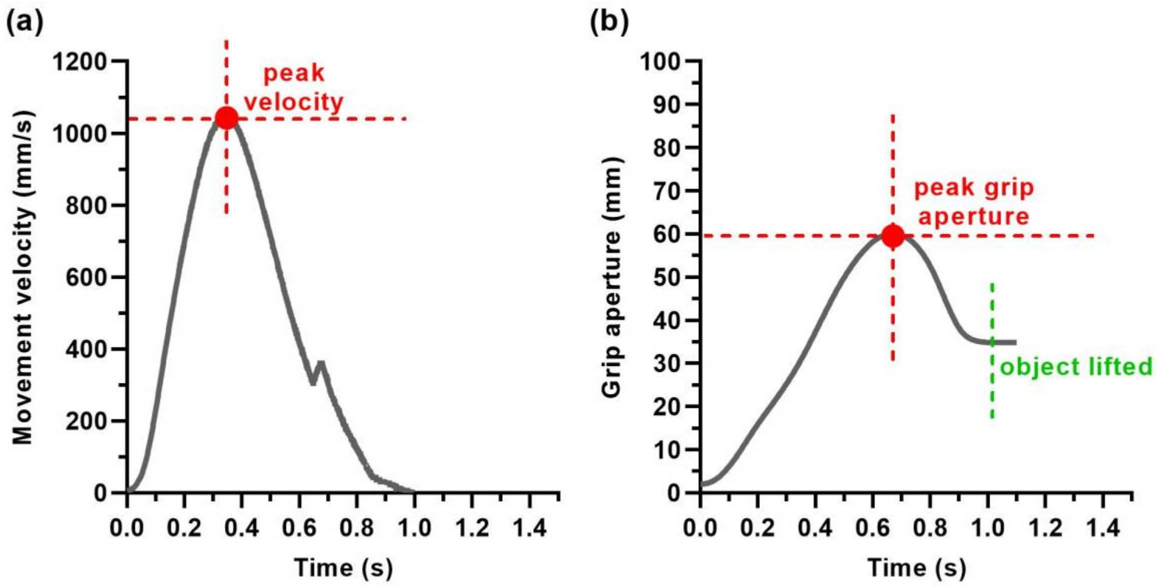


Figure 2.5. Typical velocity and grip aperture profiles. (a) Wrist velocity for a single hand-grasping movement, as a function of time. The red data point and dashed lines denote peak velocity and the time at which it occurred. (b) Grip aperture (3-D separation of index finger and thumb) as a function of time, for the same movement. The red data point and dashed lines indicate peak grip aperture, and time of occurrence. The vertical dashed green line represents the time point identified as when the object was lifted (see main text).

2.5 Indices of interest

To examine grasping movements, a number of kinematics measures were derived from the 3-D coordinates on each trial. Extraction of these indices was semi-automated, using custom-written analysis software in MATLAB. Graphical representations of each trial, showing identified kinematic parameters, were also visually inspected to ensure no errors were present.

2.5.1 Peak velocity

The Peak velocity is the maximum 3-D velocity of the reaching movement, and is used to quantify the overall speed of the movement. It was identified analytically in each profile by localising the point of inflexion at the largest overall magnitude. It has been shown to scale reliably with object distance (Jeannerod, 1984, 1988). Peak velocity decreases when uncertainty is introduced, for example by removing visual feedback during the movement (Connolly & Goodale, 1999; Keefe et al., 2019; Melmoth & Grant, 2006), suggesting a strategy by the visuomotor system of slowing down to compensate for perceptual uncertainty. Thus, peak velocity cannot be used to make direct inferences about the distance estimate used by the visuomotor system. Because peak velocity occurs early in the movement in time, it primarily reflects planned aspects of grasping movements, rather than online corrections.

The peak velocity is typically extracted from the wrist marker, to provide a measure of speed that is biomechanically independent from grip formation. It also allows direct comparisons of hand speed in our tool and hand-grasping conditions.

Across the thesis, we will analyse the peak velocity to investigate the presence of scaling of peak velocity to object distance. We will not however analyse potential interactions between object distance and effectors. Our main focus remains on the control of the tool-tips. Further, we will compare peak movement velocity between the different effectors (hand vs. 1:1 tool: to test the effect of using one of our pliers-like tool; between the tools: to test if a certain tool geometry has an impact on movement velocity). Differences between effectors could be informative on their own, identifying a tool geometry being more difficult to account for or requiring more online control. An absence of difference in movement velocity between the tools would also ease the interpretation of the peak grip aperture, as it would be indicative that no trade-offs were made between movement velocity and peak grip aperture for a specific tool geometry.

2.5.2 Peak grip aperture

Peak grip aperture is typically defined as the maximum separation between the index finger and the thumb during a hand grasping movement, reached before the object is lifted. We defined it similarly in tool conditions, as the maximum separation between the tool-tips. Similar to peak velocity, it was identified analytically in each profile by localising the point of inflexion at the largest overall magnitude. We sometimes refer to this measure as 'peak end-effector aperture' when both hand-grasping and tool-grasping data are presented on the same graph. Otherwise, it is referred to as 'peak hand aperture' when grasping with the hand, and 'peak tool-tip aperture' when grasping with the tools.

Peak grip aperture has been found to scale linearly and reliably with object size (Jeannerod, 1984, 1988). The magnitude of this scaling, calculated as the slope of the best fitting linear regression to the mean peak grip aperture plotted as a function of object size (Fig. 2.6), is typically around 0.8 (Smeets & Brenner, 1999).

Peak grip aperture is also thought, as mentioned in the introduction, to include a margin-for-error as a response to uncertainty, increasing the grip aperture to reduce the chances of not grasping the object (Keefe et al., 2019; Schlicht & Schrater, 2007). When visual uncertainty is increased, for example by blurring vision, it leads to larger grip apertures (Keefe et al., 2019), as does moving faster (Wing et al., 1986). Similarly, when visual feedback is removed, larger grip apertures are observed (Jakobson & Goodale, 1991; Melmoth & Grant, 2006). Thus, as with peak velocity, although peak grip varies primarily with object properties, it also reflects more refined calculations associated with uncertainty and controlling the probability of a successful grasp (Keefe et al., 2019; Schlicht & Schrater, 2007). As such, although object-size scaling in peak grip aperture does indicate sensitivity to object size in planning movements, the precise estimate of size used cannot directly be 'reverse-engineered' from the grip aperture data.

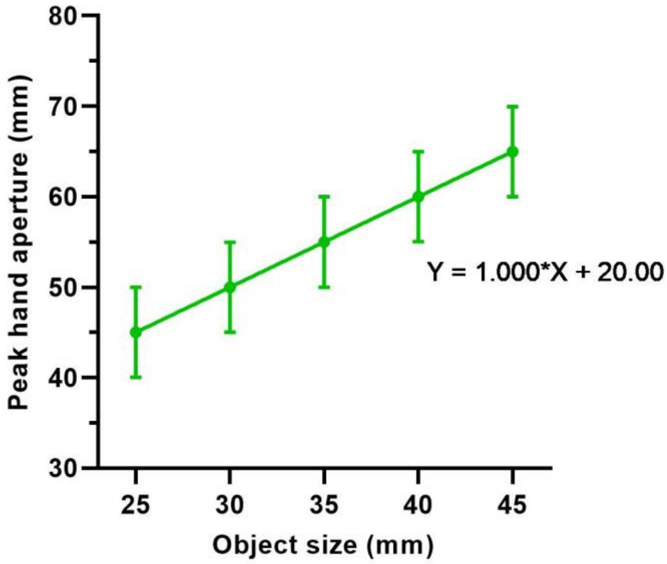


Figure 2.6. Scaling function. Peak hand aperture as a function of object size (collapsed across object distance). The solid line represents the best fitting linear regression to the data (the equation is displayed). The error bars denote +/- 95% confidence interval.

For the tool conditions in this thesis we sometimes present peak aperture data in units of tool-tip opening, and sometimes in units of hand opening, depending on purpose. Apertures in hand opening units were calculated from tool-tip opening by dividing the tool data by the tool ratio.

We are particularly interested peak grip aperture because our principal questions relate to whether participants account for the different tool geometries (ratio between tool and hand opening) in planning their movements. The magnitude of peak grip apertures across tool conditions should be a key indicator of this. Moreover, the presence or otherwise of peak grip aperture scaling with object size in the tool conditions will be an important indicator of whether anticipatory control of the tools is occurring. If the visuomotor system has no understanding of the properties of the tool, it may not be able to adjust tool opening to reflect object properties. Or alternatively, it may produce the same movements with the hand for all tools, showing no adjustment to reflect the tool geometry. However, if participants do develop internal models of the tools, we expect to see grip aperture scaling, and compensatory adjustments to overall grip opening, to take account of tool geometry.

2.5.3 Overall movement time

Movement time was defined as the time between the start of the movement (participants releasing the starting button), and the object being grasped. There is no one accepted way to evaluate when an object is lifted, partly because grasping movements are typically continuous, rarely exhibiting a distinct point of inflexion that corresponds to a stable grasp being achieved. We therefore chose a standard spatial criterion instead, defining the point at which the object was lifted as the first frame on which the object marker reached a height 5 mm above its starting point. This criterion was only triggered if the aperture was also essentially constant during this period, so the accidentally knocking over would not be counted as an 'object lifted' event. By defining movement time in this way we intentionally included both the main portion of the movement, and also any fumbling and final adjustments required to achieve a stable grasp. As such, this index is a sensitive 'catch all' not only for overall slower movements, but also for inaccuracies in the programmed movement or in online control.

Note that in some cases, particularly when grasping with the tools, and without visual feedback, participants failed altogether to grasp the objects. Here, no movement endpoint could be defined. These trials were entered into other analyses (peak grip, peak velocity) because they reflect real variation in movements, but obviously had to be excluded from movement duration analyses.

We did not analyse movement duration directly, but that measure was required for the overall grasping profiles (see below).

2.5.4 Overall grasping profiles

In this thesis, we study changes in kinematic parameters as a way to measure underlying differences between movements made with the hand, and with different tools. However, those parameters are only a single point out of the entire movement and so their use reduces a complex movement to a handful of parameters. Attempting to characterize the entire movement based on those parameters may be misleading, because differences may lay elsewhere (consider the extended plateau observed in tool use studies, which is not evident in peak grip aperture data per se). For visualisation purposes we therefore also created average grasp profiles across whole experiment conditions. The process involved, for each participant, normalization in time (from movement onset to object grasp) and space of individual trials, before the averaging of those trials for a specific condition. Those average conditions were averaged again across participants. The profiles were then stretched in time to scale with overall movement duration. These profiles were generally averaged across object size and distance, and were plotted as a function of time (the standard method) and also as a function of space (normalised by object distance). Precise details are given in the relevant chapters. Note that the trials without identifiable endpoints could also not be included in these overall profiles because they could not be normalised in time and space. Note also that simple averaging across 'bumpy' movements produces average profiles that artificially smooth.

Time spent in the 'plateau phase'

Following previous studies (Bongers, 2010; Gentilucci et al., 2004; Golenia et al., 2014; Itaguchi & Fukuzawa, 2014) we also computed the duration of the 'plateau phase' of the overall grip aperture profiles, defined as the time spent with an end-effector aperture of >= 90% of the peak grip aperture (as seen in Fig. 2.7).

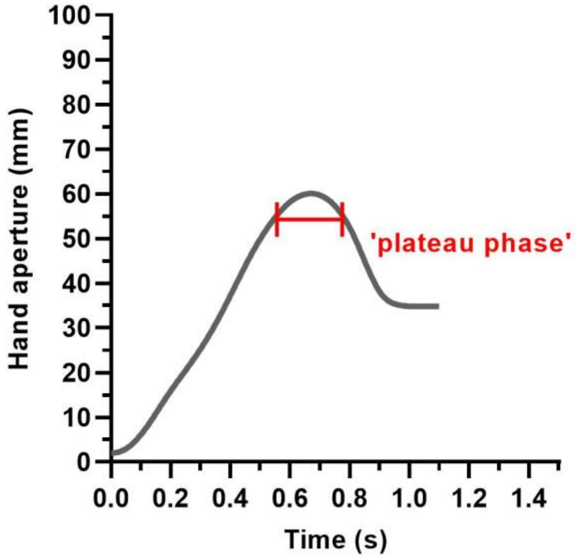


Figure 2.7. Plateau phase. Example of a ‘plateau phase’ on a hand grasping profile.

Chapter 3 – Are tools ‘used as body parts’ ?

3.1 Introduction

In the General Introduction, we discussed how one way to define tools, from the perspective of visuomotor control, is as devices that transform the relationship between body movements and their consequences in the world. This includes transformations such as altering the relationship between hand opening and tool-tip opening (Arbib et al., 2009; Takahashi & Watt, 2014, 2017). This Chapter examines the extent to which people account for these geometrical transformations in the planning and execution of grasping movements with simple tools.

An emergent idea in the existing literature is that tools are ‘used as body parts’. We have argued that this idea implies that the same visuomotor control principles would be used for grasping movements made with the hand and for grasping with tools. Normal grasp control is thought to rely on internal models of the relationships between motor commands and hand posture (the end-effector in hand grasping; McNamee & Wolpert, 2019; Wolpert et al., 1995; Wolpert & Kawato, 1998). These models allow anticipatory features such as appropriate scaling of movement velocity with object distance (Jeannerod, 1981, 1984; Marteniuk et al., 1990) and scaling of the maximum grip aperture with object size (Jeannerod, 1981, 1984; Smeets & Brenner, 1999), even when visual feedback is unavailable (Jakobson & Goodale, 1991). They also are thought to support the planning and control of grasping in units of ‘end-effector movements’ in the world (rather than joint angles etc.), simplifying the problem of controlling a complex effector such as the hand, with its many joints and muscles (Diedrichsen et al., 2010; Todorov, 2004; Todorov & Jordan, 2002). When viewed this way, the idea of tools ‘used as body parts’ implies that internal models are developed of the tools we use, which take into account the additional ‘remapping’ of the relationship between hand posture and tool-tip posture, to allow tool movements to be controlled in the anticipatory manner described above.

In this study, we look for evidence that such internal models of tool properties are present. Specifically, we probe the presence and fidelity of internal models of tools by examining the effects of removing visual feedback on grasping movements made with tools, so that movement control must rely on feedforward processes, and non-visual information about the tool's movements. We do not attempt here to distinguish between different possibilities for how tool properties are modelled (e.g. altering the representation of the hand in the body schema vs. adding additional components representing the tool), but instead test the general proof-of-principle idea that the brain can predict (and interpret) the relationship between motor commands and tool movements/posture.

Moreover, as argued in the General Introduction, internal models of tool properties (and of the hand) need ideally to be metrically accurate, so that predictions and control signals are accurate. This aspect of tool use is sometimes overlooked. More qualitative analyses are sometimes applied (inspection for presence of features such as identifiable peaks in grip aperture, for example), and/or direct quantitative comparisons are made between grasping the same object with the hand and with a tool (Gentilucci et al., 2004; Golenia et al., 2014; Itaguchi & Fukuzawa, 2014). Although interesting, it is difficult to infer the accuracy of internal models of tools from these comparisons, because the conditions differ in other ways likely to affect movement kinematics, including the mechanical constraints imposed by tools, and the attenuation of sensory signals (Gentilucci et al., 1994, 1997). We therefore probed the accuracy of tool models in a different way. We varied the geometry (ratio of tool-opening to hand-opening) of otherwise similar tools, to see if their different properties were appropriately taken into account.

Our experiment used three pliers-like tools with three different ratios between handle opening and tool-tips opening. One tool opened less than the hand, one tool opened the same as the hand, and a third opened more than the hand (similar to Golenia et al., 2014; Takahashi & Watt, 2014). We reasoned that, all else being equal, if the brain has accurate internal models of the three tools, it would plan similar movements *of the tool-tips* in all three cases, independent of the tool geometry. That is, different grasp profiles of the hand would be programmed, taking into account the variations in tool geometry, so as to produce the same movement of the end-effector. Thus, if our tools are 'used as body-parts', and so behaviour relies on accurate internal models for anticipatory control, we would expect to see several 'signatures' in the resulting movement kinematics.

First, normative patterns of scaling of movement indices with object properties should be present (e.g. grip apertures scaling with object size). An absence of such scaling would be indicative of movement control that differs from control ‘as a body part’. On its own, this is not unambiguous evidence that the visuomotor system has an internal model of the tool geometry, however, because movements based on the normal hand model could nevertheless result in similar scaling.

A second signature would therefore be *quantitatively appropriate* opening of the tool-tips, taking into account the geometry of the tools. Considering the two extreme possibilities, if the normal hand model were used for all three tools (i.e. there was no internal model of the tool) then hand-opening profiles would be the same across all three tools, resulting in tool openings that varied according to variations in tool ‘gain’. If, on the other hand, the visuomotor system has an accurate internal model of the remapping introduced by each tool, and planned similar movements of the tool-tips in each case, then peak grip apertures of the tool-tips would be similar, when grasping the same object, independent of the tool used (i.e. the hand opening would be changed to take into account the tool geometry).

Third, if the visuomotor system has access to a model of the tool mapping that is truly equivalent to that of the hand, both (i) the scaling of kinematics with object properties, and (ii) the ‘compensation’ for effects of tool geometry, should be evident even when visual feedback is removed (by occluding vision at movement onset). As mentioned earlier, this manipulation forces movement control to rely more on feedforward control, and on non-visual sensory signals about the movement as it progresses (e.g. proprioception about hand position and posture). In normal grasping, loss of visual feedback has consistent, but relatively minor, effects. Grip apertures are increased (presumably reflecting need for an increased margin-for-error; Jakobson & Goodale, 1991), and sometimes movement speeds are slower (Connolly & Goodale, 1999), but otherwise the scaling of grip aperture to object size is largely preserved, indicating that anticipatory control remains possible. Similarly minor effects in tool use would indicate that feedforward/non-visual control was possible here too, pointing to the presence of useful internal tool models. Alternatively, a collapse of scaling, or of compensation for different tool geometries, would indicate a relatively impoverished internal model of tool geometry compared to that of the hand. In a sense this can be thought of as a hard test for the existence of accurate internal models of tools, as it probes performance under impoverished conditions, when vision cannot be used to help support accurate behaviour.

In addition to these principal indicators, for which we have clear predictions, comparing hand grasping to performance with the 1:1 tool may also inform us about the effects of using one of our tools per se. Moreover, consideration of other movement parameters such as success rate may provide additional insights into the level of performance in different conditions.

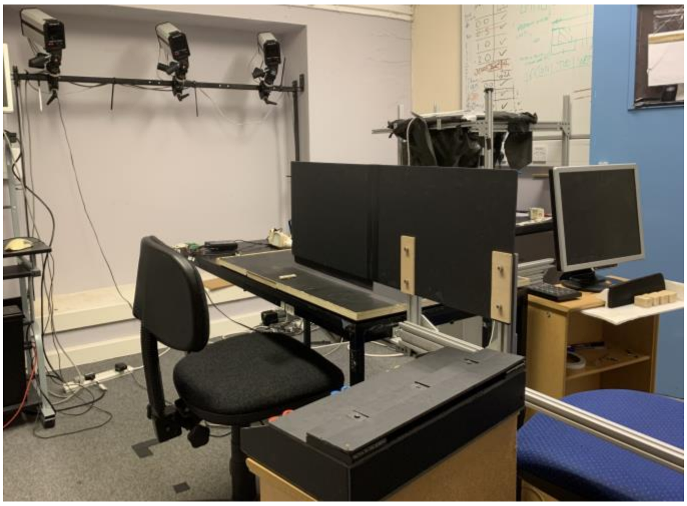
3.2 Methods

3.2.1 Participants

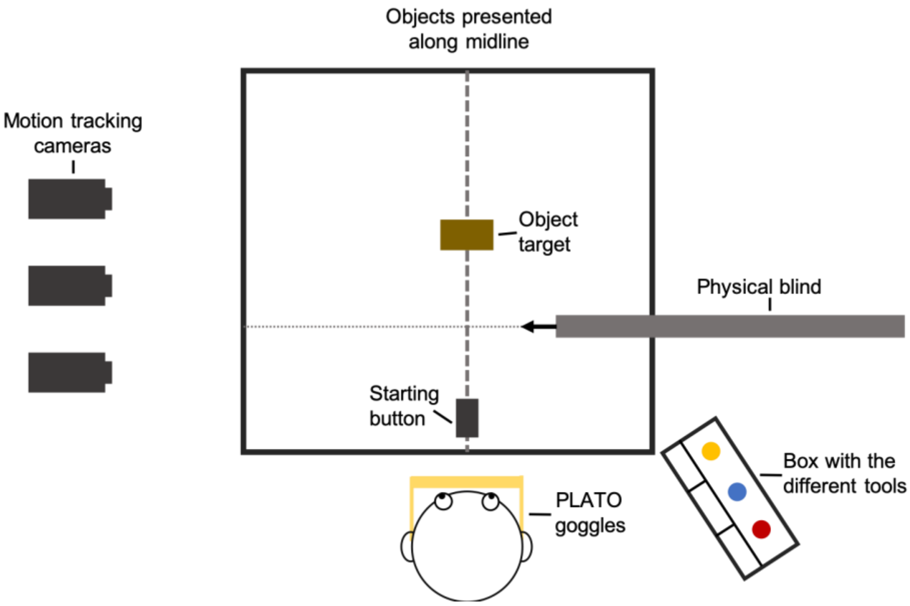
20 right-handed participants completed this experiment (17 female, 3 male; aged 22-31 years old). All participants had normal or corrected-to-normal vision, and no known impairments that would affect their ability to grasp. Participants were reimbursed £50 for completing the experiment. Participants gave informed consent prior to taking part, and all procedures were in accordance with the Declaration of Helsinki.

3.2.2 Apparatus and stimuli

Most of the setup method was as described in the Chapter 2. Additional details for this study are presented below. The experiment apparatus is shown in Fig.3.1 and the tools are shown in Fig. 3.2.



(a)



(b)

Figure 3.1. Representation of the experimental setup (a) by picture and (b) by schematic

General setup was as described in Chapter 2, excepting a box containing the different tools in different compartments placed on the right of the participant (see Fig. 3.1). At the beginning of each trial, coloured lights on the box indicated which tool should be used for the upcoming trial.

Figure 3.2. Pictures of the three pliers-like tools (same as Fig. 2.4). The yellow tool has a ratio of 0.7:1 between hand opening and tool-tips opening. The blue tool has a ratio of 1:1 and the red tool has a ratio of 1.4:1.

Availability of vision was controlled using a pair of ferro-electric shutter-glasses. Vision was required for participants to switch tools between trials. Thus to ensure that participants could pick up the next tool, while not seeing the next object being placed on the table, a physical 400 x 800 mm blind, sliding in a rail outside the table, was used.

The objects grasped were the five balsa wooden blocks described in Chapter 2 (25, 30, 35, 40 and 45 mm front-to-back), presented at three distances from the start button (150, 300 and 450 mm (see Fig. 3.1b).

3.2.3 Procedure

Grasping with the hand

At the beginning of each trial the PLATO goggles were clear, and participants could see to pinch their index finger and thumb together to press the start button. The PLATO goggles then switched to occlude vision while the experimenter positioned the object to be grasped. Following this, the goggles again opened, initiating the trial. The participant was instructed to view the object, but not to initiate their movement until an auditory ‘go’ signal, 1000 ms after the object became visible. Participants were instructed to grasp the object on hearing the go signal, using only their index finger and thumb to grasp the object front to back. Movements initiated before the auditory signal, or >1000 ms after it, were considered void. This response window was used to prevent participants substantially extending viewing times (and therefore movement planning times) in certain conditions. Void trials were repeated, such that we obtained complete data sets (same number of grasps to each object size, at each distance) that met the response criteria for all subjects in all conditions.

On trials with visual feedback (visually closed-loop conditions) the PLATO goggles remained open, allowing full vision of the hand/arm, object, and surroundings throughout the entire movement. On trials without visual feedback (visually open-loop conditions), the goggles closed when participants released the start button, preventing all visual feedback. Participants did not receive any feedback about their performance from the experimenter (in any conditions), but could feel whether or not they grasped the object.

Grasping with tools

In the tool conditions, the trial procedure was broadly similar to the hand-grasping conditions, with the following exceptions. The PLATO goggles were initially left open between trials, and the physical blind was used to block participants’ view of the object being placed. This allowed participants to see while they put down the current tool, and picked up the one required for the next trial (indicated by a light on the tool box). Once the tool was picked up, participants pressed the start button with the tool-tips, and the PLATO goggles were closed, and the blind retracted. The trials then proceeded as per the hand-grasping trials, with availability of visual feedback controlled in the same way, as required.

At the start of each trial, when holding the start button, participants were instructed to close their hand as much as possible with all tools. The tips of the 1:1 and the 0.7:1 tools could be closed completely (so that they touched), physical constraints of the 1.4:1 tool meant there was a minimum gap of 19 mm between the tool-tips. That gap could influence slightly the beginning of the movement, but should not influence the peak grip aperture (Hesse & Deubel, 2009).

Blocking of trials

A block of trials in the hand conditions consisted of two repetitions of each object size at each distance, making 30 trials (5 object sizes x 3 object distances x 2 repetitions). A block of trials in the tool conditions consisted of each object size presented at each distance, grasped with each of the three tools, making 45 trials (5 object sizes x 3 objects distances x 3 tools). The order the tools were used in was randomised, but with the constraints that the same tool was never used twice in a row, and within every three trials, all three tools were used once. This was done to minimise the likelihood of tool geometry being taken into account by 'classical adaptation' of felt hand size, over repeated trials using the same tool[1]. Moreover, random practice has been identified as being beneficial for motor learning (Contextual Interference Effect: Magill & Hall, 1990; Shea & Morgan, 1979) and would likely lead to a 'deeper' learning.

Structure of experiment conditions

Each participant completed four experiment sessions, across four consecutive days. Each took around 2 hours to complete. The order of conditions within each daily session is shown in Fig. 3.3. Note, that we find it helpful to use the terminology of 'baseline', 'training', and 'post-test', to describe in short-form how we measured participants' visually open-loop performance with tools before and after blocks of trials with vision available ('training'). However, measurement of the 'training' blocks

[1] Note that consistent with previous work from our lab, we have assumed here that developing internal models of tools is at least somewhat distinct from classical adaptation (e.g. to felt hand opening), and that such an effects could obscure findings relevant to our key question, or even result in a 'false positive' regarding the existence of internal models of tools. We assume this partly because the apparent modelling of tool spatial offsets observed by Takahashi et al. (2009) was found, in a control experiment, not to rely on adaptation of felt arm position in space. It remains to be determined, however, whether adaptation of felt size is in fact the mechanism by which different tool gains is taken into account. We explore this in Chapter 4.

is at least as important as the other blocks, indicating as it does performance with tools under relatively naturalistic conditions of having vision available.

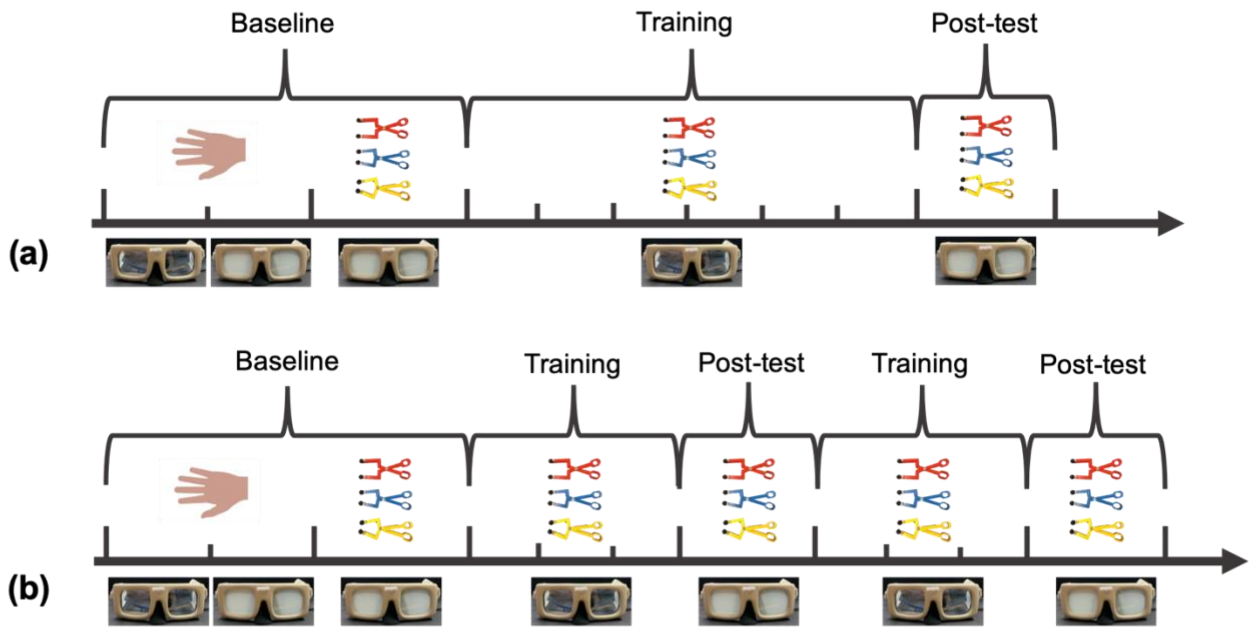


Figure 3.3. Overview of the experiment design. (a) The blocks comprising a session during the first day of the experiment. (b) The blocks comprising a session on the second, third and fourth days of the experiment. The images of the PLATO Goggles represent visually open- and closed-loop blocks (white lenses indicate open-loop).

The first day was slightly different from the following days to maintain the time duration of the experiment across days constant (the first day included explanation of the task). The first day started with a baseline, consisting of (i) one block of hand grasping with visual feedback, (ii) one block of hand grasping without visual feedback, and (iii) one block of tool grasping *without* visual feedback, always in that order. The baseline was followed by a 'training' phase composed of six blocks of tool grasping with visual feedback. Each session ended with a 'post-test', consisting of a block of tool grasping without visual feedback. The first day was therefore composed of 420 trials in total. During the following days, the training phase was divided into two training phases of three tool-grasping blocks with visual feedback by the insertion of a tool grasping block without visual feedback, as seen in Fig. 3.3b. This allowed us to monitor closely the development of the tool mappings. Those days were composed of 465 valid trials. In total, over the four days, each participant completed 1815 valid trials. There was no compelling evidence in the motor learning literature that a given number of trials would be 'enough' to observe learning of the tool models. Moreover, grasping with tools is a more complex manipulation than most motor learning studies (this point will be discussed in section 6.3). To ensure the highest probability of observing the learning of the tool mappings, we decided to expose participants to as many trials as possible in each condition during each 2h session to maximise exposure to each tool geometry. By doing so, we exposed participants to 525 trials with each tool (more than some studies in dual adaptation: Woolley et al., 2007: 275 trials per condition; Krakauer et al., 1999: 264 trials per condition; this point will be discussed in the Discussion, section 4.4)

3.2.4 Data analysis and predictions

We aim to address specific a priori questions. Therefore, rather than carrying out global analyses, we constrained our analyses to testing a small number of well-specified predictions, for specific dependent measures. In this Chapter, we are investigating whether tools are used as 'body parts'. As discussed in the Introduction (section 3.1), based on the literature, we defined three key signatures that are to be expected if tools are indeed used as 'body parts'. Those signatures of movement control are (i) the presence of anticipatory control of grasp (scaling of movement velocity to object distance and scaling of peak grip aperture to object size), (ii) accounting for the tools' geometrical properties in grasp opening, and (iii) normal responses to removal of visual feedback. We will analyse those signatures separately, thus separating the analysis of the conditions with and without visual feedback. Principal analysis will be performed on the data collected during the fourth day, when we expect acquisition of internal models of tools to be most complete. As discussed in the Introduction, the hand will only be directly compared to the 1:1 tool.

In each visual condition, we will investigate the presence of velocity and grip scaling, and of accounting for the tool geometries. To investigate the presence of scaling, we will test whether the slopes of the scaling functions (movement velocity with object distance; grip aperture with object size) are significantly greater than zero (i.e. a one-tailed prediction). To test for accounting for tool geometry, we will analyse grip aperture data for both tools that opened different amounts than the hand (i.e. the 0.7:1 and 1.4:1 tools). We will compare the tool data to expected data under two boundary conditions: (i) tool geometry is completely accounted for, and (ii) tool geometry is not accounted for at all. In the first case tool opening should be the same across different tool geometries, and so hand openings should differ significantly, in predictable directions (smaller hand opening with 1.4:1 tool; larger hand opening with 0.7:1 tool). We will therefore examine whether hand opening differed across tool conditions, using planned pair-wise comparisons (one-tailed t-tests, Bonferroni corrected for multiple comparisons). Second, if tool geometry is not accounted for at all, hand movements will be the same across tools, but tool opening will be significantly different. Again, there is a strong predicted direction of these differences (the same hand movement produces larger tool opening for the 1.4:1 tool, and smaller opening of the 0.7:1 tool). So again we will examine this with one-tailed t-tests (Bonferroni corrected for multiple comparisons). This approach is intended to avoid the problem of null-hypothesis testing (testing predictions of *no difference* between conditions). By making the analysis highly sensitive to deviations from either of these boundary conditions, it reduces the risk of falsely concluding that the tool properties are perfectly (or not at all) taken into account.

Removing visual feedback normally causes larger peak grip apertures (Jakobson & Goodale, 1991), and occasionally decreased movement velocity (Connolly & Goodale, 1999). Thus, we will probe the significance of those effects (i.e. a one-tailed prediction).

We will also explore the functional effect of using our pliers-like tools by examining success rates and overall grasping profiles. We do not have clear predictions concerning these parameters, however, and so these analyses will be exploratory in nature. Lastly, we will investigate potential learning of the tool properties across the experiment by comparing kinematic indices (previously analysed for the fourth day) across the first and fourth day of the experiment using planned pair-wise comparison (one-tailed t-tests). Here the strong prediction is that learning would be evident in higher compensation for each tool geometry (characterised by smaller hand opening with 1.4:1 tool; larger hand opening with 0.7:1 tool; and no change with the 1:1 tool). Learning could manifest in faster movement and in higher success rate with all tools. We do not have clear predictions concerning how learning could be perceived in overall grasping profiles.

3.3 Results

As noted in the introduction to this chapter, our data analysis focuses on answering questions related to anticipatory control, and taking tool geometry into account. We therefore present the kinematic indices that relate most closely to these questions first, before reporting more exploratory data analysis later. We focus our analysis on performance during the fourth day, when learning of the tool mappings would be expected to be at its highest, when exploring questions related to the ‘integrity’ of tool models.

3.3.1 Overview of movement speed and grip aperture data

We first present summary data of overall movement speed and grip apertures. Analyses of our specific questions are based on subsets of these data, but these figures provide a useful overview of the experiment. We will also refer back to those overall figures when necessary.

We first examined movement velocity. Fig. 3.4 plots average peak movement velocity, collapsed across all object sizes and distances, for each condition on each day. It can be seen that peak velocity increased slightly over the course of the experiment. It can be seen that the effector used has an effect, as movement velocity was higher when using the hand (independent of visual feedback availability) than when using tools. Between the tools, movement velocity appears similar in each condition. Peak velocity was also overall faster when visual feedback was available compared to when it was not.

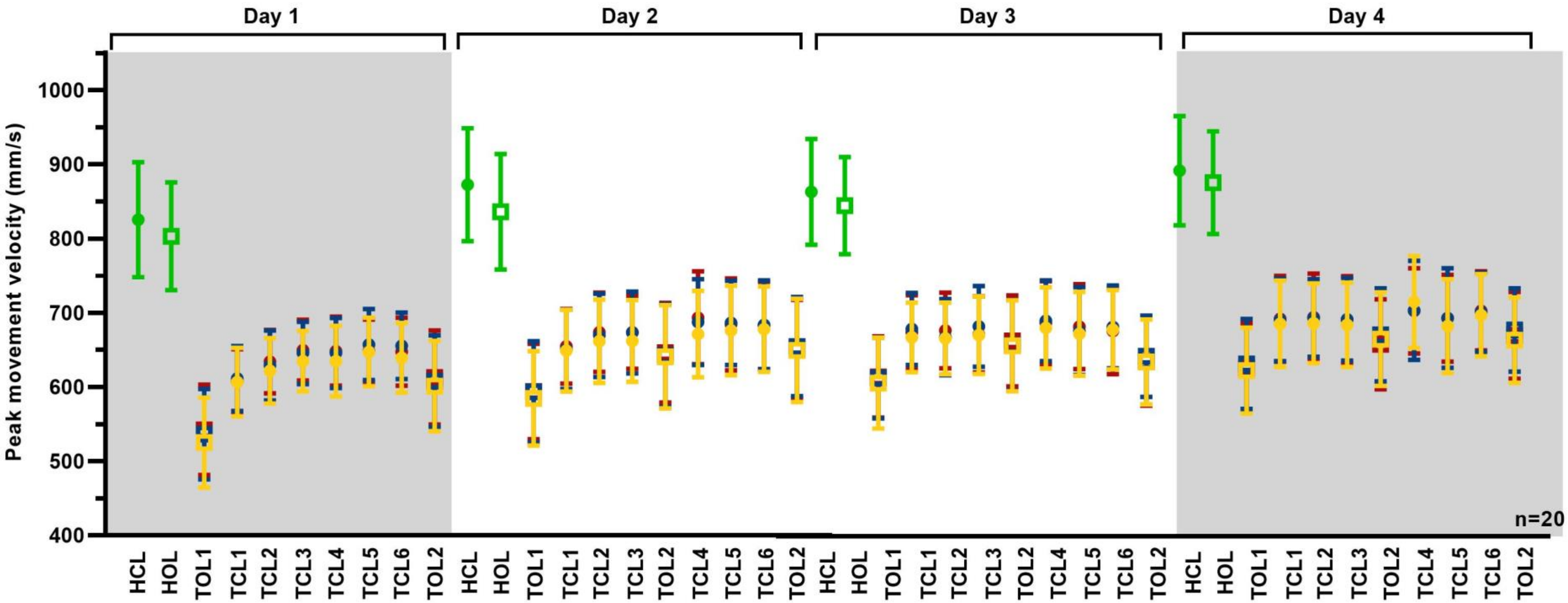


Figure 3.4. Overall peak velocity results. Mean peak movement velocity for each of the four day of the experiment. The x-axis represents each block during the time course of the experiment. The closed circles represent closed-loop conditions (‘CL’ on the x-axis labels). The open squares represent the open loop conditions (‘OL’ on the x-axis labels). Tools block are denoted by ‘T’ prefix, while hand blocks are denoted by ‘H’. The numbers represent the block numbers. The red, blue, and yellow data points denote the 1.4:1, 1:1, and 0.7:1 tools respectively. The error bars denote +/- 95% confidence interval.

Fig. 3.5 plots the overall peak end-effector aperture data for the entire experiment, again collapsed across all object sizes and distances. To allow for comparison of tool data across different days (and as the hand data varied slightly across days), the data in this figure were normalised by calculating peak end-effector apertures as a proportion of each participant's peak hand aperture in the closed-loop hand grasping condition for that day. Thus, the hand grasping data lie on a horizontal line at 1.0 (the solid green line). Normalising to that performance allows for examination of how much tool geometry was accounted for on different days in comparable units. It also normalises for different overall grip apertures across participants (e.g. due to different hand sizes). The solid red and yellow lines show the expected performance if tool geometry was not accounted for at all (i.e. same grasp profile with the hand across different tools), calculated by multiplying the closed-loop hand grasping data by the different tool geometries. The dashed red and yellow lines show the same calculation for the open-loop data, based on the hand-grasping open-loop data (dashed green line). We will examine performance with each tool separately, below.

For the 1:1 tool, it can be seen that, in closed-loop condition, participants started with the tool opened wider than the hand, on day 1, before performing similarly to hand grasping for the rest of the experiment. In open-loop condition, the 1:1 tool was not opened as wide as their hand on each day. Complete compensation for the tool geometry is represented by that 1:1 tool opening (i.e. same grasp profile with the different tools).

With the 0.7:1 tool, it can be seen that tool geometry was never really accounted for when visual feedback was available (overlapping with no account of tool geometry on day 4). When visual feedback was removed, it appears the tool geometry was not accounted for as tool-tips aperture was under the zero accounting for the tool geometry.

For the 1.4:1 tool, it can be seen that tool geometry was not accounted for in day 1 when visual feedback was available (overlapping with no account of tool geometry). Across day 2, 3 and 4, it can be seen that the tool-tips aperture with the 1.4:1 tool decreased, getting closer to complete compensation (1:1 tool grasping) without ever reaching it (stopping before 50% of complete compensation). It suggests tool geometry was gradually taken into account during the experiment. When visual feedback was removed, tool-tips aperture with the 1.4:1 tools stayed ‘constant’ across the experiment, showing no real account of the tool geometry (just under the no account for tool geometry).

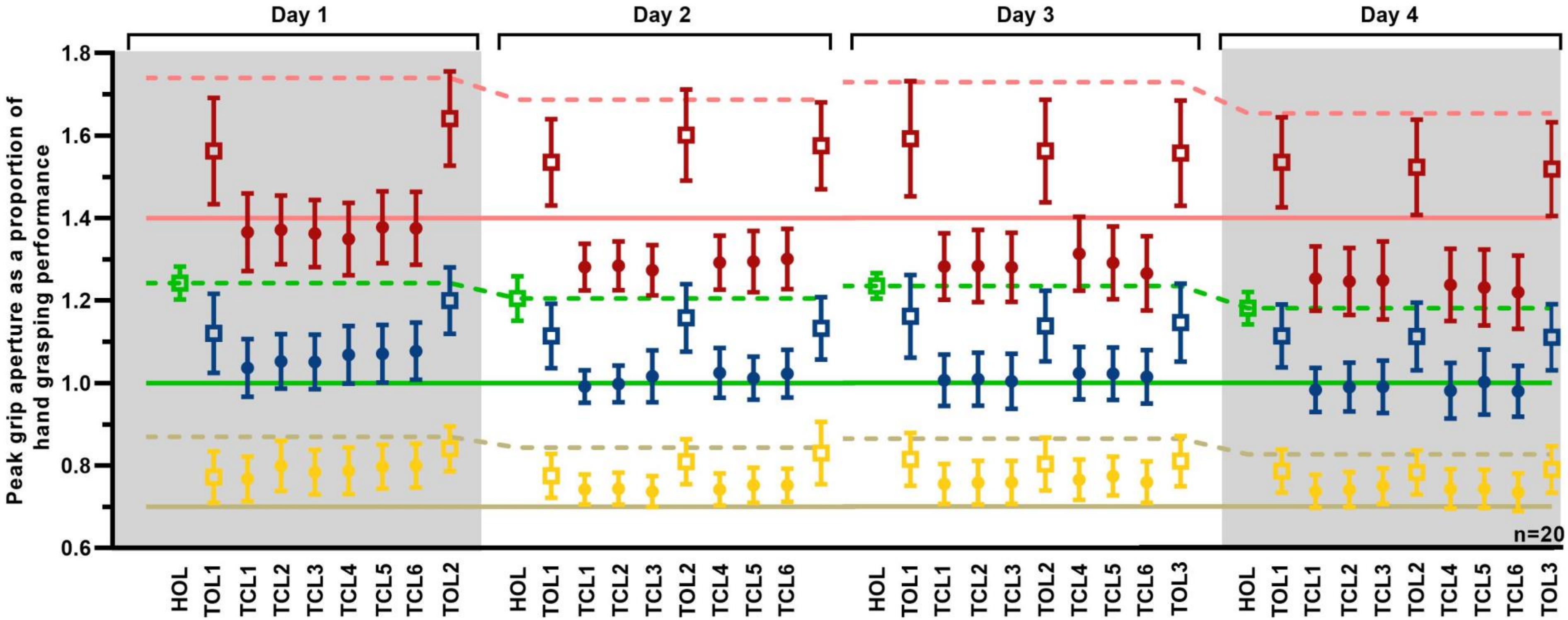


Figure 3.5. Overall peak grip aperture results. Mean peak end-effector aperture in each condition. Each days' data are plotted as a proportion of the peak grip aperture in the closed-loop, hand-grasping condition for that day (collected during the baseline period). The x-axis represents each block during the time course of the experiment. The closed circles represent closed-loop conditions ('CL' on the x-axis labels). The open squares represent the open loop conditions ('OL' on the x-axis labels). Tools block are denoted by 'T' prefix, while hand blocks are denoted by 'H'. The numbers represent the block numbers. The green line represents the mean peak aperture when grasping with the hand in closed-loop conditions (always 1.0 because this was the normalisation baseline). The red, blue, and yellow data points denote the 1.4:1, 1:1, and 0.7:1 tools respectively. The solid lines (darker colour for the 0.7:1 and lighter colour for the 1.4:1 tool) in each case represent the expected performance in closed loop conditions if participants produced the same hand opening in each condition (computed by multiplying the closed-loop hand data by the tool geometry; see main text). The dashed lines represent the same data for open-loop conditions (open-loop hand data multiplied by tool geometry). The error bars denote +/- 95% confidence interval.

3.3.2 Does tool use show anticipatory scaling with object properties?

One expected 'signature' of using tools as a body part is the presence of anticipatory features of hand grasping, including the scaling of peak movement velocity with object distance, and the scaling of peak end-effector aperture with object size (Jeannerod, 1981, 1984; Marteniuk et al., 1990; Smeets & Brenner, 1999; Wing et al., 1986). As noted above, the data from day 4 would be expected to offer the clearest picture, because any internal model of the tools should be most established by the end of the experiment. We therefore initially examined the data from day 4 to look for evidence of such scaling. For both velocity and grip aperture we combined data across all blocks of the visually closed-loop conditions on day 4.

Peak velocity scaling in closed-loop tool use

We first examined whether peak velocity in the closed-loop conditions of day 4 scaled with object distance. Fig. 3.6 shows the peak velocity with each effector at each object distance (collapsed across object size). First, it can be seen that the hand grasping data show the normal scaling pattern of systematically faster movements to farther objects. Second, the tool movements are overall slower, but also clearly show scaling of peak movement velocity with object distance.

To examine the scaling effects statistically we first computed the slopes of the object-distance scaling functions for each participant in each effector condition, yielding a sample (n=20) of slopes in each case. We then ran one sample t-tests to examine if those slopes were on average different from zero for each effector. In all cases, the one-tailed t-tests revealed that the slopes of the object-distance scaling were significantly greater from zero (hand: $t(19) = 25.48$, $p < .001$, $d = 5.76$; 0.7:1 tool: $t(19) = 18.62$, $p < .001$, $d = 4.16$; 1:1 tool : $t(19) = 19.85$, $p < .001$, $d = 4.4$; 1.4:1 tool: $t(19) = 19.09$, $p < .001$, $d = 4.04$).

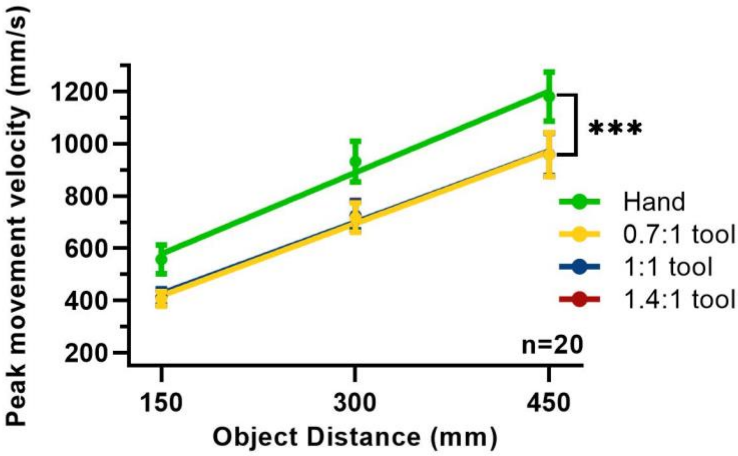


Figure 3.6. Peak velocity scaling with object distance in closed-loop conditions (day 4). (a) Mean peak velocity of grasping movements with each effector as a function of object distance (collapsed across object size). Solid lines show the best fitting linear regressions to the data in each case. (b) Same data collapsed across object distance. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

Fig. 3.6 suggests that movement velocity was higher when grasping with the hand than with the tools. To investigate the differences in peak velocity between effectors, we collapsed the peak movement velocity across distances and sizes. We then ran a one-way repeated measures ANOVA on the peak velocity with effector as the factor. Mauchly's test indicated that the assumptions of sphericity had been violated ($\chi^2(5) = 84.15$, $p < .001$), so the Greenhouse-Geisser correction was applied. The ANOVA revealed a main effect of effector (F(1.043,19.836) = 87.56, $p < .001$, $\eta_p^2 = .82$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that movement velocity was significantly higher when grasping with the hand than with the three tools, and there was no difference between the tools. Thus, movement velocity remained unaffected by differences in tool geometry. Thus, we can interpret differences in peak grip aperture as the effect of using a specific and not some sort of trade-off between movement velocity and grip aperture.

Peak grip aperture scaling in closed-loop tool use

Another feature of anticipatory behaviour in normal grasping is that peak grip aperture scales with object size, with larger openings for larger object sizes. Fig. 3.7 shows the peak end-effector aperture for the different effectors (hand and tools) as a function of object size. The figure suggests that participants clearly scaled their end-effector aperture with object size in all cases. To examine the effect, as with velocity/distance scaling, we analysed whether end-effector aperture scaling was significantly different to zero in each condition by computing the slopes of the grip aperture/object size scaling functions for each participant in each condition. We used one-sample t-tests in each case to examine whether the mean slope of the scaling functions was greater than zero. For all effectors, the one-tailed t-tests revealed that the slopes of the object-size scaling functions were significantly greater than zero (hand = .66, $t(19) = 15.91$, $p < .001$, $d = 3.57$; 0.7:1 tool = .60, $t(19) = 16.31$, $p < .001$, $d = 3.65$; 1:1 tool = .80, $t(19) = 17.65$, $p < .001$, $d = 3.95$; 1.4:1 tool = 1.07, $t(19) = 16.99$, $p < .001$, $d = 3.8$).

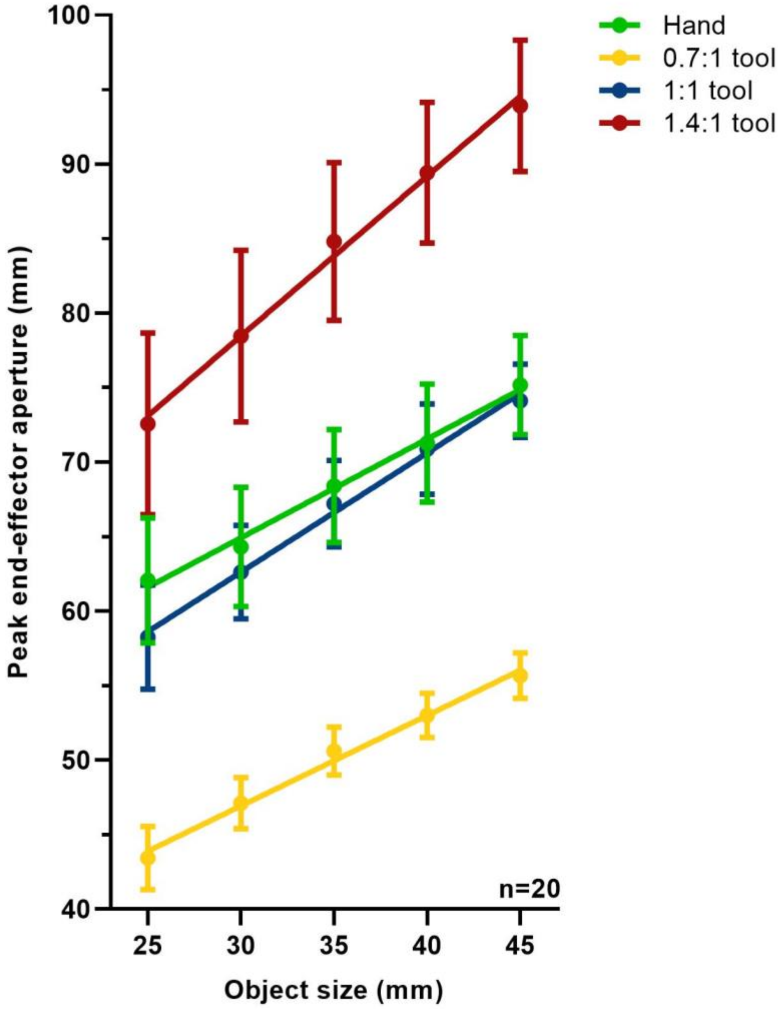


Figure 3.7. Peak end-effector aperture scaling with object size in closed-loop condition (day 4). Mean peak aperture as a function of object size (collapsed across object distance) for the end-effector aperture. Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence intervals.

When using our different tools, the normal patterns of anticipatory scaling of movement velocity with object distance, and grip aperture with object size, were present with all three tools (Jeannerod, 1981, 1984; Marteniuk et al., 1990; Smeets & Brenner, 1999; Wing et al., 1986). However, this does not inform about the development of a tool model, as the same pattern would still be evident if participants used their normal hand model, without accounting for changes in tool geometry. We turn to this next.

3.3.3 Is tool geometry taken into account in closed-loop conditions?

We looked for evidence that variations in tool geometry were taken into account in a quantitatively appropriate manner. As stated in the introduction to this Chapter, if the visuomotor system controlled tools using the same processes as the hand, and had accurate and reliable internal models of the different tools, it is reasonable to expect that the same movements of the tool-tips would be programmed in all cases, independent of the tool geometry. If this were the case, the data in Fig. 3.7 would all lie on the same line. Clearly this is not the case, indicating that this 'ideal' case was not met.

Note, however, that this prediction—identical movements in tool-tip units, independent of tool geometry—provides an upper bound on taking tool geometry into account. We can also specify a lower bound, which is the expected pattern of results if tool geometry is not taken into account at all. That is, what would performance look like if the same pattern of hand movements was programmed (the same grasp profile with the hand) regardless of the tool used? These lower-bound predictions can be calculated simply by multiplying the grip aperture data from the 1:1 tool condition by the tool gain. Fig. 3.8a replots the data from Fig. 3.7, superimposed on a plot of these lower-bound predictions (shaded areas, in corresponding colours). It can be seen that the data for the 1.4:1 tool, in particular, and to a lesser degree for the 0.7:1 tool, lie outside the predictions for not taking tool geometry into account at all (the shaded zones and error bars denote 95% confidence intervals). That is, the data lie between the extremes of 'completely' taking tool geometry into account, and not taking it into account at all, suggesting that hand movements are adjusted to some extent to take into account the properties of the tools; smaller hand openings are programmed when the tool opens wider than the hand, and larger hand openings are programmed when the tool opens less than the hand.

To visualise this another way, Fig. 3.8b plots the same data transformed into units of hand opening, rather than tool-tip opening. Plotted in this way the converse pattern of upper- and lower-bound predictions for taking tool geometry into account hold. Now, 'ideally' (completely) taking into account tool geometry would manifest as very different hand openings shown by the shaded zones in Fig. 3.8b (calculated by dividing the 1:1 tool data by the tool gain). Conversely, taking no account of tool geometry would here result in identical data with each tool (same hand opening regardless of tool). Fig. 3.8b reveals that different hand openings were programmed for the three different tools (in a direction consistent with taking tool geometry at least partially into account). We can also see that hand grasping and grasping with the 1:1 tool resulted in similar grip apertures. We examine this specifically in section 3.3.7.

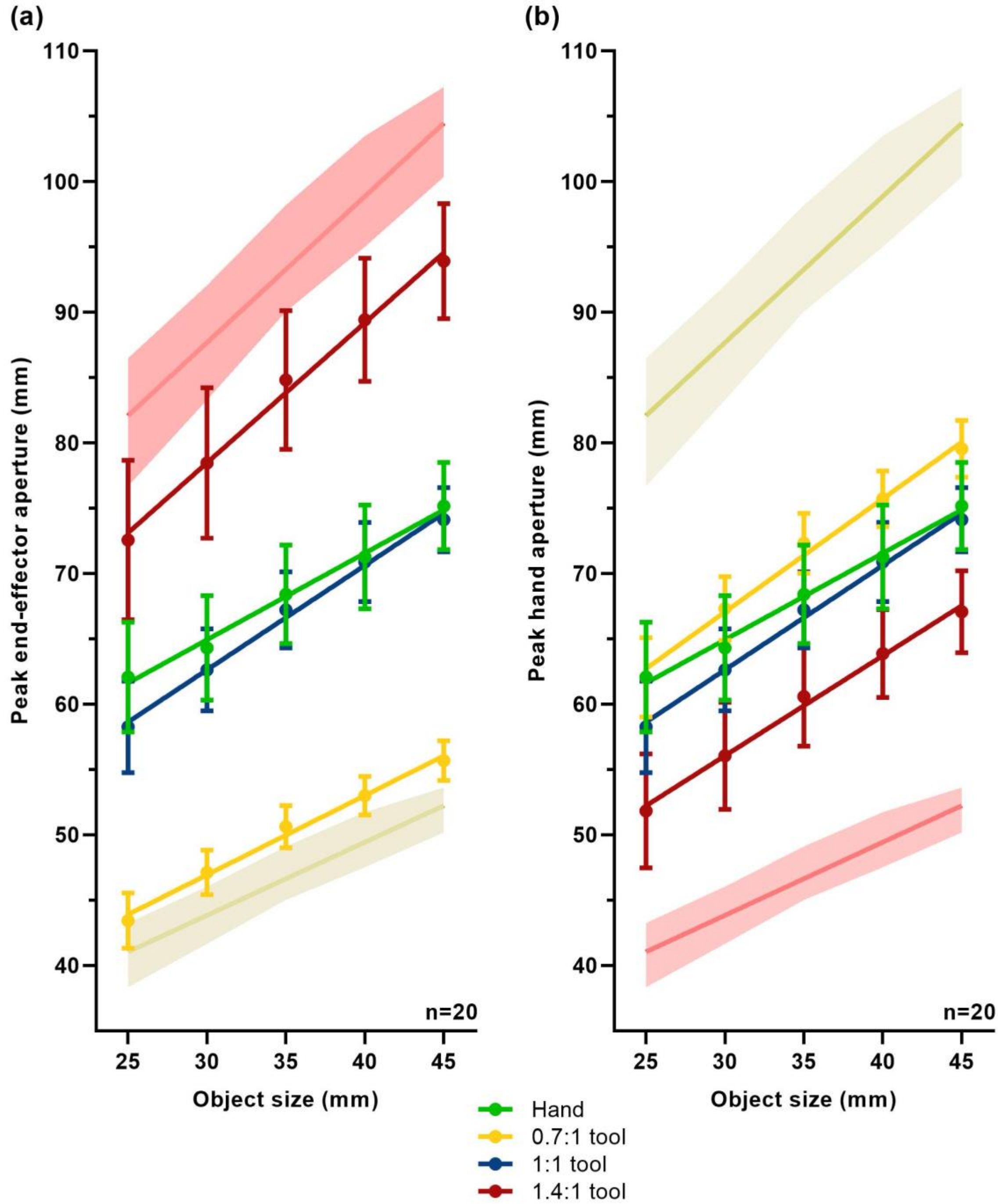


Figure 3.8. Peak end-effector aperture results in closed-loop condition (day 4). (a) Mean peak end-effector aperture replotted from Fig. 3.7. Shaded areas represent the expected peak end-effector aperture if participants did not take into account the tool geometry at all. (b) The data from panel (a) plotted in units of hand aperture. Here, shaded areas represent the expected peak hand aperture if participants completely took into account the tool geometry. Solid lines show the best fitting linear regressions to the data in each case. In all cases, the error bars denote +/- 95% confidence intervals.

To examine the compensation for tool geometry statistically we first collapsed across object size to produce single overall mean grip apertures for each tool. These are shown in Fig. 3.9, in tool-tip (end-effector) units (left panel), and hand-opening units (right panel). The basic pattern of effects of course resembles those in Fig. 3.8, from which they were derived. Using the logic outlined above, we then tested whether the data differed from (i) completely taking into account tool geometry, by examining whether the tool-tip apertures were different across different tools (Fig. 3.9a), and (ii) zero taking account of tool geometry, by examining whether hand opening differed across tool conditions (Fig. 3.9b). First, we compared tool-tip aperture of both the 0.7:1 tool and the 1.4:1 tool to the 1:1 tool, using separate one-tailed paired-sample t-tests (Bonferroni corrected for multiple comparisons). The 0.7:1 tool was opened significantly less than the 1:1 tool ($t(19) = -21.52$, $p < .001$, $d = -4.81$) and the 1.4:1 tool was opened significantly wider than the 1:1 tool ($t(19) = 13.72$, $p < .001$, $d = 3.07$). Similar analyses of the hand opening were again statistically significant. When using the 0.7:1 tool the hand was opened significantly wider than when using the 1:1 tool ($t(19) = 7.66$, $p < .001$, $d = 1.71$). When using the 1.4:1 tool, the hand was opened significantly less wide than with the 1:1 tool ($t(19) = -10.39$, $p < .001$, $d = -2.32$). Thus, our results indicate that tool geometry was taken account to some degree, but not completely.

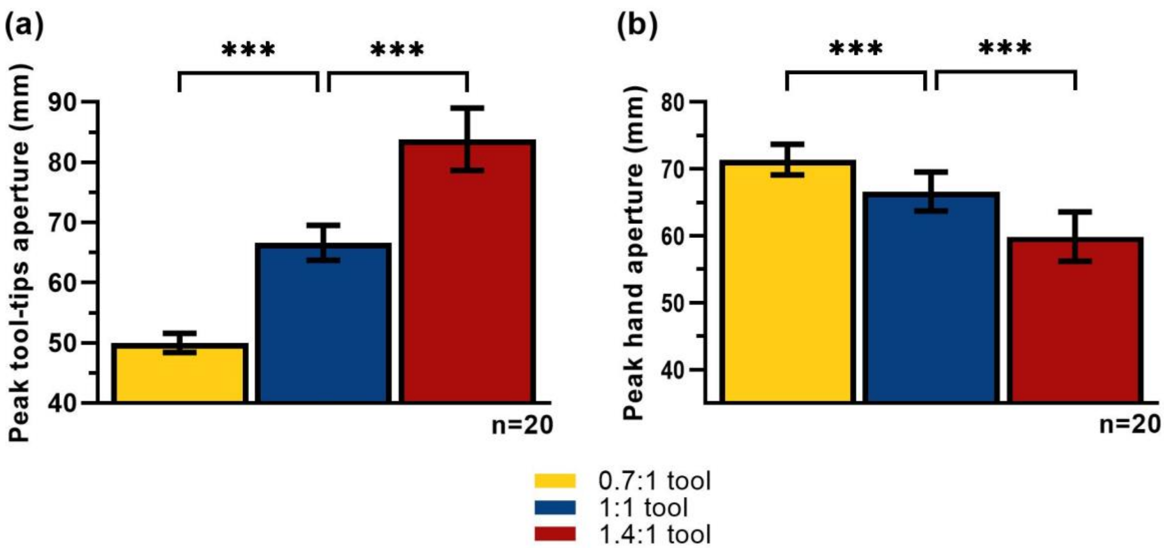


Figure 3.9. Peak end-effector aperture in closed-loop condition (day 4). (a) Mean peak tool-tips aperture (collapsed across object distance and object size) in closed loop condition. (b) Same data plotted as mean peak hand aperture. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

Degree of 'compensation' for tool geometry: closed-loop

Given that tool geometry was taken into account incompletely (rather than ideally, or not at all) it is useful to quantify the extent to which it was taken into account, and especially to compare across the 1.4:1 and 0.7:1 tools. We refer to this as the degree of 'compensation' for tool geometry. Based on the logic above, and for each participant, we computed the peak grip apertures that would have resulted from zero compensation, and from ideal compensation, with each tool, based on their 1:1 tool data. We then calculated their actual degree of compensation in each case as a proportion of the ideal prediction. Thus, no compensation at all (same hand movements regardless of tool geometry) is scored 0.0, and ideal compensation (quantitatively 'correct' adjustment to hand aperture to match the tool opening across tools) is scored 1.0. Fig. 3.10 shows the average compensation values for the 1.4:1 and 0.7:1 tools, with individual participant's data superimposed (it does not make sense to compute a compensation value or the 1:1 tool). Several points are noteworthy in this figure. First, while participants did compensate for tool geometry with both tools, the effects were overall not large—less than half the ideal value even in the case of the 1.4:1 tool. Second, the degree of compensation for the 0.7:1 tool was smaller than for the 1.4:1 tool (and only quite small). A paired sample t-test showed that this difference was statistically significant ($t(19) = -7.92$, $p < .001$, $d = -1.77$). Finally, there was individual variability in the degree of compensation. We explore this last point further in the Discussion.

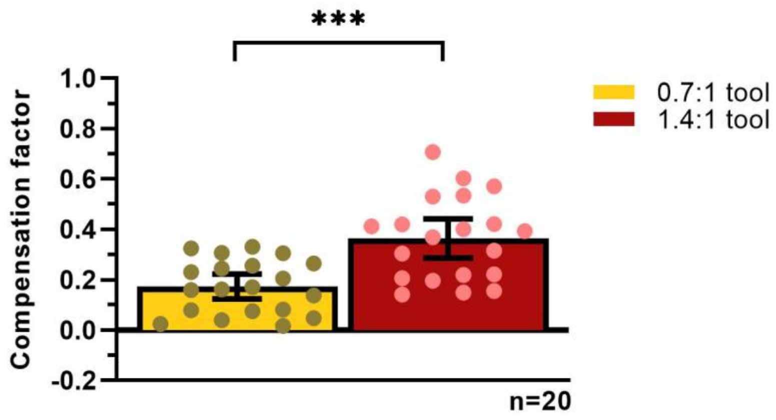


Figure 3.10. Compensation for tool geometry in closed-loop condition (day 4). Compensation factors for the 1.4:1 and 0.7:1 tools in visually closed-loop condition. See main text for how these values were calculated. The dots represent individual participant's compensation factors. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

Thus, overall, compensation for tool geometry was evident with both tools, but a higher degree of compensation was found with the 1.4:1 tool than with the 0.7:1 tool, and compensation was less than complete with both tools.

3.3.4 Evidence for internal models of tools in the absence of visual feedback?

As a 'hard test' of whether internal models of tools are equivalent to those relied on for normal grasping, we also examined performance when visual feedback was removed at movement onset (visually open-loop conditions), forcing participants to rely on feedforward control and non-visual feedback signals. Following the approach employed for the closed-loop data, we first explore whether the visually open-loop performance per se shows anticipatory scaling of grasp parameters, and whether tool geometry was taken into account quantitatively—both of which would be expected if the visuomotor system has an internal model of the tools similar in nature to that for the hand. We then examine the effects of removing visual feedback during tool use (i.e. comparing closed-loop vs open-loop performance), and compare these to the effects of the same manipulation on normal grasping. If participants did use tool as body parts, we would expect that removing visual feedback when grasping tools with would have similar effects as removing visual feedback when grasping with the hand. For this analysis, we combined data from all three blocks of tool grasping without visual feedback on day 4 of the experiment.

Peak velocity scaling in open-loop tool use

Fig. 3.11a shows peak movement velocity as a function of object distance. The pattern of results is qualitatively similar to the closed-loop conditions (Fig. 3.6). Tool movements were again overall slower than hand movements, and peak movement velocity scaled with object distance in all conditions. We again assessed whether the slopes of the scaling functions were significantly greater than zero by running one-tailed one-sample t-tests on slopes computed for each participant (see above). In all cases, peak velocity scaling was greater than zero (hand: $t(19) = 19.14$, $p < .001$, $d = 4.28$; 0.7:1 tool: $t(19) = 19.15$, $p < .001$, $d = 4.28$; 1:1 tool: $t(19) = 18.43$, $p < .001$, $d = 4.13$; 1.4:1 tool : $t(19) = 16.81$, $p < .001$, $d = 3.76$).

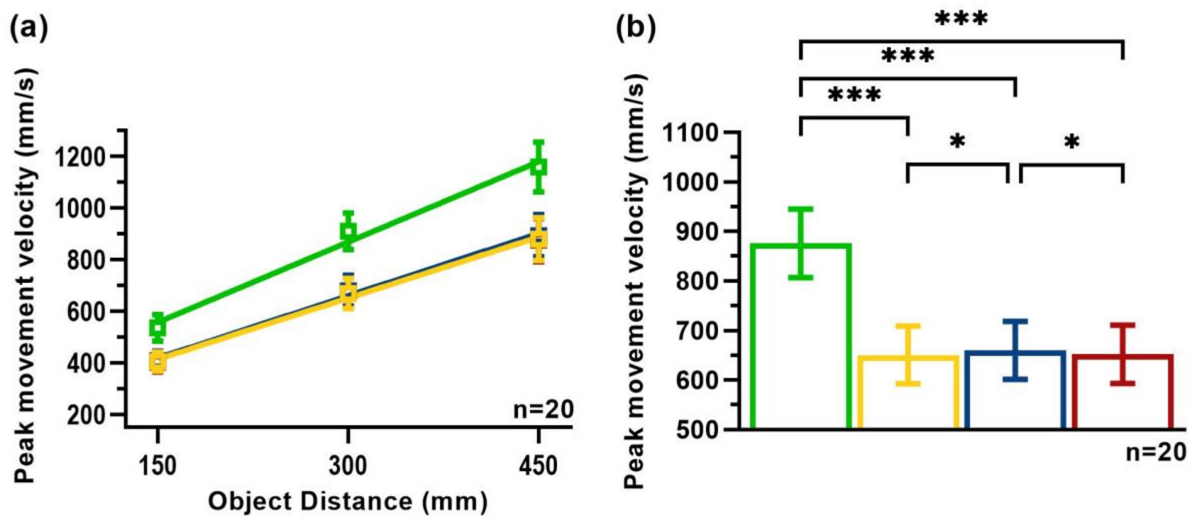


Figure 3.11. Peak velocity scaling with object distance in open-loop condition (day 4). (a) Mean peak velocity of grasping movements with each effector as a function of object distance (collapsed across object size). Solid lines show the best fitting linear regressions to the data in each case. (b) Same data collapsed across object distance. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

As for the closed-loop conditions, we examined how the effector used affected peak velocity by collapsing the data across object distance (Fig. 3.11b). It can be seen that participants again moved faster when grasping with the hand than with the different tools. As for the closed-loop data we ran a one-way repeated measures ANOVA on the peak velocity with effector as the factor. Mauchly's test indicated that the assumptions of sphericity had been violated ($\chi^2(5)$ = 94.55, *p* < .001), so the Greenhouse-Geisser correction was applied. The ANOVA revealed a main effect of effector (F(1.062,20.173) = 101.04, *p* < .001, η_p^2 = .084). As for the closed-loop conditions, post hoc (Bonferroni corrected) pairwise comparisons indicated that movements were significantly faster when grasping with the hand than with the three tools. Surprisingly, movement velocity was significantly higher (around 9 mm/s) when using the 1:1 tool than when using the 0.7:1 tool (*p* = .043) and the 1.4:1 tool (*p* = .04). Thus, contrary to closed-loop conditions, movement velocity was slightly affected by tool geometry. The effect is difficult to interpret however, as without visual feedback to monitor the movement, difference in movement velocity would not bring any distinct advantage.

Peak grip scaling in open-loop tool use

Fig. 3.12 shows peak grip apertures as a function of object size for the open-loop conditions. It can be seen that grip aperture scaling with object size is again present in all conditions. Analysing the data as before (one-tailed one-sample t-tests on each participant's slopes) we found scaling was significantly greater than zero in all conditions (hand = .49, t(19) = 13.54, *p* < .001, *d* = 3.03; 0.7:1 tool = .32, t(19) = 12.09, *p* < .001, *d* = 2.7; 1:1 tool = .44, t(19) = 11.21, *p* < .001, *d* = 2.51; 1.4:1 tool = .65, t(19) = 9.43, *p* < .001, *d* = 2.11).

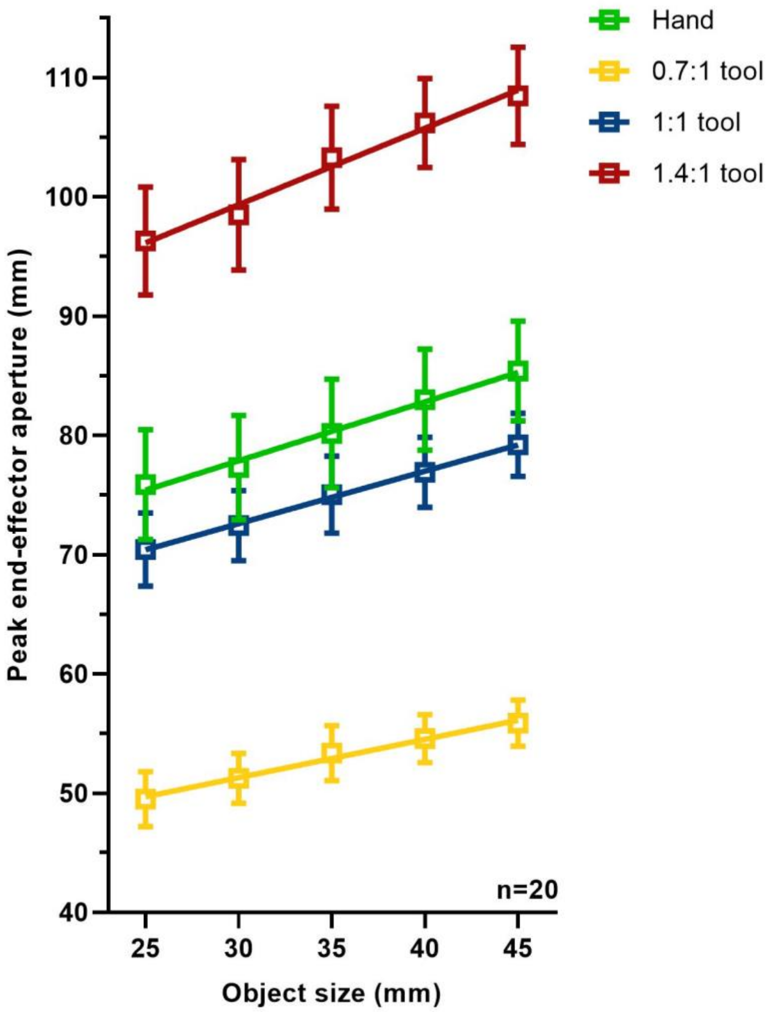


Figure 3.12. Peak end-effector aperture scaling with object size in open-loop condition (day 4). Mean peak aperture as a function of object size (collapsed across object distance) for the end-effector aperture. Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence intervals.

Is tool geometry taken into account in open-loop conditions?

As for the closed-loop conditions, we examined end-effector apertures to explore whether the different tool geometries were taken into account in controlling open-loop movements. Fig. 3.13 shows the peak grip aperture data in the same form as Fig. 3.12. The left panel shows the data in tool-tip, or end-effector, units and the right panel shows the data in units of hand opening. The shaded zones show the predictions in the same form as previously (here computed with respect to the open-loop 1:1 tool data). Thus, the zones on the end-effector plot (left panel) depict the prediction for zero tool compensation, and the zones on the hand-units plot (right panel) depict predictions for ideal compensation. It can be seen that overall the degree to which tool geometry is taken into account appears less pronounced than in closed-loop conditions. The peak end-effector opening (left panel) was very different across different tools, and was close to the prediction for zero compensation. Accordingly, it can be seen that hand opening (right panel) varied very little when using the different tools.

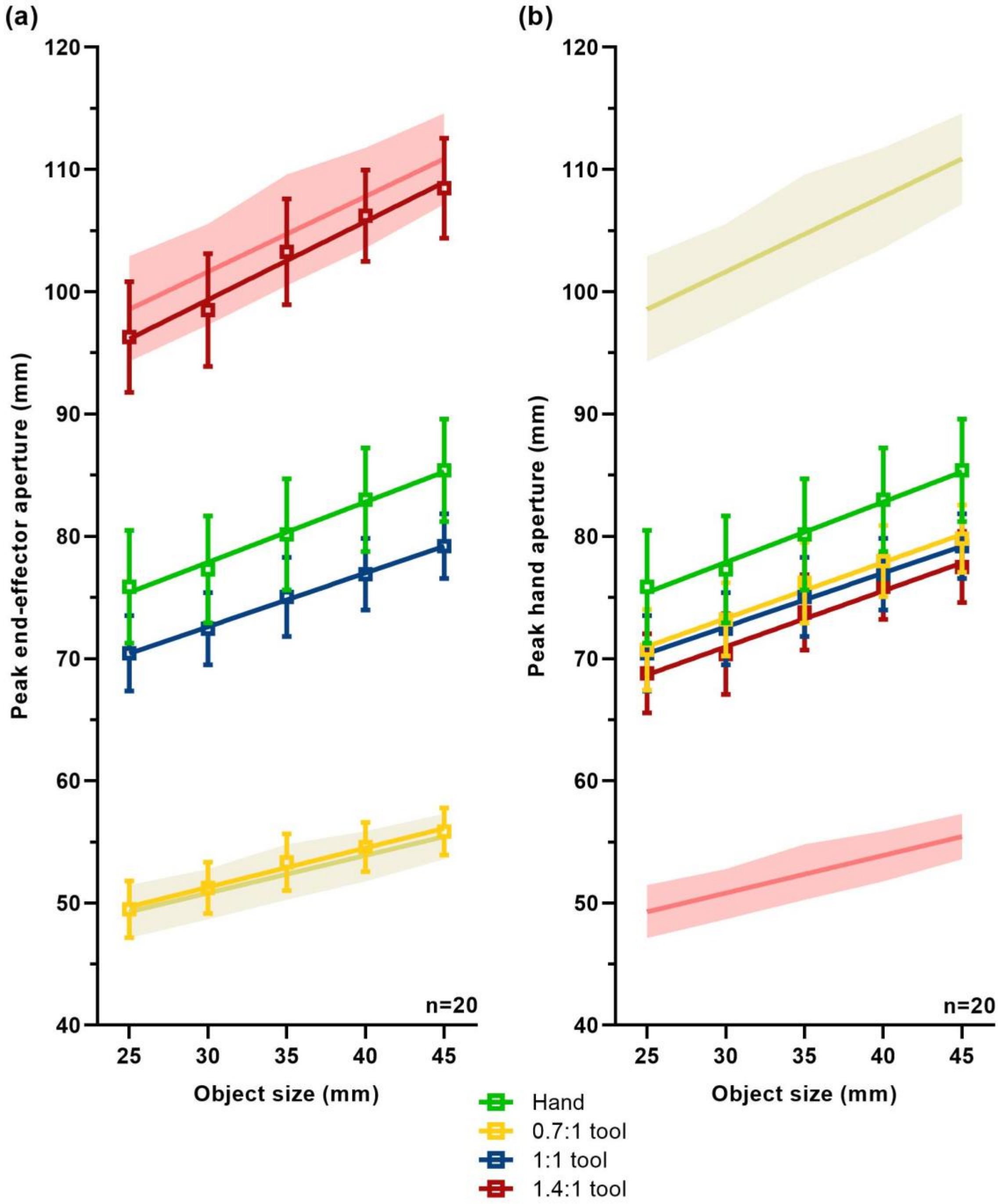


Figure 3.13. Peak grip aperture results in open-loop condition (day 4). (a) Mean peak aperture replotted from Fig. 3.12. Shaded areas represent the expected peak end-effector aperture if participants did not take into account the tool geometry. (b) Data presented as the hand aperture for each effector. Shaded areas represent the expected peak hand aperture if participants did take completely into account the tool geometry. Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence interval.

As for closed-loop condition, we first tested whether the data differed from ideally taking into account tool geometry by examining whether the tool-tip apertures were different across tools (Fig. 3.14a). We then examined whether tool geometry was taken into account at all by comparing hand opening across tool conditions (Fig. 3.14b). Tool-tip apertures with both the 0.7:1 tool and the 1.4:1 tool were significantly different (Bonferroni corrected one-tailed paired sample t-tests), in the expected direction, from the 1:1 tool (0.7:1 tool: t(19) = -49.2, $p < .001$, $d = -11$; 1.4:1 tool: t(19) = 40.74, $p < .001$, $d = 9.05$). A similar analysis on hand apertures showed that hand opening with both tools was significantly different from the hand aperture with the 1:1 tool (0.7:1 tool: t(19) = 2.61, $p < .034$, $d = .58$; 1.4:1 tool: t(19) = -5.22, $p < .001$, $d = -1.17$).

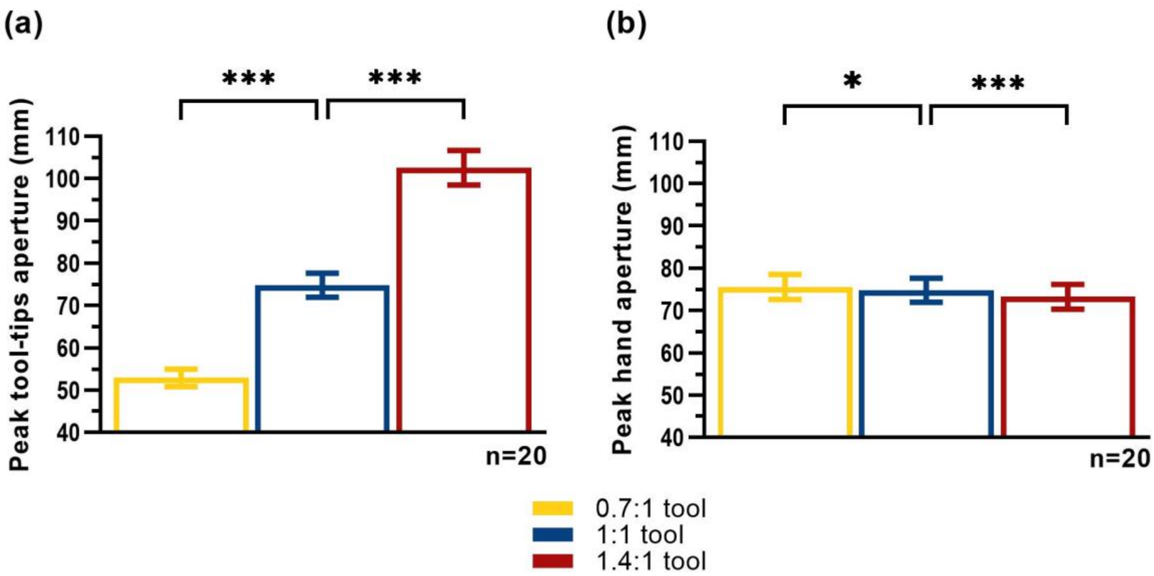


Figure 3.14. Peak end-effector aperture in open-loop condition (day 4). (a) Mean peak tool-tips aperture (collapsed across object distance and object size). (b) Same data plotted as mean peak hand aperture. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

It appears therefore that the both tool geometries were significantly accounted for, however the difference in hand opening was very small (0.7:1 tool: 0.75mm compared to a difference of 4.76mm in closed-loop conditions; 1.4:1 tool: 1.55 mm, compared to a difference of 6.74 mm in closed-loop conditions). The magnitude of tool compensation therefore appears substantially lower when visual feedback was unavailable, providing little evidence of the tool geometry being accounted for.

Degree of 'compensation' for tool geometry: open-loop

To supplement the above analysis we again examined quantitatively the degree to which participants compensated for tool geometry in the open-loop conditions. Fig. 3.15 plots the overall mean compensation, and individual's data. As expected from the preceding analyses, the disparity in compensation for the two tools was preserved, but the overall magnitude of tool compensation was substantially lower in open-loop conditions—less than 0.1 for the 1.4:1 tool, and nearly zero for the 0.7:1 tool. These data therefore provide only very limited evidence that tool geometry was taken into account when vision was unavailable.

As in closed-loop condition, we ran a paired sample t-test to examine if the compensation was greater for the 1.4:1 tool than the 0.7:1 tool (as seen for closed-loop conditions). There was significantly more compensation with the 1.4:1 tool (0.07) than with the 0.7:1 tool (0.02; $t(19) = 3.78$, $p = .001$, $d = .85$). Thus, this 'asymmetry' was still evident when visual feedback was removed.

The degree of compensation was extremely low (less than 0.1) for both tools, suggesting that no internal models of tools were developed. Interestingly, the asymmetry found in closed-loop conditions (more compensation for the 1.4:1 tool than for the 0.7:1 tool) was also evident in open-loop conditions.

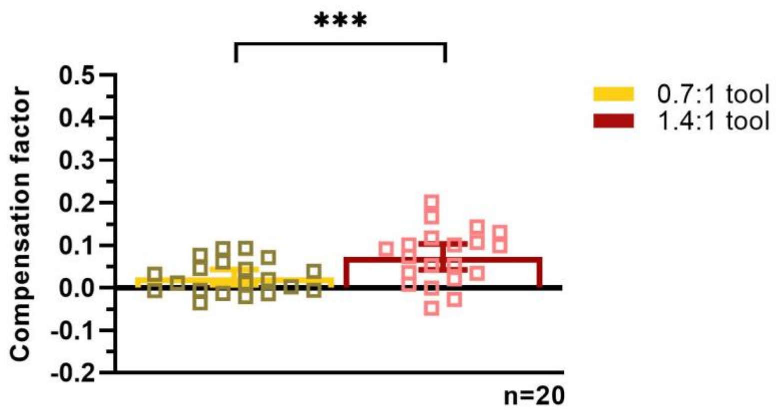


Figure 3.15. Compensation for tool geometry in open-loop condition (day 4). Compensation factors for the 1.4:1 and 0.7:1 tools in open-loop condition. See main text for how these values were calculated. The empty squares represent individual participant's compensation factors. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparison.

Open-loop vs. closed-loop performance

Taken together, the data on anticipatory scaling, and on taking tool geometry into account, do not provide compelling evidence for tools being controlled as a body part when visual feedback was unavailable. As mentioned previously, the presence of anticipatory scaling per se does not necessarily indicate that the brain has effective internal models of the tools. And the ‘compensation data’ suggest tool geometry was taken into account only to a very limited degree. It is possible that the lack of variation in hand apertures with the different tools was because grip apertures simply opened to the maximum possible amount when vision was removed. However, the presence of reliable grip aperture scaling suggests that this was not the case. Thus, it seems most likely that under the conditions of our experiment the visuomotor system did not acquire a model of tool geometry equivalent to that of the hand.

A further way to probe the presence of a ‘hand-like’ model of the tool is to consider the effect that removing visual feedback has on tool use conditions, compared to grasping with the hand. If participants did use tools as body parts, we would expect removing visual feedback to have similar effects, namely reliable increases in grip aperture, and perhaps slowing of movement velocity, thought to reflect the visuo-motor system actively controlling the probability of errors in the face of increased uncertainty (Connolly & Goodale, 1999; Hesse & Franz, 2009b; Jakobson & Goodale, 1991; Keefe et al., 2019; Schlicht & Schrater, 2007; Tang et al., 2016; Wing et al., 1986).

To analyse this we calculated difference scores between performance with and without visual feedback (open-loop minus closed-loop), for both peak velocity and peak grip aperture. The left and right panels in Fig. 3.16 plot these difference scores for velocity and grip data (expressed here in both tool and hand units), respectively. Fig. 3.16a suggests that removing visual feedback caused a small but consistent reduction in movement speed for the tool conditions (~40 mm/s reduction with the tools) but not for grasping with the hand. Consistent with this, removing vision slowed the movement significantly with all three tools (one-tailed one-sample t-tests; 0.7:1 tool : $t(19) = -2.88$, $p = .01$, $d =$

-.64; 1:1 tool : t(19) = -2.45, p = .024, d = -.55; 1.4:1 tool: t(19) = -3.19, p = .005, d = -.71) but not with the hand (t(19) = -1.33, p = .2, d = -.3). The effect of removing vision was not significantly smaller with the hand than the effect with the three tools (paired sample t-tests, Bonferroni corrected, 0.7:1 tool: t(19) = 1.61, p = .374, d = .36; 1:1 tool: t(19) = 1.23, p = .705, d = .27; 1.4:1 tool: t(19) = 1.79, p = .266, d = .4). Thus, the performance with tools is broadly consistent with an appropriate margin-for-error response to loss of visual feedback.

The lack of accounting for tool geometry in open-loop conditions makes it difficult to interpret the magnitude of effects of removing visual feedback on grip apertures (the same change in hand opening would result in different tool-tip changes due to different tool geometry, for instance). Nonetheless, Fig. 3.16c shows that, with all of the tools, tool-tips apertures were increased in response to loss of visual feedback (as found in Tang, Whitwell & Goodale, 2016), as was the hand aperture. A ceiling effect can also be seen in the opening of the 0.7:1 tool at the larger object size (45 mm) in both vision conditions. Plotting the data in hand units (Fig. 3.16d) revealed the same ceiling effect (for the 45 mm object size), but this time with all the tools in both vision conditions (~80 mm of hand opening). The hand was opened larger in open-loop conditions, but considering holding the tool (having to bend the last phalanx of the finger to hold the tool), the hand aperture observed when using a tool in open-loop conditions appears to have reached a ceiling. To analyse the ‘most likely’ effect of removing vision, the difference score between open- and closed-loop conditions was calculated on the performance at the smallest object size (25 mm, Fig. 3.16b). These effects (analysed here in hand units) were statistically significant (hand: t(19) = 10.6, p < .001, d = 2.37; 0.7:1 tool: t(19) = 4.07, p < .001, d = .91; 1:1 tool: t(19) = 6.06, p < .001, d = 1.35; 1.4:1 tool: t(19) = 7.49, p < .001, d = 1.68). This is qualitatively consistent with an appropriate margin-for-error strategy in response to the loss of visual feedback when using tools. Examined in more detail, however, the picture is mixed. The geometry of the tools means that, if anything, the hand opening should be increased more with the 0.7:1 tool, and less with the 1.4:1 tool, compared to the 1:1 tool and/or hand grasping, in order to create an appropriately sized margin-for-error in grasp. Alternatively, assuming zero tool compensation, we might expect that hand opening would be increased by a similar amount across the different tools. We found the opposite pattern, however. Compared to the 1:1 tool, the hand opening was increased less with the 0.7:1 tool (paired sample t-test: $t(19) = 5.03$, $p < .001$, $d = 1.13$) and more with the 1.4:1 tool (paired sample t-test: $t(19) = -5.69$, $p < .001$, $d = 1.27$). Thus, our data suggest that insufficient margin-for-error was added when using the 0.7:1 tool in the absence of visual feedback. We consider this further when examining error rates, in a later section.

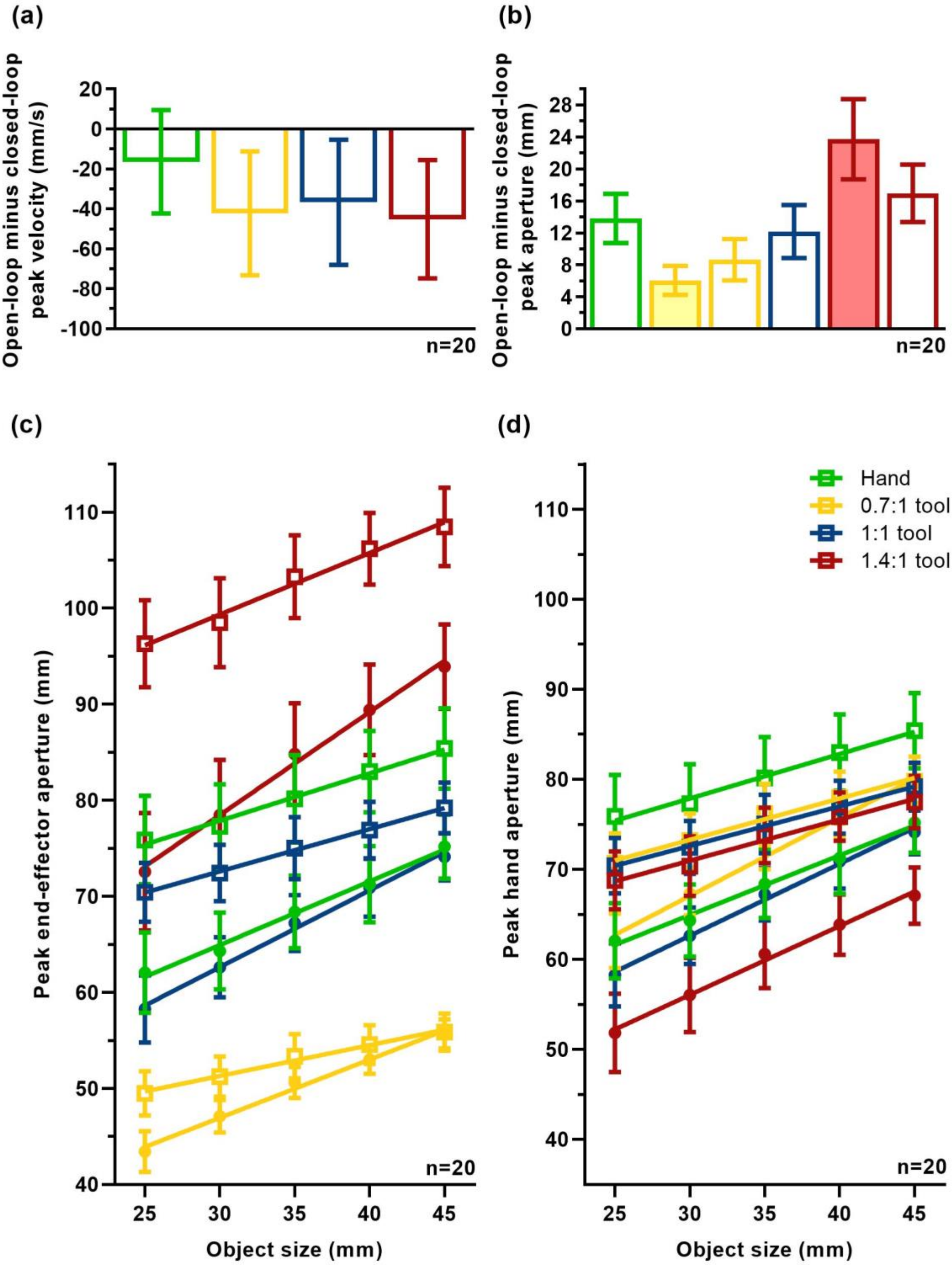


Figure 3.16. Effect of removing visual feedback on velocity and grip aperture (day 4). (a) Open-loop minus closed-loop performance for peak velocity. (b) Open-loop minus closed-loop performance for peak hand aperture for the 25 mm object. The empty bars represent data in hand units. The full bars with lighter colour represent data in tool units. (c) Mean peak aperture as a function of object size (collapsed across object distance) for the end-effector aperture in both vision conditions (replotted from Fig. 3.7 and Fig. 3.12). (d) Same data as in (c) presented in hand units (replotted from Fig. 3.8b and Fig. 3.13b). Solid lines show the best fitting linear regressions to the data in each case. In all cases, the error bars denote +/- 95% confidence intervals.

As mentioned previously, the compensation factor in open-loop conditions suggested that tool geometry was only accounted for to a very small degree if at all, whereas in closed-loop conditions we saw significant (albeit incomplete) compensation. To analyse whether this reduction in tool compensation with loss of visual feedback was significant, we first calculated difference score between each participant's compensation factor in open- and closed-loop conditions (Fig. 3.17). We then tested whether these difference scored differed from zero, using one sample t-tests. Removing visual feedback significantly reduced the compensation factors for both the 0.7:1 tool ($t(19) = -6.46$, $p < .001$, $d = -1.44$) and the 1.4:1 tool ($t(19) = -7.82$, $p < .001$; $d = -1.75$).

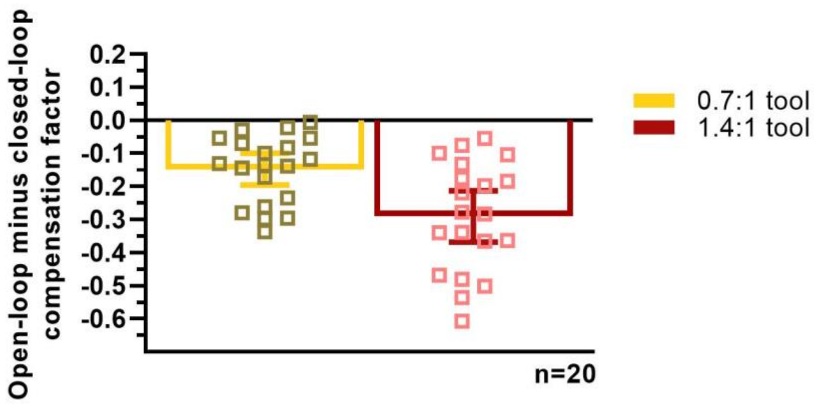


Figure 3.17. Effect of removing visual feedback on tool compensation for tool geometry (day 4). Open-loop minus closed-loop compensation factors for the 0.7:1 and 1.4:1 tool. The squares represent individual participant's difference in compensation factors. The error bars denote +/- 95% confidence intervals.

Overall, removing visual feedback did not eliminate participants' ability to produce anticipatory landmarks of grasp behaviour, as both object-distance velocity scaling, and object-size tool-opening scaling, remained present. Participants also altered their movements somewhat appropriately in response to the loss of feedback, by opening the tools wider and by slowing the movement down—two features associated with normal grasping behaviour without visual feedback. However, contrary to the idea of tools being 'controlled as body part', we found little quantitative evidence that tool geometry per se was taken into account when visual feedback was removed, with compensation for tool geometry decreasing to near zero. Thus, we did not find compelling evidence that tools were controlled in a truly equivalent manner to hand movements when visual feedback was unavailable.

3.3.5 Functional implications of not taking tool geometry into account?

The above analyses suggest that the visuomotor system took tool geometry into account when vision was available, albeit incompletely, but by-and-large failed to do so when visual feedback was unavailable. Our consideration of tool-compensation values was based on significant (unverified) assumptions, however, including that the ideal movement is to try to produce the same spatial pattern of tool-tip movement regardless of the tool geometry. Moreover, peak grip aperture (our main index) occurs while the hand is ‘in-flight’, and so is only indirectly related to global functional outcomes of the movements. It is entirely possible, then, that what our analysis might label ‘incorrect’ opening of the tool-tips (e.g. in open-loop conditions) has no discernible effect on success or failure of the movements.

We considered this by analysing the number of trials on which the object was successfully grasped, in each condition. Successful grasps were defined as trials on which participants did grasp the object front to back, lifting the object at least 5 mm above the table. Fig. 3.18 plots the percentage of successful trials for all effectors, for closed- and open-loop viewing conditions. The figure shows that overall success rates in the closed-loop conditions were near to 100%, though they appear slightly lower with the tools than with the hand (particularly with the 0.7:1 tool). The open-loop data show a different pattern. As expected from previous literature (Gentilucci et al., 1995; Hesse & Franz, 2009b; Jakobson & Goodale, 1991; Keefe et al., 2019), removing visual feedback had very little effect on the success rate for grasping with the hand, which remained near 100%, suggesting that changes to the movement to mitigate the increased risk of error were successful (Keefe et al., 2019). Removing visual feedback had a marked effect on grasp success rates with the tools, however, falling to around 70% for the 1.4:1 and 1:1 tools, and <50% for the 0.7:1 tool.

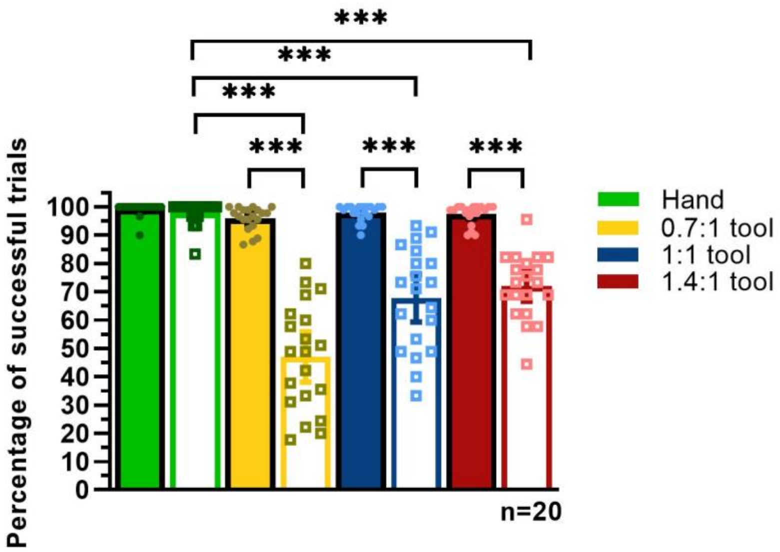


Figure 3.18. Grasping success rates in both vision conditions (day 4). Percentage of successful trials for each effector in each viewing condition. The coloured bars represent the closed-loop data. The empty bars represent open-loop data. The dots and empty squares represent individual participant's percentage for closed-loop and open-loop condition respectively. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

To analyse these effects statistically we ran a two-way (effector x viewing condition) repeated measures ANOVA. The ANOVA revealed a main effect of effector (F(3,57) = 81.73, p < .001, η_p^2 = .81), a main effect of viewing condition (F(1,19) = 115.93, p < .001, η_p^2 = .86). The ANOVA also revealed a significant interaction (Greenhouse-Geisser corrected; F(1.740,33.064) = 55.26, p < .001, η_p^2 = .74). Post hoc (Bonferroni corrected) pairwise comparisons indicated that in closed-loop conditions, there was no significant difference between the success rates with the hand and with the three tools. In open-loop conditions, the success rate was significantly higher with the hand than with the three tools (p < .001). The success rate with the 0.7:1 tool was significantly lower than the success rate with the 1:1 tool and the 1.4:1 tool (p < .001). There was no significant difference between the success rate with the 1:1 tool and the 1.4:1 tool. Post hoc comparisons also indicated that removing visual feedback did not affect the success rate during hand grasping. In contrast, removing visual feedback affected significantly negatively the success rate with the three tools (p < .001).

Success rate with the tools was heavily influenced by the availability of visual feedback. Removing it led to large, significant decreases in success rate with all of the tools (~49, 30 and 25%

with the 0.7:1, 1:1, and 1.4:1 tools, respectively) while the hand was only marginally affected (~1.3% less successful, and still over 98% success rate). These results suggest that participants' relied heavily on visual feedback in order to use the tools effectively, in a way that was not evident for hand grasping. The apparent lack of internal models of tools (evidenced by the tool-compensation values in open-loop conditions) therefore appears to have had clear negative effects on the functional effectiveness of movements.

We also noticed the large variability in individual's success rates with the tools in open-loop conditions. For example, with the 0.7:1 tool, several participants had less than 30% success rate while others were above 70%. We explore the idea that some people might be better overall at taking tool geometry into account in the Discussion.

3.3.6 Overall average movement profiles

So far we have analysed specific kinematic indices of movements related to our hypotheses. These indices capture only a tiny portion of the movement (although they are highly auto-correlated), and so may not reflect other differences (and similarities) between movements across different conditions. As discussed in Chapter 2, we address this by using overall average grasp profiles to visualise the movements as a whole. We again examined data from day 4 of the experiment. However, for the tool data, only the three last blocks of closed-loop grasping were included[2].

We could only include successful trials in the average profiles because our analysis required a defined movement endpoint so as to normalise profiles with respect to time and space (allowing comparisons of movements to different object distances, which take different amounts of time, for instance). We therefore only present this analysis for the closed-loop data, in which success rates remained high overall. Overall grasp profiles computed from the open-loop data would not be representative of performance as we would have removed a substantial proportion of trials (see Fig. 3.18) that may well have relatively outlying—and therefore informative—profiles (since they

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[2] Producing those profiles is a lengthy process. As they are produced as a visualisation tool, it was decided to focus on the last three blocks only.

resulted in errors). We also removed profiles of trials in which the tracking of one or more markers was disrupted, and so a complete profile was not available. For hand grasping, we included 93.8% of the trials. For tool grasping, we included 96.2% with the 1.4:1 tool, 93.7% with the 1:1 tool, and 92.8% of the trials with the 0.7:1 tool.

Fig. 3.19 plots the overall grasping profiles for all effectors. The top-left panel (Fig. 3.19a) plots end-effector (tool-tip) aperture as a function of time. The profiles are normalised in time such that overall durations are a proportion of the hand-grasping data. The top-right panel (Fig. 3.19b) plots the same in units of hand opening. The middle row plots the same data as the panels above, but as a function of space. Here, space was normalised with respect to the movement end point (when the object was lifted), and computed with respect to the midpoint between the two markers used to characterise grip aperture. Finally, the bottom-left panel shows the duration of the plateau part of the grasp profile, as a proportion of movement duration (see below). A version of those plots with error bars is available in section 7.1.1 (Section 7.1.1; Fig. 7.1) and overall grasping profiles for each object size, for all effectors are also available (hand and 1:1 tool: Fig. 7.2, 0.7:1 tool and 1.4:1 tool: Fig. 7.3).

We first examined the end-effector profiles normalised in time (Fig. 3.19a). Grasping profiles produced with the 1:1 tool and the 1.4:1 tool broadly resemble the hand grasping profile while the 0.7:1 grasping profile appears substantially more skewed. It can be seen that more time was needed to grasp the object with the 0.7:1 tool than with the 1:1 tool and the 1.4:1 tool.

Fig. 3.19b plots the same average grasp profiles in units of hand opening, again as a function of (normalised) time. It can be seen that for the early stages of the movements hand opening profiles are very similar with the three different tools. Movements made with the 1.4:1 tool started to separate from the others at around 30% of the movement time, and movements with the 0.7:1 tool were extremely similar to those with the 1:1 tool until 50% of the movement time. This suggests that the initially programmed movements were quite similar across different tools, even though the peak grip apertures showed evidence of compensation for tool geometry. In the Discussion we explore the idea that this pattern may be indicative of a primarily visual control strategy. This pattern maps on to the pattern of tool compensation factors reported above (greater compensation for the 1.4:1 tool than the 0.7:1 tool). Assuming the compensation reflects the fidelity of the internal models, a 'worse' internal model might be expected to lead to a more 'generic' initial movement plan (and reliance on later visual control).

Examining the profiles in space (Fig. 3.19c and d), we can observe the same pattern as in the time normalised profiles. We also noticed that the peak end-effector aperture was happening after 90% of the distance to object target with the tools and after 95% with the hand. That extra time spent in the 'plateau' seems then to happen around the object location, strengthening the idea that the movement was visually controlled, particularly the closure phase of the grasp.

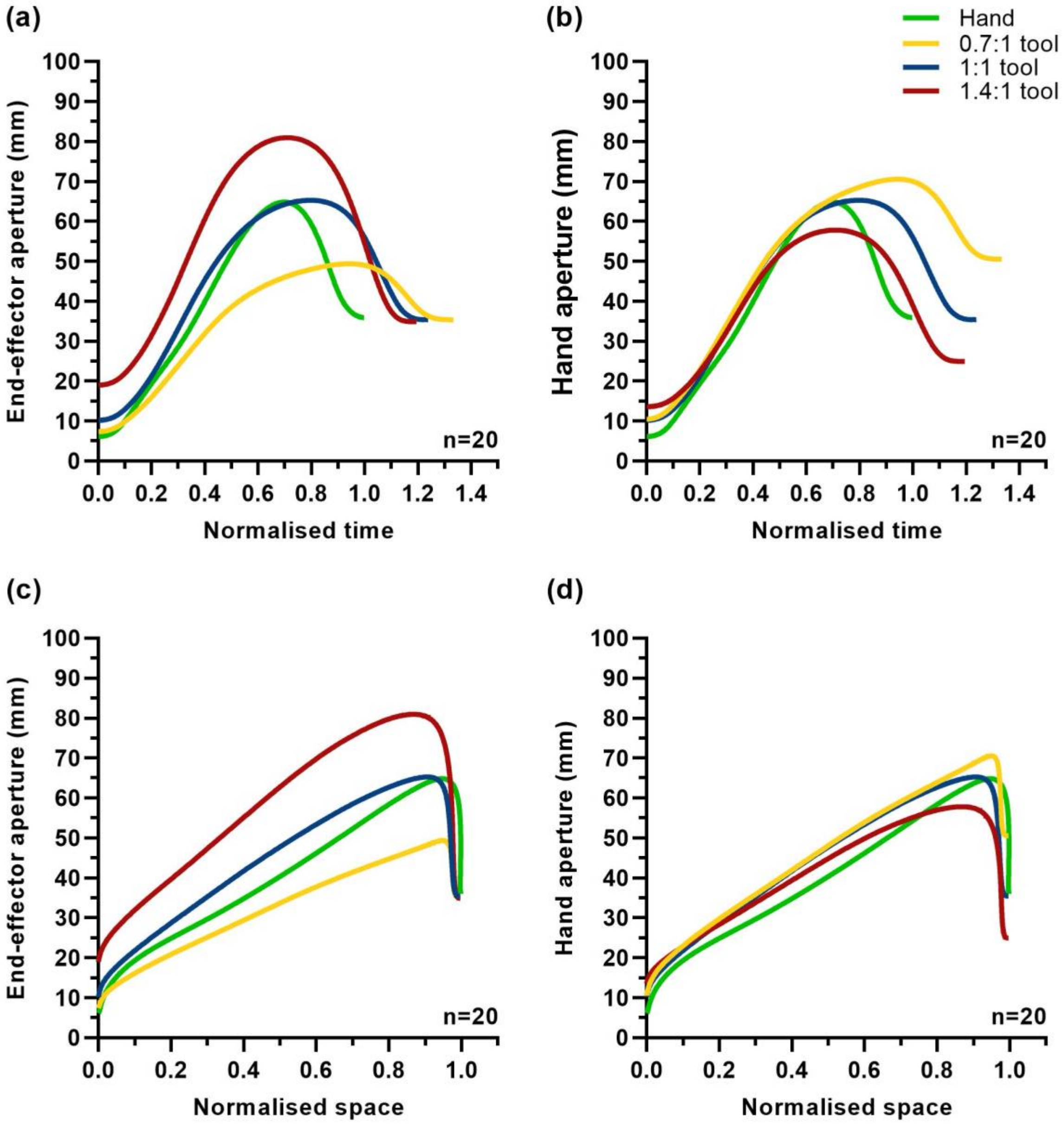


Figure 3.19. Average grasp profiles in closed-loop condition (day 4). Overall grasping profiles collapsed across object sizes and distances in closed-loop condition during the last 3 blocks of closed-loop grasping with the tools in day 4. (a) The end-effector profiles (b) The hand profiles when using the different effectors. Both are normalised in time adjusted to the hand grasping profile. (c) The end-effector profiles are normalised in space. (d) The hand profiles when using the different effectors are normalised in space.

Moreover, all the tools appear to be opened wide for a greater proportion of the movement duration, compared to grasp opening with the hand. Similar findings have been reported before (Bongers, 2010; Golenia et al., 2014; Itaguchi & Fukuzawa, 2014), with tool use being described as showing an extended 'plateau' in grasp opening. Itaguchi & Fukuzawa (2014) defined this plateau as the proportion of movement during which participants opened the tool tips more than 90% of the peak tool-tip aperture. We adopt this definition for our analysis. The derived plateau durations for our data are shown in Fig. 3.20. As the profiles suggest, the plateau phase was longer with the tools than with the hand, and longest of all with the 0.7:1 tool. A one-way repeated measures ANOVA revealed a main effect of effectors (F(1.674,31.798) = 27.70, p = .001, η_p^2 = .59; Greenhouse-Geisser corrected). Post hoc pairwise comparisons (Bonferroni corrected) confirmed that plateau duration was significantly shorter with the hand than with the three tools. Between the tools, plateau duration with the 0.7:1 tool was significantly longer than with the other two tools. Finally, plateau duration was significantly shorter with the 1.4:1 tool than with the 1:1 tool. Thus, the overall pattern of different performance with the 0.7:1 tool is present in this index too.

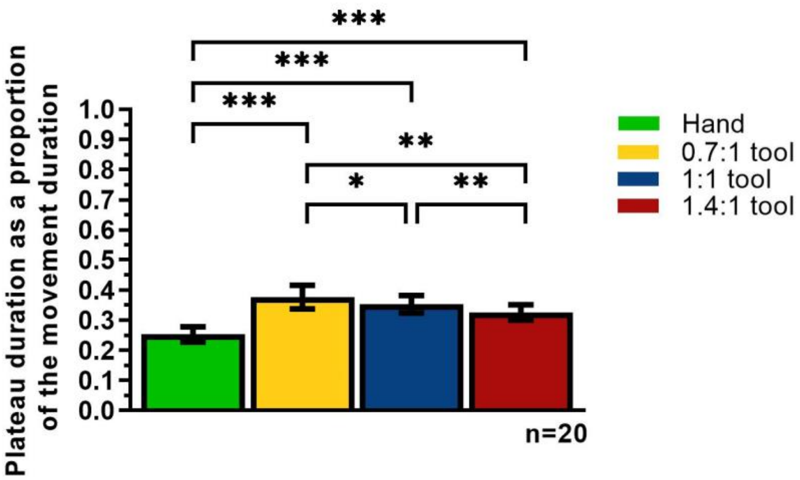


Figure 3.20. Plateau duration as a proportion of movement duration. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

3.3.7 Comparison of hand grasping with 1:1 tool performance

As noted in the Introduction, comparing across different tools allows us to isolate how different tool geometries affected movements while holding constant the factors associated with using a tool (reduced tactile signals, biomechanical constraints of holding the handles etc.). We can gain insight into these factors, per se, by comparing movements with the 1:1 tool (which does not alter the relationship between hand opening and tool-tip opening) to movements made with the hand. We will draw on previous sections, as most of the analyses have already been done in those sections.

In both closed- and open-loop viewing conditions, anticipatory velocity/distance scaling, and grasp/size scaling was evident in hand and 1:1 tool movements, although in both conditions we found slower movement velocity when using the 1:1 tool than during hand grasping (closed-loop: Fig. 3.6; open-loop: Fig. 3.11b). 1:1 tool performance most closely resembled hand grasping performance in the closed-loop conditions, however. First, as shown in Fig. 3.5, from the second day onwards grasp opening with the 1:1 tool practically lined up with the hand opening (on day 4, tool-tip aperture was 99% of the hand aperture). Success rates were also similar across hand and 1:1 tool (Fig. 3.18), suggesting that using a tool per se did not impact participants' success rate at the task. Examining overall grasping profiles (Fig. 3.19) showed, however, that grasping movements made with the hand and with the 1:1 tool are different at the detailed level. Using a tool per se appears to result in a more skewed grasp closure profile, with a statistically longer 'plateau' phase duration (Fig. 3.20), as well as slower overall movements.

In visually open-loop conditions, the differences between kinematics of hand grasping and 1:1 tool use were not dramatically altered. However, and, most notably, removing vision had a substantially larger effect on success rate with the 1:1 tool than with the hand. Thus, although the primary kinematic markers are present (Gentilucci et al., 2004) tool use per se has significant effects on grasping, which should be taken into account when interpreting data from tool experiments.

3.3.8 Changes in performance across the experiment?

The data analyses around our main hypotheses concentrated on day 4 of the experiment, at which point participants had had the most opportunity to acquire the tool mappings. Here we examine the evidence for learning of the tool mappings over the course of the experiment, by comparing data on day 1 and day 4 of the experiment. In general, we expect learning of the tool properties to be accompanied by faster movement speeds, smaller grip apertures (less margin-for-error required with increasing knowledge of tool properties), higher 'tool compensation' (taking greater account of tool geometry), and higher success rates. We consider each of these in turn, for both closed- and open-loop viewing conditions.

Peak velocity

Fig. 3.21a and b shows peak movement velocity for the first and fourth day for each effector, in closed-loop viewing, and in open-loop viewing, respectively. The figures show that with all effectors participants moved faster on day 4 than on day 1, in both viewing conditions. To examine the effect, we ran one-tailed paired-sample t-tests on the peak velocity, collapsed across object sizes and distances, for each effector. With all effectors, movement velocity was significantly higher on day 4 than on day 1 of the experiment, both for closed-loop (hand: $t(19) = -2.3$, $p = .016$, $d = -.40$; 0.7:1 tool: $t(19) = -4.29$, $p < .001$, $d = -.96$; 1:1 tool: $t(19) = -4.12$, $p < .001$, $d = -.52$; 1.4:1 tool: $t(19) = -4.08$, $p < .001$, $d = -0.50$) and open-loop (hand: $t(19) = -2.18$, $p = .011$, $d = -.46$; 0.7:1 tool: $t(19) = -5$, $p < .001$, $d = -.67$; 1:1 tool: $t(19) = -4.93$, $p < .001$, $d = -.67$; 1.4:1 tool: $t(19) = -3.98$, $p < .001$, $d = -.56$) conditions. This pattern could reflect either a learning of the task, or a learning of the tools (as ‘better’ internal models would allow faster movements). Our experiment does not allow us to differentiate these ‘types’ of learning unambiguously. However, the fact that movement velocities increased similarly with the tools and with the hand—for which a high-fidelity internal model was presumably present at the outset of the experiment, and so could not be further learned—suggests that the major factor in increased movement speed was learning of the task.

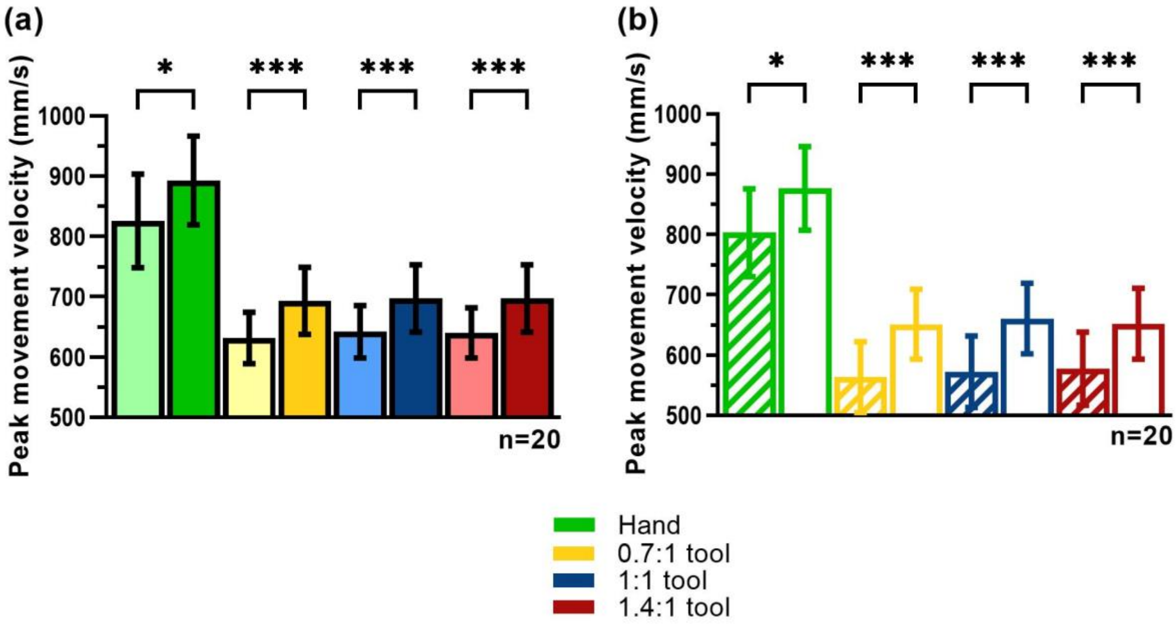


Figure 3.21. Day 1 vs. day 4 peak velocity. (a) Mean peak velocity of grasping movements, in closed-loop conditions, for each effector collapsed across object distance and size. The lighter coloured bars represent day 1. The darker coloured bars represent day 4. (b) Mean peak velocity of grasping movements, in open-loop conditions with each effector collapsed across object distance and object size. The diagonal stripes bars represent day 1. The empty bars represent day 4. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

Peak grip aperture

Fig. 3.22 shows the peak tool-tips aperture for the first and fourth day for all the tools. Fig. 3.23a shows the peak tool-tips aperture (on the left panel), in closed-loop conditions, as a proportion of hand grasping. The right panel (Fig. 3.23b) shows the same data in units of hand opening. The bottom row represents the open-loop data plotted the same way. The data for each day were normalised based on the hand grasping aperture from that day. We observed in Fig. 3.5 that the hand data varied slightly across days (also visible in Fig. 3.24a), and we assume that those changes are related to the overall learning of the task. Our interest lies in potential changes in the tool-tips aperture with the different tools across the experiment. Normalising tool-tips aperture (based on hand grasping performance) allows for examination of how much tool geometry was accounted for on different days in comparable units

Fig. 3.22a shows the peak tool-tips aperture (on the left panel), in closed-loop conditions, as a proportion of peak hand aperture. The right panel (Fig. 3.22b) shows the same data in units of hand opening. The bottom row represents the open-loop data plotted the same way. In closed-loop conditions (Fig. 3.22a) it can be seen that the peak tool-tips aperture decreased across the experiment with the three tools (as seen in Fig. 3.5). To examine those effects across tools, we ran one-tailed paired-sample t-tests on the hand peak aperture when using the tools between day 1 and day 4. With each tool, participants opened their hand significantly less in day 4 than in day 1 (0.7:1 tool: $t(19) = 2.66$, $p = .004$, $d = .59$; 1:1 tool: $t(19) = 2.59$, $p = .005$, $d = .58$; 1.4:1 tool: $t(19) = 3.21$, $p = .001$, $d = .72$).

In open-loop conditions (Fig. 3.22c), contrary to closed-loop conditions, it appears there was no change in tool-tips aperture (or in hand aperture, Fig. 3.22d). As before, we ran one-tailed paired sample t-tests on the hand peak aperture when using the tools between day 1 and day 4. With each tool, there was no significant difference in hand opening between day 4 and day 1 (0.7:1 tool: $t(19) = -1.03$, $p = .421$, $d = -.23$; 1:1 tool: $t(19) = -.36$, $p = .320$, $d = -.08$; 1.4:1 tool: $t(19) = -.09$, $p = .267$, $d = -.02$).

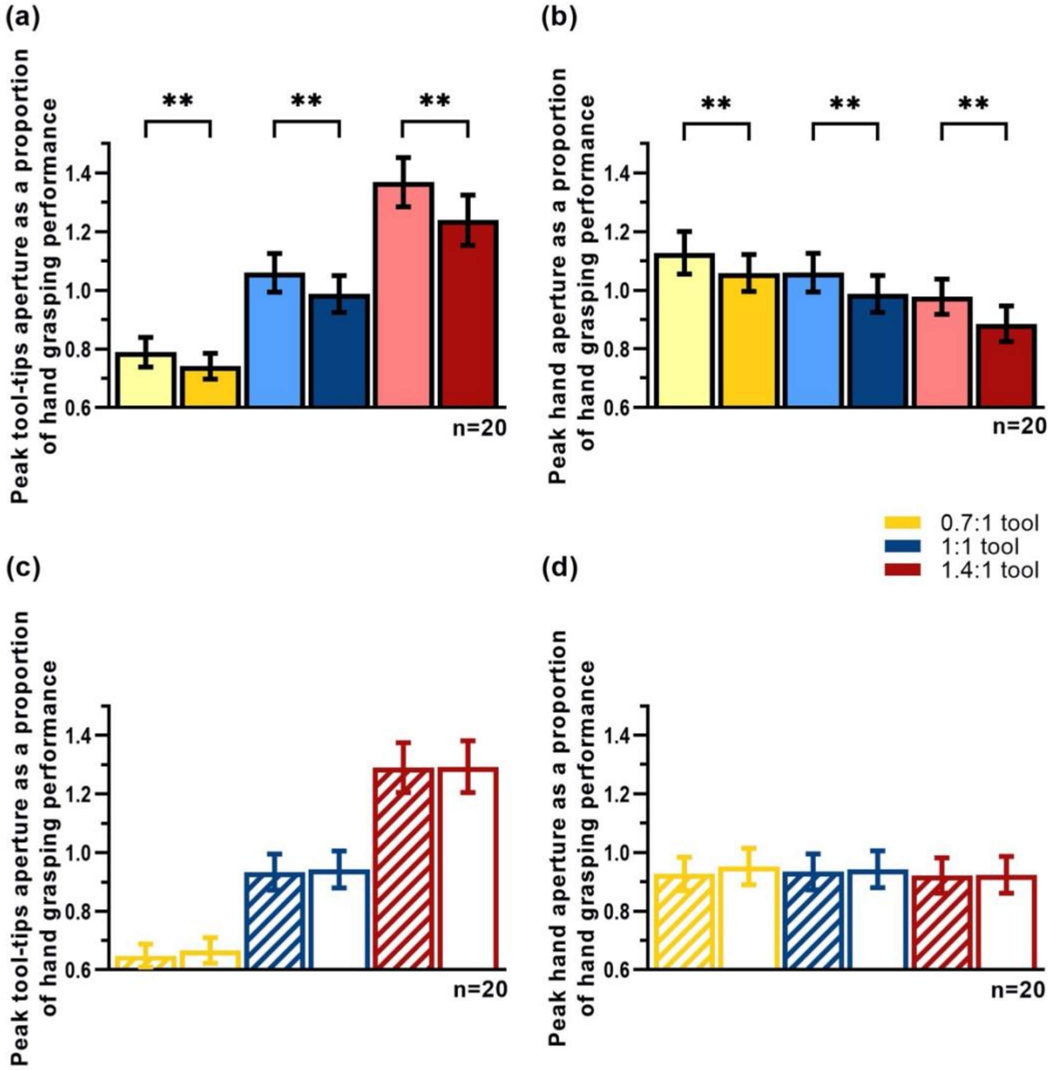


Figure 3.22. Day 1 vs. day 4 peak tool-tips aperture. (a) Mean peak tool-tips aperture collapsed across object distance and object size as a proportion of hand grasping in closed-loop conditions. (b) Same data plotted as hand peak aperture. The lighter coloured bars represent day 1. The darker coloured bars represent day 4. (c) Mean peak tool-tips aperture collapsed across object distance and object size as a proportion of mean hand peak aperture in open-loop conditions. (d) Same data plotted as hand peak aperture. The diagonal stripes bars represent day 1. The empty bars represent day 4. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

We only observed a reduction of hand aperture in the closed-loop conditions across the experiment and no differences in open-loop. Again, this pattern of reduction of tool-tips opening could represent of learning of the task, or a learning of some control process that supports visually guided closed-loop control, but not a complete ‘non-motor’ model (internal model) of the tools, both leading to less uncertainty, leading to the production of movements with less margin-for-error. We are however unable to differentiate those two possibilities.

Across the experiment, the increase of movement velocities with the three tools, combined with less margin-for-error, shows those movement parameters were not traded off (as the visuomotor system might have increased their margin-for-error to diminish the risk of faster movement, Wing et al., 1986). This suggests that participants learned to better perform at the task.

Compensation for tool geometry

Fig. 3.23 plots the degree of compensation for tool geometry on day 1 and day 4, for the closed-loop conditions (left panel) and for the open-loop conditions (right panel), computed as previously. In closed-loop conditions (Fig. 3.23a), it can be seen that compensation for the 0.7:1 tool geometry was not higher in day 4 than in day 1. For the 1.4:1 tool, however, there is an increase between day 1 and day 4. Moreover, it can be seen that the asymmetry of compensation between the 1.4:1 tool and the 0.7:1 tool the observed in day 4 was already present in day 1. To analyse the effects statistically, we ran a two-way (day x tool) repeated measures ANOVA on the compensation factors. The ANOVA revealed a main effect of day (F(1,19) = 14.81, p = .001, η_p^2 = .44), a main effect of tool (F(1,19) = 45.57, p < .001, η_p^2 = .71), the interaction was also significant (F(1,19) = 10.13, p = .005, η_p^2 = .35). Post hoc (Bonferroni corrected) pairwise comparisons indicated that there was not more compensation in day 4 than in day 1 with the 0.7:1 tool, but for the 1.4:1 tool, there was significantly more compensation in day 4 than in day 1. Moreover, in day 1, there was already more compensation for the 1.4:1 tool than for the 0.7:1 tool.

In open-loop conditions (Fig. 3.23b), it can be seen that the compensation for that there is only a slight increase of compensation with both tools. Again it appears that there was more compensation with the 1.4:1 tool than with the 0.7:1 tool. As for closed-loop conditions, we ran again a two-way (day x tool) repeated measures ANOVA. The ANOVA revealed a main effect of day (F(1,19) = 11.06, p = .004, η_p^2 = .37) and a main effect of tool (F(1,19) = 18.45, p < .001, η_p^2 = .49). The interaction was not significant (F(1,19) = 0.27, p = .612, η_p^2 = .01).

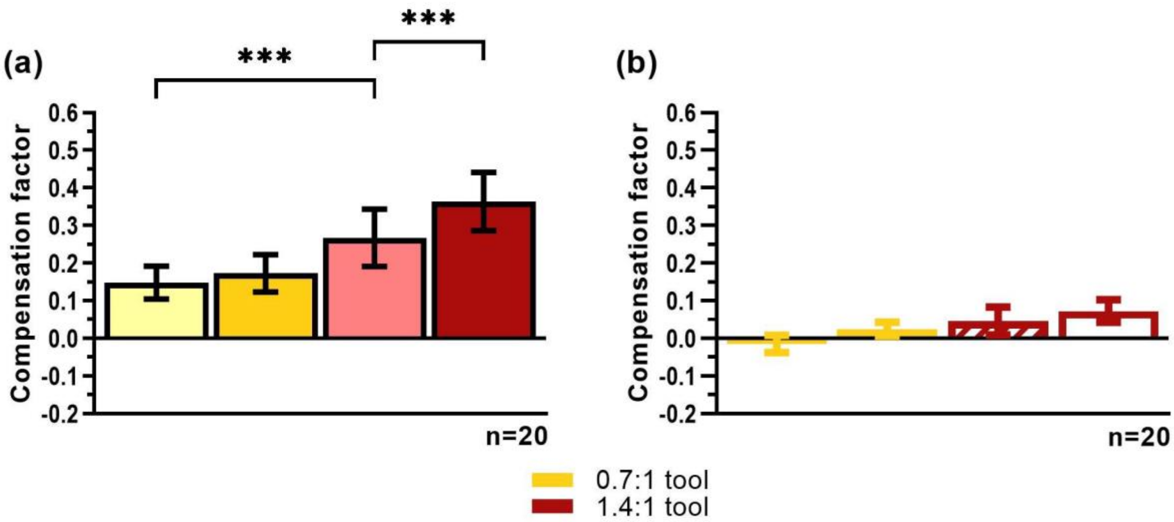


Figure 3.23. Day 1 vs. day 4 compensation factors. (a) Compensation factors for the 0.7:1 tool and the 1.4 tool in closed-loop conditions. The lighter coloured bars day 1. The darker coloured bars represent day 4. (b) Compensation factors for the 0.7:1 tool and the 1.4:1 tool in open-loop conditions. The diagonal stripes bars represent day 1. The empty bars represent day 4. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Over the course of the experiment, in closed-loop conditions, compensation increased only for the 1.4:1 tool. This suggests participants learned more about the 1.4:1 tool geometry than about the 0.7:1 tool. This again reflects the overall the pattern of difficulty of learning the 0.7:1 tool geometry. That is, in open-loop conditions, compensation only significantly increased with the 0.7:1 tool (but it is not really informative as the compensation factor on day 4 is only 0.02). Those patterns reflect the absence of learning of internal models of tool across the experiment.

Percentage of successful trials

Fig. 3.24 shows the percentage of trials on which the object was successfully grasped for each effector on day 1 and day 4, for the both vision conditions. In closed-loop conditions (Fig. 3.24a), it can be seen that, success rates for hand grasping were at ceiling even on day 1, and so no improvements were observed across days. The success rates did appear to improve across the experiment with the tools, however. To examine the effect, we ran paired sample t-tests on the percentage of successful trials between the first and fourth day of the experiment for each effector.

With the 0.7:1 tool, success rate improved significantly across the experiment ($t(19) = -2.00$, $p = .031$, $d = -.52$) but not with the other effectors (hand: $t(19) = .28$, $p = .39$, $d = .009$; 1:1 tool: $t(19) = -.97$, $p = .171$, $d = -.24$; 1.4:1 tool: $t(19) = -1.65$, $p = .058$, $d = -.37$).

In open-loop conditions (Fig. 3.24b) it can be seen that the percentage of successful trials improved on day 4, most clearly in the tool conditions, where the success rate on day 1 was relatively low. To examine the effect, we ran one-tailed paired sample t-tests on the percentage of successful trials for all effectors. Participants were more successful, albeit non significantly, with all effector on the fourth day (hand: $t(19) = -1.03$, $p = .080$, $d = -.23$; 0.7:1 tool: $t(19) = -1.14$, $p = .067$, $d = -.29$; 1:1 tool: $t(19) = -0.7$, $p = .124$, $d = -.21$; 1.4:1 tool: $t(19) = -0.85$, $p = .102$, $d = -.23$).

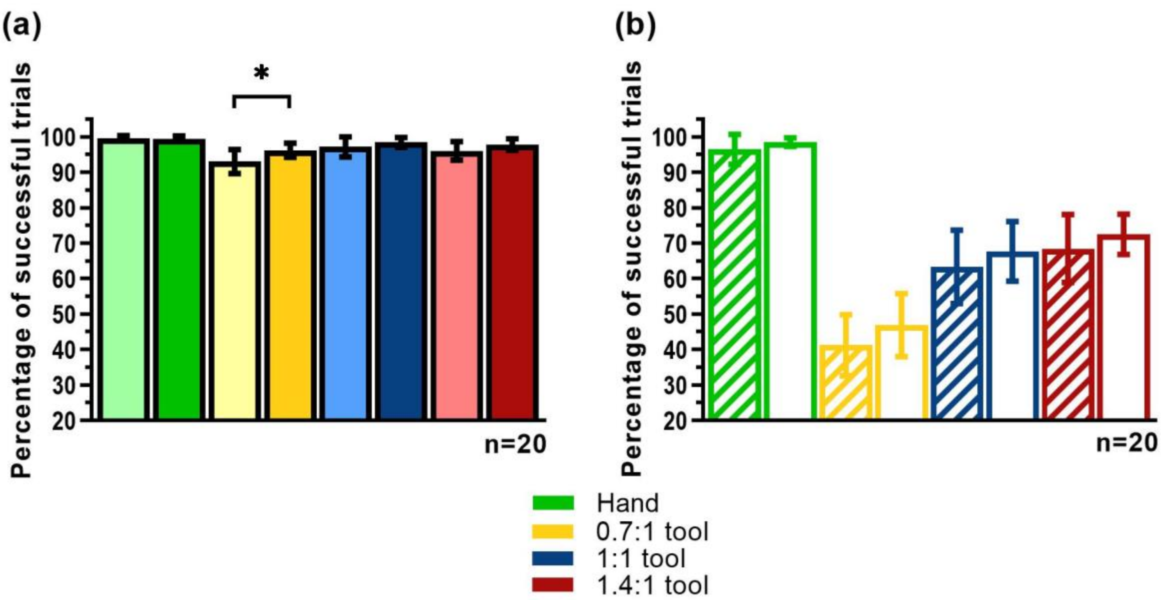


Figure 3.24. Day 1 vs. day 4 success rate. (a) Percentage of successful trials for all effectors tool in closed-loop conditions. The lighter coloured bars represent day 1. The darker coloured bars represent day 4. (b) Percentage of successful trials for all effectors tool in open-loop conditions. The diagonal stripes bars represent day 1. The empty bars represent day 4. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

Taken together, it appears that in most conditions (except hand grasping in closed-loop conditions, which was at ceiling), success rate improved, but non-significantly. Overall, performance with the tools in open-loop viewing conditions stayed poor, and did not represent a clear improvement of performance that could have been expected with a clear development of internal models of tools.

Thus, those results are consistent with the idea that no internal models of tools were learned across the experiment.

Overall average grasp profiles

Fig. 3.25 shows the overall grasping profiles for day 1 and day 4 of the experiment for all effectors (following the same structure as the previous figure on overall grasp profiles, Fig. 3.19). Fig. 3.25a shows that with all effectors movement duration (time to grasp the object) was quicker on day 4 than on day 1. On day 1, as on day 4, movement duration was also shorter with the hand than with the tools. Participants were the slowest to complete their grasping movement when using the 0.7:1 pliers-like tool.

Considering Fig. 3.25a, it can be seen that, within each effector, grasp profiles did not differ qualitatively between day 1 and day 4, but instead are essentially scaled in time. We can also observe a slight variation in hand opening between day 1 and day 4.

An interesting observation in Fig. 3.19b was that the hand movement made with the three tools was highly similar at the beginning of the movement. It is possible that that pattern was already evident during day 1, or it may have been developed across the experiment. Examining Fig. 3.25b, we noticed that the same pattern of overlapping hand movement with the three tools visible in day 4 was already present in day 1. If anything, the pattern is clearer in day 1 than in day 4, as the beginning of the movements appear identical even with the 1.4:1 tool.

When looking at the profiles as a function of space, as seen in Fig. 3.25c and d, we noticed that the peak end-effector aperture is reached earlier in the movement, thus farther in space from the object in day 4, suggesting participants started the closure phase of grasp sooner.

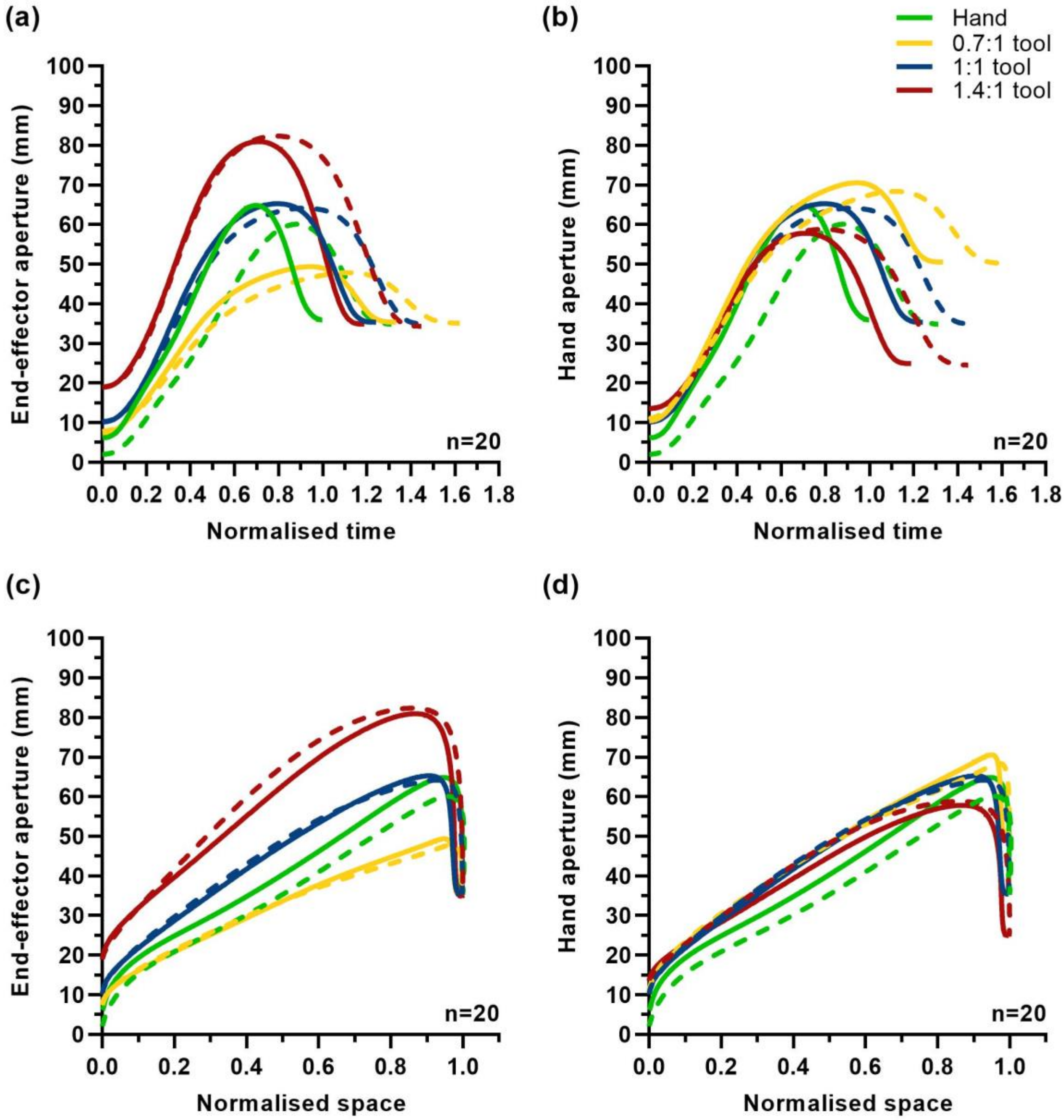


Figure 3.25. Day 1 vs. day 4 overall average grasping profiles. (a) End-effector aperture (collapsed across object sizes) normalised in time for all effectors. (b) Same data plotted as hand aperture. For clarity, only the data from day 1 were plotted (day 4 data are visible in Fig.3.19) (c) Data presented in (a) normalised in space. (d) Data presented in (b) normalised in space. Dashed lines represent day 1. Plain lines represent day 4.

As before, we computed the plateau duration as a proportion of movement duration (Fig. 3.26). The figure shows that the proportion of the movement spent in the plateau phase appears similar between day 1 and day 4. To examine the effect, we ran paired sample t-tests on plateau duration between day 1 and day 4. The proportion of time spent in the plateau duration did not vary significantly with any effector (hand: t(19) = -.69, *p* = .249, *d* = -.16; 0.7:1 tool: t(19) = -.32, *p* = .375, *d* = -.08; 1:1 tool: t(19) = .81, *p* = .214, *d* = .17; 1.4:1 tool: t(19) = .82, *p* = .212, *d* = .19). Although movement duration was shorter in day 4 compared to day 1, the proportion of time spent in plateau duration did not change.

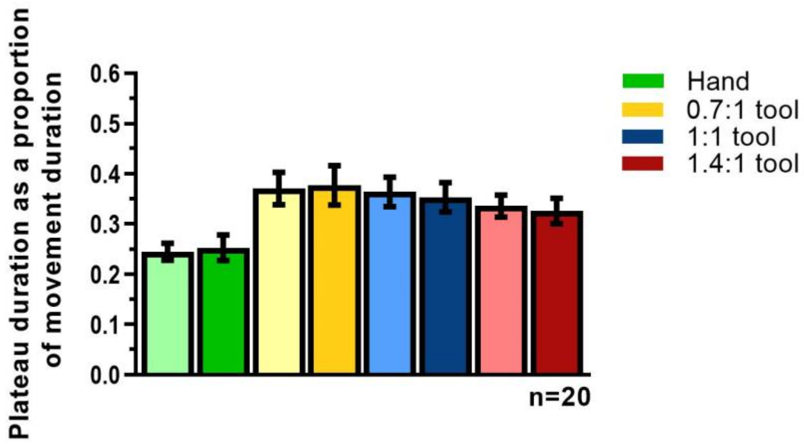


Figure 3.26. Day 1 vs. day 4 plateau duration. Plateau duration as a proportion of movement duration. The lighter coloured bars represent day 1. The darker coloured bars represent day 4. The error bars denote +/- 95% confidence interval.

3.4 Discussion

In this experiment we aimed to investigate if tools were ‘used as body parts’. We defined several expected ‘signatures’, such as a normative patterns of scaling of movement indices with object properties, a quantitatively appropriate opening of the tool-tips, an accounting for the geometry of the tools, and the presence of both when visual feedback is unavailable, suggesting the existence of an internal model of the tool geometry. First, in closed-loop conditions, our results indicated that the expected normative patterns of scaling of movement indices was found with the three tools. That is, with all tools, we observed evident scaling of movement velocity with object distance and evident scaling of tool-tips aperture with object size. Second, our results indicated that the geometry of the tools was accounted for, albeit not completely. Third, in open-loop conditions, while both scalings were preserved, we only found little evidence of compensation for the geometry of the tools. That is, removing visual feedback led to very similar hand opening with all tools, suggesting that no internal models of tools were developed during the experiment. Taken together, those results suggest that the tools were not ‘used as body parts’.

Although we did not find compelling evidence that tools were used as body parts, when visual feedback was available, tool grasping performance resembled hand grasping. First, we observed evident features of natural movement during tool grasping (object-distance velocity and object-size tool aperture scalings, as observed in Gentilucci et al., 2004; Itaguchi & Fukuzawa, 2014). Second, we found evident compensation for the tool geometries. Third, success rate with the tools were at ceiling or really close to ceiling. And fourth, while using a tool reduces movement velocity, movements made with tools were not ‘slow’. When removing visual feedback, we still found evident features of natural movement (presence of both scalings). We also observed an increase of tool-tips aperture as well as a slowing of movement velocity. Those features are common when visual feedback is removed during hand grasping (Connolly & Goodale, 1999; Hesse & Franz, 2009b; Jakobson & Goodale, 1991; Tang et al., 2016; Wing et al., 1986). Taken together, we observed landmarks of natural grasping during tool grasping in both vision conditions, but no compelling evidence of compensation for tool geometry without visual feedback.

Consistent with the ‘tools use as body parts’ account, the presence of anticipatory behaviours (movement velocity and tool-tips aperture scalings), accounting for object properties, suggests the use of internal models (McNamee & Wolpert, 2019; Wolpert et al., 1995; Wolpert & Kawato, 1998) during movement planning. We have not found, however, compelling evidence for the development of such internal models of tools, or models equivalent to the existing internal models of the hand (allowing for accurate and successful grasp even without visual feedback). So how did the motor system produce those landmarks of natural movement when using a tool ? We discuss different possibilities, below.

Despite that absence of a ‘complete’ internal model, tool geometry was still partially accounted for in closed-loop condition. We discussed three possible accounts (based on the General Introduction, Section 1.5.3) on how the alteration could have been accounted for. First, the existing internal model of the hand could have been adapted to reflect, or incorporate the properties of the tools. Second, the alteration of the tool geometry could have been added to the existing hand model. Third, a completely new internal model including the alteration could have been created. Our results appear not to be consistent with the third account, as there was no evidence of the development of internal model of the tools. Our experiment design was chosen to diminish the chances of seeing classical adaptation' of felt hand size (e.g. forgetting between session, a characteristic of adaptation, was not evident in our results). Thus, it appears unlikely that the existing hand model was altered (first account). Our results are however compatible with the use of some sort of visual model of the tool geometry that could be added to the existing hand model (second account), and that could not be used once vision was removed.

Our results are indeed consistent with tool grasping movements being primarily visually controlled. That is, removing visual feedback led to an absence of compensation for the tool geometries, and to a large decrease in success rate. Moreover, when visual feedback was available, and we observed a 'plateau phase' (suggesting an increased reliance on vision). Further, initial programming of grasping movements were quite similar across tools, suggesting that the tool-tips opening was visually controlled (as if the closure phase of the movement would only occur when the tool-tips aperture was visually larger, including a margin-for-error, than the object). We explore below, some possible explanations underlying that visual strategy.

First, as mentioned previously, it is likely that to build an internal model linking the desired tool-tips movements, and specific muscle activations needed to produce them, vision would have an important role (Sailer, Flanagan, & Johansson, 2005). In tool grasping, visual signals might be more reliable than proprioceptive ones. That is tools do not send direct signals about the position or the opening of the tool-tips. The brain has to derive them from the hand proprioceptive signals (Proske & Gandevia, 2012) and the knowledge of the tool geometries. As mentioned previously, participants only accounted partially for the tool geometries. Thus, interpreting hand proprioceptive signals with that incomplete understanding of the geometry would only lead to more uncertainty in the proprioceptive signals. Thus, to compensate, the reliability of the visual signals would likely increase (Jeannerod, 1997; Gentilucci et al., 1997; van Beers et al., 1999, 2002)

Second, it is possible that the system developed some kind of 'visual model' of the tools (e.g. relating visual space to hand posture). That is, there is evidence in the literature that vision could be mainly used in the first stage of motor planning, helping the system to define a movement plan in visual coordinates (Sarlegna & Sainburg, 2009). In the Optimal Control Theory framework, such a 'visual model' could be used to predict the potential visual consequences of the movement. Those predictions would then be compared to the actual outcome (allowing for continuous update of the model). Such a model is reminiscent of the distinction between forward (allowing for the prediction of future states of the movement based on the current state) and inverse (allowing to produce the desire motor outcome) internal models (McNamee & Wolpert, 2019; Mehta & Schaal, 2002; Wolpert et al., 1995; Wolpert & Kawato, 1998). A visual model resembles a forward model. Such a model would be the first to be learned (Wolpert & Kawato, 1998). It is likely that to operate a tool without visual feedback, the system would need an inverse model, to produce an accurate and successful movement (as the system could not rely on feedback). Our result suggest that such a model was not developed (no compensation for tool geometry without visual feedback to correct). Thus to operate a tool optimally, 'as a body parts', it is likely that both kinds of model would have to be learned (Itaguchi & Fukuzawa, 2014).

Compensation for tool geometries was evident, although not complete, when visual feedback was available. It seems there was a bias in the perception of the tool geometry. That is participants did not account for the full alteration introduced by the tool geometry. Assuming that the compensation factor reflects the actual internal representation of the tool geometry, we can interpret the compensation factors (as the percentage of the alteration accounted for). We observed a compensation of 0.36 with the 1.4:1 tool, suggesting the brain has an estimate of the tool geometry of ~1.144. For the 0.7:1 tool, the compensation factor (0.17) suggest an estimate of the tool geometry of ~0.949. Thus the brain does not appear to have a ‘complete understanding’, or a metrically accurate model of the remapping introduced by the tool geometry.

An evident characteristic of our compensation results is the asymmetry between the 0.7:1 and 1.4:1 tool, as participants reliably showed more compensation for the 1.4:1 tool than for the 0.7:1 tool. This is interesting because both tools have the same mechanical complexity. Similar results about the ‘difficulty’ of learning the mapping of a tool opening less than the hand have been reported by Golenia et al. (2014). Moreover, our results suggest that the visuomotor system had less of an understanding of the 0.7:1 tool geometry. This ‘lack’ of understanding of the 0.7:1 tool geometry had direct implications, such as a more skewed grasping profile, and a small success rate (under 50%) in open-loop conditions. Another evidence comes from the evolution of performance over time. Over the course of the experiment, participants opened the 0.7:1 tool-tips less while complete compensation would have required the opposite pattern. That is, planning similar tool-tips movement with all tools would have required larger 0.7:1 tool-tips opening (than what participants produced). This further suggests the brain did not have a clear understanding of the remapping induced by the 0.7:1 tool, or had a large bias in the perception of that alteration. We discuss possible explanations below. The first one comes from the statistics of the world. That is, the visuomotor system is exposed, across the lifespan, to some transformations more often, while others are never encountered. The visuomotor system may have developed internal models for the encountered transformations. We assumed participants may have experienced similar tools in their life (e.g. pliers opening when the hand is open, like a pair of scissors). It is unlikely however that they had encountered a tool opening less than the hand (such a tool requires more effort to operate, without bringing a clear advantage). Second, to operate the tool ‘optimally’, a larger hand opening than usual is required. As mentioned in the General Introduction, grasping can be interpreted as an optimisation problem, where the system has to maximise the chance of success, while minimising some other costs, such as energy, discomfort, jerk, muscle activation, etc. (Todorov & Jordan, 2002; Wolpert et al., 1995). The 0.7:1 would require an extra movement, requiring more jerk, more muscle activation, more energy and likely some discomfort. As success rate was nearly at ceiling level, it is then possible that the movements produced with that tool were the optimised version of the movement, minimising most of the costs. Third, it is possible that participants could not produce the ‘extra’ movement required to use the tool optimally. That is there is a ceiling in hand opening for the larger object sizes. This ceiling effect might explain the difference in success rate observed when visual feedback was removed (and the absence of compensation for the tool geometry). Indeed, hand opening was highly similar with the three tools in that condition. This would directly affect the success rate, as the same hand opening would lead to large margin-for-error with the 1.4:1 tool and small ones with the 0.7:1 tool, increasing the chances of grasping the object with the 1.4:1 tool.

Some participants may have been better ‘compensators’ than others. Our results showed individual variability in the degree of compensation. A correlation analysis revealed there was a positive relationship (Fig. 3.27; $r(19) = .77$, $p < .001$) between the compensation factors for both tools. This suggests that some participants were indeed better at compensating for tool geometries in general. Different individual patterns of learning have been observed in Golenia et al. (2014), suggesting that some individual differences play a role during motor learning. Thus it is likely that some participants would be better at developing model of tools than others.

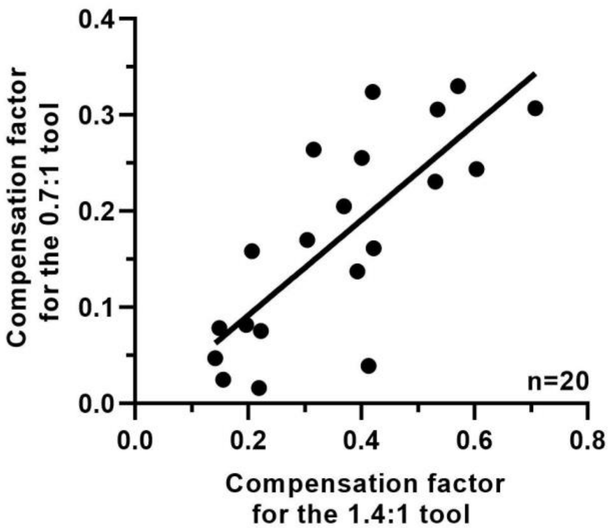


Figure 3.27. Relationship between compensation factors for the 1.4:1 tool and the 0.7:1 tool. Solid lines show the best fitting linear regressions to the data.

We expected participants to develop internal models of tools. Our results did not show compelling evidence of their presence. Different factors may have impaired the learning of internal models. First, the experiment design may have favoured the learning of a more ‘general mapping’. Second, the design of our experiment (constantly switching between the different tools) may have hindered the learning. Third, our tools ‘behaved’ like the hand. Fourth, the timescale of our experiment might not have captured the development of internal models. We discuss those potential explanations, below.

One factor that may have impacted the learning of internal models of tools is the task structure. When facing a task, the motor system extracts a set of general principles and motor strategies (Braun et al., 2009, 2010). In our experiment, participants are constantly exposed to three different tools with similar mechanical complexity, it is then possible that the motor system extracted general principles about the three tools. That is, our design may have inadvertently pushed participants to develop a ‘generic’ tool model. On a given trial, the brain would then ‘fine-tune’ the movement to the tool that has to be used (using different parameters depending on the specific tool used). This interpretation is supported by the similar hand movements produced with all tools, and by the decrease of tool-tips aperture observed with all tools.

A second factor is the constant tool switching. That feature might have impacted the learning is by making the ‘credit assignment problem’ more complex. That is, the attribution of error signals to the correct underlying cause may have been difficult. The error signal from a single trial is noisy, and by nature difficult to attribute to the correct source (Wolpert & Landy, 2012). As the tool was changed at every trial, information about an error (direction, magnitude, …) would have to be stored to be used in a few trials (between two and four trials), potentially degrading the quality of that information (until there is no information left). Hence, by making ‘classical adaptation’ less likely, we may have unwillingly made the ‘credit assignment problem’ very complicated, and the feedback coming from error signals less efficient. Further, randomisation of trials represents high contextual interference (Brady, 1998; Magill & Hall, 1990; Merbah & Meulemans, 2011) and thus requires a higher cognitive activity. It has been hypothesised that it would lead to increase retention (Magill & Hall, 1990). However, when learning some new skills (dependent on the type of skill), high degrees of contextual interference might actually impair motor learning (Brady, 2008; Magill & Hall, 1990), by making learning too difficult. In that situation, it may be beneficial for participants to start a task with less contextual interference (e.g. blocked trials) before increasing the degree of interference (Brady, 1998; Magill & Hall, 1990). Thus our 'learning environment' may have render the development of internal models really slow, or not possible. In the next chapter, we will investigate if a different 'learning environment', in which participants would be constantly exposed to a single tool mapping at a time, can produce different learning outcome.

In some studies (Takahashi & Watt, 2014, 2017), participants had to learn and store different mappings without impacting the retention of the other mappings. Our experimental design requires the same process. This situation is reminiscent of so-called dual-adaptation experiments in which participants have to adapt to both conflicting transformations (Martin, Keating, Goodkin, Bastian, & Thach, 1996; Welch, Bridgeman, Anand, & Browman, 1993). Those experiments show that adaptation appears, although after longer training period. That is, the process of consolidation of the two opposite mappings interferes (creating conflict in the credit assignment problem; Krakauer, Ghilardi, & Ghez, 1999). Eventually, participants are able to switch between the transformations without a decrease of performance response (Krakauer et al., 1999; Wada et al., 2003; Woolley et al., 2007). In those experiments participants were only exposed to two transformations in a controlled environment. Our experiment introduces three transformations, added to the challenges of using our tools (reduction of tactile sensitivity, mechanical constraints, …), thus making the learning process of internal model for the three tools through adaptation (if adaptation is the mechanism underlying the development of internal tool model) even more difficult.

A third factor is that our tools 'behaved' like the hand (Arbib et al., 2009), as the movement of the tool-tips closely 'followed' the movements of the thumb and index finger (varying only in terms of a gain parameter). This relates to the distinction between adaptation versus skill learning

(Wolpert & Flanagan, 2016). In that framework, tools ‘behaving’ like the hand favour adaptation of existing models as a mode of acquisition of internal models. It is possible that adaptation is the main mechanism used by the visuomotor system to develop internal model of tools. And by rendering adaptation less likely, we may have rendered the task of learning internal model really difficult, if not impossible. Our experiment however, does not allow for direct testing of adaptive processes. We will investigate the potential adaptation underlying compensation for tools that ‘behave’ like the hand in Chapter 4, and the use of tool not behaving qualitatively like the hand in Chapter 5.

Another factor that may have limited the mappings learning is that the time window in which we examined the development of internal models of tools. The duration of the experiment (8h) matters, but not as much as the active exposure duration to each tool (525 trials: 360 trials in closed-loop conditions and 165 in open-loop conditions). It is difficult to know if such a number of trials is ‘enough’ to expect evident sign of development of internal model. The dual-adaptation literature shows that the number of trials can vary greatly (e.g. Over 5000 trials per condition, Martin et al., 1996; 1670 trials per condition, Wada et al., 2003; 275 trials per condition, Woolley et al., 2007; 264 trials per condition, Krakauer et al., 1999). We reasoned that we had ‘enough’ trials compared to some studies to be able to expect signs of development of internal models. Our results may indicate a lack of exposure to the different tools. Nevertheless, as discussed previously, by rendering adaptation less likely, it is possible that internal models of tools would be developed through ‘skill learning’. This process would likely be slow (Abe et al., 2011; Reis et al., 2009) and require longer training than during an adaptive process. Taken together, it is possible that our ‘learning environment’ failed to capture the development of internal models of tools, and that more training would be needed for internal models of tools to be developed.

Using only kinematic indices to define a movement, or a certain level of performance could be misleading. Our results showed that similar kinematic indicators might have been produced by ‘different’ control processes. When comparing the hand to the 1:1 tool in closed-loop conditions, only examining movement end-effector opening, success rate and movement velocity lead to the impression that the movements were similar and thus were similarly controlled. Observing the movement as a whole (through the use of overall grasping profiles) revealed that although those indicators do represents the movements, they don't tell 'the entire story', as they mask subtle differences in movement control ('plateau phase', difference in opening and closing phase of the grasp). This indicates that we need to be careful in interpreting and giving meaning to kinematic indicators. They should be interpreted in the larger context of the whole movement.

No a-priori analysis was done because we could not rely on existing literature to define an expected effect size. Thus, we performed some sensitivity analysis for the expected signatures of tools being used as body parts. First, during closed-loop conditions, sensitivity analysis revealed that, with each effector, we found larger effect size than the minimal detectable effect size for both the movement velocity scaling to object distance (minimal detectable effect size is 0.58; 0.7:1 tool: d = 4.26; 1:1 tool: d = 4.4; 1.4:1 tool: d = 4.04) and the scaling of tool-tips aperture with object size (mdes = 0.58; 0.7:1 tool: d = 3.65; 1:1 tool: d = 3.95; 1.4:1 tool: d = 3.8) and for presence of compensation for the tool geometries (mdes = 0.76; 0.7:1 tool: d = 1.71; 1.4:1 tool: d = 2.32). Second, for the presence of those key signatures in open-loop conditions, sensitivity analysis revealed that we found larger effect size than the minimal detectable effect size for both movement velocity scaling to object distance (mdes = 0.58; 0.7:1 tool: d = 4.28; 1:1 tool: d = 4.13; 1.4:1 tool: d = 3.76), the scaling of tool-tips aperture with object size (mdes = 0.58; 0.7:1 tool: d = 2.7; 1:1 tool: d = 2.51; 1.4:1 tool: d = 2.11) and the presence of compensation for tool geometries (mdes = 0.76; 0.7:1 tool d = 0.58; 1.4:1 tool d = 1.17). Interestingly, the effect size for the compensation for the 0.7:1 tool, although is statistically significant, is lower than the minimal detectable effect size. This suggests that the found effect is below the bound of what our study was set to detect, but this effect, however small (0.75mm difference in hand opening) was reliable. Overall, most of our effects can be categorized above 'large' effect size and taken together, those analysis suggest that we have a large enough sample size to detect the effects we are looking for and that the detected effects are practically significant.

3.5 Conclusion

Our results indicated that the visuomotor system was able to produce the anticipatory features of hand grasping. Tool geometry was partially accounted for when visual feedback was available. We did not find however evidence for the development of internal models of tools geometry, similar to those existing for the hand. Thus, our results appear non consistent with the framework of the 'tool used as a body part'.

Chapter 4 – Is adaptation the principal mechanism by which tool geometry is accounted for ?

4.1 Introduction

We saw in Chapter 3 that participants were able to show anticipatory behaviours, such as scaling of the maximum tool-tip opening to object size and scaling of the movement velocity to object distance. However, we did not find compelling evidence that the visuomotor system had developed an accurate internal model of the tool mappings similar to that thought to exist for the hand. Participants showed only partial compensation for the differences in tool geometries when vision was available, and this was further reduced (to a very low level) when visual feedback was removed.

In this chapter we investigate several issues arising from Chapter 3, with the aim of building a clearer picture of what is learned when using our tools, and how. First, we examined whether more consistent exposure to the same tool mapping results in increased compensation for tool geometry. Second, we probed the mechanisms behind the learning of tool mappings by examining whether compensation for tool geometry results from adaptation of the felt opening of the hand per se, or is more consistent with developing a distinct mapping/model of the tool. Third, we probed the integrity, and generality, of the learning of tool mappings by asking participants to produce sizes with the unseen tools/hand, and by measuring the ability to discriminate the sizes of objects felt with the different tools. We explore each of these issues in turn, below.

One possibility is that acquisition of internal models of the tools is possible in the timescale of the experiment in Chapter 3, but that the process was substantially slowed by the requirement to change tools on every trial. We structured the experiment this way because we wished the average tool gain in any block of trials to be 1:1, to prevent ‘classical’ adaptation of felt hand size. We reasoned that such adaptation could cause results consistent with an internal mapping of the tool via a different mechanism (i.e. a false positive). It is possible, however, that the requirement to switch tools frequently, and learn three tool geometries at the same time, interfered with learning (see work on dual adaptation for similar findings: Krakauer et al., 1999; Martin et al., 1996; Wada et al., 2003; Woolley et al., 2007). To examine this, in this experiment participants completed blocks of trials using the same tool, only switching between sessions. This manipulation would also reduce the degree of interference, likely improving learning and performance at the task (Brady, 1998, 2008; Magill & Hall, 1990) . If this results in faster acquisition of tool mappings, we would see greater compensation for tool geometry in this experiment than in Chapter 3.

We also probed the mechanisms underlying compensation when tool geometry was consistent. We consider several possibilities in the following paragraphs. By blocking tool use we increased the likelihood that compensation for different tool geometries could be achieved by adaptation of the felt opening of the hand. From the perspective of internal models of tool mappings this appears to be a false-positive result, as discussed above. It is possible, however, that such adaptation is in fact the normal mechanism by which we 'learn' to use tools such as this when possible (and which we unwittingly prevented in Chapter 3). As discussed in Chapter 3, our simple pliers *behave* like the hand in that grasp aperture qualitatively 'follows' the opening of the thumb and index finger (allowing for the use of existing motor programmes), varying only in terms of a gain parameter. Thus, adaptation of felt hand opening could in principle be used to adjust the hand internal model to take account of tool geometry changes. Critically, this account does not imply an explicit or distinct mapping 'stage' that relates hand posture to tool-tip positions. Evidence that felt hand size can be adapted comes from the demonstration that systematically altering the opening of graphical representations of the finger and thumb in normal grasping movements causes after-effects in subsequent movements (Cesanek & Domini, 2018). To examine whether this occurred during tool use we asked participants to produce the size of a seen object by opening their unseen hand, immediately following each block of trials with a tool. The expectation is that alterations in the felt opening of the hand caused by using the 0.7:1 and 1.4:1 tools would result in opposite 'classical adaptation' after-effects in the opening of the unseen hand during size production (c.f. Cardinali et al., 2009).

It is possible that the different experiment protocols in Chapter 3 and Chapter 4 result in different mechanisms for compensating for tool geometry. For instance, adaptation could occur where possible (i.e. in this experiment), yet the incomplete compensation we saw in Chapter 3 (when steps were taken to minimise adaptation) could be due to a different mechanism. We cannot readily distinguish between these possibilities. For example, in principle, one could prevent adaptation, yet present tool geometries blocked, in order to isolate whether the costs of switching tool models per se limits the amount of compensation. But to our knowledge this experiment is not possible in practice. Similarly, if adaptation contributes to effects with trial-by-trial tool changes, and effects would likely be very small. Thus, if we find adaptation of felt hand opening in this chapter, we cannot infer that it was also present in Chapter 3. If we find no evidence of adaptation in the current experiment (when it is most likely to occur), however, along with high levels of compensation, we can reasonably conclude that adaptation of felt hand size is not the principal mechanism by which tool geometry is compensated for.

A lack of adaptation of the felt hand opening implies that the required change may include a distinct stage that takes into account the (changing) relationship between hand and tool. For tools that transform the mapping between hand and end-effector in complex ways that differ qualitatively from hand movements (consider actions involved in driving a car, for instance) it seems likely that the system must create a new internal model or control process (Telgen et al., 2014). Indeed, all tools may require *de novo* models. It seems plausible that where tools *behave* like the hand, however, it may be possible to quantitatively adjust, or fine-tune, a ‘copy’ of the normal hand control programmes to account for tool geometry, which might be expected to be quicker/easier than acquiring altogether new models (Telgen et al., 2014). Our size-production task cannot distinguish between these possibilities, but is instead designed to determine whether compensation for tool geometry was caused by adaptation of felt hand size or some other process. Chapter 5 explores the idea of adapting existing grasp control processes in more detail.

Finally, this experiment also probed the nature of the acquired tool mappings in two additional ways. Firstly, we asked whether ‘training’ with grasping movements with the tools transferred to perceptual experience of tool opening. To do this we asked participants to open the tool-tips to produce the size of a visual object, with neither the tool nor hand visible. Similar to grasp control, achieving this accurately requires the haptic signal about hand opening to be interpreted taking into account the effect of tool geometry. As discussed in previous chapters, the capability to interpret afferent signals from the hand in terms of what they indicate about the movements of the tool tips is presumably important for calibrating models used to control movements, and for online control. We might therefore expect a close relationship between these processes, or even a common mapping. Differences between tool compensation across grasping and size-production would constitute evidence that there are distinct processes for perceptual control of tools and interpreting sensory signals from them. Conversely, similar patterns of effects would be consistent with (though not definitive evidence for) a common underlying remapping. We also reasoned that a similar asymmetry in tool compensation for the 1.4:1 and 0.7:1 tools in this perceptual task would provide stronger evidence that it reflects underlying differences in acquiring the tool mapping for the 0.7:1 tool, rather than reflecting constraints due to movement per se. Secondly, participants completed a psychophysical haptic size-discrimination task with each tool, following blocks of grasping trials. Performance in this task is thought to reflect the noise in the brain's estimate of haptic size (Ernst & Banks, 2002). Normally we would expect haptic size-discrimination performance to be constant in units of hand opening (i.e. the sensitivity of the hand, per se, would not be expected to be altered by the tool geometry; Takahashi & Watt, 2014). However, results of a previous pilot study in our lab hinted at significantly noisier haptic size estimates when using the 0.7:1 tool, raising the prospect that noise in the brain's knowledge of the tool mapping might propagate into perceptual estimates of sizes experienced via the tools.

The experiment was divided in three sessions, one session for each tool. Each session was composed of a training phase followed by the size-production task with the hand, the size-production and size-discrimination tasks with the tools.

4.2 Methods

4.2.1 Participants

8[3] right-handed participants completed this experiment (4 female, 4 male; aged 21-36 years old). All participants had normal or corrected-to-normal vision, and no known impairments that would affect their ability to grasp. Participants were rewarded at the rate of £6 per hour. Participants gave informed consent prior to taking part, and all procedures were in accordance with the Declaration of Helsinki. No participants took part in the experiment in Chapter 3. One participant took part in the second experiment in Chapter 5 (which did not involve learning different tool 'gains').

4.2.2 Apparatus, stimuli and tasks

The experiment was composed of three different tasks, each completed with the same three 'different-gain' tools used in Chapter 3, and with the hand: a grasping task (exactly as the full-vision condition in Chapter 3), a size-production task, and a perceptual size-discrimination task. The new tasks and apparatus required are described below.

Size-production task

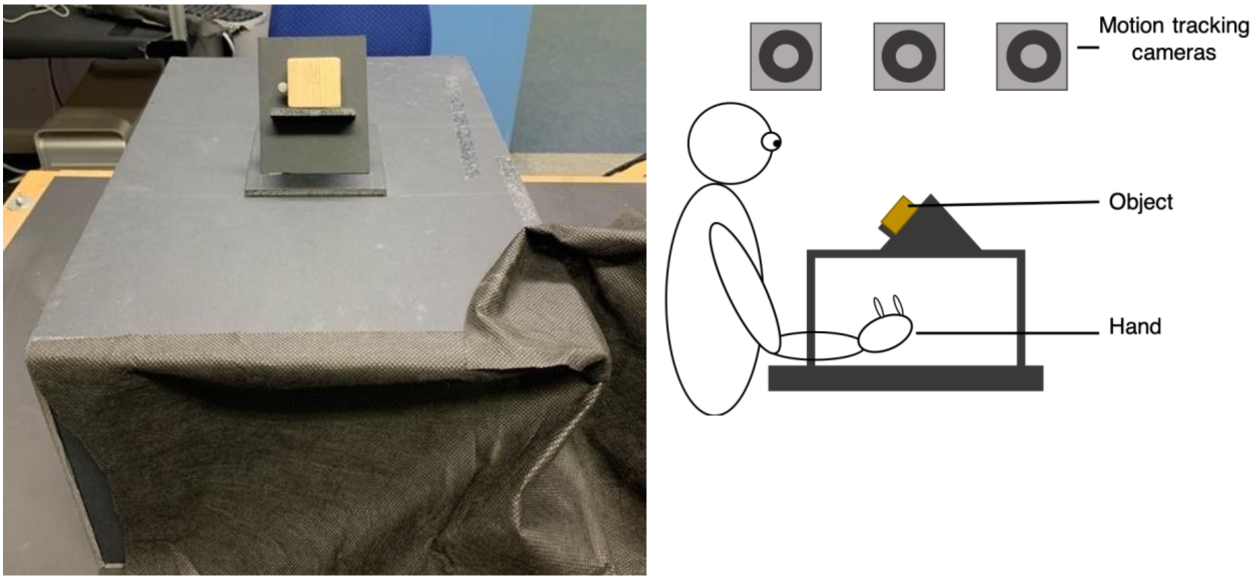
The size-production task required participants to open their unseen hand/tool to match the size of an object they could see. The stimuli were the same objects used in Chapter 3, sized 25, 30, 35, 40, & 45 mm.

To hide the hand/tool, a box 300 x 400 x 210 mm was placed in front of participants, as shown in Fig. 4.1. The box was opened on the sides, allowing the ProReflex motion cameras to record the position of the markers, and the experimenter to monitor what the participants were doing. The box prevented participants from seeing their hand or the tool while performing the task. An object was displayed on a stand on top of the box, as seen in Fig. 4.1. The task required participants to open their index and thumb to match the size of the object. Specifically, they were asked to produce the grasp

[3] Testing was stopped at a certain date after a decision made by the PhD comity. We were unable to test more participants before that date.

opening that they would make if they were holding the object (i.e. the object size had to be represented between the pulpar surfaces of the thumb and index finger or between the insides of the rubber balls on the tools). Participants were instructed to inform the experimenter when they had opened their hand/the tool to the intended opening. We capture the 3-D separation between the markers (corrected for marker positions to reflect the actual separation between the pulpar surfaces of the digits or the insides of the rubber balls) for 60 frames (250 ms).

When the size-production task followed the tool training phase (size-production: adaptation in Fig. 4.3), we aimed to capture the current state of adaptation. We feared vision of the hand could allow the motor system to recalibrate, and thus adaptation would disappear. To maintain a hopefully reasonably pure measure of the current of adaptation, we kept the goggles closed during the transition between the task. That is, at the end of the grasping training phase, the goggles stayed closed and participants were asked to move their hand inside the box with the tool, and then to drop the tool. Markers were then attached to their finger-tips (in the same position each day). Only then were goggles opened, allowing for normal viewing and for the task to start.

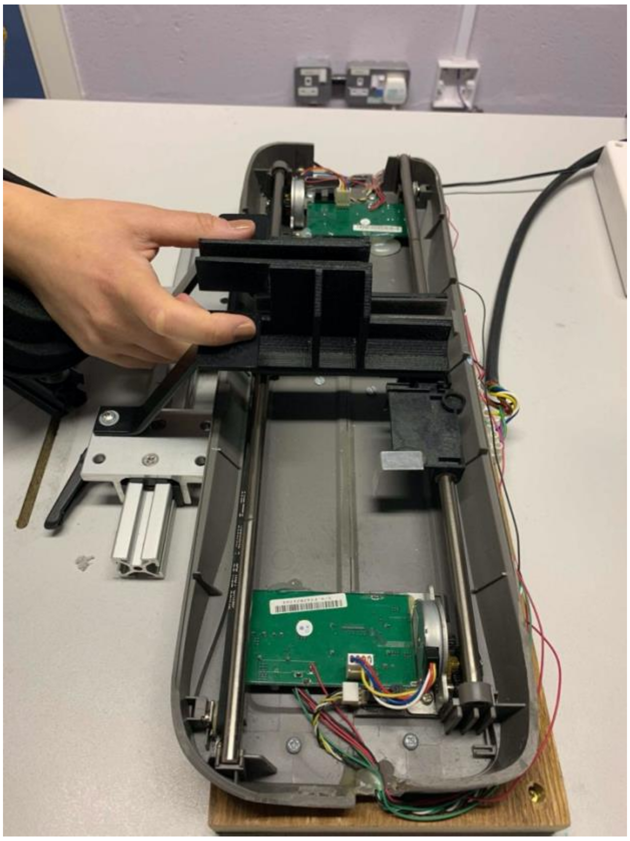


(a) **(b)**

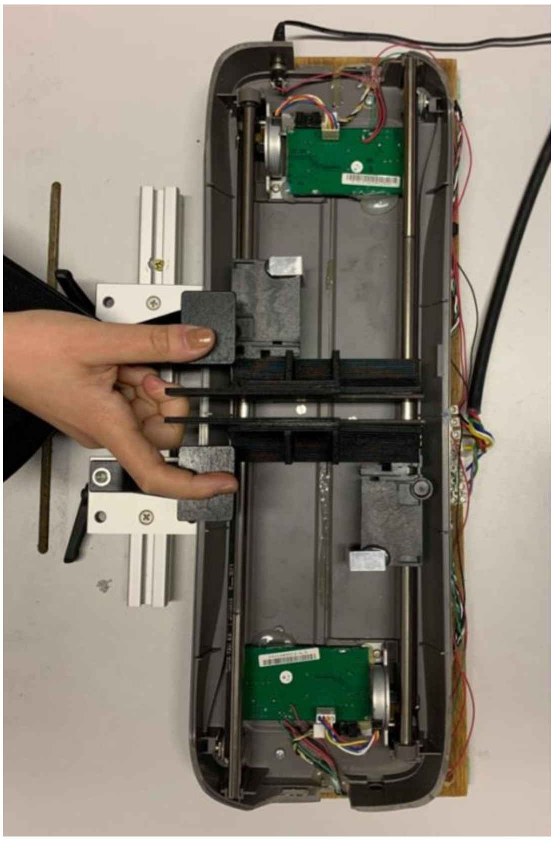
Figure 4.1. Size-production task. (a) Picture of the box used to obstruct vision of the hand and/or the tool and the object presentation during a trial from the perspective of a participant. (b) schematic of the experimental set up from the perspective of the experimenter.

Size discrimination task

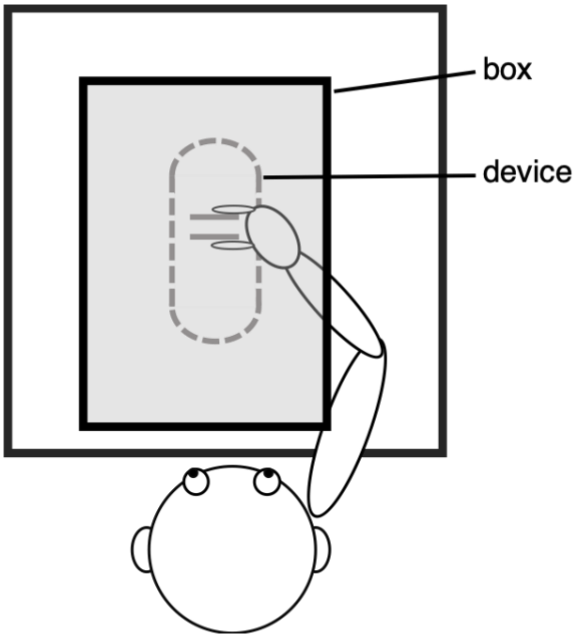
The ability to discriminate object size was measured using a two-interval, forced-choice psychophysical task (2-IFC). Different object ‘sizes’ were presented using a device that moved two motorized plates, using stepper motors, controlled by a computer (shown in Fig. 4.2). Each plate could be moved independently to create differently sized “objects“, at different distances. The resolution in size was ~0.1 mm. Between stimulus intervals participants rested their fingers (or the tool tips) on two platforms, which can be seen in Fig. 4.2. The pads did not move with the plates, but provided a resting position between trials/stimulus intervals. These were employed to minimize the movement required to feel the object, thereby minimising both the risk that the object would not be grasped successfully, and the participants’ uncertainty about when they were feeling the object (potentially a problem when using the tools, which greatly reduced tactile feedback; see below).



(a)



(b)



(c)

Figure 4.2. Device used for the size-discrimination task. (a) Picture from the side. (b) Picture from above. The black plastic plates are the surfaces moved to change 'object' size. A participant is shown positioning her thumb and index finger on the finger platforms, prior to feeling the 'object'. (c) Schematic of the actual experiment. The entire apparatus, including the hand/tool, was covered by a box, to prevent any visual signals to object size, or hand/tool opening.

Participants were asked to put their index finger and thumb, or the tool-tips, on the pads. On each trial they were asked to feel two “object“ sizes, one after the other, and to indicate which was larger. On each stimulus interval the plates moved until the desired object size, and an auditory signal conveyed to the participants when they should feel the object. They were given practice so that they learned to squeeze each object briefly, and release, so that the mechanism could move in-between unimpeded. The time between presentation of each interval was 1500 ms. On each trial within a block, one interval was the same standard size (see below), and the comparison size was controlled using an adaptive staircase. Two types of staircase were used: (i) 1-up, 2-down, and (ii) 2-up, 1-down. For a 1-up, 2-down staircase, for example, this means that the difference between the standard and comparison sizes increased (making the task easier) following one incorrect answer, and decreased (making the task harder) after two consecutive correct answers. The staircases changed with an initial step of 8 mm, which was halved after each of the first three reversals, resulting in steps of 4, 2, then 1 mm). This method distributes data along the psychometric function, with data points concentrated at the most informative positions (Hillis, Watt, Landy, & Banks, 2004). The order of presentation of the standard and comparison intervals was randomised on each trial. The objects’ position (distance from the participant) was also jittered by a small amount on each trial, by moving both planes in the same direction, to ensure that the task could not be completed by comparing the position of a single digit across stimulus intervals. Participants did not wear headphones as the sounds of the device were not informative about which interval was larger. No feedback was given to the participants regarding their performance during the experiment. A block finished after 10 staircase reversals (when the staircase changed direction) or after 100 trials had been completed.

Object-size discrimination thresholds vary somewhat idiosyncratically as a function of object size/hand opening (Takahashi & Watt, 2014). Thus, we needed to match the hand opening used across the different tools (and hand). We chose a ‘base’ hand opening of 40 mm for all conditions, resulting in object sizes felt with the tools of 28 mm with the 0.7:1 tool, and 56 mm with the 1.4:1 tool. The object size with the 1:1 tool was of course 40 mm.

Because the tools reduced tactile feedback we were concerned that participants might find it difficult to know when they were squeezing the object, making the task more difficult. To counter this, we replaced the rubber balls on the tool-tips with hard plastic balls of the same diameter (leaving tool geometry unaffected), providing a clearer tactile signal, and an auditory cue, to object contact.

With each tool, and with the hand, participants completed two repetitions of each staircase type (i.e. four staircases per psychometric function), resulting in approximately 160 trials per psychometric function.

4.2.3 Procedure

Each day, participants performed all of the tasks with a different tool, and some tasks with the hand. Fig. 4.3 shows the evolution of the testing blocks on the first day (top panel) and the remaining two days (bottom panel). The day on which each tool was used was counterbalanced across participants.

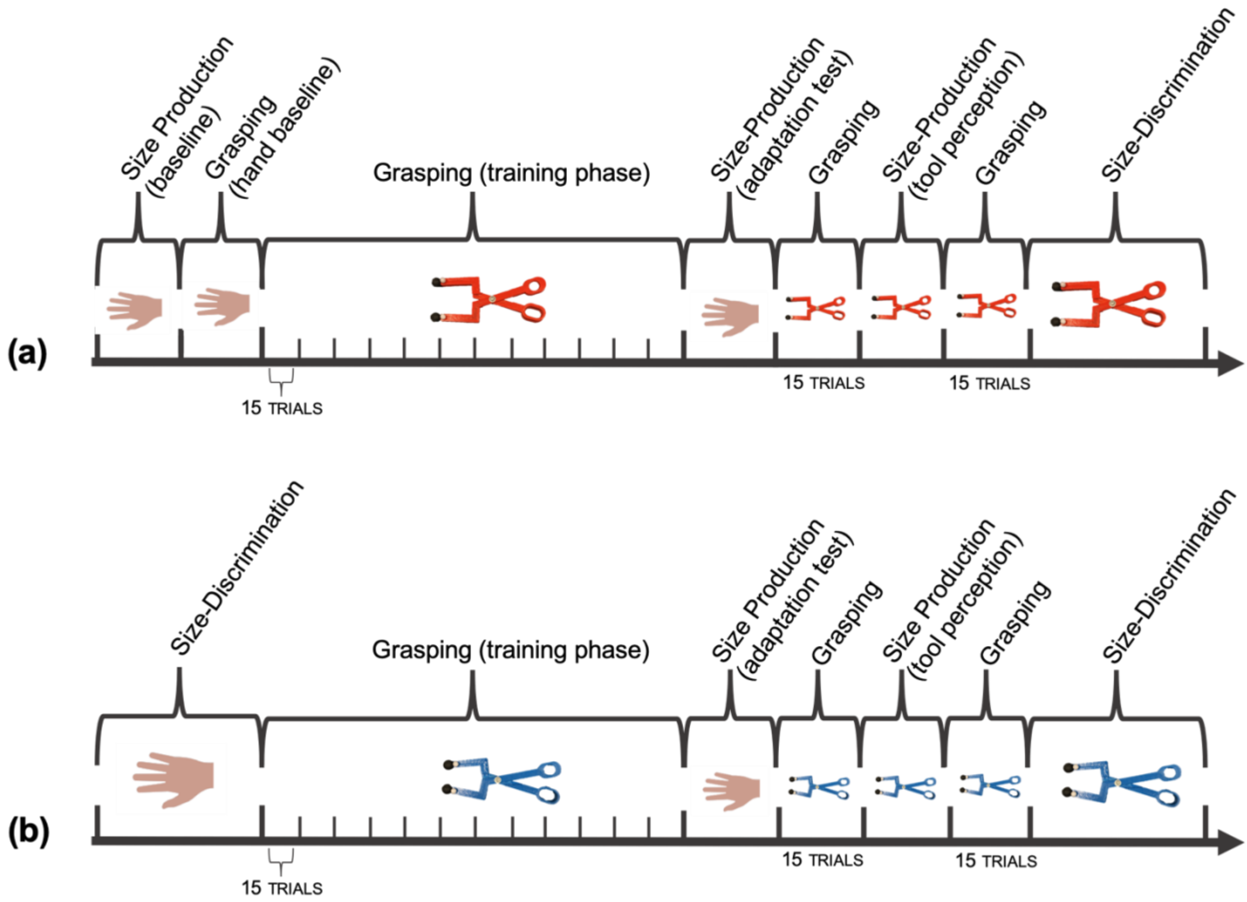


Figure 4.3. Experiment design. Schematic representation of the design of (a) first session and (b) the second and third session. The tool pictures represent examples of which tool was used.

In the grasping task, the procedure was the same as in Chapter 3. A block of grasping trials consisted of one presentation of each object size at each distance, making 15 trials. A block of size-production consisted of 3 presentations of each object size, making 15 trials. The order of presentation of object size and distance (where applicable) was randomized.

On the first day, participants started with one block of hand-grasping, followed by one block of size-production with the hand, providing baseline measures for each task. Then, they performed a tool-training period, consisting of 12 blocks of grasping with the defined tool for this day. After training, participants performed a block of size-production with their hand, to measure the after-effect of using the different tools (making sure participants could not see their hand, by keeping the goggles closed) Then, participants performed one top-up block of tool grasping (15 trials), to mitigate any ‘forgetting’ of the tool geometry while the hand and tool were unseen. They then completed one block of size production with the defined tool for the session, followed by another top-up block of grasping. Finally participants completed the size discrimination task with that day's tool. On the second and third days, participants began by completing the size-discrimination task with the hand. Then, the remainder (from tool training onwards) was the same as for day 1, except with different tools. The number of trials was, as in Chapter 3, chosen to maximise the exposure to each tool in a certain time window, as we were uncertain about the effect of changing from randomisation to blocked trials. Further, here, the goal was not to observe the development of a tool model, so less trials were required.

4.2.4 Data analysis and predictions

As in Chapter 3, we aim to address specific a priori questions. We will therefore use the same approach, constraining our analysis primarily to testing a small number of well-specified predictions, for specific dependent measures (Section 3.2.4). First, we aim to investigate whether giving constant exposure to a single tool geometry (by blocking the trials) improves the acquisition of tool mappings. To investigate this, we applied the same analysis structure to Chapter 3 (as the visual feedback condition). Thus we will investigate the presence of velocity and grip scaling, and of accounting for the tool geometries by analysing the presence or absence of compensation for the tool properties of the 0.7:1 and 1.4:1 tools by comparing the data to expected data under two boundary conditions: (i) tool geometry is completely accounted for, and (ii) tool geometry is not accounted for at all. Mainly, we expect that the blocking of trials will improve the amount of compensation for the tool geometry (for the 0.7:1 and 1.4:1 tools). We will therefore investigate this by comparing directly the amount of tool compensation for both tools between this experiment and the experiment in Chapter 3, using planned comparisons (one-tailed t-tests). We will explore whether a difference in amount of compensation is reflected in the overall grasping profiles. We will then investigate the presence of learning effect during the training phase of the grasping task by comparing the 30 first to the 30 last trials of that training phase using pair-wise planned comparisons (one-tailed t-tests) on previously analysed kinematic indices. Here, the prediction is that learning would be evident in higher compensation values and faster movement velocity.

Second, we aim to investigate whether accounting for the tool properties is the result of adaptation of felt hand opening during the training phase of the grasping task. We will investigate this during the Size Production (adaptation) test by comparing hand aperture when not using a tool, immediately following using the 0.7:1 tool or 1.4:1 tool, using planned pair-wise comparisons (one-tailed t-tests, Bonferroni corrected for multiple comparisons). We will also examine hand aperture immediately after using the 1:1 tool—which should cause no adaptation of felt hand size under any circumstances—to account of possible effects of using a tool per se. If adaptation is the main mechanism underlying the accounting for tool properties, hand aperture during size production should be different following use of the different tool geometries. There is a clear predicted direction of these differences: smaller hand aperture after the use of the 1.4:1 tool (would make the hand opening feel larger), and larger hand aperture after the use of 0.7:1 tool.

Third, we aim to investigate whether the tool mappings built during the training phase of the grasping task could be transferred, and used in a Size Production task (tool perception) with the tools (i.e. the 0.7:1 and 1.4:1 tools). Using the same approach as for the kinematics grasping data, we will analyse the presence or absence of compensation for the tool properties of the 0.7:1 and 1.4:1 tools by comparing the data to expected data under two boundary conditions: (i) tool geometry is completely accounted for, and (ii) tool geometry is not accounted for at all. We will also correlate (one-tailed Pearson's correlation) the compensation factors in both tasks. If participants used the same tool model in the grasping task and the size-production (tool perception) task, we expect to observe a positive relationship across tasks between the amount of compensation with both tools.

Lastly, we aim to investigate whether tool geometry influences the Size Discrimination task. To examine this, we will compare using pair-wise comparisons (t-tests) the Just Noticeable Differences between the 0.7:1 and 1.4:1 tools, and the 1:1 tool (Bonferroni corrected for multiple comparisons). A difference in JND would imply that the tool model (and the noise in the brain's perception of the tool geometry) influences the perceived size.

4.3 Results

4.3.1 Grasping task: Does tool use show anticipatory scaling with object properties?

We expected that anticipatory scaling of (i) peak velocity with object distance, and (ii) peak grip aperture with object size, would again occur in this study, when learning of the tools should if anything be enhanced by blocking the tool type. We analysed this in the same manner as in Chapter 3.

Peak velocity scaling with blocked tools

Fig. 4.4a shows the peak velocity with each effector as a function of object distance (collapsed across object size). The figure shows participants did scale the peak velocity of their movement with object distance, in all conditions. We examined the statistical significance of this in the same manner as previously, by testing whether the mean scaling slopes differed from zero in each condition (see Section 3.3.2). One sample t-tests showed that in all cases, the scaling of peak velocity with distance was significant (hand: t(7) = 9.22, $p < .001$, $d = 3.24$; 0.7:1 tool: t(7) = 19.46, $p < .001$, $d = 6.8$; 1:1 tool: t(7) = 17.31, $p < .001$, $d = 6.01$; 1.4:1 tool: t(7) = 13.18, $p < .001$, $d = 4.63$).

The figure also suggests that, as in Chapter 3, movements with tools were overall slower than hand grasping. To investigate this we collapsed the peak movement velocity across object distance and size (Fig. 4.4b). It can be seen that movement velocity appears higher during hand grasping. To analyse the effect statistically, an one-way repeated measures ANOVA on the peak velocity with effector as the factor. The ANOVA revealed a main effect of effector (F(3,21) = 8.85, $p = .001$, $\eta_p^2 = .084$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that movement velocity with the hand was significantly higher than with the 1.4:1 tool ($p = .019$) but not with the other tools (0.7:1 tool, $p = .066$; 1:1 tool, $p = .207$). There was no significant difference between the tools. Thus, we can interpret differences in peak grip aperture as the effect of using tools with different geometry, and not some sort of trade-off between movement velocity and grip aperture.

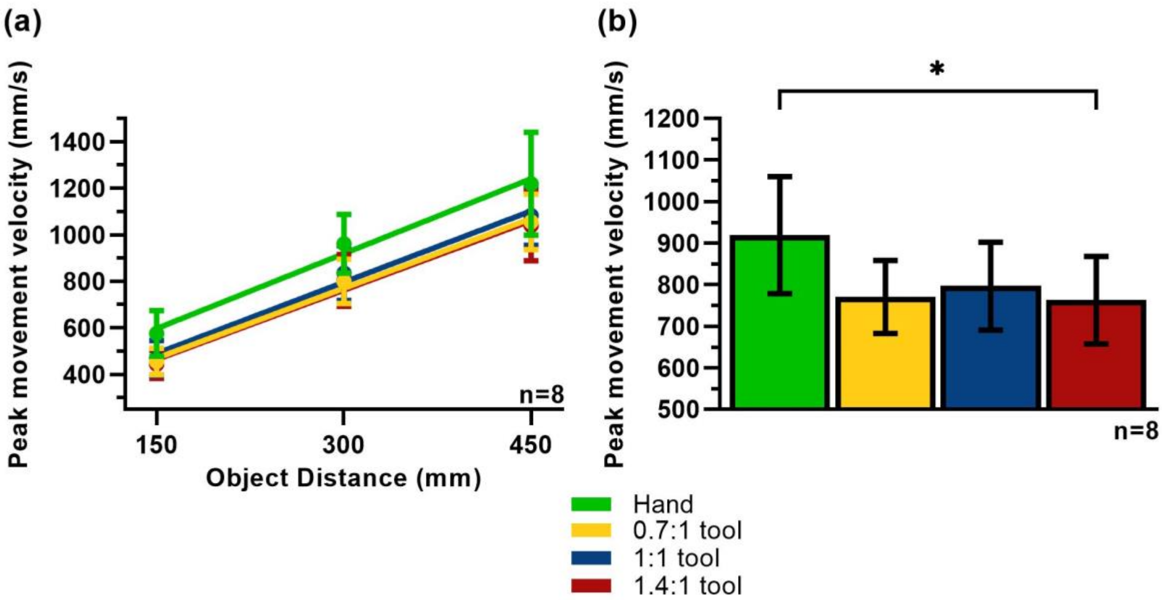


Figure 4.4. Peak velocity with blocked tools. (a) Mean peak velocity of grasping movements with each effector as a function of object distance (collapsed across object size). Solid lines show the best fitting linear regressions to the data in each case. (b) Same data collapsed across object distance. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Overall, participants scaled their movement velocity with object distance with all effectors, as observed in Chapter 3 (see Section, 3.3.2). However movement velocity with the hand (in this experiment) was only reliably different from the 1.4:1 tool, which is different from the experiment in Chapter 3, where movement velocity during hand grasping was reliably higher than during tool grasping. Average hand movement velocity was similar between this experiment (919 mm/s) and the experiment in Chapter 3 (893 mm/s), while average tool movement velocity (collapsed across tools) was higher in this experiment (777 mm/s) than in the experiment in Chapter 3 (697 mm/s). To examine the differences statistically, we ran independent t-tests for all effectors. Movement velocity was not significantly higher in this experiment than in the experiment in Chapter 3 with all effectors (hand: t(26) = .4, p = .694, d = .02; 0.7:1 tool: t(26) = 1.51, p = .144, d = .63; 1:1 tool: t(26) = 1.96, *p* = .061, *d* = .82; 1.4:1 tool: t(26) = 1.23, *p* = .207, *d* = .54). Taken together, it appears movement velocity with tools in this Chapter was closer to hand movement velocity.

Peak grip aperture scaling with blocked tools

As in Chapter 3, we examined the object-size scaling. Fig. 4.5 shows the peak end-effector aperture for the different effectors as a function of object size (collapsed across distance). It can be seen that larger peak end-effector apertures were produced for larger objects, with all effectors. We again analysed mean slopes, using one-sample t-tests, and found that grip scaling was significantly greater than zero for all effectors (hand = 0.83, t(7) = 9.98, $p < .001$, *d* = 3.48; 0.7:1 tool = 0.52, t(7) = 9.1, $p < .001$, *d* = 3.31; 1:1 tool = 0.66, t(7) = 12.49, $p < .001$, *d* = 4.4; 1.4:1 tool = 0.72, t(7) = 13.34, $p < .001$, *d* = 4.8).

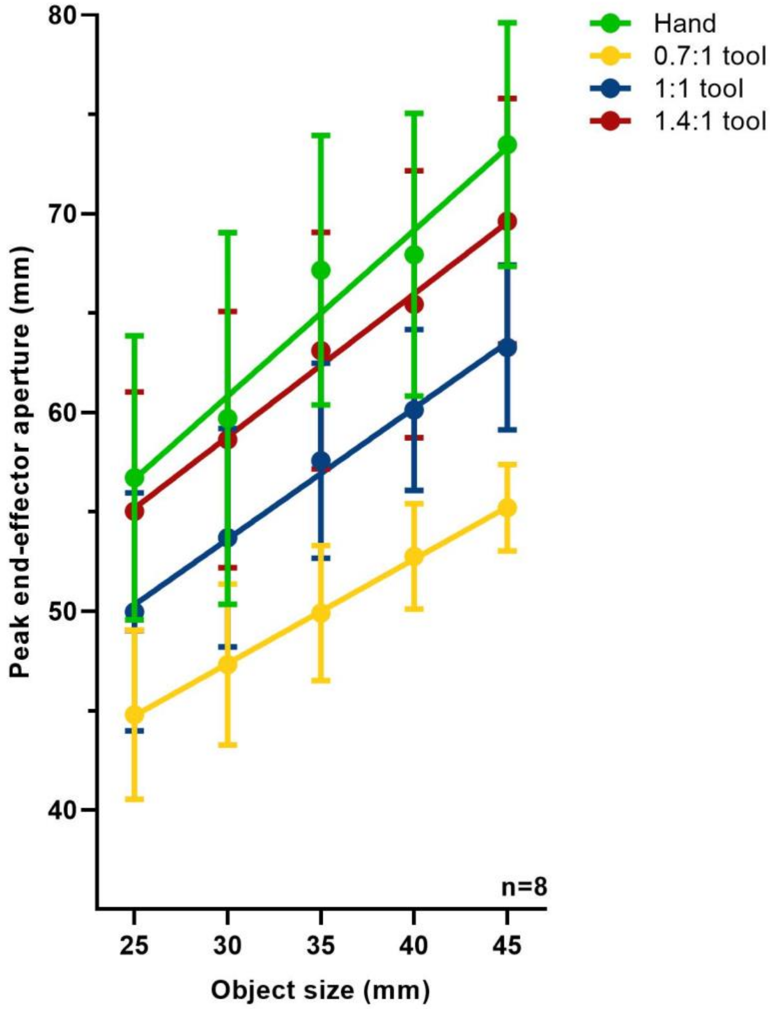


Figure 4.5. Peak end-effector aperture results with blocked tools. Mean peak aperture as a function of object size (collapsed across object distance) for the end-effector aperture. Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence interval.

As in Chapter 3, the normal patterns of anticipatory scaling of movement velocity with object distance, and grip aperture with object size, were present with all three tools (Jeannerod, 1981, 1984; Marteniuk et al., 1990; Smeets & Brenner, 1999).

4.3.2 Grasping task: Degree of 'compensation' for tool geometry with blocked tools

We analysed the extent that tool geometry was taken into account in the grasping task in a similar manner to Chapter 3. Fig. 4.6. plots the peak grip aperture for the different effectors (as a function of object size) in both end-effector/tool-tip units (left panel) and units of hand opening (right panel). As in Chapter 3, we specified lower bounds representing the expected tool opening if tool geometry was not accounted for at all (the same pattern of hand movements programmed regardless of the tool geometry). Complete account of tool geometry would manifest as the 1:1 tool performance (same tool opening regardless of the tool geometry). Fig. 4.6a replots the data from Fig. 4.5, with the lower-bound predictions (shaded areas in the corresponding colours). We can observe that the data for the 1.4:1 tool and the 0.7:1 tool lie outside the predictions for not accounting for tool geometry (shaded areas). That is, the data lie between the extremes of taking complete account for the tool geometry and not taking it into account at all. It suggests that the hand movements were adjusted to some extent to the properties of the tools.

To visualise the data another way, Fig. 4.6b plots the same data transformed into units of hand opening (no longer tool-tip opening). We again used the pattern of upper- and lower-bound predictions for accounting for tool geometry. However, now, completely taking into account tool geometry would manifest as very different hand openings shown by the shaded zones in Fig. 4.6b. Conversely, taking no account of tool geometry would here result in identical data with each tool (same hand opening regardless of the tool geometry). Fig. 4.6b reveals that different hand openings were programmed for the three different tools (in a direction consistent with taking tool geometry into account to some extent). We can also see that hand grasping and grasping with the 1:1 tool resulted in different grip apertures. This is a significant change from Chapter 3 (see Section 3.3.3).

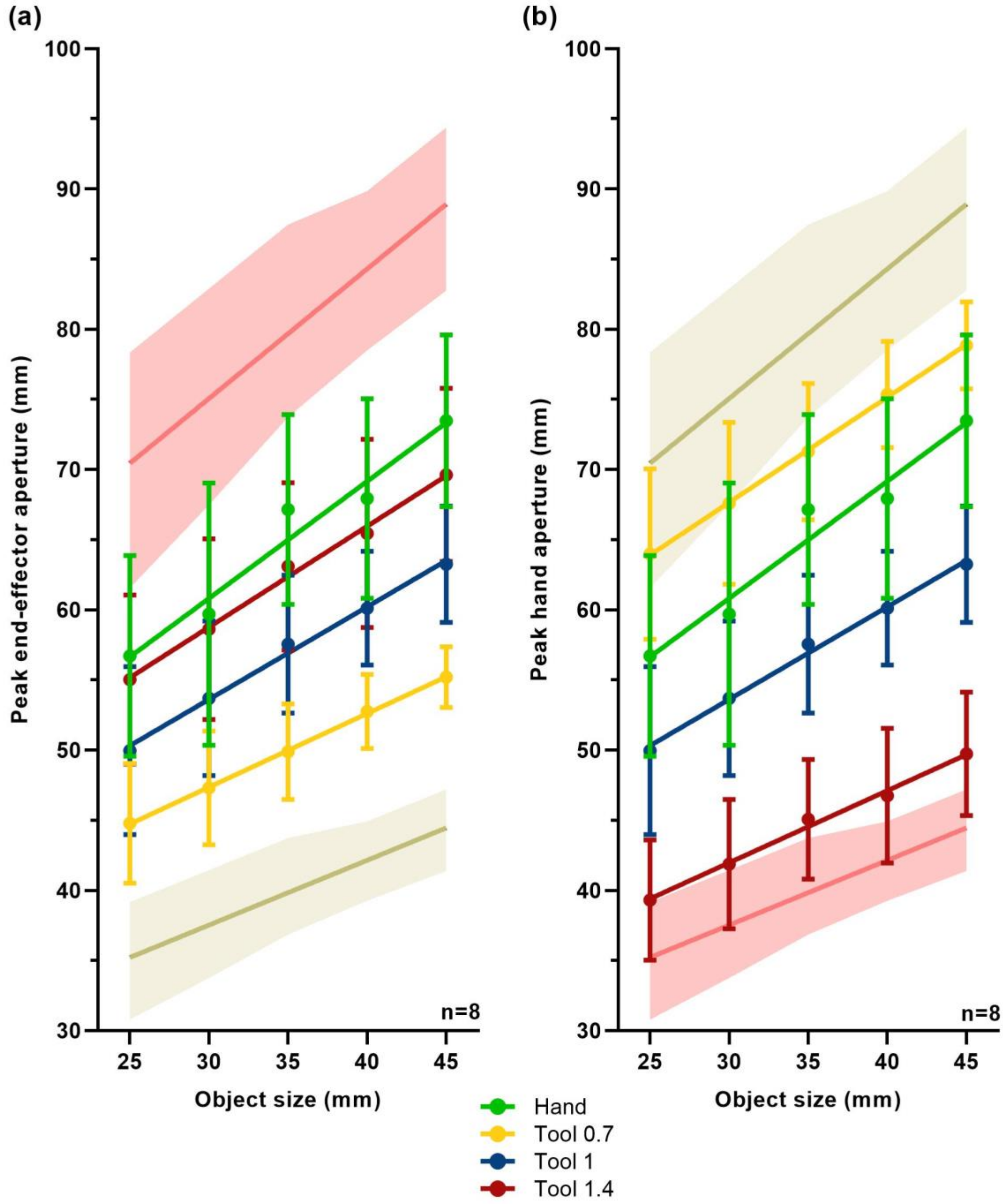


Figure 4.6. Peak end-effector aperture results with blocked tools. (a) Mean peak end-effector aperture replotted from Fig. 4.5. Shaded areas represent the expected peak end-effector aperture if participants did not take into account the tool geometry at all. (b) Same data plotted in units of hand aperture. Here, shaded areas represent the expected peak hand aperture if participants fully took into account the tool geometry. Solid lines show the best fitting linear regressions to the data in each case. In all cases, the error bars denote +/- 95% confidence interval

To examine the compensation for tool geometry statistically, as in Chapter 3, we first collapsed across object size to produce single overall mean grip apertures for each tool. These are shown in Fig. 4.7 (end-effector units in the left panel and hand-opening units in the right panel). It can be seen the same basic pattern of effects as before (as they are derived from Fig. 4.6). We tested whether the data differed from (i) completely taking into account tool geometry, by examining whether the tool-tip apertures were different across different tools (Fig. 4.7a), and (ii) zero taking account of tool geometry, by examining whether hand opening differed across tool conditions (Fig. 4.7b). First, we compared tool-tip aperture of both the 0.7:1 tool and the 1.4:1 tool to the 1:1 tool, using separate one-tailed paired-sample t-tests (Bonferroni corrected for multiple comparisons). The 0.7:1 tool was opened significantly less than the 1:1 tool ($t(7) = -6.49$, $p < .001$, $d = -2.29$) and the 1.4:1 tool was opened significantly wider than the 1:1 tool ($t(7) = 3.53$, $p = .019$, $d = 1.25$). Similar analyses of the hand opening were again statistically significant. When using the 0.7:1 tool the hand was opened significantly wider than when using the 1:1 tool ($t(7) = 14.86$, $p < .001$, $d = 5.26$). When using the 1.4:1 tool, the hand was opened significantly less wide than with the 1:1 tool ($t(7) = -10.03$, $p < .001$, $d = -3.55$). Thus, our results indicate that tool geometry was taken account to some degree, but not completely.

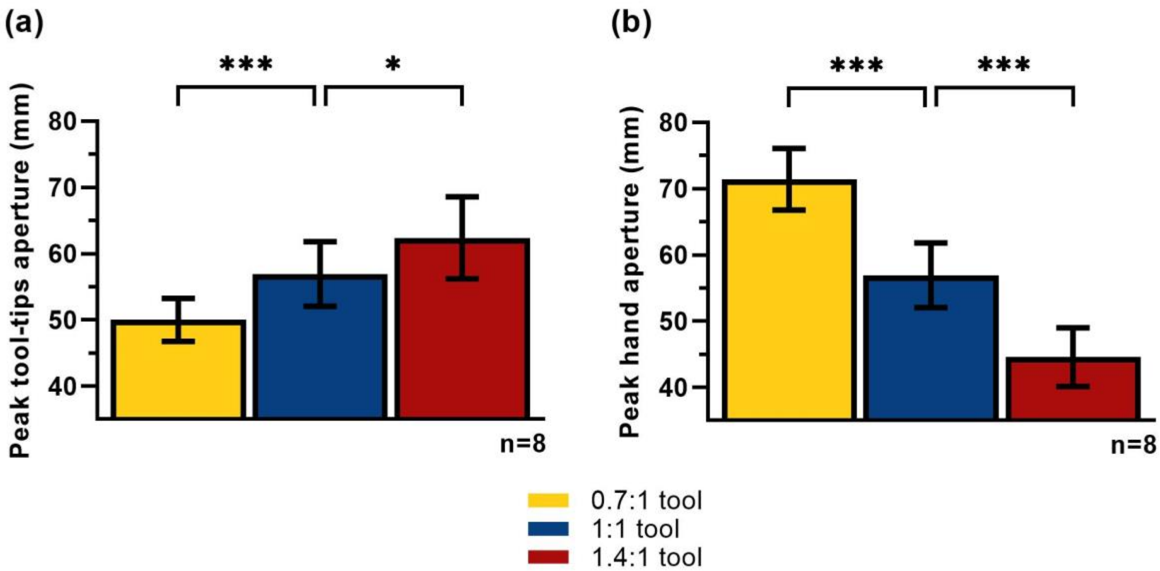


Figure 4.7. Peak end-effector aperture. (a) Mean peak tool-tips aperture (collapsed across object distance and object size) in closed loop condition. (b) Same data plotted as mean peak hand aperture. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

To examine the degree of tool compensation quantitatively (allowing comparison to Chapter 3) we again computed the 'compensation factors' with respect to 1:1 tool performance (see Section 3.3.3)

The result is plotted in Fig. 4.8. Visually inspecting the figure reveals two main points. The overall degree of compensation is larger than that seen in the comparable closed-loop conditions of Chapter 3 (0.36 vs. 0.76 with the 1.4 tool; 0.17 vs. 0.6 with the 0.7:1 tool), yet the greater compensation for the 1.4:1 tool *appears* preserved. We first examined the difference in compensation factors across tools by running a paired t-test on the compensation factors for the 0.7:1 and the 1.4:1 tools. This revealed that there was not significantly more compensation with the 1.4:1 tool than with the 0.7:1 tool ($t(7) = -1.66$, $p = .142$, $d = -0.87$). This contrasts with the pattern of results observed in Chapter 3 (significant difference between the compensation for the tools in favour of the 1.4:1 tool).

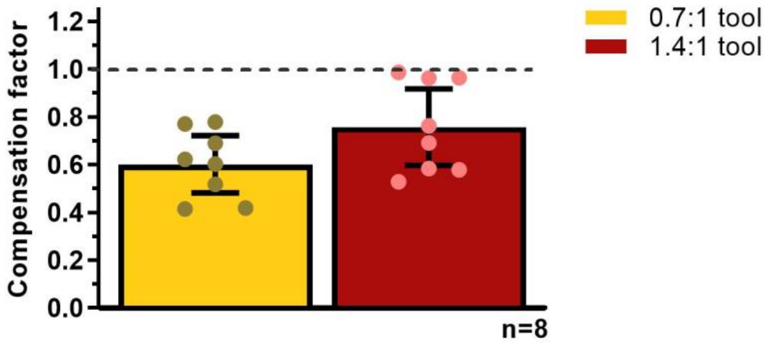


Figure 4.8. Compensation factor with blocked tools. Mean compensation factors for the 0.7:1 and 1.4:1 tools. The dots represent individual participant's compensation factors to show the data distribution. The dashed line represents complete compensation for the tool geometry. The error bars denote +/- 95% confidence interval.

We then compared the compensation data presented above to the compensation data from Chapter 3 for both tools. This experiment data are replotted side-by-side in Fig. 4.9. The figure shows that there was more compensation in this experiment than in the experiment in Chapter 3. To examine the effect, we ran one-tailed independent t-tests for each tools. For both tools, the degree of compensation was significantly greater in this experiment than in the experiment in Chapter 3 (0.7:1 tool: $t(7) = 5.54$, $p < .001$, $d = 1.96$; 1.4:1 tool: $t(7) = 4.64$, $p < .001$, $d = 1.64$).

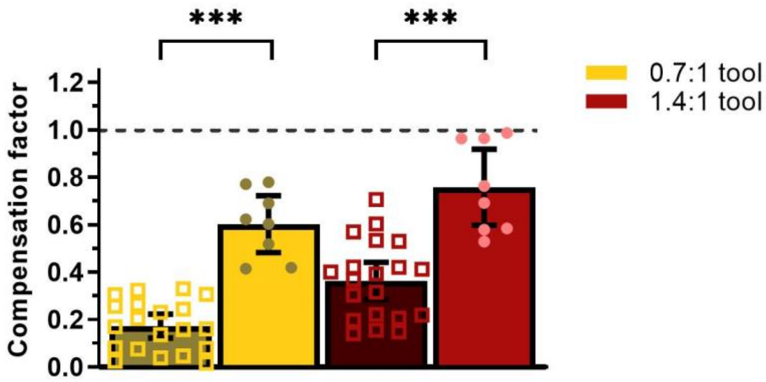


Figure 4.9. Compensation factor between Chapters. Mean compensation factors for the 0.7:1 and 1.4:1 tools. The dots and empty squares represent individual participant's compensation factors. The darker coloured bars represent the compensation factor on day 4 in Chapter 3. The lighter coloured bars represent the compensation factor for this experiment. The dashed line represents complete compensation for the tool geometry. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Overall, we observed more compensation for the tool geometry for both tools than in Chapter 3. The asymmetry observed in Chapter 3 (more compensation for the 1.4:1 tool than for the 0.7:1 tool) was no longer significant.

We do not report the success rates in this Chapter as they were at ceiling level.

4.3.3 Grasping task: Overall average movement profiles

As in Chapter 3, we computed the overall grasping profiles for all conditions (see Section 3.3.6). For the hand grasping, all trials were included. For the tools, we included 4224 trials out of 4320 (97.7% of trials).

Fig. 4.10 plots the overall grasping profiles for each effector, collapsed across object size and distance. The top-left panel (Fig. 4.10a) plots end-effector aperture as a function of time. The profiles are normalised in time such that overall durations are expressed as a proportion of the hand-grasping data. The top-right panel (Fig. 4.10b) plots the same in units of hand opening. The bottom row plots the same data as the panels above, but plotted as a function of space (normalised with respect to the movement end point in space, when the object was lifted). A version of those plots with error bars is available in section 7.2.1 (Fig. 7.4) and overall grasping profiles for each object size, for all effectors are also available (hand and 1:1 tool: Fig. 7.5, 0.7:1 tool and 1.4:1 tool: Fig. 7.6).

We first examined the end-effector aperture normalised in time (Fig. 4.10a). It can be seen that the tool overall profiles are qualitatively different from the hand grasping profile. Most noticeably, they show evidence of the ‘plateau phase’ reported elsewhere (Bongers et al., 2010: Golenia et al., 2014; Itaguchi & Fukuzawa, 2014), and seen in Chapter 3. The plateau duration will be analysed below.

We then examine the overall profiles in hand units (Fig. 4.10b). we noticed that the hand movements performed with each tool differed from the start. This contrasts with the pattern observed in Chapter 3 (very similar beginning of hand movement for all three tools). Here, there is evidence for ‘compensation’ for the tool geometry early in the movement (reflecting difference in movement planning).

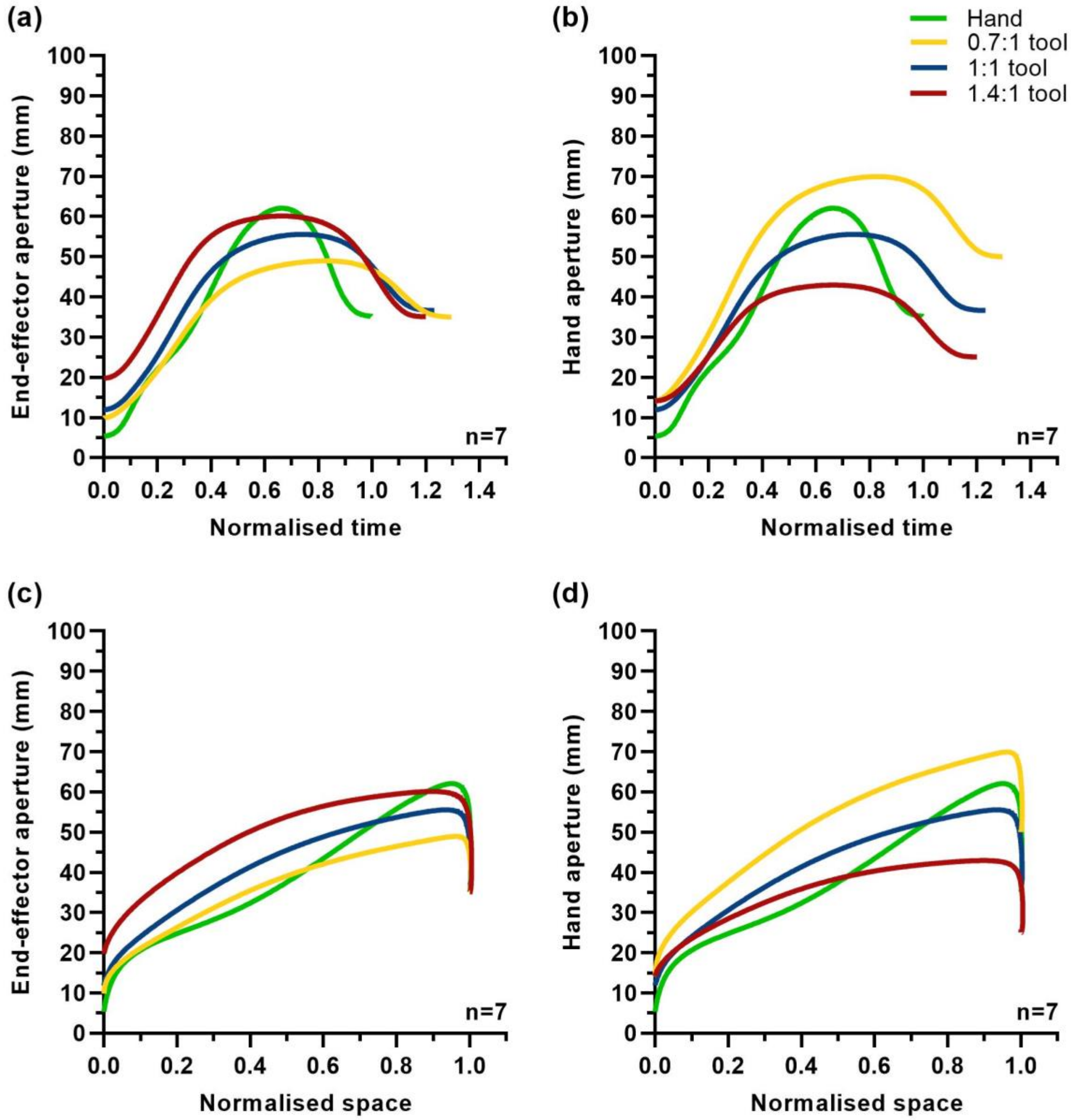


Figure 4.10. Overall grasping profiles. (a) Effector grasping profiles. (b) Same data as (a) plotted in hand grasping units. The profiles in (a) and (b) are collapsed across object distances and object size and normalized in time adjusted to the hand grasping profile. (c) Tool-tips grasping profiles normalized in space. (d) Same data as (c) plotted as hand grasping. The profiles in (c) and (d) are collapsed across object size.

As in Chapter 3, we calculated the duration of the plateau phase for each effector, shown in Fig. 4.11. As in Chapter 3, plateau duration was shorter with the hand than with the tools. To examine the effect, we ran a repeated measures ANOVA on the plateau duration for each effector. The ANOVA revealed a main effect of effector ($F(3,21) = 38.75$, $p < .001$, $\eta_p^2 = .85$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated the plateau phase was significantly shorter during hand grasping. There was no significant differences between the tools. This suggest that reliance on visual feedback was greater during tool grasping movements.

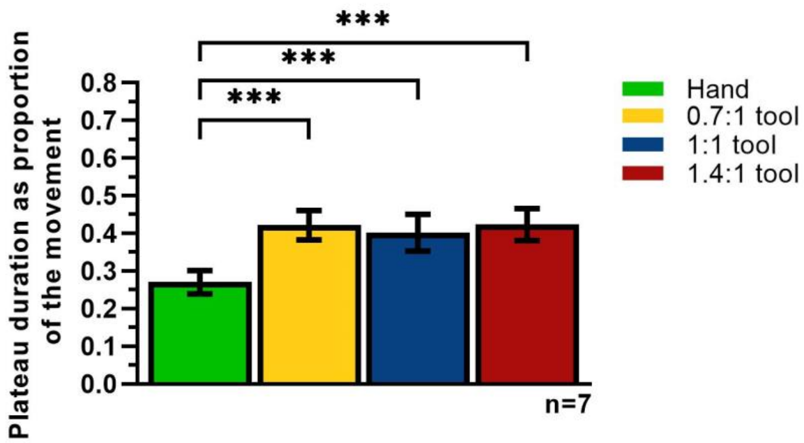


Figure 4.11. Plateau duration with blocked tools. Plateau duration as a proportion of the movement duration/ The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

4.3.4 <u>Grasping task: learning during the training phase?</u>

Our data suggest that continuous exposure to the same tool mapping improves the degree to which tool geometry is taken into account. Consistent with this, we might also expect that continuous exposure to the same tool allows gradual development of the mapping (or gradual adaptation), which would be evident as progressive change in performance across the training session. Such learning might be evident as faster movements at the end of training compared to the beginning, and greater tool compensation. As for the compensation factors, we examined whether performance differed between the first 30 trials and last 30 trials of that phase.

Peak velocity

Fig. 4.12 shows the movement velocity for each tool for the first and last 30 trials of the training. To investigate if participants' peak velocity did improve, we ran separate one-tailed paired t-tests for all tools. When using the 1:1 and the 0.7:1 tool, participants moved significantly faster on the last 30 trials than on the first 30 trials (0.7:1 tool: t(7) = -2.79, p = .014, d = -.65; 1:1 tool: t(7) =

-2.1, *p* = .037, *d* = -.36) but not with the 1.4:1 tool (t(7) = - 1.61, *p* = .075, *d* = .3). Movement velocity increased significantly during the training phase for the 0.7:1 tool and the 1:1 tool.

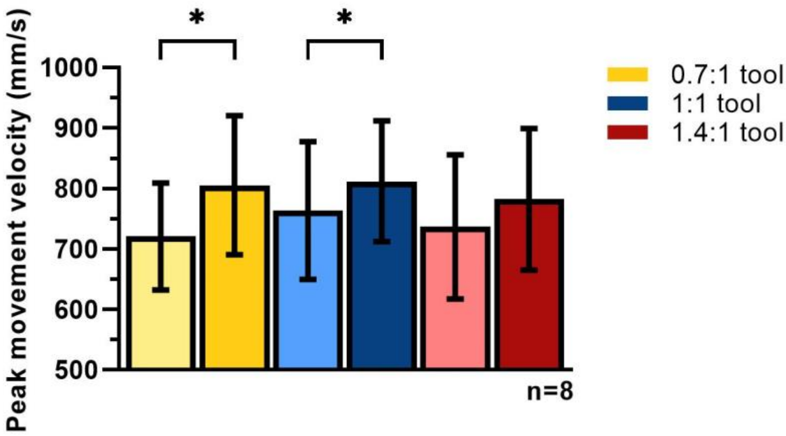


Figure 4.12. Peak velocity first 30 trials vs. last 30 trials. Mean peak velocity of grasping movements for each effector collapsed across object distance and object size. The lighter coloured bars represent the first 30 trials. The lighter coloured bars represent the last 30 trials. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Compensation for tool geometry

Fig. 4.13 shows that there was no appreciable change in compensation with the 0.7:1 tool, and only a slight increase with the 1.4:1 tool. We ran separate one-tailed paired sample t-tests (first vs. last 30 trials) for both tools . There was no significant difference in compensation between the first and last 30 trials with both tools (0.7:1 tool: t(7) = -0.004, *p* = .500, *d* = 0; 1.4:1 tool: t(7) = -1.05, *p* = .165, *d* = -.29). Compensation for tool geometry did not increase over the course of the training phase.

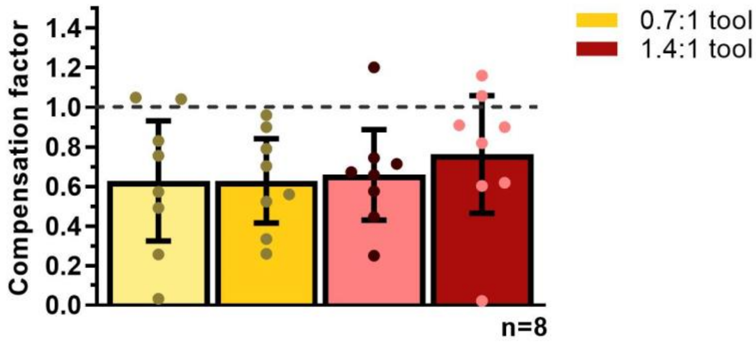


Figure 4.13. Compensation factor first 30 trials vs. last 30 trials. Mean compensation factors for the 0.7:1 and 1.4:1 tools. The lighter coloured bars represent the first 30 trials. The darker coloured bars represent the last 30 trials. The dots represent individual participant's compensation factors to show the data distribution. The dashed line represents complete compensation for the tool geometry. The error bars denote +/- 95% confidence interval

Overall grasping profiles

As before, we also compared overall grasp profiles between the first and last 30 trials of the training phase (Fig. 4.14). It can be seen that the profiles were very similar (no qualitative difference) between the first and last 30 trials. The main difference being shorter movement duration with the 1:1 and 0.7:1 tools following training (left panel). This is consistent with the pattern of increased movement velocities following training reported above.

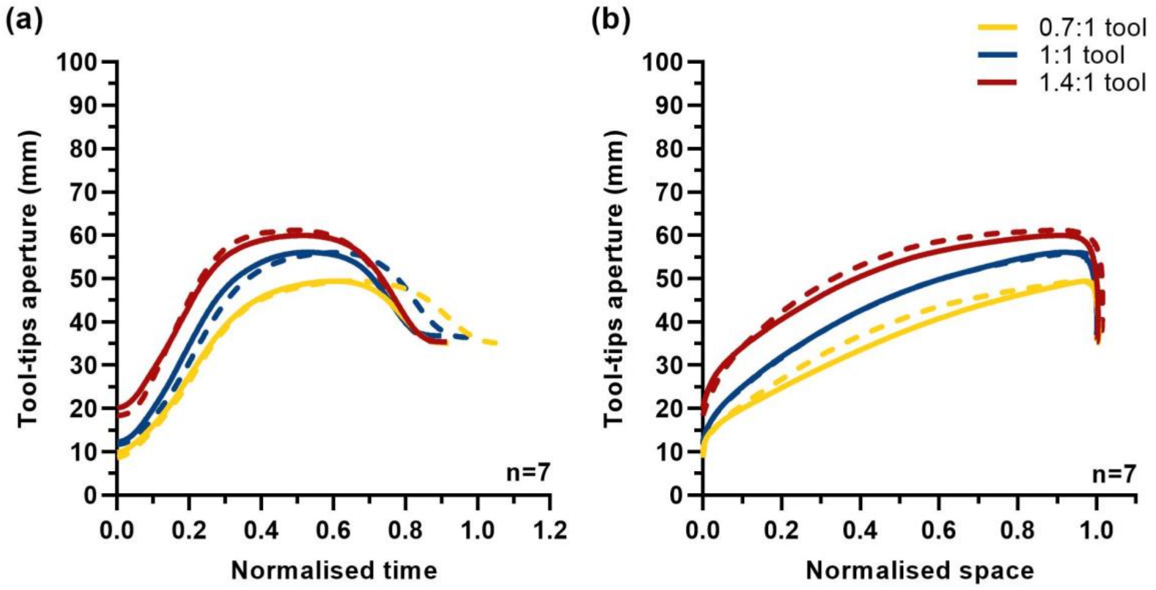


Figure 4.14. Overall grasping profiles from the first 30 trials vs. the last 30 trials (collapsed across object distance and object size). (a) The profiles are normalized in time adjusted to the hand grasping profile. (b) Same data normalized in space. Dashed line represents data from the 30 trials. Plain line represents data from the last 30 trials.

As before, we computed the time spent in the plateau phase of the movement for the first and last 30 trials of the training phase (Fig. 4.15). It can be seen that the proportion of time spent in the plateau phase of the movement did not change during the training phase. We ran separate paired one-tailed sample t-tests for all tools. There was no significant difference between the plateau duration during the first and the last 30 trials of the training phase (0.7:1 tool: $t(7) = 1$, $p = .175$, $d = .32$; 1:1 tool: $t(7) = -.19$, $p = .427$, $d = -.07$; 1.4:1 tool: $t(7) = -.85$, $p = .213$, $d = -.29$). Interestingly, although participants moved faster (shortening movement duration), they still spent the same proportion of their movement in the plateau phase.

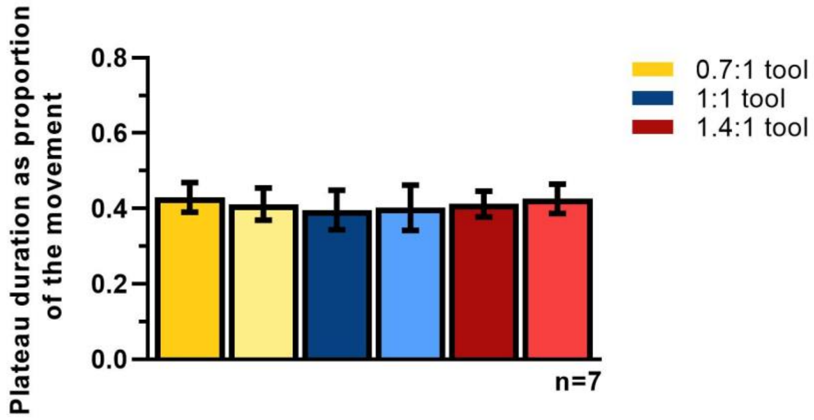


Figure 4.15. Plateau duration first 30 trials vs. last 30 trials. Plateau duration as proportion of the movement duration. The darker coloured bars represent the mean plateau duration for the 30 first trials. The lighter coloured bars represent the mean plateau duration for the last 30 trials. The error bars denote +/- 95% confidence interval.

Summary

Substantial compensation for the 0.7:1 and 1.4:1 tool geometries was evident when tools were used continuously for a sustained period, and this compensation was significantly greater than observed in Chapter 3, when the tool geometry was changed on each trial. We again saw some evidence that participants compensated more, albeit non-significantly, for the 1.4:1 tool than for the 0.7:1 tool. Participants again showed signs of anticipatory behaviour, such as scaling of their movement velocity to object distance and of their peak end-effector aperture to the object size.

4.3.5 Size-production task: adaptation of felt hand size during tool grasping?

Here we examined whether grasping training with the tools—which lead to their geometrical properties largely being taken into account—resulted in a concomitant adaptation of the felt opening of the hand. If so, it would suggest that adaptation of the hand representation is the mechanism for the tool compensation we observed in this experiment. Alternatively, substantial compensation co-existing with no adaptation of felt hand opening suggests distinct mechanisms or representations. Here, all data will refer to responses with the hand (following tool training), but are labelled with the tool that was used before the size-production task. One participant's data had to be removed because many trials were missing due to a tracking issue during data collection. Thus, the data presented are from seven participants.

Adaptation to the 1.4:1 tool would result in a reduction in post-test hand opening because a ‘small’ hand opening would feel larger than it is. Conversely, adaptation to the 0.7:1 tool would result in larger hand post-test opening (the hand opening would feel smaller than it is). Fig. 4.16a shows the different hand openings produced after the use of each of the three tools, as a function of stimulus object size, as well as the initial hand ‘baseline’. Given that the 1:1 tool should result in no adaptation under any account, it is reasonable to attribute the slight differences between training with the 1:1 tool and the baseline as being due to using our tools per se. We therefore interpret adaptation effects with respect to the 1:1 tool-training data, rather than the hand. Fig. 4.16a shows that participants were able to do the task appropriately, they produced larger hand opening for larger object in each condition, with similar object-size scaling (hand: 1.27; after using the 0.7:1 tool: 1.21; after using the 1:1 tool: 1.14 ; after using the 1.4:1 tool: 1.12). Overall the hand opening was larger than the actual object size (dashed black line). The figure also shows small, but consistent differences between training with the 0.7:1 and 1:4 tools, and the 1:1 tool, in the expected direction (larger hand openings for the 0.7:1 tool; smaller hand openings for the 1.4:1) consistent with adaptation of felt hand size. To examine these effects, we ran one-tailed paired sample t-tests (Bonferroni corrected for multiple comparisons) on the hand opening after the use of the 0.7:1 tool and the 1.4:1 tool, and the 1:1 tool. There was no significant pre-vs.-post difference in hand opening after using the 0.7:1 tool ($t(6) = 1.14$, $p = .298$, $d = .43$) or the 1.4:1 tool ($t(6) = -1.14$, $p = .299$, $d = -.43$) and after using the 1:1 tool. Thus, using the 0.7:1 and the 1.4:1 tools did not significantly changed hand performance compared to the use of the 1:1 tool. Although we observed small changes in the expected directions, this suggests that the felt hand size was not adapted during the tool training phase.

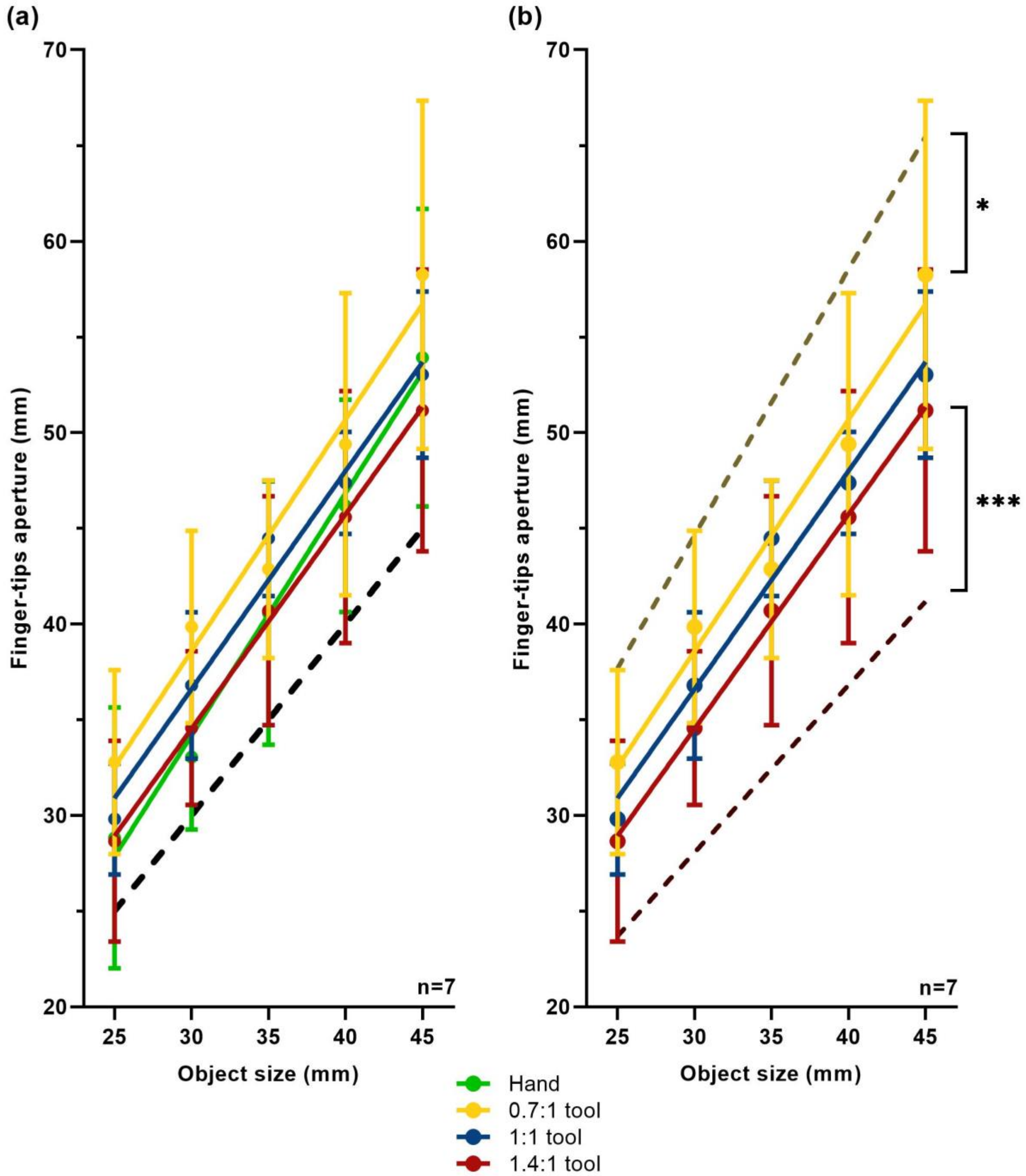


Figure 4.16. Results of size-production task with the hand after the tool training phase . (a) Mean finger-tips opening as a function of object size (collapsed across object distance). Solid lines show the best fitting linear regressions to the data in each case. The dashed black line represent the optimal response. (b) Same data without the hand size-production performance. The darker dashed lines represent the predictions of after-effect based on tool performance in the grasping task. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

While these non-significant differences are consistent with no significant adaptation of felt hand size following tool use, this may result from our small sample size. We can understand the data better, however, by considering what size of effect would be expected under the hand-adaptation account, and given the amount of tool compensation we observed. That is, if we assume that the tool compensation observed in the grasping task was entirely caused by adaptation of the felt hand opening, it can be assumed to reflect the bias in the tool model (the amount of adaptation). Thus, the tool compensation factors can be used to directly compute the expected adaptation effects (assuming no change in the felt hand opening when the tool is put down prior to the size-production task).

To do this, we needed to compute an estimate of the updated mapping between felt hand size and actual size indicated by the tool compensation factors. Consider the 1.4:1 tool. A compensation factor of 1.0 (perfect/complete compensation) would imply that felt hand size was 1.4 times actual hand size, whereas a compensation factor of zero implies a felt hand size of actual hand size x 1.0. Similarly, a compensation factor of 0.5 implies a felt hand size halfway between these two cases: actual hand size x 1.2. Thus we can compute the predicted (adapted) hand size when trying to produce a given object size as follows:

Produced hand size = unadapted hand opening / (1 + (tool gain -1) x compensation factor)

where the unadapted hand opening is the performance with the 1:1 tool.

Fig. 4.16b replots the size production data following tool training, and shows the predicted adaptation effect computed as above, using the tool compensation factors from the grasping task. It can be seen that following training with both the 0.7:1 and 1.4:1 the observed effects are closer to zero effect than the effect predicted by adaptation. Moreover, as the confidence intervals suggest, the observed data differed statistically from the predictions (paired sample t-tests; 0.7:1 tool: $t(6) = 2.93$, $p = .026$, $d = 1.1$; 1.4:1 tool: $t(6) = -6.47$, $p < .001$, $d = -2.45$). Thus it appears that there is very little adaptation of felt hand size and that adaptation cannot explain the degree of tool compensation seen in the grasping data.

4.3.6 Size-production task: is tool geometry taken into account ?

We next examined size production with the different tools, to determine whether tool geometry was taken into account for this task. The same participant had to be removed as in the adaptation analysis, due to missing data.

We first examined whether participants' tool openings were sensitive to changes in object size by examining the object-size scaling functions, in a similar manner to how we analysed grip apertures. Fig. 4.17a shows the effector opening as a function of object size. The figure indicates that participants did scale their end-effector opening with changes in object size with all effectors (one-tailed one sample t-tests on the slopes; hand: $t(6) = 9.71$, $p < .001$, $d = 1.27$; 0.7:1 tool: $t(6) = 8.73$, $p < .001$, $d = .63$; 1:1 tool: $t(6) = 10.17$, $p < .001$, $d = 1.03$; 1.4:1 tool: $t(6) = 5.35$, $p = .002$, $d = 1.06$) .

As for the grasping task, we examined the presence of compensation for the tool geometry. We first looked at the presence of complete compensation by comparing tool-tips opening with the 0.7:1 tool and the 1.4:1 tool with the tool-tips opening with the 1:1 tool (complete compensation would be evident if the same tool-tips openings were produced, independent of tool geometry). We then looked at the absence of compensation (zero compensation) by comparing the hand opening with the 0.7:1 and the 1.4:1 tools, and the 1:1 tool (zero compensation would be evident if the same hand opening were produced, independent of too geometry). We first examined tool-tips opening (Fig. 4.17a). It can be seen that the 1.4:1 data is both overlapping with the 'no-compensation' and the full compensation lines, while the 0.7:1 data are closely matching the line of 'no compensation'. One-tailed paired sample t-tests (Bonferroni corrected for multiple comparisons) revealed the 0.7:1 tool opening (collapsed across object size) significantly smaller than the 1:1 tool ($t(6) = -8.74$, $p < .001$, $d = -3.3$) and the 1.4:1 tool opening (collapsed across object size) being different, albeit not significantly, from the 1:1 tool ($t(6) = 2.04$, $p = .174$, $d = .77$). Second, the same pattern of results can be seen in hand units (Fig. 4.17b). One-tailed paired sample t-tests revealed there was no significant difference between the hand opening (collapsed across object size) with the 1:1 tool and the 0.7:1 tool ($t(6) = .24$, $p = 1$, $d = .09$) and the 1.4:1 tool ($t(6) = 1.96$, $p = .196$, $d = .74$). Overall, there was no evidence for compensation for both tools. As the substantial observed variability may hinder the interpretation for the 1.4:1 tool, we decided to explore the individual compensation scores.

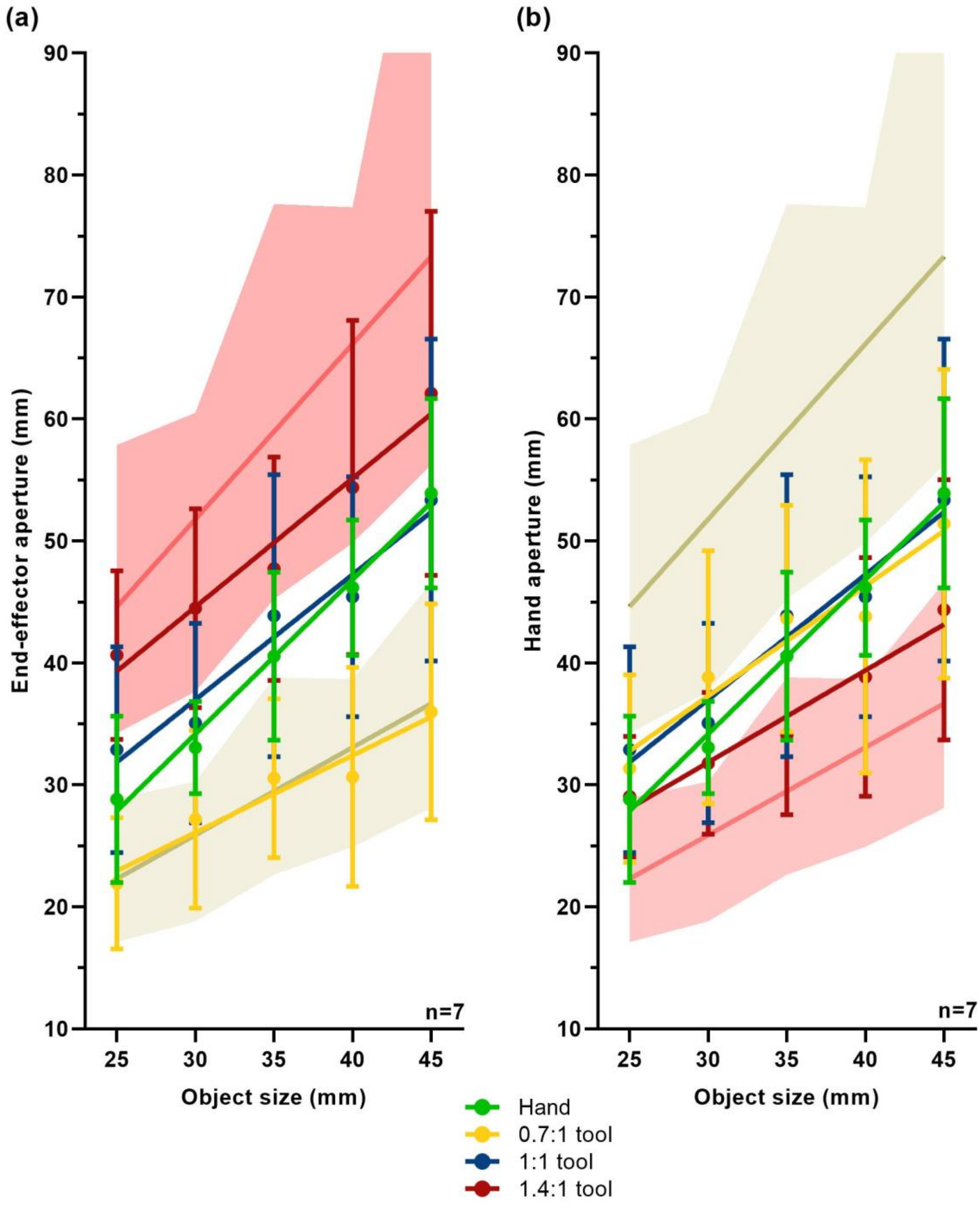


Figure 4.17. Results from the size-production task. (a) Mean end-effector opening as a function of object size. Shaded areas represent the expected peak end-effector aperture if participants did not account for the tool geometry. (b) Same data plotted in hand units. Shaded areas represent the expected peak hand aperture if participants did account fully for the tool geometry. Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence interval.

To assess the degree of compensation for the tool geometries quantitatively we computed compensation factors based on the 1:1 tool performance (as done in the grasping task). Consistent with the pattern observed before, Fig. 4.18 shows there is no compensation for the 0.7:1 tool geometry, and a slight compensation for the 1.4:1 tool geometry. The asymmetry between the compensation for the 0.7:1 tool and the 1.4:1 tool observed during the grasping task (and in Chapter 3) can also be seen. While most participants did not compensate at all for the 0.7:1 tool, there is high variability in individual's compensation factors with the 1.4:1 tool (from absence of compensation to near complete compensation, likely leading to the pattern of absence of significant compensation observed in Fig. 4.17). A paired sample t-test revealed that there was more compensation for the 1.4:1 tool than for the 0.7:1 tool, albeit not significantly (t(6) = 2.22, p = .068, d = .84).

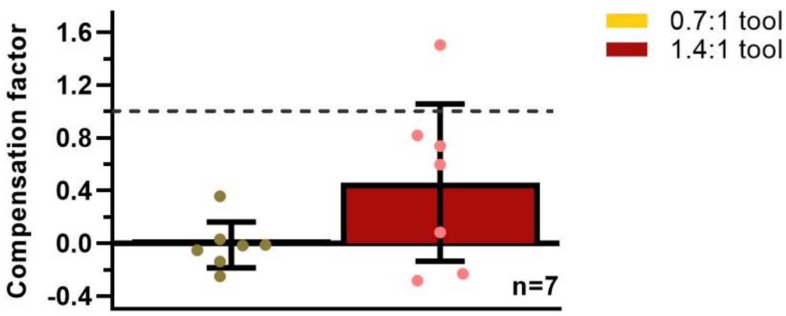


Figure 4.18. Compensation factors for the size-production task. Compensation factors for the 0.7:1 and 1.4:1 tools . The dots represent individual participant's compensation factors to show the data distribution. The dashed line represents complete compensation for the tool geometry. The error bars denote +/- 95% confidence interval.

If the exact same internal model of the tool geometry was used in both tasks, we would have expected (naively) to find the same compensation factors in the size-production task than in the grasping task. However, it appears there was less compensation in this task than in the grasping task. We statistically compared the size production compensation factors and the grasping compensation factors, for both tools, using paired sample t-tests. Significantly more compensation was found in the grasping task for the 0.7:1 tool (t(6) = 6.99, p < .001, d = 2.64) and there was more compensation, but not significantly, in the grasping task for the 1.4:1 tool ($t(6) = 1.3$, $p = .240$, $d = .49$) than in the size-production task.

Overall, it appears compensation was smaller in a more perceptual task than in a motor task. The asymmetry between compensation for 1.4:1 and 0.7:1 tool was also present. However, in this task, as participants did not have to open the tool-tips larger than the object (grasping task), potential hand opening limits cannot explain the asymmetry.

4.3.7 Relationship between tool mapping for perception and for action ?

While the grasping task is more action-control oriented, and the size-production task is more perceptual, and despite the differences in overall compensation discussed above, we might nonetheless expect that better knowledge of the tool geometry in a given participant would manifest as better compensation in both tasks. We can gain insights into this by examining the relationship between each participant's compensation factors for grasping and size production. To do this we examined whether there was a positive correlation between the compensation factors for the two tasks with the 1.4:1 tool. As we did not find compensation in the size-production task, it does not make sense to expect a correlation between the compensation factors for grasping and size-production for the 0.7:1 tool. Fig. 4.19 shows the relationship between the compensation factors from the two tasks. The figure suggests a positive correlation for the 1.4:1 tool. One-tailed Pearson's correlation coefficient showed that the relationship between the compensation factors for the 1.4:1 tool was nearly statistically significant ($r(7) = .646$, $p = .058$). Although this suggests that the same 'knowledge' of the 1.4:1 tool geometry may have been used in both tasks, we need to be careful as there is a large variability in the size production compensation factors. It is possible, then, that some participants were just 'better compensators', and produced high compensation while using distinct models for both tasks. We are unable to differentiate between the two possible accounts.

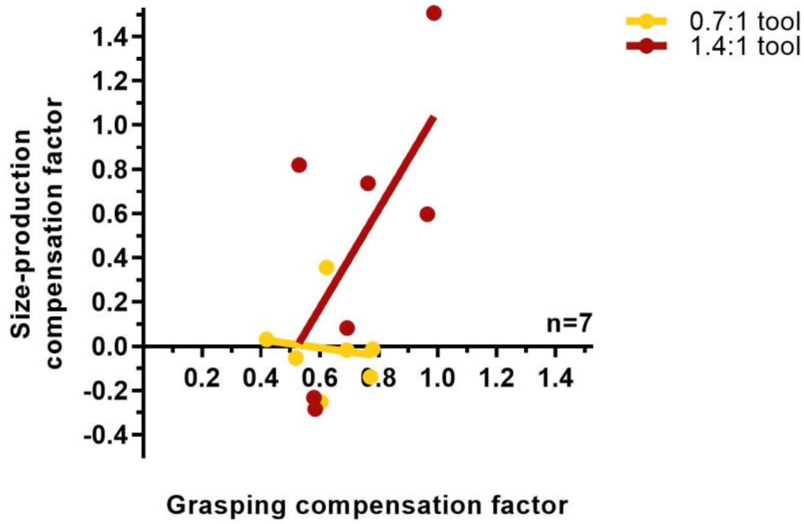


Figure 4.19. Relationship between compensation factors for tool grasping and size-production with tools. Size-production compensation factor as a function of grasping compensation factor for the 1.4:1 tool and for the 0.7:1 tool. Solid lines show the best fitting linear regressions to the data for each tool.

4.3.8 Size-discrimination task

We computed Just Noticeable Differences (JNDs) in size with each effector by fitting the data for each participant with a cumulative normal distribution psychometric function. Examples of fitted psychometric functions are shown in Fig. 4.20a and b. Following previous work (e.g. Ernst & Banks, 2002) we defined the discrimination threshold as the standard deviation of the fitted function. This corresponds to 84% correct discrimination performance. We calculated the JND in units of hand opening, by dividing the JND obtained for the tool-tips by the respective tool gain. This yielded JNDs around the same hand opening (40 mm), in comparable units, independent of tool geometry.

The JNDs in each effector condition are shown in Fig. 4.20c. The figure suggests there were no dramatic differences in performance (in units of hand opening) between the effectors, although the JNDs with the 0.7:1 tool are slightly higher than with the other tools. To analyse the effect statistically, we ran one-tailed paired sample t-tests (Bonferroni corrected for multiple comparisons) between the 0.7:1 and 1.4:1 tools, and the 1:1 tool. There was no significant difference in JND between the 1.4:1 tool and the 1:1 tool ($t(7) = -.61$, $p = .563$, $d = -.22$) and between the 0.7:1 tool and the 1:1 tool (t(7) = 2.13, *p* = .071, *d* = .75). Thus, using tools of different geometries did not impact significantly participants' performance in a size discrimination task, assessed in units of hand opening. There is however a trend toward significance between the JNDs when using the 0.7:1 tool and the 1:1 tool. That is, using the 0.7:1 tool, for which the participants' tool mapping appeared to be most impoverished, may have resulted in poorer discrimination of different hand openings.

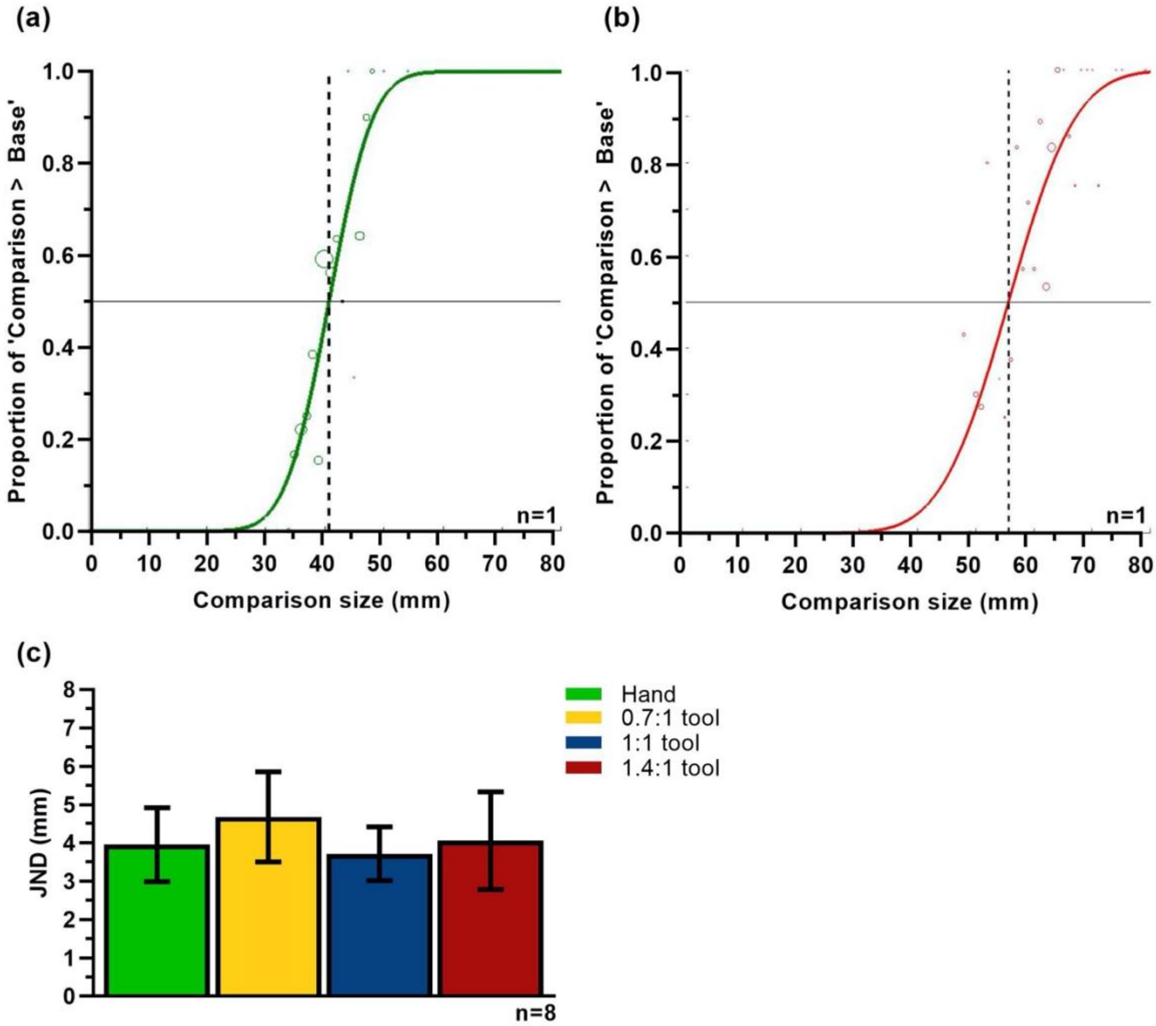


Figure 4.20. Results of the size-discrimination task. (a) Example of a cumulative normal distribution psychometric function for the hand (participant SM). (b) Example of a cumulative normal distribution psychometric function for the 1.4:1 tool in tool unit (participant SM) (c) Just Noticeable Difference in hand units. The error bars denote +/- 95% confidence interval.

4.4 Discussion

In this experiment we aimed to investigate whether giving continuous exposure to a single tool mapping during the grasping task would increase compensation for the tool geometries (compared to Chapter 3). We also examined if adaptation of felt hand size could be the underlying mechanism behind the compensation for the tool geometry. And lastly, we examined if the knowledge about the tool geometry (internal model) could be used in perceptual tasks, during which vision was occluded. First, results of the grasping task revealed increased compensation for both tool geometries compared to Chapter 3, suggesting ‘better’ model of the tools were developed. Second, results of size-production task (adaptation test), showed no evidence that the felt hand size had been adapted. This would imply that adaptation of felt hand size was not the principal mechanism underlying tool compensation. Thus, the development of new model must include a distinct stage that takes into account the relationship between hand and tool. This stage could represent adding components representing the tool geometry to the existing hand model, or developing a new tool model. In this experiment, we did not test directly grasping without visual feedback (the internal model ‘hard test’ of Chapter 3). We did however, probe the nature of the tool model in different, more ‘robust’ ways (size-production – tool perception and size-discrimination), requiring participants to interpret haptic signals from the hand without visual feedback, using knowledge about the tool geometry. Our size-production task (tool perception) did not indicate compelling evidence of compensation for both tool geometries. Compensation for the 1.4:1 tool however was nearing significance (here our small sample impedes our ability to make a clear statement). This suggests that *some* participants may have developed an internal model for that tool. This pattern is reinforced by the (non-significant) positive correlation between the compensation factors of the grasping and size-production task with the 1.4:1 tool. Those results suggest that some participants may have been able to use the same ‘non-visual’ knowledge (internal model) about the 1.4:1 tool in both tasks. This result is important, as it appears consistent with a common tool model that can be use in different task. This is the first sign we have of the potential development of an internal model of the tool geometry. In contrast, in the absence of development of such a model for the 0.7:1 tool, participants appear to have resorted to using the existing hand model. Lastly results from the size-discrimination task showed that using different tools with different geometries did not impact participants' performance, as predicted by the literature (Takahashi & Watt, 2014). There is an interesting however (non-significant) difference when using the 0.7:1 tool, suggesting that the fidelity of the internal model may have affected the performance, as the use of an impoverished model may have led to poorer discrimination performance (here again, we need to consider our small sample). This suggest that the noise from the tool model could propagate to the proprioceptive signals.

Taken together, as in Chapter 3, our results are consistent with an increase reliance on vision, and the development of some sort of visual model for tools, with encouraging signs that some internal model may have been developed for the 1.4:1 tool.

The 'better' tool models developed in this Chapter (compared to Chapter 3) are also evident in other movement parameters, such as movement velocity and overall grasping profiles. First, evidence for 'better model' come from movement velocity. Indeed during tool grasping movement velocity was not different from movement velocity during hand grasping (except with the 1.4:1 tool). Comparing movement velocity across Chapters revealed similar movement velocity during hand grasping, and movement velocity being faster (albeit not significantly) during tool grasping in this Chapter. As participants moved faster in this experiment, they had less time to use sensory feedback and generate feedback commands (reflecting underlying computation processes). That is moving faster increases the constraints on the system (Telgen et al., 2014). To maintain the chances of grasping the object while moving faster, the visuomotor system might have produced larger hand aperture (Wing et al., 1986) to guarantee the chances of success of the grasping movements by adding larger margin-for-error (Keefe et al., 2019). End-effector aperture (collapsed across object size and distance) for this Chapter and Chapter 3 are presented in Fig. 4.21. It can be seen that the hand was opened less in this experiment than in Chapter 3 when using the 1:1 tool and the 1.4:1 tool, but not with the 0.7:1 tool. Thus, it appears that participants produced faster movements, while adding the same (0.7:1 tool) or less margin-for-error (1.4:1 tool and 1:1 tool). It appears that a 'better' model of the tool geometry was developed in this Chapter, allowing the visuomotor system to produce faster and more accurate movement.

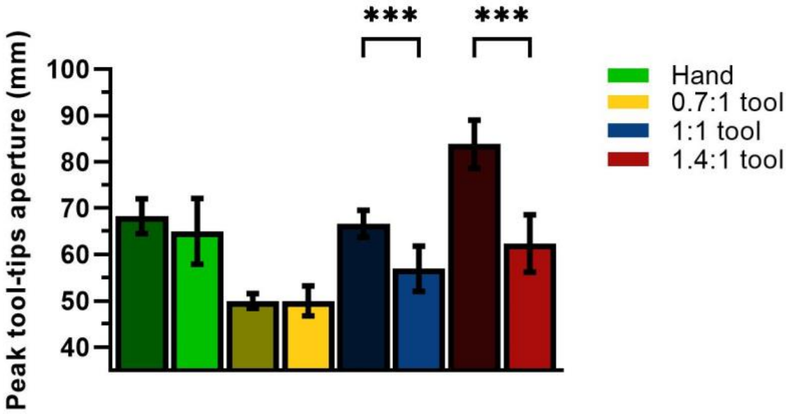


Figure 4.21. Peak hand aperture for Chapter 3 and Chapter 4. Peak hand aperture for the 35 mmm object. The darker coloured bars represent Chapter 3. The lighter coloured bars represent Chapter 4. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

The second evidence that continuous exposure led to 'better' tool models comes from the overall grasping profiles. Our results indicated distinct hand movements when using the different tools in this experiment. This could reflect the fidelity of those tool models (suggested by the higher degree of compensation), as the use of 'better' tool models would have likely produced distinct hand movements for all tool. It can be seen in this experiment (Fig. 4.22a) that participants did open their hand differently for all tools quite early in the movement. In comparison, in Chapter 3 (Fig. 4.22b), on the fourth day of the experiment, participants did show a more 'stereotypical' beginning of movement with all tools. Results in Chapter 3 (Section 3.4) were possibly explained by the constant switching of tools, potentially leading to the development of a 'generic' tool model and to stereotypical movements with all tools. That is the visuomotor system may have extracted a more 'general' task structure (Braun et al., 2009, 2010; Wolpert et al., 2011). On the contrary, in this experiment, as the tools were learned on separate sessions, the brain could have learned three different 'tasks', each task corresponding to a specific tool. Thus, the brain could have developed three different tool mappings while starting each new session with the knowledge of the task structure (general tool grasping task) obtained from previous session(s).

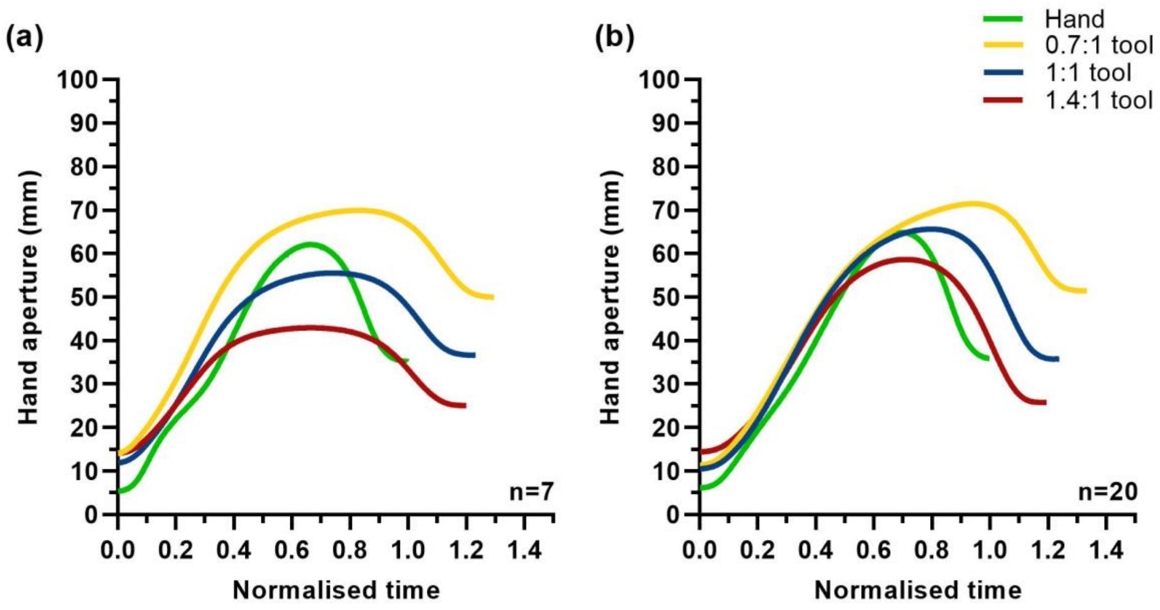


Figure 4.22. Overall grasping profiles for all effectors from this Chapter and Chapter 3. (a) Overall hand grasping profiles for this experiment during the training phase. (b) Overall hand grasping profiles for day 4 in Chapter 3.

The 'learning environment' also has implications on the number of trials required to observe certain degree of compensation. The higher degree of compensation observed in this experiment. That is the fourth day of the experiment in Chapter 3 represented the 90 last trials of the 360 trials done in total in that experiment. In comparison, in this chapter, participants made 180 trials during the training phase. That is participants had more exposure to the tool mappings in Chapter 3 than in this Chapter. We however found higher compensation in this Chapter, suggesting continuous exposure appears to favour the development of tool models. This is consistent with the idea that there was interference in learning of the tool geometry in Chapter 3 (similar to work on dual adaptation for similar findings: Krakauer et al., 1999; Martin et al., 1996; Wada et al., 2003; Welch et al., 1993; Woolley et al., 2007). Thus the task structure, and by extension, the 'learning environment' need to be carefully developed, as it can greatly influence participants' ability to account for tool geometry.

In this 'new' learning environment, we expected participants to improve 'gradually' over the course of the training phase. Continuous exposure should 'ease' the error attribution process, as participants have the opportunity to attribute directly any error signal to their most likely cause and then to act on it in the subsequent trial (Shadmehr et al., 2016), allowing for gradual improvement of performance (Krakauer & Mazzoni, 2011). The motor system should then constantly update the internal models during the training phase (Wolpert & Flanagan, 2010), aiming at planning and executing 'better' (more efficient, accurate) movements (Albert & Shadmehr, 2016; Krakauer & Mazzoni, 2011). This assumption however is supported by the idea that tool transformations are accounted for by adapting existing internal models. In contrary, our results did not reveal evidence for adaptation being the principal mechanism underlying tool compensation. Moreover, our results showed no significant improvement in the degree of compensation for tool geometry across the training phase. Our results also indicated that there was no qualitative alteration in tool grasping movements over the course of the training phase. Thus, we did not find evidence for a 'gradual' improvement. We explore possible reasons, below.

First, as adaptation was not the principal mechanism underlying the development of our tool models, it is likely that tool models would have to be developed by either adding components representing the tool geometry to the existing 'untouched' hand model, or by developing tool models *de novo* (Telgen et al., 2014). We are unable to unambiguously differentiate the two mode of acquisition. Our results from the size-production task hinted that some internal tool model may have been developed (for the 1.4:1 tool). This suggest internal models of tool may be developed *de novo*. Such a process would likely be slow (Abe et al., 2011; Reis et al., 2009). We have argued that the development of a visual model could be the first step in the acquisition of an internal model. Thus, we may have captured that first step, but not the development of a more internal.

Second, participants may have developed explicit strategies to deal with each tool geometry early in the experiment (e.g. "I need to open my hand less with that tool"). As suggested by Wolpert et al. (2011), the initial part of motor learning could be more cognitively driven. That is participants could voluntarily correct for the larger errors arising early in the training phase. In our experiment, participants, when potentially facing large error signals at the beginning of the task, might attribute those errors to external or environmental factor (Kluzik et al., 2008), such as our tools. It is then possible that participants may have gained explicit knowledge about the ‘nature’ of the perturbation and decided to develop a compensatory strategy (explicit learning; Taylor & Ivry, 2011; Taylor, Krakauer, & Ivry, 2014). That explicit learning is usually followed (with some degree of independence) by an implicit learning, related to the update of an internal model (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011). So participants could have been able to use explicit knowledge early on to adapt their movements in the right direction. It is likely that most of the knowledge about the tool geometry was visual. That is, visual consequences of the movement would be more salient in the early stage of development of tool models (Sailer et al., 2005), as it is likely that proprioceptive information was either not available, or too noisy and difficult to interpret. This account is consistent with the development of a visual model of the tool geometry. It is then possible that we failed to capture the more implicit learning of the tool geometry (although some participants may have developed more implicit knowledge for the 1.4:1 tool).

Third, it is possible however that the system did optimise the movement to the best of its ability early in the training phase. Grasping can be seen as an optimisation problem, with the goal of increasing the chances of that movement to reach a certain level of performance (Scott, 2004; Todorov, 2004; Todorov & Jordan, 2002). It is possible that during our task, participants quickly optimised the chances of success of the tool grasping movements. That is, the system could have ‘decided’ that the compensation was ‘enough’ for the grasping movements to be successful. And as compensating more might require non-trivial calculation (Keefe et al., 2019; Schlicht & Schrater, 2007; Trommershäuser et al., 2003; Wolpert & Landy, 2012), the cost of optimising compensation for the tool geometry was found to be too high, and the system may have optimised other movement parameters, such as movement velocity. This behaviour was likely rendered possible because there was no cost for failing at the task or no reward for successfully grasping the object. The potential effect of reward/punishment will be explored in the General Discussion (Section 6.6).

Our results have implication for the tools ‘used as body parts’ account. The ‘tool as body part’ account comes from studies showing that using a tool alters the representation of the body (Canzoneri et al., 2013; Cardinali et al., 2009, 2012; Martel et al., 2019; Miller et al., 2019; Sposito et al., 2012). We argued that tools used as body parts implies that the same visuomotor control principles used for hand grasping would be used for tool grasping. This implies that tool grasping would exhibit normative patterns of scaling of movement indices with object properties (such as object-size tool-tips aperture scaling and object-distance movement velocity scaling), and the presence of compensation for the tool geometry. Our results are consistent with that idea. However, as in Chapter 3, we did not find compelling evidence for the development of internal models (although we found encouraging signs that some participants may have developed internal models). Moreover, the ‘tools as body parts’ account suggest that the system would *adapt* existing body parts representations during tool use. In tool grasping, we argue that the hand representation was the most likely to be adapted. Our results however do not support that account. Taken together, our results don’t fully support the ‘tools as body parts’ account. However, the idea that the tool can be control like the hand is still relevant, as it is possible that once an internal model of the tool is developed, the same visuomotor control principles used for the hand could be used to control the tool.

Compensation for the tool geometry was not complete. Although we observed more compensation for both tools geometries than in Chapter 3, we still did not observe complete compensation for both geometries. Again, assuming the compensation factor reflect the actual representation of the tool geometry, we computed the brain’s perceived estimate of each tool alteration. For the 1.4:1 tool, the compensation factor (0.76) suggests the brain has an estimate of the tool geometry of ~1.304. For the 0.7:1 tool, the compensation factor (0.6) suggests an estimate of tool geometry of ~0.82. Those results suggest the visuomotor was still biased in its perception of the tool geometry, but less biased than in Chapter 3. Moreover compensation value did not improve across the training phase. Thus, as in Chapter 3, we still did not observe a metrically accurate model of the actual alterations produced by the tool geometries.

The asymmetry in compensation between the tools observed in Chapter 3 is still present, although no longer being significant in the grasping task. In our grasping tasks, using a tool might have hindered the ability of the system to open the tool-tips as wide as required (as discussed in Chapter 3, Section 3.4) producing some sort of hand opening ceiling effect. That asymmetry was however present in perceptual tasks, during which hand opening was not constraint by any possible ‘ceiling effect’, or any ‘extra energy consumption’ due to the demand for larger hand opening. That is, in the size-production task, while there are signs for compensation for the 1.4:1 tool, indicating some model of the tool may have been developed, there was zero compensation for the 0.7:1 tool, suggesting an absence of model of that tool. Further, in the size-discrimination task, there is a trend for poorer discrimination with the 0.7:1 tool than with the 1.4:1 tool (for which participants appears to have a better ‘model’). Taken together, our results suggest those two alterations might be accounted for by different mechanisms, or that the 0.7:1 transformation is less easily accounted for by the visuomotor system. As discussed in Chapter 3 (Section 3.4), that difference could be the result of the statistic of the world, or the cost of producing the required hand movement.

Noise in the estimate of the tool properties could propagate to the perceptual estimates (like size opening) obtained through the tools. In the size-discrimination task, there are signs that there was poorer discrimination with the 0.7:1 tool. Results from Takahashi & Watt (2014) suggest that the sensitivity of the hand should not be altered by the tool geometry. Our result however might reflect the effect of the model fidelity. Indeed, participants have to interpret proprioceptive and tactile signals from the hand, and factoring in the knowledge about the tool geometry. If the brain has a noisy estimate of the tool geometry, the noise would likely propagate into the perceptual estimates of sizes perceived via the tool, leading to poorer size discrimination performance.

A visible effect of the training is a shortening of the duration of the plateau phase, as suggested by Golenia et al. (2014). Their interpretation is that shorter plateau phase is a sign of learning, as the system learns to use the visual feedback effectively. Our results indicated a shortening of that plateau phase with more training, however that shorten plateau phase was still the same proportion of total movement duration. It suggests that the proportion of movement duration spent in plateau phase might be a programmed feature of tool grasping. Thus the decrease of length of that phase would just be the result of a shorter movement and might not reflect learning of the tool model.

Using the size-production task with the hand after tool use showed evidence that the felt hand size was not adapted during grasping with tools. It is still possible that adaptation was present, with tiny effects (we observe small effects in the expected direction after tool use). One way to be sure that adaptation is not present in the compensation of the tool geometries is to develop a control experiment that would measure hand adaptation. That experiment would use a simple hand grasping paradigm, during which, in a proportion of trials, we would manipulate the visual size of the objects. That is, we would mismatch the visual and physical sizes of objects, the physical size would be a ratio of the visual size (same ratio as the tools) in different blocks. This manipulation would give the opportunity to examine how the same alterations of hand opening are accounted for when no tool is being used. By comparing the after-effects of such a task with the after-effects of tool use, we would be able to get a better insight about the presence of adaptation in the process of accounting for tool geometry. Similar after-effect would give clearer indication that the felt hand size was adapted during the grasping task with the tools. Different after-effect would suggest that the mechanism resides in the development of a new mapping for the tool geometry.

As our sample size was small, we performed sensitivity analysis for each of the tasks used in this Chapter. *First*, in the grasping task, for the key signatures of tools being used as body parts (as in Chapter 3), sensitivity analysis revealed that we found larger effect size than the minimal detectable effect size for both the movement velocity scaling to object distance (mdes = 0.98; 0.7:1 tool: $d = 6.8$; 1:1 tool: $d = 6.01$; 1.4:1 tool: $d = 4.63$) and the scaling of tool-tips aperture with object size (mdes = 0.98; 0.7:1 tool: $d = 3.31$; 1:1 tool: $d = 4.4$; 1.4:1 tool: $d = 4.8$) and for the presence of compensation for the tool geometries (mdes = 0.98; 0.7:1 tool $d = 5.26$; 1.4:1 tool $d = 3.55$). Already with eight participants, those effects were practically significant. For the comparison of compensation values with the previous Chapter, sensitivity analysis revealed that we found larger effect size than the minimal detectable effect size (mdes = 1.07; 0.7:1 tool: d = 1.96; 1.4:1 tool: d = 1.64). Those analysis suggest that the study was already sufficiently powered to detect the desired effects in the grasping task. *Second*, for the size production task (adaptation), sensitivity analysis revealed that we found smaller effect size than the minimal detectable effect size (mdes = 1.07; 0.7:1 tool: d = 0.43; 1.4:1 tool: d = 0.43). This suggest that either no effect was present, or that an effect was present, but too small to be certain, given our sample size. *Third*, for the size production task (tool perception), for the presence of compensation for the tool geometries, sensitivity analysis revealed that we found smaller effect size than the minimal detectable effect size (mdes = 1.07; 0.7:1 tool: d = 0.09; 1.4:1 tool: d = 0.74). The result for the 1.4:1 tool is interesting as it suggest that an effect might be present, but not large enough to be detected given our sample size. This suggests that our study was underpowered. *Fourth*, for the size discrimination task, (mdes = 0.98; 0.7:1 tool: d = 0.75; 1.4:1 tool: d = 0.22). Here, the result for the 0.7:1 tool is interesting, suggesting that an effect might be present, but not large enough to be detected, suggesting again that our study was underpowered. Taken together, those analysis suggest that our study was likely underpowered and that a larger sample size could allow us to make more conclusive statements and interpretations of our data.

4.5 Conclusion

The experiment revealed that continuous exposure to a single tool does increase the compensation for that tool mapping. Adaptation does not appear to be the principal mechanism underlying compensation for the tool geometries. There are some signs (albeit light) that some participants may have developed a ‘non-visual’ internal model of the 1.4:1 tool geometry.

Chapter 5 – The effect of using a tool that does not behave qualitatively like the hand

5.1 Introduction

To plan and execute a desired movement with a new tool, assuming the brain knows what the movement of the tool-tips has to be to carry out the task, the visuomotor system must (1) know the mapping between hand and end-effector movement, to know what hand movement needs to be produced, and (2) establish motor programmes that allow those hand movements to be achieved. In this chapter we explore these stages further and attempt to decouple them.

In Chapters 3 and 4 the tools opened when the hand opened, only altering the ratio between hand and tool-tips opening. Thus, they could have been controlled effectively by adapting, or co-opting pre-existing hand representations and existing hand grasping motor programmes (though they would need tweaking to account for the tools' spatial offset, mechanical constraints, alteration of haptic feedback, etc.). Under these conditions, participants were able to show anticipatory behaviour, such as scaling of the tool-tips opening to object sizes, and could compensate, albeit incompletely, for the tool geometries when visual feedback was available. Here we explore grasping performance with a tool that cannot be used by altering existing hand representations, in order to better understand how readily new tool mappings and motor programmes for tool use can be acquired.

One way to do this is to make a more mechanically complex tool, which participants have not previously experienced. The degree of complexity is likely to affect the difficulty of acquiring new tool mappings, however, and so this manipulation does not isolate the acquisition of new mapping/motor programmes per se. We therefore examined movements made with 'reverse pliers', which open when the hand is closed. We reasoned that it was unlikely that participants already possessed experience with such a tool, and so appropriate movements of the tool-tips would still require the development of a new internal model of the tool geometry and new control programmes (Telgen et al., 2014). Such a tool is *no more* mechanically complex than those used in Chapters 3 and 4, however, allowing us to determine the effects of the need to acquire a new tool mapping/motor programme while holding tool complexity constant.

In Experiment 1 we therefore compared grasping movements with our previous 1:1 tool, and with a reverse tool. Because we already found (in the open-loop conditions in Chapter 3) that the visuomotor system likely did not have access to a non-visual tool model even for 'normal' tools, we kept vision available throughout the trial in this experiment. To preview the results, we found very little evidence of anticipatory control of the opening of the reverse tool. In Experiment 2 we probed whether the lack of anticipatory control could be attributed entirely to the difficulty of acquiring an unusual tool mapping, or to the requirement to make an unusual hand movement per se (opening the hand to grasp objects).

In both experiments we again examined the anticipatory features of grasping movements, such as the scaling of tool opening with object size, and scaling of movement speed with object distance. Following the earlier logic, if the brain has accurate internal models of the two tools, and is able to produce the required movements, then we would expect it to plan similar movements of the tool-tips in both cases. That is similar performance between the two tools would be a sign that the visuomotor system accounted for the challenges of the reverse tool.

5.2 Experiment 1 Methods

5.2.1 Participants

15 right-handed participants completed this experiment (14 female, 1 male; aged 18-30 years old). All participants had normal or corrected-to-normal vision, and no known impairments that would affect their ability to grasp. Participants were rewarded at the rate of £6 per hour. Participants gave informed consent prior to taking part, and all procedures were in accordance with the Declaration of Helsinki.

5.2.2 Apparatus and stimuli

The experimental apparatus was the same as in Chapter 3. For this study, the 'normal' tool had an opening ratio of 1:1 (the same tool as used in Chapters 3 and 4). The other was a reverse pliers-like tool, operating by closing the finger and thumb in order to open the tool-tips (bottom right in Fig. 5.1).

The objects and distances were the same as in Chapters 3 and 4: depths of 25, 30, 35, 40, & 45 mm, positioned at 150, 300, & 450 mm from the start button, along the body midline.

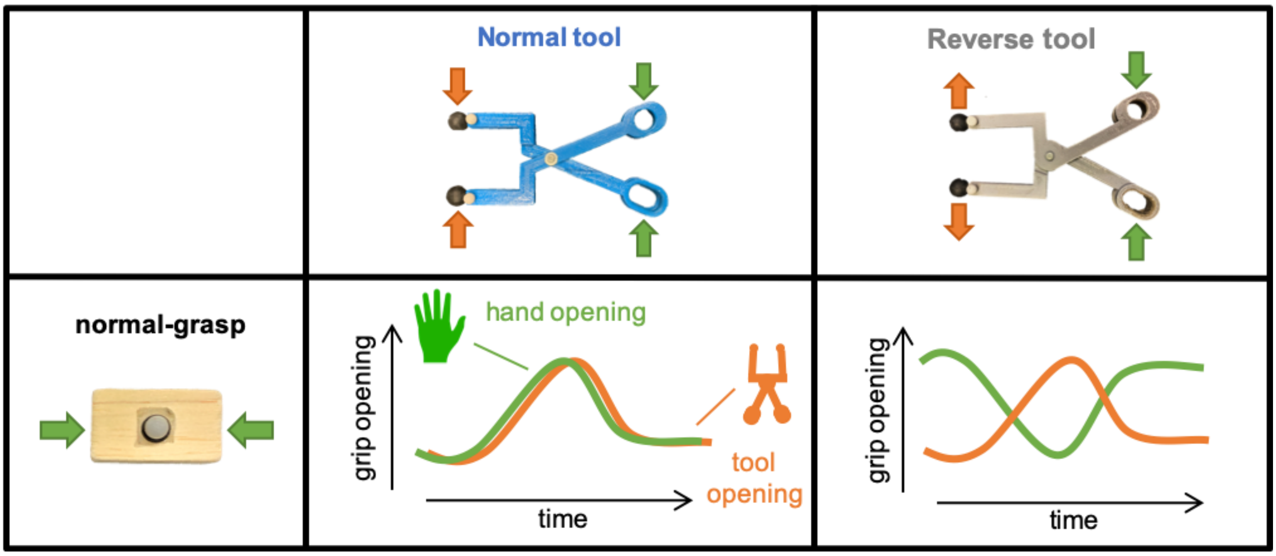


Figure 5.1. Schematic of the tools used and grasp opening-closing movements required in each condition. Picture of one of the objects used in the experiment, the green arrows represent where participants were instructed to grasp the object. The orange profiles represent the required movement with the end-effector. The green profiles represent the required hand movement to produce the desired tool-tips opening, for both tools.

5.2.3 Procedure

Individual trials followed the same format as in the closed-loop conditions of Chapters 3 and 4. The experiment was divided into three sessions. One session was dedicated to grasping with the hand. The two other sessions were dedicated to grasping with both tools. During the tools sessions, the tools were randomly interleaved[4]. The experimenter instructed the participant which tool would be used on the upcoming trial, and handed him/her the other tool as necessary. Participants were asked to start each trial with the tool-tips closed (with the hand open when using the reverse tool). Each session was divided into two blocks of 60 trials (for hand grasping: 4 repetitions x 5 object sizes x 3 object distances; for tool grasping: 2 tools x 2 repetitions x 5 object sizes x 3 object distances)

[4] This experiment was chronologically run after Chapter 3, thus the same rationale concerning randomization applies here.

making 240 trials in total (the number of trials was chosen to maximise exposure to both tools in a one hour session). Movements were recorded as previously.

5.2.4 Data analysis and predictions

As in previous chapters, we will examine whether movements—including with the reverse tool—show evidence of anticipatory scaling with object properties (movement velocity with object distance; grip aperture with object size). The presence of those anticipatory behaviours would reflect learning of the reverse tool properties, as it would indicate that the tool is 'used as a body part'. Our main manipulation relates to grip, so the scaling of grip aperture to object size will be the *key* measure in understanding if the reverse tool was 'learned'. Thus, our primary analysis will investigate the presence of scaling of the movement velocity with object distance and of grip aperture with object size by testing whether the slopes of the scaling functions are significantly greater than zero (one-tailed prediction). Then, depending on the results, we will carry out follow-up exploratory analyses to better understand the picture revealed by the scaling functions. We will also explore the functional effect of using the reverse tool by examining success rates and overall grasping profiles. Lastly, we will investigate potential learning of the tool properties across the experiment by comparing kinematic indices (previously analysed) across the first and last block of 60 trials of the experiment using planned pair-wise comparisons (one-tailed t-tests). Learning would be evident in faster movement velocity, higher grip scaling and less errors.

5.3 Experiment 1 Results

5.3.1 Does tool use show anticipatory scaling with object properties?

Peak velocity scaling

As in previous Chapters, we analysed peak velocity in order to examine if participants scaled their movement velocity to object distance, with faster movement for further distances. We expected this 'signature' to be evident when grasping with the hand and also with the normal tool. We do not have clear expectations regarding the reverse tool. Fig. 5.2 shows the peak velocities with the hand, the normal tool and the reverse tool for each object distance. It can be seen that participants did scale their movement velocity to object distance in all conditions. Mirroring the pattern of earlier chapters, movements appear to be faster overall for the hand compared to the tools. And movement velocity was overall similar with the two tools, albeit slightly slower with the reverse tool. To examine the statistical significance of the scaling, as previously, we tested whether the mean scaling slopes differed from zero in each condition (see section 3.3.1). One-tailed one sample t-tests showed that in all cases the slopes of the object-distance scaling functions were significantly greater than zero (hand: $t(14) = 16$, $p < .001$, $d = 4.13$; reverse tool: $t(7) = 20.33$, $p < .001$, $d = 5.25$; 1:1 tool: $t(7) = 18.88$, $p < .001$, $d = 4.88$).

It can be seen that the degree of scaling of peak velocity with object distance was similar with all three effectors. However, the figure suggests overall differences in movement velocity across effectors, with the hand quickest, and the reverse tool slightly slower than the normal tool. To investigate these differences in peak velocity between effectors, we collapsed the peak movement velocity across distance, and ran an one-way repeated-measures ANOVA with effector as the factor. Mauchly's test indicated that the assumptions of sphericity had been violated ($\chi^2(2) = 12.23$, $p = .002$), so the Greenhouse-Geisser correction was applied. The ANOVA revealed a main effect of effector ($F(1.242,17.395) = 41.51$, $p < .001$, $\eta_p^2 = .75$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that movement velocity was significantly higher in hand grasping than with both tools ($p < .001$). Between the tools, movement velocity was higher with the normal tool than with the reverse tool ($p = .003$).

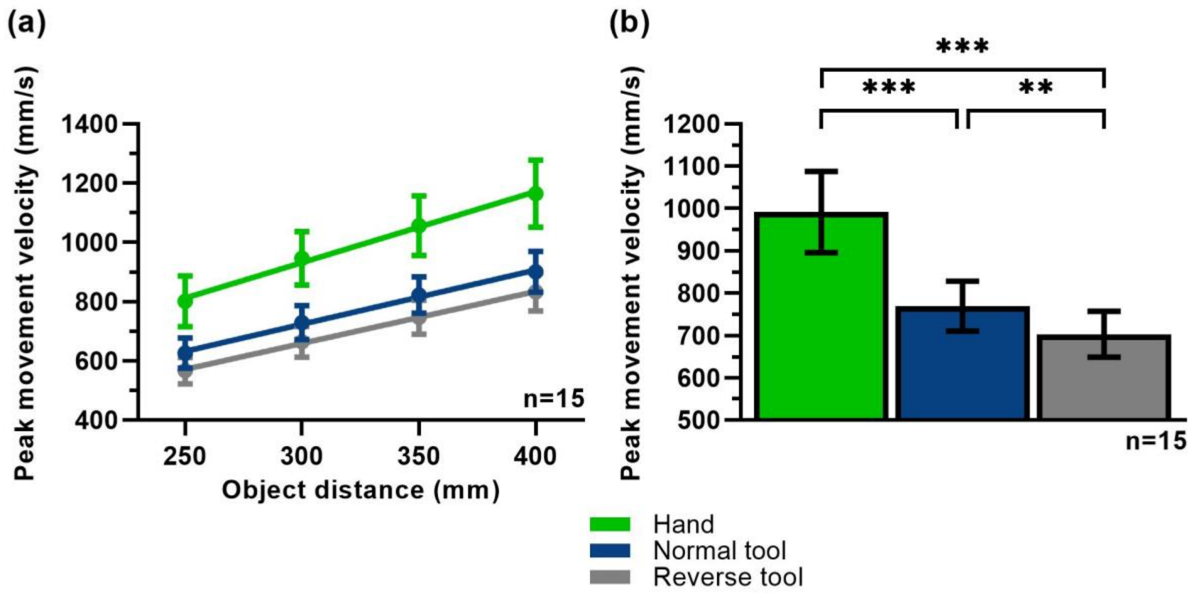


Figure 5.2. Peak movement velocity results in Experiment 1. Mean peak velocity of grasping movements with each effector as a function of object distance (collapsed across object size). Solid lines show the best fitting linear regressions to the data in each case. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Peak grip aperture scaling

As before, we also analysed peak end-effector aperture to examine if grip apertures scaled with object size. Tool aperture scaling with object size with the reverse tool would indicate anticipatory control of the tool, thus providing strong evidence for 'control as a body part' even of this tool that does not behave in an analogous manner to the hand. Fig. 5.3a shows the peak end-effector aperture with all end-effectors for each object size. It can be seen that while grip aperture scaling was present with the hand, and with the normal tool, such scaling was absent with the reverse tool. Instead, the tool-tips were opened the same (large) amount whatever the object size, suggesting a lack of anticipatory control of grasp aperture. Analysis of the mean scaling slopes (Fig. 5.3b), using one-tailed one sample t-tests, revealed that object-size scaling was significant with the hand ($t(14) = 32.67$, $p < .001$, $d = 8.44$), and with the normal tool ($t(14) = 13.68$, $p < .001$, $d = 3.53$) but not with the reverse tool ($t(14) = 1.35$, $p = .099$, $d = .35$).

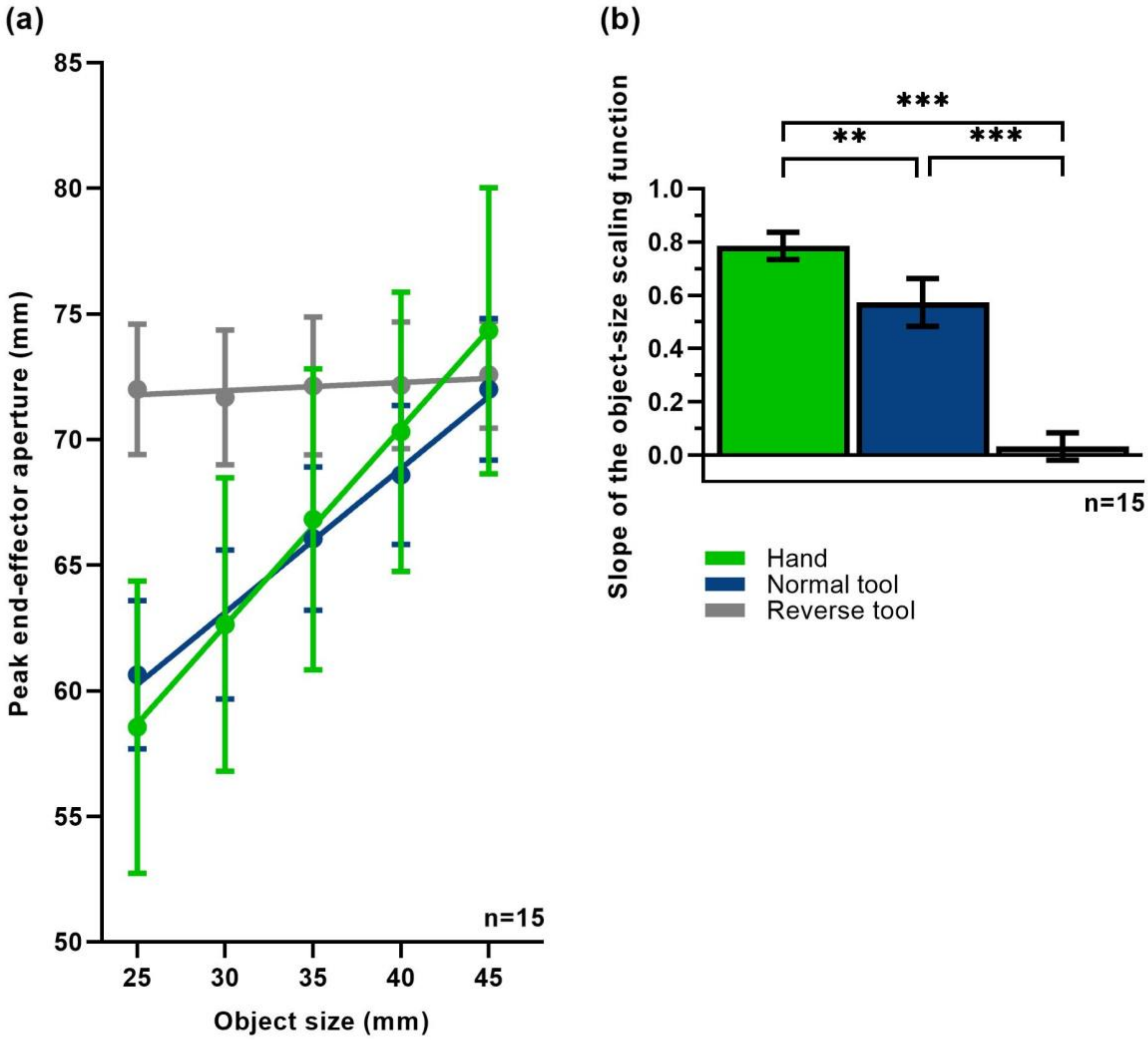


Figure 5.3. Peak end-effector aperture results in Experiment 1. (a) Mean peak end-effector aperture as a function of object size (collapsed across object distance). Solid lines show the best fitting linear regressions to the data in each case. (b) Mean of the individual participant's slope of the fitted regression lines in panel (a). In all cases, error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

The figure suggests overall differences in grip aperture scaling across effectors, we therefore examined the magnitude of the scaling function using a one-way repeated measures ANOVA on the mean slopes for all effectors. The ANOVA revealed a main effect of effector ($F(2,28) = 150.5$, $p < .001$, $\eta_p^2 = .92$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that object-size scaling was higher with the hand (0.78) than with the normal tool (0.57, $p = .003$). And object-size scaling with both the hand and the normal tool was higher than with the reverse tool (0.03, $p < .001$).

Thus, this canonical anticipatory feature of grasping with the hand, which we observed with our normal tool in this study, and with the non-1:1 geometry tools in Chapters 3 (hand = .66; 1:1 tool = .80) and 4 (hand = .83, 1:1 tool = .66), was not present with the reverse tool.

5.3.2 Functional implications of not accounting for tool geometry?

As discussed previously, the redundancy in movement control means that kinematic changes, while sensitive, do not necessarily translate directly into functional consequences, such as success or failure at grasping the object. To examine this directly we again examined the number of failures in the different conditions (here we plot error rate rather than success rate). Errors were defined as trials during which participants failed to grasp the object front to back, lifting that object at least 5 mm above the table. Fig. 5.4. shows that the proportion of errors was near zero with the hand and normal tool, but higher with the reverse tool. A one-way repeated measures ANOVA (Greenhouse-Geisser corrected for violation of the assumptions of sphericity; $\chi^2(2) = 7.46$, $p = .024$) revealed a main effect of effector ($F(1.392,19.488) = 17.35$, $p < .001$, $\eta_p^2 = .55$). Post hoc tests (pairwise comparisons, Bonferroni corrected) confirmed that the error rate with the reverse tool was significantly higher than with the hand ($p < .001$) and normal tool ($p < .001$). Thus, the lack of object-size scaling observed previously with the reverse tool was associated with a direct reduction in functional performance during the grasping task.

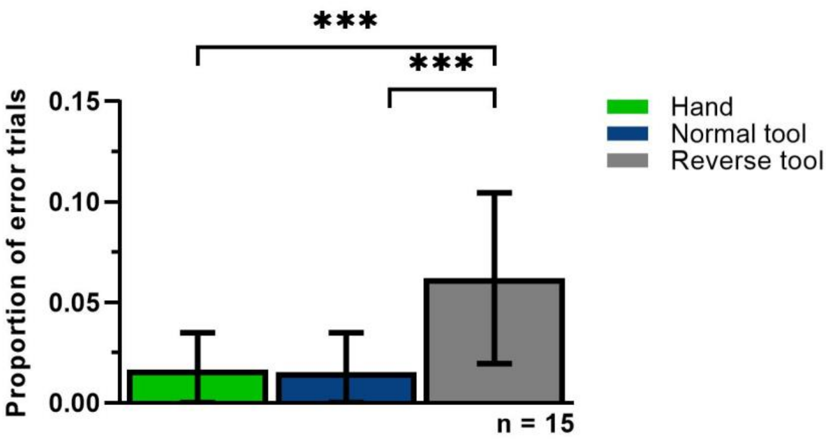


Figure 5.4. Error rates in Experiment 1. Proportion of error trials for all effectors. An error was defined as a failure to grasp the object for the different effectors. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

5.3.3 Changes in performance across the experiment?

It is possible that participants learned to use the reverse tool effectively by the end of the session, but this was masked by plotting and analysing overall data, averaged across the entire experiment, including at the beginning when performance may have been particularly poor. To explore this, we examined whether performance differed between the first and fourth block of 60 trials. Comparing the fourth vs. first block of trials such learning would presumably be evident as faster movements, increased scaling of tool opening with object size, and lower error rates.

Peak velocity

Fig. 5.5a shows the peak velocity was higher with both tools in the last block of the experiment. One-tailed paired sample t-tests showed that for both tools, movement velocity was faster in the last block than in the first block (normal tool: $t(14) = 3.776$, $p = .001$, $d = .63$: reverse tool: $t(13) = 4.476$, $p < .001$, $d = .53$).

Grip aperture scaling

Fig. 5.5b shows that the scaling of tool opening with object size was essentially unchanged across the first and fourth block of the study (one-tailed paired sample t-tests; normal tool: t(14) = -0.47, p = .324, d = -0.14; reverse tool: t(14) = 1.2, p = .875 , d = .27). Notably, scaling with the reverse tool was essentially zero even at the end of the experiment, when we might expect it to be highest.

Error rates

We do not expect the number of errors to reduce with the normal tool because they were very low overall (Fig. 5.4). Fig. 5.5c shows that number of errors with the normal tool did not change (one-tailed paired sample t-test; t(14) = -0.51, p = .617, d = - .16). With the reverse tool, participants failed more at grasping the object in the first block than the last block of the experiment, reaching a similar level to the normal-tool performance (one-tailed paired sample t-test; t(13) = 5.29, p < .001, d = 1.48).

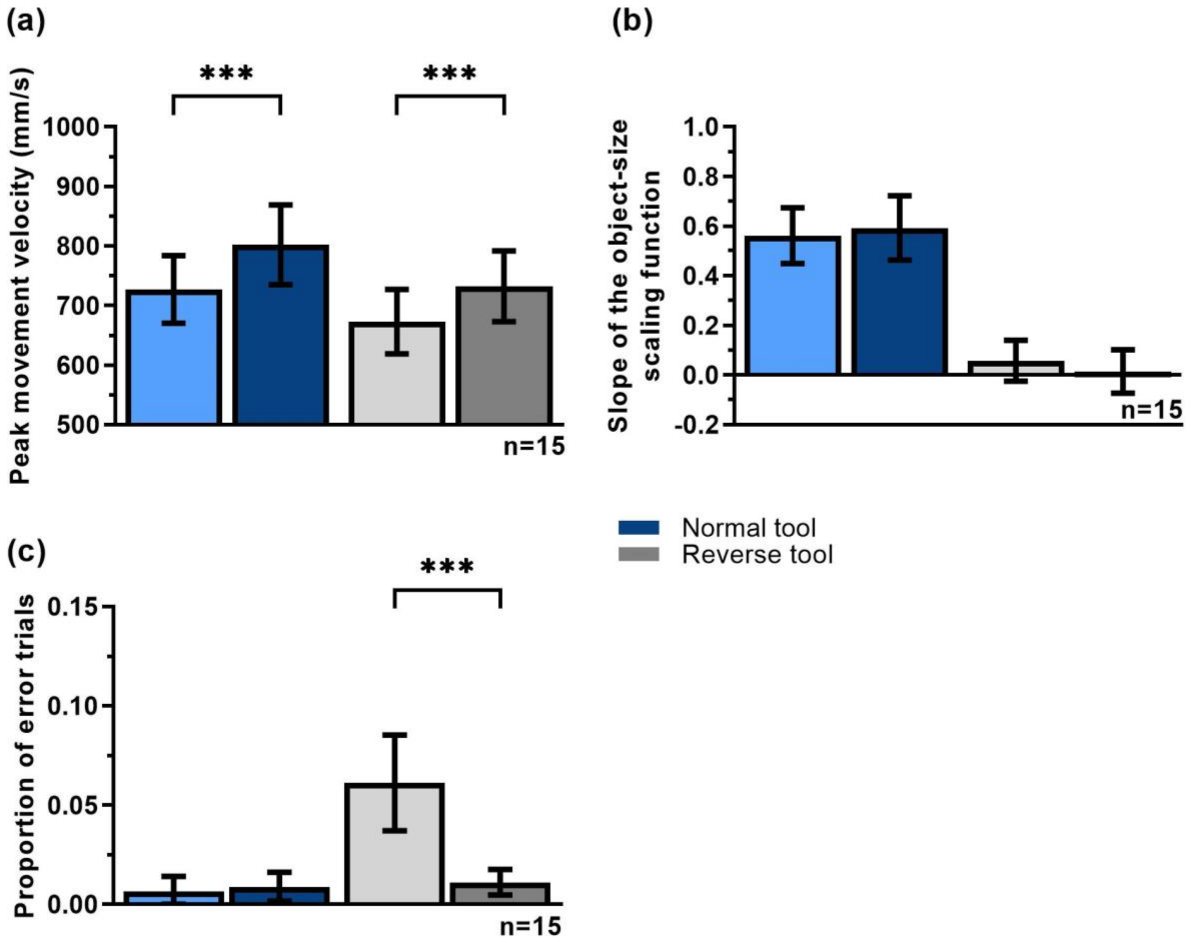


Figure 5.5. Performance across blocks in Experiment 1. (a) Mean peak velocity of grasping movements for each effector collapsed across object distance and object size. (b) Slope of the object-scaling function. (c) Proportion of error trials. The lighter coloured bars represent the first block of the experiment. The darker coloured bars represent the last block of the experiment. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

5.4 Experiment 1 Discussion

In this experiment we explored performance at grasping with a reverse tool. We have argued that using this tool 'as a body part' requires the development of knowledge of the mapping of the new tool's geometry, and new motor control programmes to control the hand (opening the hand to squeeze the object), allowing 'normal' anticipatory control to occur. Overall, the results of Experiment 1 suggest that participants did not show compelling evidence of anticipatory behaviour when using the reverse tool. Although there was significant scaling of movement velocity with object distance, and some evidence of learning from reduction in error rates across the experiment, there was no scaling of the tool tip aperture with object size. This is a canonical feature of hand grasping, and with our normal tools (including those with different gain ratios). Instead, the tools were opened the same amount independent of object size. Thus, in our study, the reverse tool did not appear to be controlled 'as a body part'.

As discussed previously, to plan and execute a movement with the tool-tips the visuomotor system must develop an internal model linking the desired movement to the hand movement required to produce it (the tool mapping). Then, it must be able to produce that correct hand movement (i.e. the required motor programmes must be formed). In this framework, the lack of anticipatory control with the reverse tool could be caused by a problem at either stage — lack of understanding of the tool mapping or an inability of the system to produce the appropriate hand movement (opening the hand to grasp). Experiment 1 does not dissociate these components because both factors—unusual tool geometry and unusual hand movement—co-varied. We consider each in more detail here, before introducing Experiment 2, which attempts to dissociate the two components or stages.

First, why might it be difficult to develop an internal model for the reverse tool than the normal (1:1) tool? If the only determining factor is mechanical complexity, we would expect no difference, because the normal and reverse tools have similar mechanical complexity. It is possible, however, that our ability to learn tool geometry is a function of experience with different tool mappings (for instance if internal models of tools can be developed by altering pre-existing models), and that we have relatively limited experience with reversing tools compared to 'normal' tools. It is also possible that not all tool transformations can be represented equally easily by the relevant underlying neural structures. In engineering terms, with the right set of basis functions, any mapping can be represented (Donchin et al., 2003; Santello et al., 2016). But the visuomotor system may not be configured in this way, and so certain types of mappings may be difficult or even impossible to internalise in such a way as to allow 'control as a body part' (though the study by Umiltà et al., 2008, suggests the latter is unlikely).

Second, the absence of anticipatory behaviour with the reverse tool could be caused by the inability of the system to perform the correct hand movement, even if the tool mapping was known. Using the reverse tool forced participants to produce an unusual hand movement—opening the hand to grasp an object. Movements such as grasping are thought to rely on 'motor primitives', that can be seen as 'building blocks' for complex movements (Santello et al., 2016; Thoroughman & Shadmehr, 2000; Wolpert & Ghahramani, 2000). As mentioned in the General Introduction, it is conceivable that pre-existing motor primitives for hand grasping, and even well-practised combinations of them, could be altered to control the normal tool, because the movements required are fundamentally similar to hand movements. It seems less likely that this is possible for the reverse tool. Even if the appropriate basic 'component' motor primitives exist, the system may need to learn how to combine them to produce appropriate movements.

A problem with either of the above 'stages' could prevent the reverse tool being used as a body part. It is also possible that there is an interaction between the challenge of learning a new internal model, and learning a new hand movement, making it particularly difficult to learn both at once. This relates to the credit assignment problem in motor learning, discussed previously. The causes of errors may be harder for the system to determine in the presence of two 'sets' of unknowns, making it difficult to know which aspects require updating. The system normally weights the different signals to locate the most likely source of error (Wolpert & Flanagan, 2010; Wolpert & Kawato, 1998; Wolpert & Landy, 2012). So, for instance, with normal tools it seems reasonable the participants could correctly attribute large error signals to the tool model because there should not be large errors in the (typical) hand movements per se (Kluzik et al., 2008). However, when grasping with the reverse tool, large error signals could result from errors in either the tool model or the hand movement, making it difficult to determine which aspect needs altering. Thus, the system could not update appropriately either the tool model or the motor programme.

Another factor that may have impaired the learning of the tool model is that participants were not exposed to a constant tool geometry, or hand movement, but were instead required to switch between the reverse and normal tool after a random number of trials. This situation is again reminiscent of so-called dual-adaptation experiments (as discussed in previous Chapters, Krakauer et al., 1999; Martin et al., 1996; Wada et al., 2003; Welch et al., 1993; Woolley et al., 2007), and may hinder the ability to track the effects of adjustments to the components of the control process over successive trials. More continuous exposure may help in localising the source of errors, resulting in better performance.

In Experiment 2 our primary aim was to dissociate learning of the tool model per se from learning of the new hand movement, in order to gain insights into the causes of the observed lack of anticipatory movements with the reverse tool. We also presented blocks of trials with the same tool, in order to rule out the (comparatively trivial) explanation that interleaving different tools/tasks was the primary cause of poor performance (due to a high contextual interference effect; Brady, 1998, 2008; Magill & Hall, 1990).

5.5 Experiment 2 Introduction

In this experiment participants not only grasped objects with normal and reverse tools, but also made two different types of grasping movement: (i) the normal closing of the tool-tips to enclose the object, as in in Experiment 1, and (ii) opening the tool-tips, to grasp the inside surfaces of a U-shaped object (see Fig. 5.6), which we refer to as ‘reverse grasping’.

The logic of these manipulations is illustrated schematically in Fig. 5.6. Consider each combination of these factors in turn. The top row shows the conditions from Experiment 1. The normal-tool, normal-grasp condition (top left in Fig. 5.6) requires a tool mapping that is relatively easily understood, according to our previous data, and a normal open-then-close hand movement. Then the reverse-tool, normal-grasp condition (top right in Fig. 5.6) requires both an unusual (reversed) tool mapping, and an unusual hand movement pattern (close-then-open hand to grasp).

The normal-tool, reverse-grasp condition (bottom left in Fig. 5.6) retains the normal tool mapping, but requires a close-then-open hand-movement pattern, very similar to normal grasping with the reverse tool in Experiment 1. Thus, this condition allows us to determine the effect on performance of having to produce an unusual hand-movement pattern per se. We have used this task (grasping U-shaped objects, but with the hand) in a previous study (Keefe et al., 2019), and found that although anticipatory grip aperture scaling was reduced, it was still statistically significant, indicating that most participants can learn this movement within the duration of a typical experiment. Here we will learn whether this can be achieved when grasping with a tool. Finally, in the reverse-tool, reverse-grasp condition the object is grasped by closing the hand, to open the tool inside the U-shaped object. That is, grasping in this condition requires the typical open-then-close hand-movement pattern, qualitatively similar to normal movements. Thus, comparing performance in this condition to the normal-tool, normal-grasp condition isolates (to some extent) the component of acquiring the novel tool mapping.

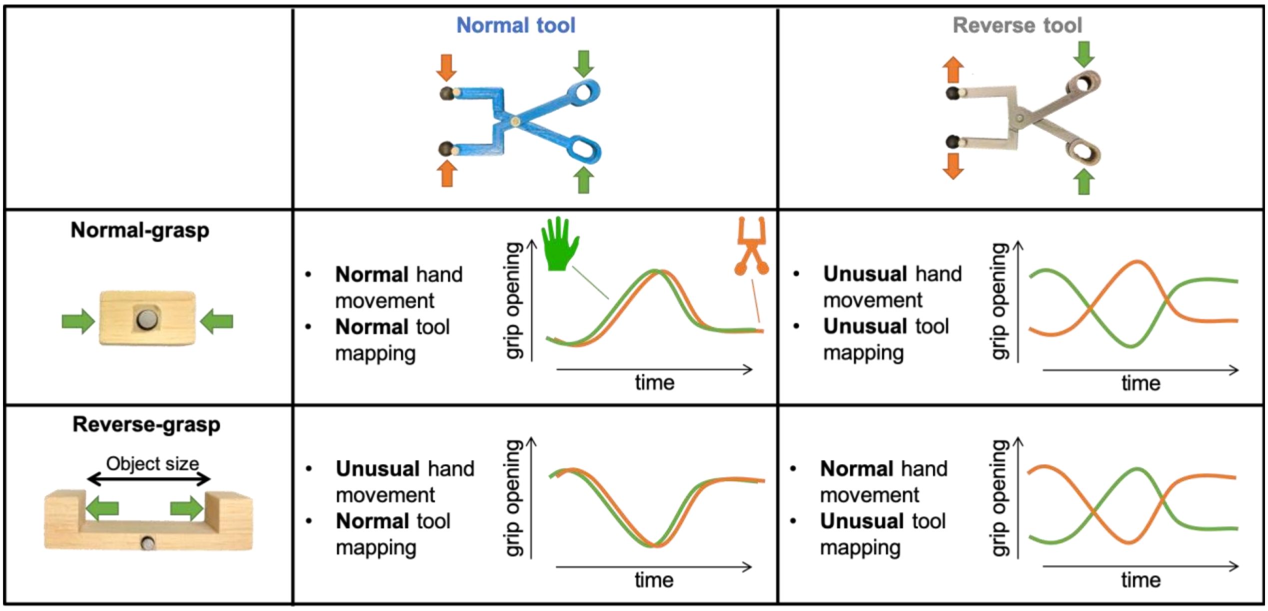


Figure 5.6. Schematic of the experimental conditions. Representation of the tool and hand opening-closing movements required in each condition. The leftmost column shows photographs of the object types used in each task. The green arrows depict how participants' tool-tips made contact with the object. The remaining columns show hand- and tool-opening profiles with each tool type. The orange lines denote the required opening of the end-effector (the tool aperture). The green lines denote the hand opening required to produce that tool tip opening.

5.5.1 Predictions

Fig. 5.7. depicts different possible outcomes of Experiment 2, under various different theoretical scenarios. For simplicity, we plot predicted 'performance' (where higher is better) rather than predictions for specific dependent measures. A first possibility (Fig. 5.7a) is that the poor performance with the reverse tool in Experiment 1 is caused solely from difficulty producing the correct hand movement (opening the hand to exert grasping force) and not from the understanding of the tool geometry per se. Here, the normal-tool, reverse-grasping performance should be similarly poor as the reverse-tool, normal-grasping (the reverse tool in Experiment 1) because the barrier to performing well is producing the unusual hand-movement pattern. In contrast, the reverse-tool, reverse-grasping condition should result in high performance, because the tool mapping is understood, and the hand-movement pattern required is normal. In reality, we might expect some impairment to performance relative to the normal-tool, normal-grasping condition because it may be non-trivial for the brain to recognise that the normal grasp movement programmes can be used in this case. However, if there is an advantage to having a normal overall grasp pattern (open-then-close the hand), we would expect to see an advantage in this condition compared to the reverse-tool, normal-grasping condition.

A second possibility (Fig. 5.7b) is that the decreased performance with the reverse tool in Experiment 1 comes solely from the lack of knowledge of the reverse tool geometry/mapping, and not from an inability to produce the correct (unusual) hand movement. If so, we would see good performance in both task with the normal tool, and poor performance in both tasks with the reverse tool, regardless of the type of grasp required. In practice, the 'perfect' performance in the normal-tool, reverse-grasp condition depicted in the figure is unlikely, given the reduced performance in reverse-grasping with the hand observed by Keefe et al. (2019). But we would expect to see an advantage compared to the performance with the reverse tool.

A third possibility (Fig. 5.7c) is that the decreased performance with the reverse tool in Experiment 1 comes from a combination of the inability to produce the correct hand movement, and poor knowledge of the reverse-tool mapping. In this case, we would see poor performance in any situation where either was required, resulting in poor performance in all conditions except the normal-tool, normal-grasping condition.

A fourth possibility (Fig. 5.7d) is that poor reverse-tool performance in Experiment 1 results specifically from the interaction of the requirement for a novel tool mapping and an unusual hand movement (as discussed earlier). Here good performance would be maintained in conditions where only one of these novel factors was introduced (normal-tool, reverse-grasping and reverse-tool, reverse-grasping), but poor performance when both were introduced together (reverse-tool, normal grasp condition).

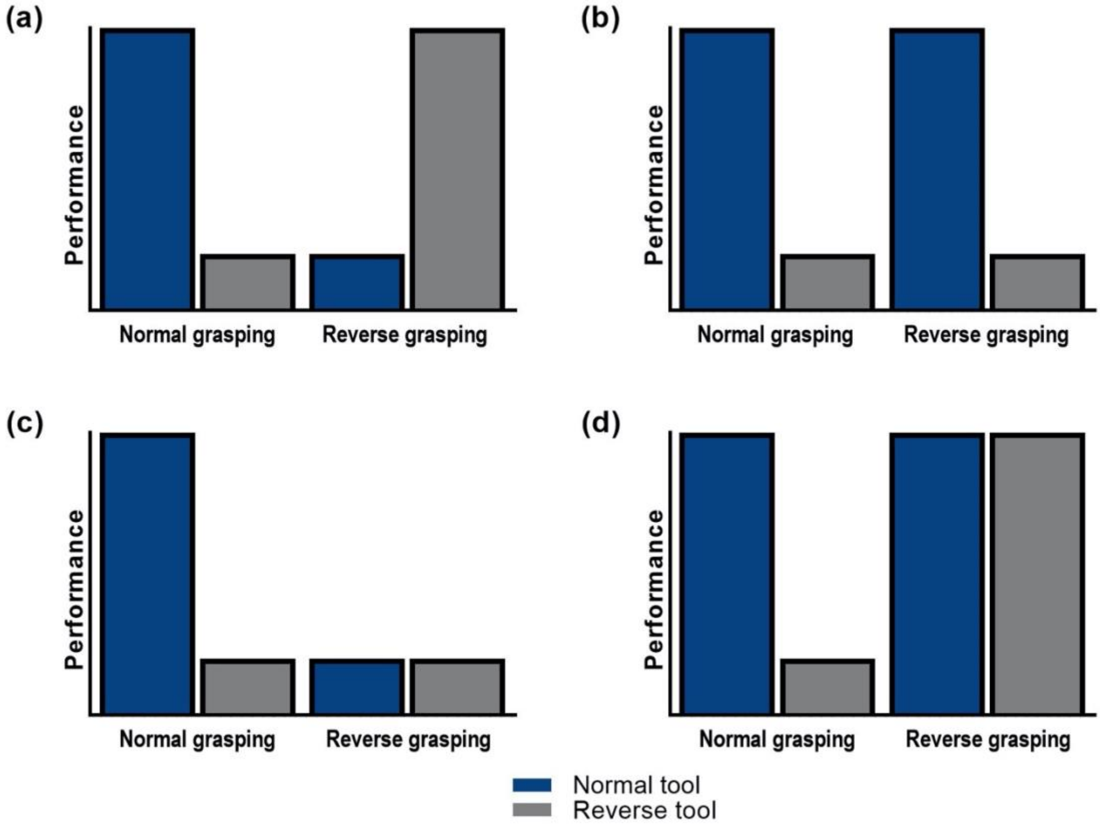


Figure 5.7. Graphical representation of the different possible outcomes of experiment 2. (a) Based on the first theoretical possibility. (b) Based on the second theoretical possibility. (c) Based on the third theoretical possibility. (d) Based on the fourth theoretical possibility

In this experiment participants also used the same tool, for the same grasping task, on a number of consecutive trials (see Method) to improve the chances of learning the novel requirements.

5.6 Experiment 2 Methods

5.6.1 Participants

20 right-handed participants completed this experiment (12 female, 8 male; aged 18-40 years old). All participants had normal or corrected-to-normal vision, and no known impairments that would affect their ability to grasp. Participants were reimbursed at the rate of £6 per hour. Participants gave informed consent prior to taking part, and all procedures were in accordance with the Declaration of Helsinki. None of them participated in experiment 1.

5.6.2 Apparatus and stimuli

The experiment apparatus and stimuli were the same as in Experiment 1, with the exception of the U-shaped balsa wood objects used for the reverse-grasp task (see Fig. 5.6). The distances between the grasping surfaces were 80, 85, 90, 95, & 100 mm. Those object sizes were chosen because they resulted in a similar range of final hand openings across the various conditions. The objects weighted from approximately 40g (80 mm object) to 60g (100 mm object).

5.6.3 Procedure

In the two normal grasping conditions, the procedure for each trial was the same as in Experiment 1. In the normal grasping conditions, participants again began each trial with the tool tips closed (i.e. with the hand open, in the reverse tool case). In the reverse grasping conditions, participants began their movement with the tool tips opened by 80 mm (matching the hand opening when using the other tool in the normal grasping condition). To do this, a small piece of wood (10 x 10 mm) was placed 80 mm in front of the start button, and participants were instructed to place one tool-tip on the start button and the other one on the small piece of wood.

The experiment was divided into four sessions of 240 trials (to equal the number of trials per condition in experiment 1), completed over four consecutive days. Participants completed two consecutive sessions of one grasping task (e.g. normal grasping), followed by two of the other grasping task (e.g. reverse grasping). Half of the participants completed the normal-grasping task first, and the other half completed the reverse-grasping task first. Within each session, participants completed three ‘mini-blocks’ with each tool type. Each mini-block comprised 40 trials (2 repetitions x 5 object sizes x 4 object distances) with one tool. Participants swapped tools at the end of each mini-block, and the starting tool was counterbalanced across participants.

5.6.4 Data analysis and predictions

For this second experiment, we will apply a similar structure to Experiment 1. Our primary analysis will investigate whether the brain can produce anticipatory scaling with object properties when performing both hand movements with both tools. We will therefore test whether the slopes of the scaling functions (movement velocity with object distance and grip aperture with object size) are significantly greater than zero (one-tailed prediction). Once more, our manipulation relates to grip, so the scaling of grip aperture will be the *key* measure in understanding if both hand movements could be performed with both tools. Indeed, presence of evidence for those anticipatory behaviours would reflect the motor system’s ability to perform a specific hand movement with a defined tool geometry. Then we will use the ‘prediction’ graphs in Section 5.5.1, allowing us to explore which scenario correspond the most to our data, and thus to better understand the effect of the each hand movement and of each tool geometry. And we will carry out appropriate follow-up exploratory analyses. We will also explore the functional effect of performing both hand movements with both tools by examining success rates and overall grasping profiles. Lastly, we will investigate potential learning of the tool properties across the experiment by comparing kinematic indices (previously analysed) across the first and last block of 40 trials of each condition using planned pair-wise comparisons (one-tailed t-tests). Learning would be evident in faster movement velocity, higher grip scaling and less errors.

5.7 Experiment 2 Results

5.7.1 Does tool use show anticipatory scaling with object properties?

Peak velocity scaling

As in Experiment 1, we started by examining the scaling of movement velocity to object distance. Fig. 5.8 shows the peak velocities as a function of object distance for the normal grasping (left panel) and reverse grasping (right panel) tasks. It can be seen that movement velocity scaled to object size in all conditions. The data for the normal grasping conditions (a near-replication of Experiment 1) showed a similar pattern to Experiment 1, in that overall movement velocities are slightly slower with the reverse tool. In the reverse-grasping condition movement velocities were similar across the two tools, and appear comparable to in the reverse-tool, normal grasping condition. We again probed the presence of velocity/distance scaling by testing (one-tailed one sample t-tests) whether the scaling function slopes were different from zero. In all conditions the scaling was significant (normal-tool, normal-grasping: $t(19) = 26.64$, $p < .001$, $d = 5.97$; reverse-tool, normal-grasping: $t(19) = 30.69$, $p < .001$, $d = 6.86$; normal-tool, reverse-grasping: $t(19) = 22.51$, $p < .001$, $d = 5.03$; reverse-tool, reverse-grasping: $t(19) = 23.58$, $p < .001$, $d = 5.28$).

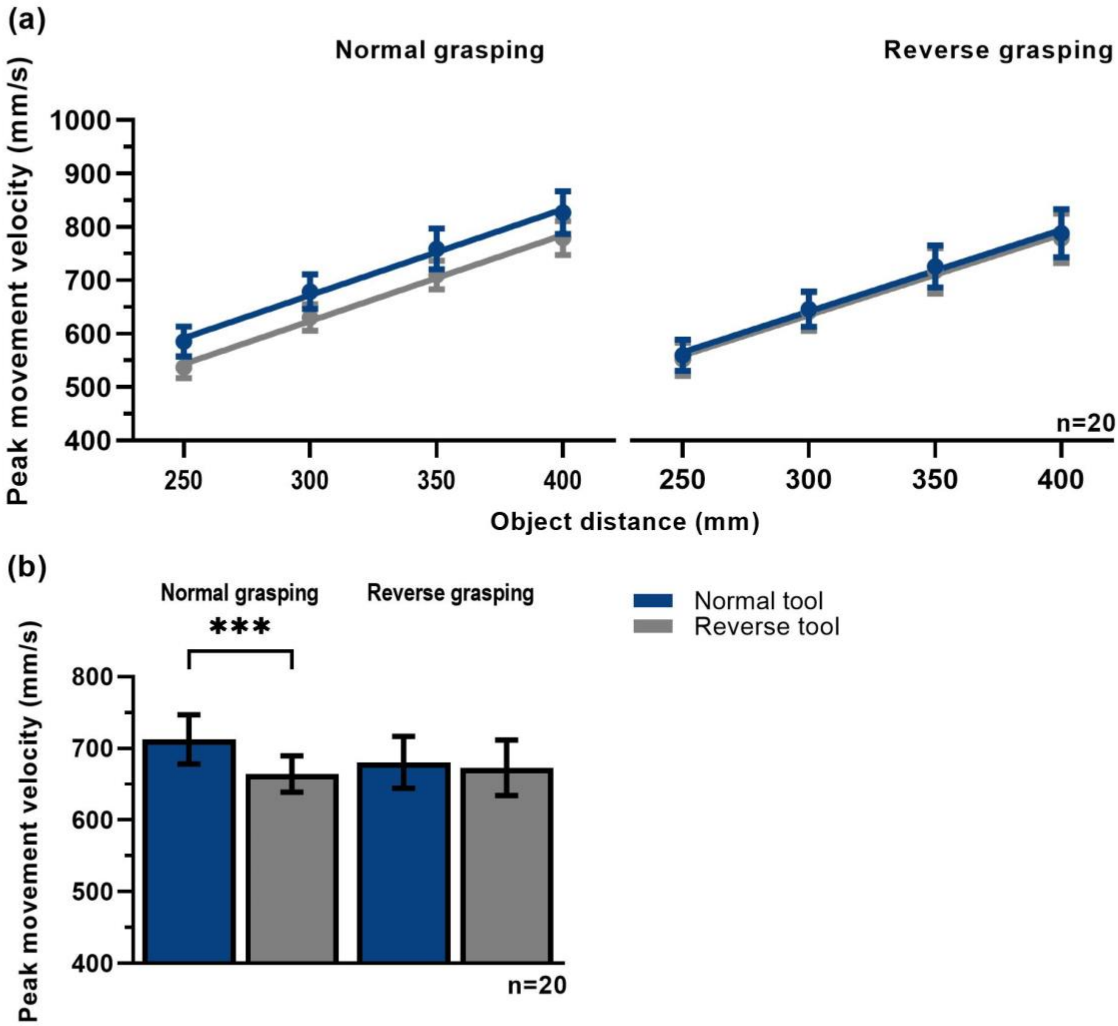


Figure 5.8. Peak velocity in Experiment 2. (a) Mean peak velocity of grasping movements with each effector as a function of object distance (collapsed across object size). Solid lines show the best fitting linear regressions to the data in each case. (b) Same data collapsed across object distance. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

The figure suggests overall differences in movement velocity across the different tasks and tools. To investigate these differences we first collapsed the peak movement velocity across distances (Fig. 5.8b). This renders the data comparable, conceptually, to the predictions plots in Fig. 5.7 (assuming that faster movements equate to better 'performance'). The data most closely resemble the predictions for a combination of both difficulty producing the correct hand movement, and poor knowledge of the reverse-tool mapping, because introducing either requirement on its own, or both together, resulted in similar slowing of movement velocity. A 2 x 2 (task x tool) repeated measures

ANOVA revealed a main effect of tools (F(1,19) = 26.68, $p < .001$, $\eta_p^2 = .58$), no main effect of tasks (F(1,19) = 0.68, $p < .42$, $\eta_p^2 = .03$), and a significant interaction between tasks and tools (F(1,19) = 9.85, $p = .005$, $\eta_p^2 = .34$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that movement velocity was significantly higher in the normal-tool, normal-grasping than in the reverse-tool, normal-grasping condition ($p < .001$), and not significantly higher than in the normal-tool, reverse-grasping ($p = .289$) and than in the reverse-tool, reverse-grasping ($p = .088$). There were no significant differences between the remaining conditions ($p = 1$). Although adding either an unusual geometry, or an unusual movement equally decreases movement velocity, the pattern of statistical effect is consistent with the predictions pattern for the case where adding both an unusual tool geometry, and an unusual movement decreases movement velocity (Fig. 5.7d)

Peak tool-tips aperture scaling

Fig. 5.9a shows the peak tool-tip aperture as a function of object size for the different conditions. As the two grasping tasks require qualitatively very different movements, the absolute magnitude of peak grip apertures cannot meaningfully be compared across tasks. We can, however, examine the degree of size scaling, as in previous experiments. The figure shows that participants show typical scaling in the normal-tool, normal-grasping condition. Relatively little scaling is seen in the three other conditions, although the reverse-tool, normal-grasping data does appear to show more scaling the comparable condition in Experiment 1. We analysed whether the tool aperture scaling differed significantly from zero by analysing the slopes of the participant's scaling functions, as previously, using one-tailed one sample t-tests. For all conditions, the tool aperture scaling was significantly different from zero (normal-tool, normal-grasping: t(19) = 14.26, $p < .001$, $d = 3.19$; reverse-tool, normal-grasping : t(19) = 5.24, $p < .001$, $d = 1.17$; normal-tool, reverse-grasping: t(19) = 5.35, $p < .001$, $d = 1.2$; reverse-tool, reverse-grasping: t(19) = 1.75, $p < .048$, $d = .39$). The scaling for the reverse-tool, reverse-grasping is very low and just slightly significant. These data suggest that, for normal grasping, the change of blocking tool type did lead to increased aperture scaling with the reverse tool compared to Experiment 1.

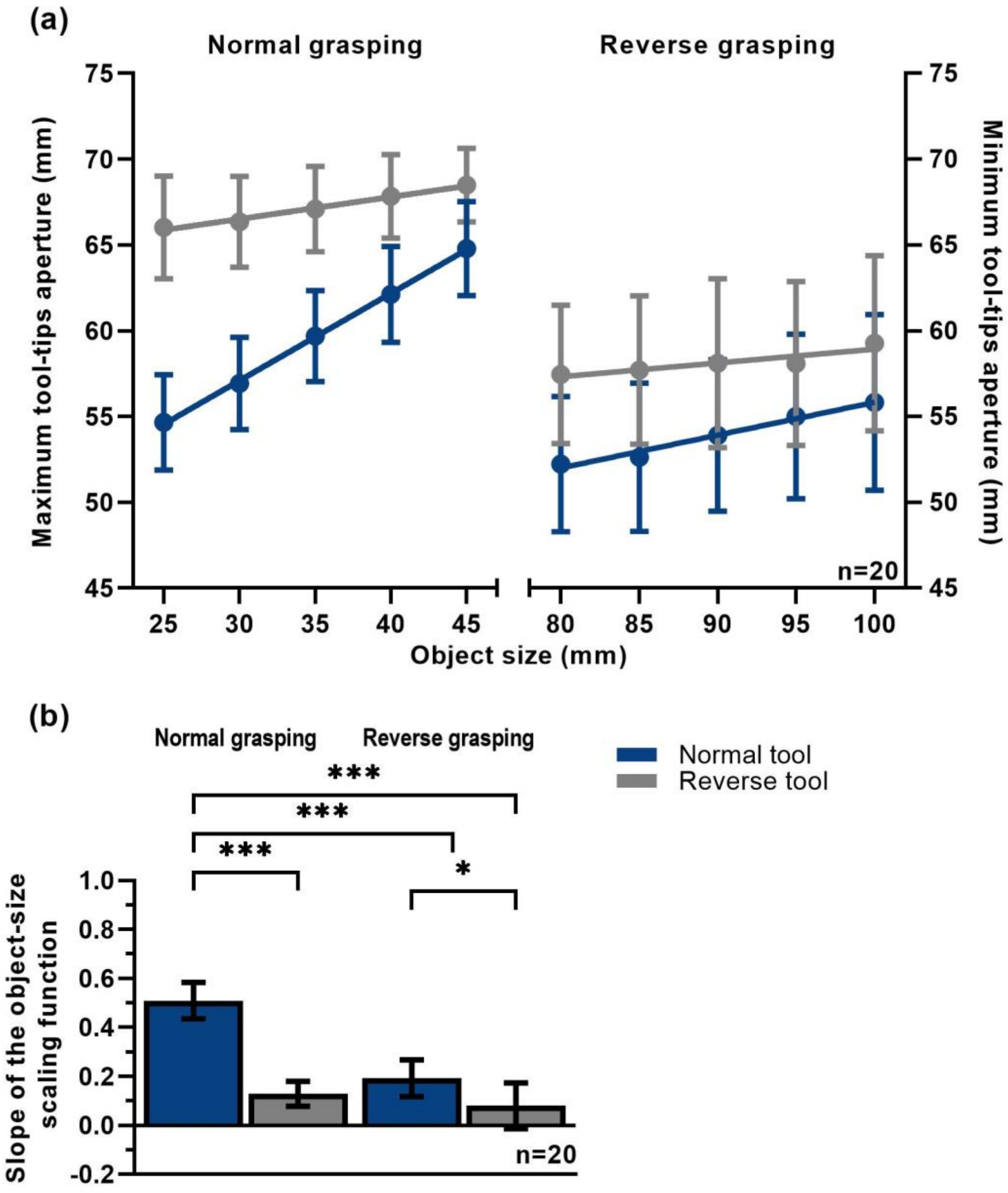


Figure 5.9. Peak tool-tip aperture results for Experiment 2. (a) Mean peak tool-tip aperture as a function of object size (collapsed across object distance). The data represent the maximum peak aperture in the normal grasping task, and the minimum peak aperture in the reverse grasping task. Solid lines show the best fitting linear regressions to the data in each case. (b) Mean of the individual participants' slope of the fitted regression lines in panel (a). The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

We next considered the grip aperture scaling data in light of the predictions plots in Fig. 5.7. Fig. 5.9b plots the mean tool aperture scaling in each condition, collapsed across object size and distance. Similar to the logic employed above, assuming that increased aperture scaling represents greater anticipatory control, and therefore better 'performance', the pattern of data in Fig. 5.9b can be compared to the predictions plots (Fig. 5.7). Qualitatively, the figure again most closely resembles the predictions for a combination of both difficulty producing the correct hand movement, and poor knowledge of the reverse-tool mapping (Fig. 5.7c). Once again, introducing either requirement on its own, or both together, resulted in similar reduction of object-size scaling. The scaling in the normal-tool, reverse-grasping data suggest, however, that performance was always better with the normal tool, even in the reverse-grasping condition. This aspect of the data therefore somewhat resembles the prediction in Fig. 5.7b, hinting that acquiring knowledge of the reverse tool mapping per se may have contributed most to the poor performance with the reverse tool.

A 2x2 (grasping task x tool) repeated measures ANOVA revealed a main effect of grasping task ($F(1,19) = 48.12$, $p < .001$, $\eta_p^2 = .72$), a main effect of tools ($F(1,19) = 73.12$, $p < .001$, $\eta_p^2 = .79$), and a significant interaction ($F(1,19) = 25.12$, $p < .001$, $\eta_p^2 = .57$). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that there was significantly more scaling in the normal-tool, normal-grasping condition (0.51) than in all of the other three conditions (vs. reverse-tool, normal-grasping: 0.13, $p < .001$; vs. normal-tool, reverse-grasping: 0.19, $p < .001$; vs. reverse-tool, reverse-grasping: 0.08, $p < .001$). Grip aperture scaling was also significantly higher in the normal-tool, reverse-grasping than in the reverse-tool, reverse-grasping condition ($p = .044$). Grip aperture scaling did not differ significantly between the reverse-tool, normal-grasping and the normal-tool, reverse-grasping ($p = .709$), and the reverse-tool, reverse grasping ($p = 1$).

Thus, the pattern of statistical effects is essentially consistent with the qualitative observations above regarding the scaling data, and their relationship to the predictions. Requiring either a novel hand movement, or understanding of the reverse-tool geometry (or both), led to a substantial reduction in anticipatory control, as indexed by aperture scaling. Thus, both components seem to have contributed to the poor reverse-tool performance seen in Experiment 1 (as per Fig 5.7b). The data provide some evidence that difficulty acquiring the mapping of the reverse tool may have made a larger contribution than the requirement to make a novel hand movement. Compared to the normal-tool, normal-grasping baseline, changing only the grasping task (normal-tool, reverse-grasping) had a significantly smaller effect than changing the tool while keeping the hand movement similar (reverse-tool, reverse-grasping; paired sample t-test: $t(19) = -2.46$, $p = .024$, $d = -.55$). This is consistent with difficulty in acquiring the tool mapping of the reverse tool causing the larger reduction in anticipatory control. Relatedly, using a normal hand movement with the reverse tool (reverse-tool, reverse-grasping) did not confer any performance advantage over using the same tool to perform normal grasping, consistent with knowledge of the tool geometry being a limiting factor. We are cautious not to over-interpret these effects, however, given the additional complication that the brain would need to have recognised that the normal grasp movement programmes can be used in the reverse-tool, reverse grasping case, which may make a distinct contribution. Moreover, the degree of scaling in all three of the 'non normal' conditions was, quantitatively, very low (slopes < 0.2) compared to that observed in normal, anticipatory control.

5.7.2 Functional implications of not accounting for tool geometry?

Error rates

As in Experiment 1, we analysed the proportion of errors made by participants to examine whether lack of anticipatory behaviour appeared to be related to success or failure at grasping. Fig. 5.10. shows the proportion of trials in which participants made errors (failed to grasp the object) in each condition. It can be seen that error rates were overall low, although more errors were made for normal grasping with the reverse tool compared to the other three conditions. It seems therefore that, compared to the normal-tool, normal-grasping condition, participants did not make more errors when only the hand movement changed (normal-tool, reverse grasping) or when only the tool changed (reverse-tool, reverse-grasping condition). In contrast to the scaling data, the pattern of error rates closely resembles the predictions for the interaction of novel tool mapping and novel hand movement causing a particular performance problem, whereas changing either one alone does not (Fig. 5.7d).

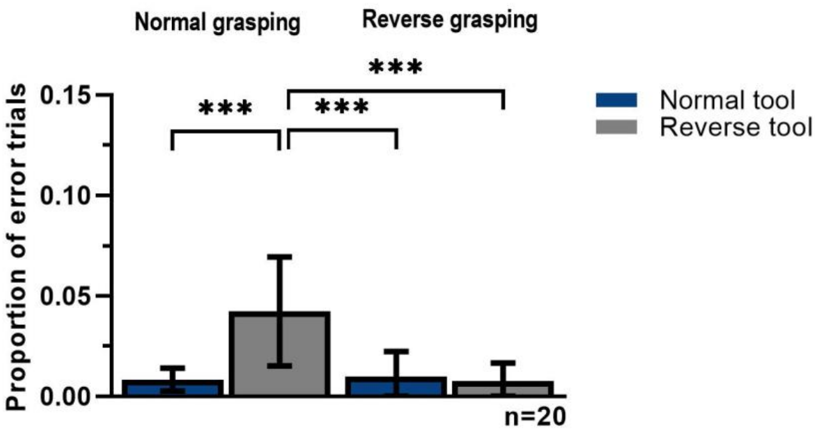


Figure 5.10. Error rates in Experiment 2. Proportion of error trials, defined as a failure to grasp the object, for both tools in each grasping task. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

A 2x2 (grasping task x tool) repeated measures ANOVA revealed a main effect of grasping task (F(1,19) = 4.76, p = .042, η_p^2 = .20), a main effect of tools (F(1,19) = 5.67, p = .028, η_p^2 = .23), and a significant interaction (F(1,19) = 7.36, p = .014, η_p^2 = .28). Post hoc analysis pairwise comparisons (Bonferroni corrected) indicated that the percentage of errors was significantly higher in the reverse-tool, normal-grasping condition than in the other conditions (normal-tool, normal-grasping, p = .005; normal-tool, reverse-grasping, p = .016; reverse-tool, reverse-grasping, p = .009). It seems that the combination of grasping with a tool with an unusual geometry and producing and usual hand movement lead to more errors (Fig. 5.7d).

Considering error rates therefore gives a similar picture than the object-distance scaling indices (and different picture than the object-size scaling indices). Here, both an unusual geometry and an unusual hand movement are needed to affect performance, whereas object-size scaling was affected by either unusual geometry or unusual hand movement alone. We explore possible reasons for this in the Discussion.

Movement corrections

As well as overall failures to grasp the objects, we observed during this study that participants frequently made distinct adjustments, or corrections during their movements. These corrections were defined as the presence of at least two peaks in the grip aperture profile. The presence of a correction during the movement would seem to indicate inaccurate movement planning. Fig. 5.11 shows the proportion of trials in which participants corrected their movement, and successfully grasped the object (i.e. these trials are distinct from the errors examined above). The figure suggests that participants made more corrections overall in the reverse grasping task than in normal grasping, and more corrections with the reverse tool than with the normal tool. A 2 x 2 (grasping task x tool) repeated measures ANOVA revealed a main effect of grasping task ($F(1,19) = 40.96$, $p < .001$, $\eta_p^2 = .68$), and a main effect of tool ($F(1,19) = 26.99$, $p < .001$, $\eta_p^2 = .59$), but no significant interaction ($F(1,19) = 0.65$, $p = .802$, $\eta_p^2 = .01$). Post hoc analysis pairwise comparisons (Bonferroni corrected) confirmed that significantly less corrections were made in the normal grasping task than in the reverse grasping task ($p < .001$), and that less corrections were made with the normal tool than with the reverse tool ($p < .001$). The pattern of statistical effect is not directly consistent with any of our predictions (Fig. 5.7), as each component (tool geometry, hand movement) seems to interact to affect the number of corrections made. That is, there is here a clear effect of task and in each task, more corrections were made with reverse tool. The ‘worst’ performance was observed in the reverse-tool, reverse-grasping. We explore possible reasons for this in the Discussion.

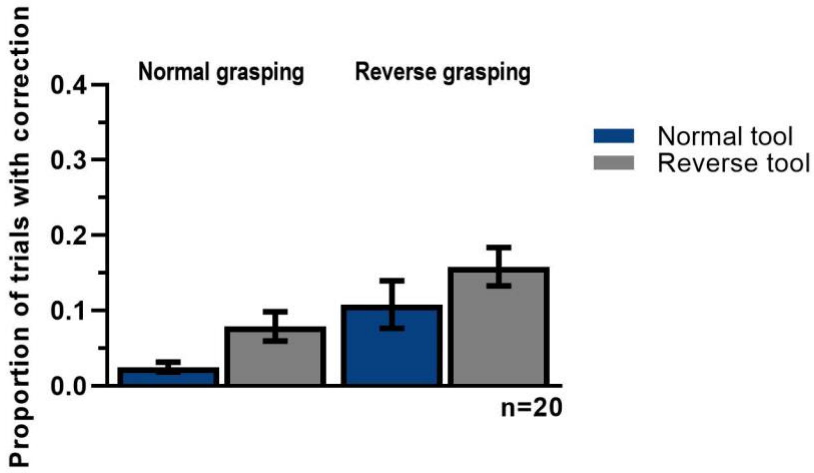


Figure 5.11. Correction rates in Experiment 2. Proportion of trials in which participants issued a correction, defined as another sub-movement before the completion of the grasping movement. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Overall average movements profiles

We have so far analysed specific kinematic indices of movements capturing only a tiny portion of the movement (although they are highly auto-correlated), and so may not reflect other differences (and similarities) between movements across different conditions. Thus, as in previous Chapters, we computed overall grasping profiles for all conditions (for detailed method see Chapter 2, section 2.6). We removed 3 participants due to noisy data collection, leading to the removal of too many trials in one or more conditions. Of the 17 participants left, for the normal grasping task, we kept 98% of the trials (out of 4080) with the normal tool and 94% with the reverse tool. For the reverse grasping task, we kept 98% of the trials with both tools. The overall grasping profiles for each condition are presented in Fig. 5.12. The top-left panel (Fig. 5.12a) plots tool-tips aperture for the normal grasping task as a function of time. The top-right panel (Fig. 5.12b) plots the same data as a function of space. The bottom row plots the equivalent data for the reverse grasping task. A version of those plots with error bars is available in section 7.3.1 (Fig. 7.7)) and overall grasping profiles for each object size, for all effectors are also available (normal-grasping: Fig. 7.8, 0.7:1 tool and reverse-grasping: Fig. 7.9).

When examining the normal grasping task as a function of time (Fig. 5.12a), we noticed that the normal tool and the reverse tool movements were quite different. The reverse tool profile presents a larger tool-tips aperture than the normal tool profile. This reflects the same pattern as observed in Fig. 5.9a. Opening the tool wider could be a 'safe' strategy, adding a margin-for-error to the grasping movements, due to uncertainty about the tool model or the hand movement required, to ensure grasp completion (Hesse & Franz, 2009a; Keefe et al., 2019; Schlicht & Schrater, 2007). We also noticed it took more time to complete the grasping movement with the reverse tool, reflecting the slower movement velocity, and the corrections made during movements. When examining the reverse grasping task normalised in time (Fig. 5.12c) we noticed the profiles resemble 'inverse' normal profiles. The profiles for both tools are similar, and don't differ qualitatively. It appears when using the normal tool, a larger margin-for-error was added than when using the reverse tool. That is, as participants have to insert the tool-tips inside the object before pressing on the surfaces, a smaller tool-tips aperture would increase the chance of success.

As we found small amount of object-size scaling (except in normal-tool, normal-grasping condition), it is possible that participants used a 'non-anticipatory' strategy, consisting of opening the hand as wide as needed really early in the movement, and only initiating the closure phase once the tool stops at the object. Evidence would come from the normalised space plots. That is, if the hand is still moving as the grip closes, it would suggest a more anticipatory, fluid control of the movement. On the other hand, if the hand was not moving as the grip closes (straight vertical line at the hand of the profile), it would suggest a 'non-anticipatory' strategy. In all conditions (except normal-tool, normal-grasping), it can be seen that the hand was no longer moving at the beginning of the closure phase of the grasp. This pattern is particularly evident in the reverse grasping task. This is consistent with a non-anticipatory control of the grasp.

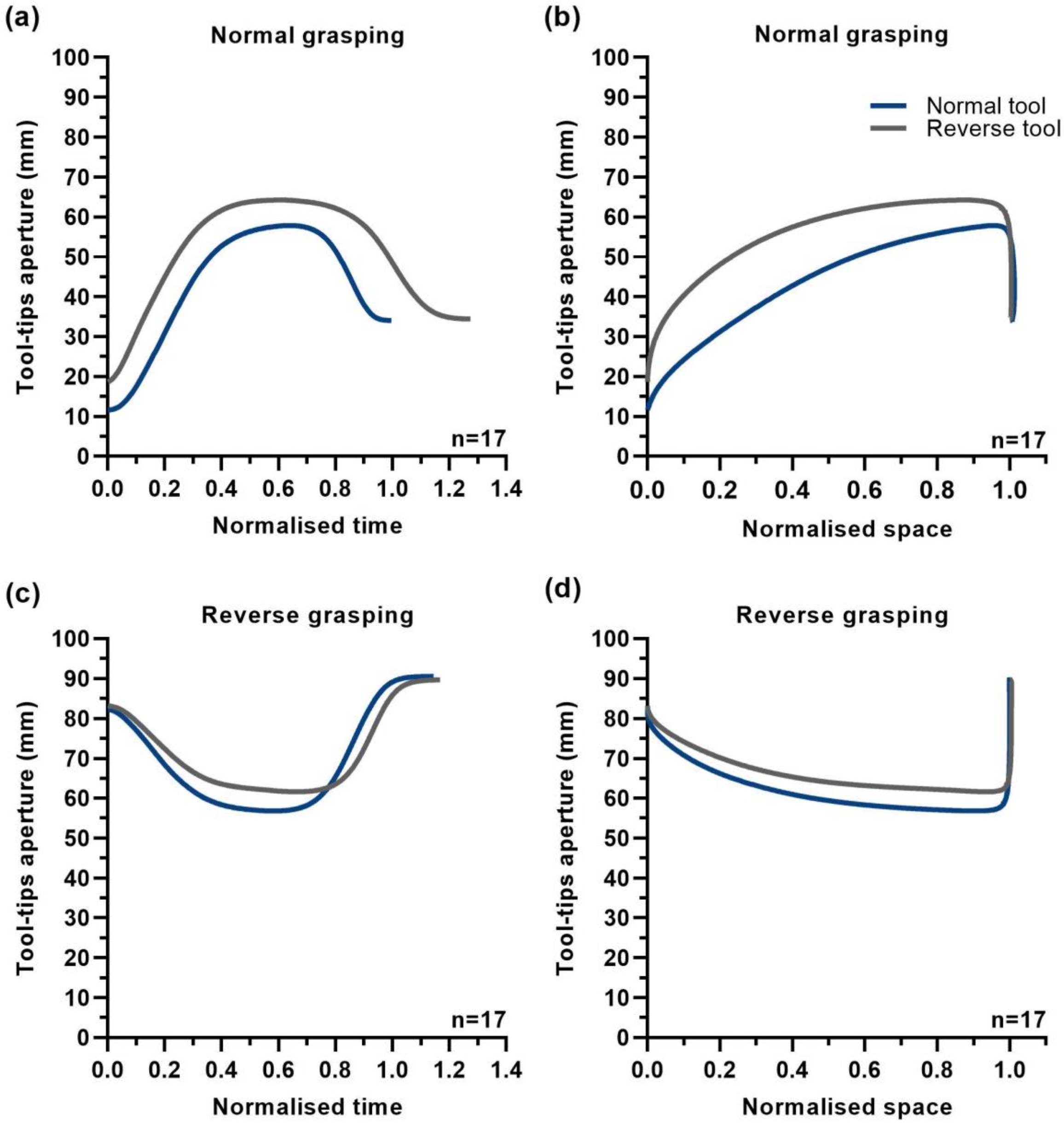


Figure 5.12. Overall grasping profiles for Experiment 2. (a) Overall tool aperture profiles for the normal grasping task (collapsed across object distance and size) as a function of time, normalised by the time the object was lifted in the normal-tool condition. (b) The normal grasping data normalised with respect to space. (c) Tool aperture profiles for the reverse grasping task, otherwise as panel (a). (d) The reverse grasping profiles normalised in space, as per panel (b).

In both tasks, the profiles show evidence of the 'plateau' phase found in the literature (Gentilucci et al., 2004; Bongers et al., 2010; Golenia et al., 2014; Itaguchi & Fukuzawa, 2014) and in both previous Chapters. As in those previous Chapters, we calculated the plateau duration in each condition (Fig. 5.13). It can be seen that more time was spent in the plateau phase in the reverse tool in both tasks. As both tasks required different movements, we decided not to analyse the differences between them (as we were unsure that a direct comparison would be meaningful), but instead to look at the effect of using the different tools within each grasping task. We ran paired sample t-tests on the plateau durations with the different tools in each task. In both cases, significantly more time was spent in the plateau phase with the reverse tool (normal grasping: $t(16) = -3.17$, $p = .006$, $d = -.65$; reverse grasping: $t(16) = -4.01$, $p = .001$, $d = -.54$). If the plateau phase duration reflects visual control of the movement, as opposed to feedforward planning (as discussed in previous Chapters), this would suggest that movements made with the reverse tool required more visual control than those made with the normal tool.

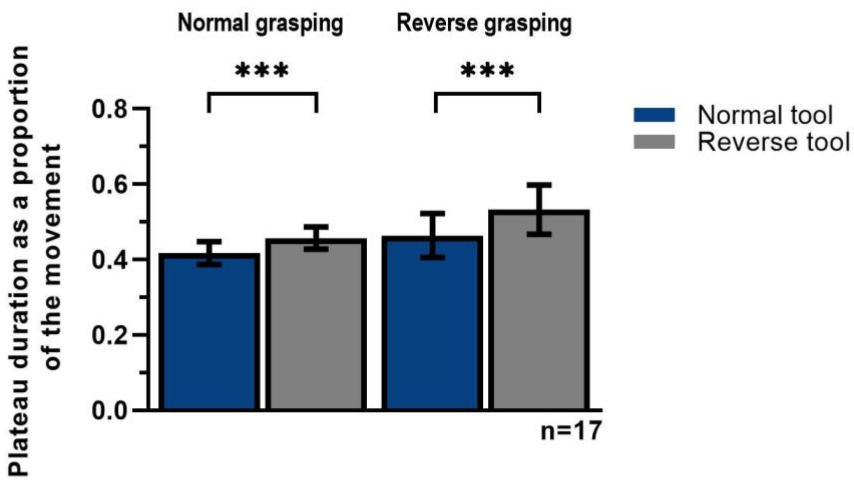


Figure 5.13. Plateau duration in Experiment 2. Plateau duration as a proportion of the movement duration. The error bars denote +/- 95% confidence intervals. Asterisks denote statistically significant pairwise comparisons.

5.7.3 Changes in performance across the experiment?

As in Experiment 1, we examined whether participants' performance differed between the first and last block of 40 trials in each condition (labelled respectively 'block 1' and 'block 6'). Evidence of learning would presumably be found in faster movements, increased tool aperture scaling with object size, and lower error rates.

Peak movement velocity

Fig. 5.14a shows the peak velocity for block 1 and block 6 of the experiment for all conditions. Movement velocity was higher in block 6 of the experiment in all conditions (one-tailed paired sample t-tests; normal-tool, normal grasping: $t(19) = -4.70$, $p < .001$, $d = -.76$; reverse-tool, normal-grasping: $t(19) = -4.9$, $p < .001$, $d = -1,15$; reverse-tool, reverse-grasping: $t(19) = -3.6$, $p = .002$, $d = -.69$) except normal-tool, reverse-grasping ($t(19) = -0.85$, $p = .202$, $d = -.14$).

Tool aperture scaling

Fig. 5.14b shows the tool aperture scaling with object size in block 1 and block 6 for all conditions. There was no significant change in object-size scaling in any condition between block 1 and block 6 (one-tailed paired sample t-tests; normal-tool, normal-grasping: $t(19) = .43$, $p = .663$, $d = .09$; reverse-tool, normal-grasping: $t(19) = .9$, $p = .810$, $d = .31$; normal-tool, reverse-grasping: $t(19) = 1.984$, $p = .969$, $d = .51$; reverse-tool, reverse-grasping: $t(19) = 1.239$, $p = .885$, $d = .27$).

Error rates

We did not necessarily expect the error rates to decrease in the normal-tool, normal-grasping, normal-tool, reverse-grasping and reverse-tool, reverse-grasping conditions as the error rates were already low. Fig. 5.14c show that, as expected, there was no changes in those conditions (one-tailed paired sample t-tests; normal-tool, normal-grasping: $t(19) = .33$, $p = .374$, $d = .09$; normal-tool, reverse-grasping: $t(19) = .82$, $p = .216$, $d = .25$; reverse-tool, reverse-grasping: $t(19) = 1.72$, $p = .51$, $d = .31$). Less errors were made in block 6 than in block 1 of the experiment in the reverse-tool, normal-grasping condition (one-tailed paired sample t-tests: $t(19) = 2.35$, $p = .014$, $d = .68$). Thus, in block 6, the error rate was similar in all conditions. This is evidence of learning (either the movement, the tool mapping or the task).

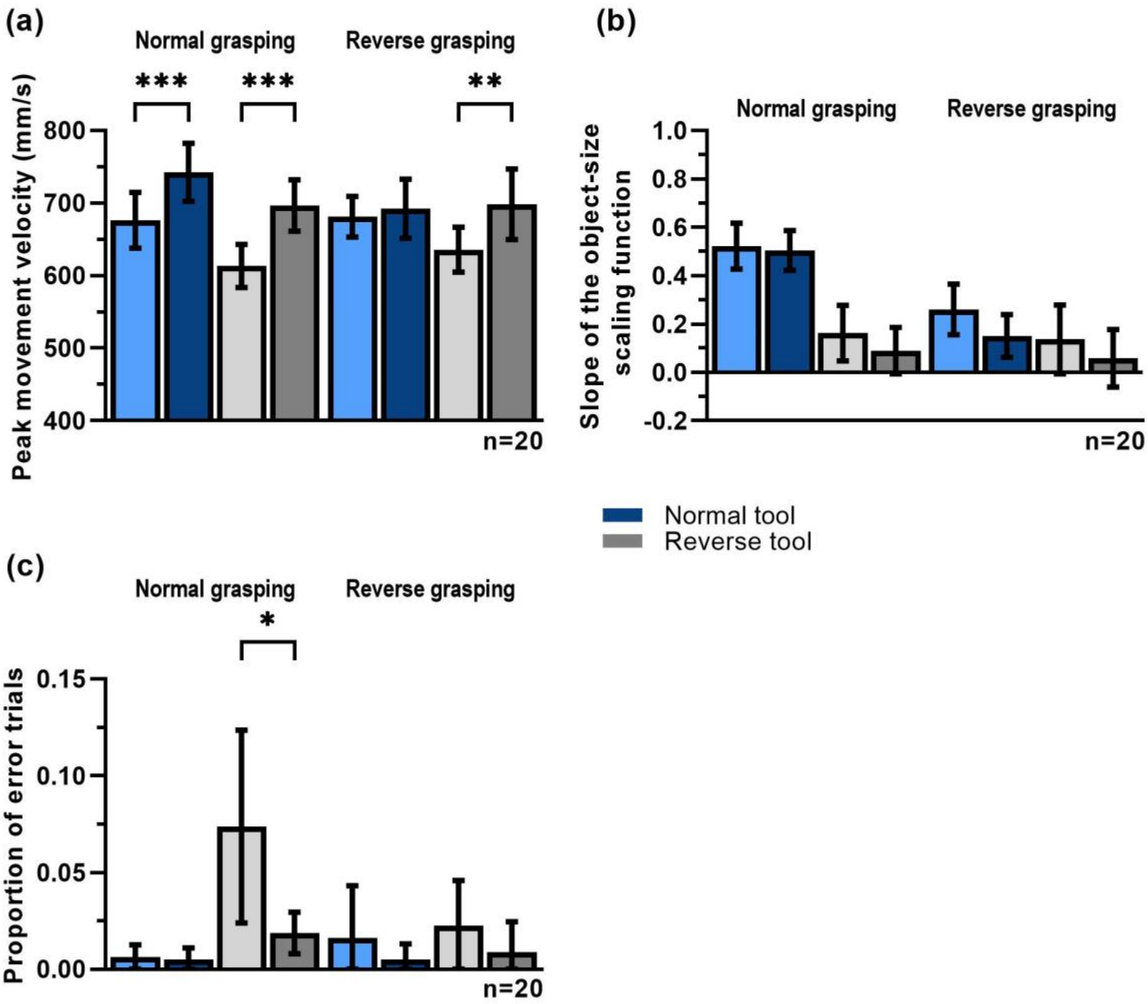


Figure 5.14. Performance in block 1 vs. block 6 in Experiment 2. (a) Mean peak velocity of grasping movements for each effector collapsed across object distance and object size. (b) Mean slopes of the object-size scaling functions. (c) Proportion of error trials. The lighter coloured bars represent block 1. The darker coloured bars represent block 6. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

Overall grasping profiles

As before, we also compared the overall grasp profiles between block 1 and block 6 of the experiment (Fig. 5.15). In the normal grasping task (Fig. 5.15a), the profiles did not qualitatively change between block 1 and block 6 with both tools. It can also be seen that the block 6 profiles with both tools are less skewed, more 'symmetrical'. We can also noticed that participants completed the movement faster in block 6, in accordance with the increase in movement velocity. The 'non-anticipatory' strategy observed in the overall profiles (Fig. 5.12) was already visible in block 1 and did not seem to change during the experiment.

In the reverse grasping task (Fig. 5.15c), while the movements made with the normal tool did not change qualitatively, it seems that the movements with the reverse tool did between block 1 and block 6 (evident in the profiles normalised in space, Fig. 5.15d). That is, in block 1, the reverse tool profile seems to gradually close the tool-tips until the minimum peak following by the opening of the tool to grasp the object. This pattern does not suggest an anticipatory control of the tool-tips, but more a visually controlled tool-tips opening. In block 6, the movement resemble more to an 'inverse' normal grasping profile, a more naturally anticipated movement. Again, time to movement completion was shorten in block 6 compared to block 1, in accordance with the observed increase of movement velocity in reverse-tool, reverse grasping. In the normal-tool, reverse-grasping condition, the increase in movement velocity was not significant, suggesting that less time was spent controlling the closure phase of the grasping movement.

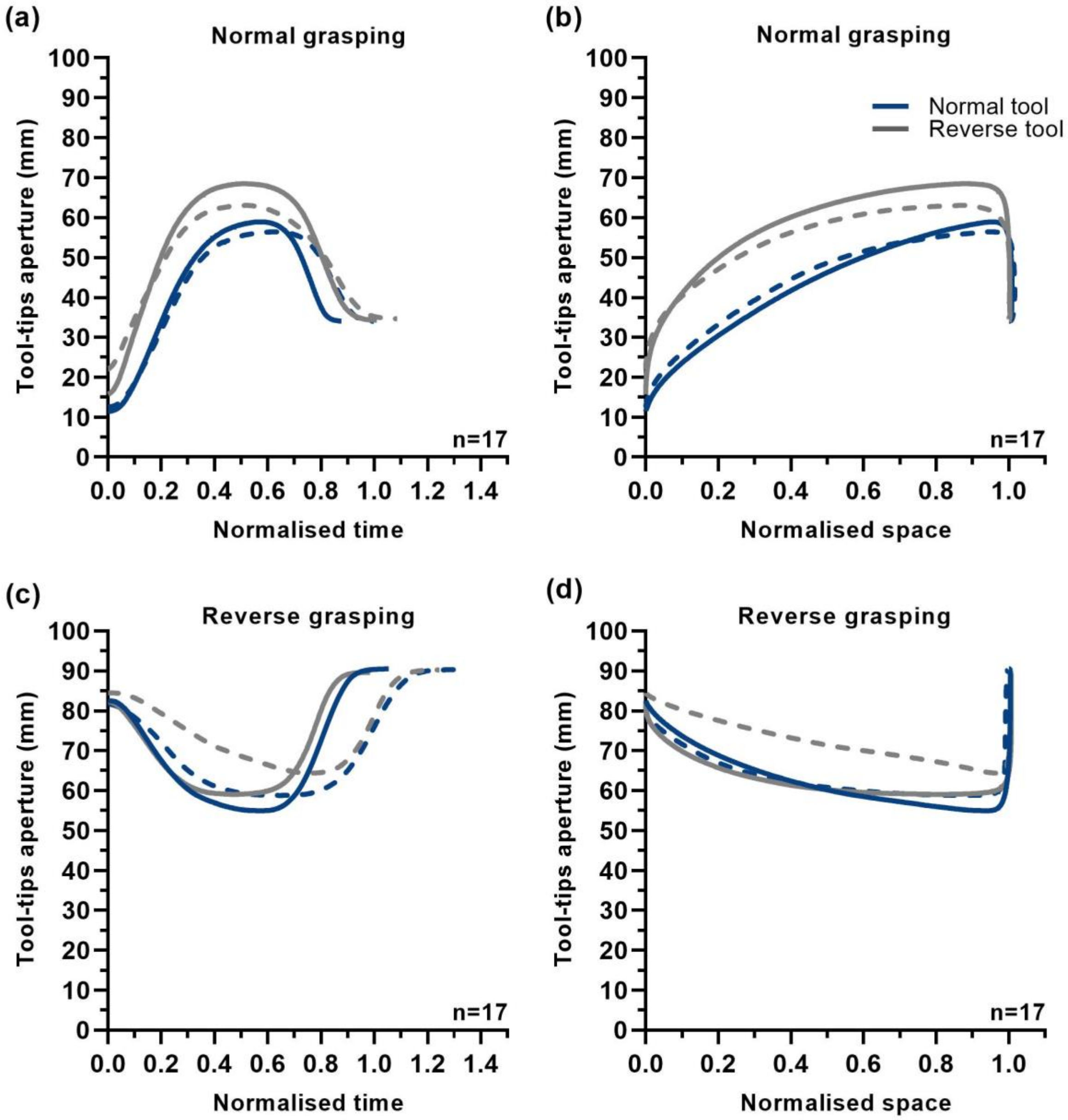


Figure 5.15. Overall grasping profiles block 1 vs. block 6. Overall tool-tips profiles for both tools collapsed across object size and distance. (a) Normal grasping condition (b) same data (a) normalised in space. (c) Reverse grasping condition (d) same data (c) normalised in space. The profiles in (a) and (c) are collapsed across object distances and object size and normalized in time adjusted to normal-tool, normal-grasping profile in block 1. The profiles in (b) and (d) are collapsed across object sizes. The dashed lines represent block 1. The plain lines represent block 6.

5.8 Experiment 2 Discussion

The aim of the second experiment was to dissociate the learning of the tool model from the learning of the new hand movement (close-then-open). Overall, the results of Experiment 2 suggest that both components affected the performance negatively. Compared to normal-tool, normal-grasping, only the presence of both an unusual tool model and an unusual hand movement led to slower movement, and to more errors. The results are more nuanced for the scaling of tool-tips aperture to object-size. That is, adding something new, either an unusual tool model or an unusual hand movement (or both) lead to a large decrease in object-size scaling. Moreover, adding only an unusual tool model led to a larger decrease of object-size scaling than adding only an unusual hand movement. Adding both components led to a similar decrease of performance, suggesting that there was no ‘additive’ effect. In contrary, movement velocity scaling to object-distance was found in all conditions, suggesting that it was unaffected by both components.

Continuous exposure to a single tool geometry led to an improvement in performance, as found in Chapter 4. Our results showed a significant object-size scaling in the reverse-tool, normal-grasping condition (compared to a non-significant scaling in Experiment 1). Continuous exposure seems to have improved the learning of the tool geometry, or the hand motor programme, or both.

As in Chapter 4, we did not observe a ‘gradual’ improvement of performance with continuous exposure to a single tool geometry. Compared to Experiment 1, there was, here, no uncertainty about what tool would be used on the next trial, and thus, no uncertainty about the possibility of using the error signal on a current trials to update the movement on a subsequent trial (Shadmehr et al., 2016). This should have allowed for gradual improvement of performance (Krakauer & Mazzoni, 2011). Although we found some evidence of learning from increase in movement velocity (in all conditions except normal-tool, reverse-grasping), and from reduction in error rates (in reverse-tool, normal-grasping, as the other conditions were already extremely low), there was no improvement in scaling of the tool-tips aperture to object-size. We instead found a slight decrease (non-significant) in three out of four conditions (reverse-tool, normal-grasping; normal-tool, reverse-grasping; reverse-tool, reverse-grasping). Those results suggest that neither the tool model, or the unusual hand movement, were improved across the experiment. Thus, it is likely that the improvement in movement velocity and in error rates, reflecting a change in the speed-accuracy trade-off (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Haith & Krakauer, 2013; Khan et al., 2006; Meyer et al., 1988), represents the learning of the tasks.

A decrease of tool-tips aperture scaling to object-size in three out of four conditions, even if not significant, is unexpected. This pattern might be however explained by the overall increase in movement velocity across the experiment, combined with really low error rates at the end of the experiment. That is to ensure the success of the movement with higher movement velocity, the brain might have added larger margin-for-error (Wing et al., 1986), leading to less object-size scaling. This would have resulted in larger tool-tips aperture in the normal grasping task and smaller tool-tips aperture in the reverse grasping task. Fig. 5.16 shows the peak tool-tips aperture for all conditions in block 1 and block 6. It can be seen that there was significantly more margin-for-error in block 6 in all conditions except normal-tool, reverse-grasping (condition with no significant improvement in movement velocity). Thus, this suggests that the pattern of results observed in the object-size scaling is consistent with the system adding larger margin-for-error to compensate for the increase in movement velocity.

Moreover, our results suggest that the visuo-motor system was able to understand 'enough' of the tool geometry, and the hand movement required, to include larger margin-for-error in both grasping tasks when necessary. This is consistent with the idea that grasping includes a flexible margin-for-error to respond to different situations (Keefe et al., 2019), while maximizing the chances of success of the intended movement. Indeed, a true lack of understanding of the tool geometry would result in the visuomotor system not knowing 'what to do', likely leading to no changes, or no sensible changes in tool-tips aperture. In contrary, our results indicated that, in all conditions, the system was doing the right thing by adding larger margin-for-error to ensure the chances of successfully grasping the object. Thus the brain had some understanding of both tool geometry and the hand movement required, enough to calculate and produce the right margin-for-error.

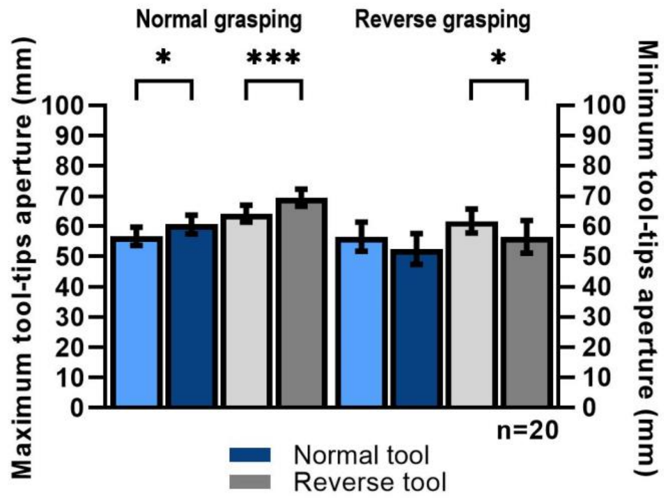


Figure 5.16. Peak tool-tips aperture block 1 vs. block 6 in Experiment 2. Mean peak tool-tips aperture collapsed across object sizes and distances. The data represent the maximum peak aperture in the normal grasping task, and the minimum peak aperture in the reverse grasping task. The lighter coloured bars represent block 1. The darker coloured bars represent block 6. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

In the normal grasping task, if the brain had some, although incomplete, understanding of the reverse tool geometry (an impoverished tool model), the margin-for-error account would suggest that the 'best' strategy would be to open the tool as wide as possible to ensure the highest chances of success. Although this could appear like a sensible strategy, our results suggest that this was not the strategy chosen by the visuomotor system. In Experiment 2, participants' peak reverse tool-tips aperture (~67 mm) was significantly smaller than the maximum possible opening of the tool (81 mm) when the handles were squeezed together (one sample t-test : t(19) = -11.59, p < .001, d = -2.59). Thus participants did not simply open the tool as wide as possible. They did, however, add a larger margin-for-error when using the reverse tool than the normal tool (particularly for smaller object size, Fig. 5.9a). In Experiment 1, peak tool-tips aperture (~72 mm) was also significantly smaller than the maximum opening of the reverse tool (one sample t-test: t(14) = -7.70, p < .001, d = -1.99). The overall margin-for-error was however larger than in Experiment 2. This suggest that while the brain had developed some knowledge about the tool geometry, uncertainty about that knowledge, or the required hand movement, or both, led to larger margin-for-error in Experiment 1.

As in previous Chapters, our results appear consistent with the idea that the visuomotor system relies on visual feedback control. Our results did not find compelling sign of anticipatory control of grasp opening (except in normal-tool, normal-grasping), suggesting the brain may not have developed a 'visual model', similar to Chapter 3 and 4. Reliance on visual control would likely result in slower movements, and the more the system would rely on vision, the slower the movements. Our results in movement velocity are consistent with that idea. That is, compared to normal-tool, normal-grasping, movement velocity was slower (albeit not significantly), when the system had to deal with either an unusual tool model, or an unusual hand movement. But the presence of both unusual tool model and unusual hand movement led to a significant decrease of movement velocity. This is consistent with more 'difficulty' leading to slower movement. Visual control of movement would also be evident in the time spent in the 'plateau phase' of the grasping movement (Bongers, 2010; Gentilucci et al., 2004; Golenia et al., 2014; Itaguchi & Fukuzawa, 2014), as this phase has been interpreted as a sign of visual control (Itaguchi & Fukuzawa, 2014). Our results indicated that the least time spent in the 'plateau phase' was in the normal-tool, normal-grasping condition. This also suggests that increased 'difficulty' results in longer time spent visually monitoring the movement. Visual control of movement can also be inferred from the pattern of early tool-tips opening, and of late (above object) closure of the tool-tips. This likely indicates an absence of anticipatory control. and suggests that the movement was visually controlled 'in flight' (due also to the absence of direct tactile or proprioceptive signals coming from the tool). Overall, results from Experiment 2 are consistent with the idea that tool grasping movements were predominantly visually controlled.

Our results showed an inconsistency between the error rates and the kinematics. That is, the pattern of corrections of the movement 'in flight' was different from the pattern of error rates, but closely resembles the pattern of 'plateau phase' duration. That is, corrections were made more often in the reverse grasping task than in the normal grasping task. And in both tasks, corrections were made more often with the reverse tool. In the reverse-tool, reverse-grasping conditions, although corrections were made, there was still the highest error rates. This pattern suggests that, while some successful corrections were issued, many inaccurate movements might not have been successfully corrected. This could have been caused by a lack of understanding of the reverse tool mapping, or an inaccurate reverse grasping hand movement, leading to inaccurate corrections. In contrast, in the reverse grasping task, although corrections were made more often, those corrections appeared to have been successful as the error rates are low. It is however interesting that corrections were made more often in that task. We explore possible explanations, below.

Task switching may have caused poor behaviour. In this experiment we asked participants to perform two different hand movements with two different tools. Errors in movement planning could therefore have resulted from failing to switch properly from one tool model or motor control programme to another across blocks of trials. This could have resulted in participants using the 'wrong' motor programme, leading to initial errors in grasp-opening direction (e.g. opening the tool-tips when it should first be closed in the reverse grasping task). Fig. 5.17 shows the proportion of trials in which participants did start their movement initially in the 'wrong' direction before correcting their movement (defined as the presence in the grasping profiles of a clear start of the movement in the wrong direction followed by a correction). Examining the figure, it can be seen that most of the initial direction errors occurred in the reverse grasping task. A 2x2 (task x tool) repeated measures ANOVA revealed a main effect of task ($F(1,19) = 75.81$, $p < .001$, $\eta_p^2 = .80$), a main effect of tool ($F(1,19) = 8.71$, $p = .008$, $\eta_p^2 = .31$) and no significant interaction ($F(1,19) = 2.26$, $p < .001$, $\eta_p^2 = .11$). Post hoc analysis pairwise comparisons (Bonferroni corrected) confirmed that significantly more initial error in grasp-opening direction occurred in the reverse grasping task than in the normal grasping task, and that more initial error occurred with the reverse tool than with the normal tool. That pattern of results closely resemble the pattern of correction rates in the reverse grasping task. This suggest that the corrections made in that task may have been the results of in initial error in the grasp-opening direction. Indeed, those errors in initial opening direction represent 69% of the number of corrections made in that task (with both tools). Thus, the majority of corrections made in the reverse grasping task were made after an initial error in grasp-opening direction.

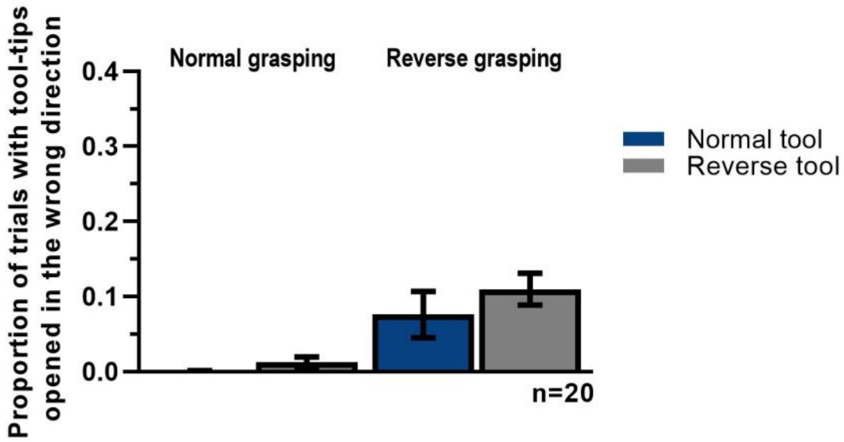


Figure 5.17. Proportion of trials in which participants started to open the tool-tips in the wrong direction before correcting their movement. The error bars denote +/- 95% confidence interval. Asterisks denote statistically significant pairwise comparisons.

The reverse grasping task might also have facilitated the amount of initial errors because participants were asked to start each trials with the tool-tips opened (80 mm). From that position, participants could start their movements by either closing or opening the tool-tips. In comparison, in the normal grasping task, participants start each trial with the tool-tips closed, leaving only the option of opening them. Thus that pattern of correction in the reverse grasping task could be a difficulty to select the appropriate motor programme, interacting with a feature of the task itself.

Learning how to perform the reverse grasping task with the reverse tool may not have been ‘straightforward’. In that reverse grasping task, participants would likely know what to do with the tool-tips (as it was demonstrated to them) but they may not have linked that tool-tips movement to the appropriate motor programmes (‘normal’ hand grasping movement). That step might have been rendered more difficult by the use of a tool with an unusual geometry. Our results indicated that more errors in the initial direction of the tool-tips opening were made in the reverse-tool, reverse-grasping condition. Moreover, there was no significant tool-tips aperture scaling to object-size in that condition. Further, comparing the overall reverse-grasping overall profiles between the first and last block of the experiment suggest that the visuomotor system ‘struggled’ to learn the movement with the reverse tool. That is on the first block, grasping profiles between the normal and reverse tool were qualitatively very different, while on the last block, grasping profiles with both tools were similar. Those results suggest that learning how to perform the reverse grasping task with the reverse tool was difficult at first, even if it required a ‘normal’ hand movement.

Experience gained with a tool model (or a hand movement) in one ‘favourable’ circumstance could lay the groundwork for better performance when the same problem is encountered later (in another task). That is, participants that learned the reverse-grasping motor programme with the normal tool (‘easy’ to use) could have performed better at using the reverse tool in the normal grasping task. That would imply that what was learned in one task (in this case, hand motor programme) could then be used in another circumstance (in this case, a new tool model in another task). To investigate that matter, we examine the effect of the starting task by observing the tool-tips aperture scaling to object-size (as it reflects control of the tool-tips). Fig. 5.18a and b shows the slopes of the object-scaling for both tools for both starting tasks for the normal grasping task and the reverse grasping task respectively. It appears participants did show slightly less object-scaling in each condition when they started the experiment with the reverse grasping task (a 2 x 2 x 2 (starting task x grasping task x tool) repeated measures ANOVA revealed no main effect of starting task; $F(1,9) = 1.41$, $p = .266$, $\eta_p^2 = .14$). Thus it seems that the starting task did not affect significantly the development of tool model or hand movement.

Although the effect is not significant, it is interesting that object-size scaling was systematically lower when participants started the experiment with the reverse grasping task. A possible explanation is that participants have to learn the required hand movements, the tool geometry and the ‘new’ task together. It is unlikely participants had been exposed to such a task before, thus they would lack of a task structure (Braun et al., 2009, 2010; Wolpert et al., 2011). Thus learning all those elements together may have interfered and slowed the learning. Another possible explanation is that using the knowledge developed in the other task (either tool model, or hand movement) is not obvious. It requires the visuomotor system to somehow know that the hand movement developed in one of the grasping task, can then be used (slightly adapted) with the other tool (with a different geometry) in the other grasping task. Thus, overall, the difficulty of using the reverse tool in the reverse grasping task, even if it requires to produce a 'normal' grasping movement, suggests that it was not trivial.

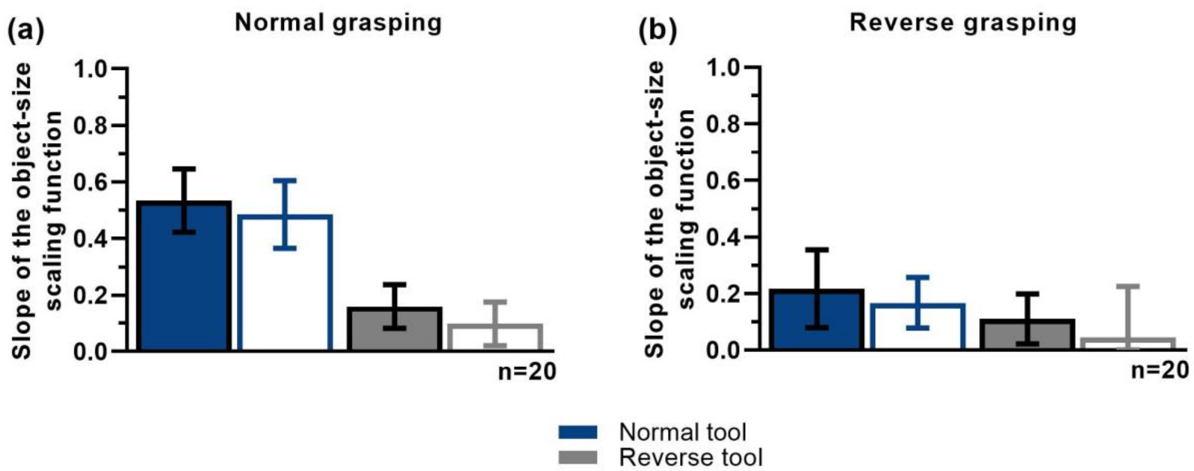


Figure 5.18. Mean slopes of the object-size scaling functions by starting task. (a) Data for the normal grasping task. (b) Data for the reverse grasping task. The filled bars represent the mean scaling for participants who started the experiment with the normal grasping task. The empty bars represent the mean scaling for participants that started the experiment with the reverse grasping task. The error bars denote +/- 95% confidence interval.

5.9 General Discussion

The tool literature has proposed that tools are 'used as body parts'. In Chapter 3 and 4, we defined that concept as movements made with tools accounting for the tool geometry and exhibiting the key anticipatory features of hand grasping such as object-distance movement velocity scaling and object-size tool-tips aperture scaling. We examined if participants could produce those features when using a tool that did not behave qualitatively like the hand, such as a reverse pliers-like tool (requiring opening of the hand to close the tool). The results in both experiments suggest that the reverse tool was not 'used as a body part'. That is, although we found significant object-distance movement velocity scaling, we did not find compelling evidence of scaling of the tool-tips aperture to object-size.

The ‘tool as body part’ account comes from studies showing that tool use alters the body representation (Canzoneri et al., 2013; Cardinali et al., 2009, 2011, 2012; Martel et al., 2019; Miller et al., 2019; Sposito et al., 2012). Further, it appears that tool use only alters the representation of the body parts whose morphology is altered by the tool (Cardinali et al., 2016; Miller, Cawley-Bennett, et al., 2017; Miller, Longo, & Saygin, 2017). That is, transposed to our experiments, the use of one of our tools would probably extend slightly the reaching ability and might alter the hand representation (in particular, index finger and thumb). When the tools behave qualitatively like the hand, that is if existing motor programmes can be used to operate the tools, the body representation could be altered when those existing motor programmes are altered to account for the tool geometry (in our experiment, index finger and thumb representations could be altered). The possible alteration of body representation is less evident when a tool does not ‘behave’ like the hand, as the functionality of the tool might not correspond to existing body movements, and as existing motor programmes likely do not exist. It is difficult to understand how our reverse tool would alter the body representation or if the body representation could actually be altered to represent such a tool.

Experiment 2 highlighted how acquiring the mapping, or building an internal model of the reverse tool geometry per se is challenging for the visuomotor system. The potential development of an internal model for the reverse tool, as it does not behave like the hand, would likely rely on the development of an internal model *de novo* (Telgen et al., 2014). That might be difficult for the system. Why might this be?

The mappings that can easily be accounted for might be determined by the statistic of the world. First, the system could learn more readily mappings that that are similar to mappings that have been experienced often. That is, the system could account for some mappings by adapting or using copy of existing internal models or motor programmes. Second, the statistics of the world could ‘determine’ what mappings could be accounted for. That is, the visuomotor system may have been configured such that its underlying neural structures are able to easily represent mappings likely to be encountered. Third, we reasoned that was likely such a tool geometry would not have been experienced before. Indeed, such a transformation is rather rare (e.g. test tube holder). Taken together, such a tool mapping would have likely been difficult to learn

There may be a fundamental limits on the kind of mappings the system can internalise. It may indeed be possible that the system is not ‘flexible’ enough to account for such a mapping in a way to control the tool ‘as a body part’. The visuomotor system has likely been developed in such a way that its underlying neural structures have evolved to control the arm and the hand. Thus, those structures may not be able to fully account for a tool that does not ‘behave’ like the hand. In engineering terms, the system might not possess the right basis functions to represent such a mapping.

It might also be that there is no problem with learning such a mapping, but the visuomotor system was not exposed enough to that mapping for an internal model to be developed. Evidence from Umiltà et al. (2008) suggest that a reverse-pliers can be controlled ‘as a body part’ (after months of training). This suggests the (monkey) visuomotor system is able to learn the reverse tool geometry. Thus, it is likely that the human visuomotor system would be able to build a tool model for such a tool. Evidence that the system might not have been exposed ‘enough’ to the tool geometry comes from previous Chapters. In those chapters, we found only little evidence for the development of internal model of tools that behave like the hand. In this Chapter, participants were exposed to 240 trials per condition with the reverse tool (compared to 525 in Chapter 3 and 180 in Chapter 4). For reasons discussed previously it is likely that development of a model for a reverse tool geometry would require more practice. Aiming to examine the development of such tool model over longer periods of time might prove itself useful to capture changes in participants’ performance that might only arise after extensive training.

Experiment 2 also highlighted the difficulty of producing the appropriate hand movement to use the reverse tool. Why might this be? We reasoned that it was unlikely the motor system would possess existing motor programmes ready to be used for that movement. We assumed the system would have to develop the appropriate motor programmes. Keefe et al. (2019) showed that this hand movement (close-then-open the hand) could be learn to grasp the same type of object (U-shaped), while still producing anticipatory grip aperture scaling to object-size. The object-size scaling was reduced but it was still significant (47% of the object-size scaling observed in normal-grasping). Our results from Experiment 2 confirmed that, even when using the normal tool, the visuomotor system was able to produce significant grip aperture scaling to object-size (normal-tool, reverse-grasping, 37% of the scaling observed in normal-tool, normal-grasping). The larger reduction of object-size scaling observed (compared to Keefe et al., 2019) could be due to the requirement of performing that unusual hand movement with a pliers-like tool. Thus those motor programmes appear to have been developed, at least enough to correctly execute the close-then-open hand movement (and enough to produce the appropriate margin-for-error). We are unsure however, on how precisely those programmes were linked to their consequences with the tools. In the Optimal Control framework, difficulty producing the appropriate movement could arise from the use of an impoverished inverse model (control policy; Haith & Krakauer, 2013), not linking properly the appropriate motor command to the desired outcome. This would likely lead to inaccurate movements.

In previous Chapters, our results were consistent with the idea that the visuomotor system developed a visual model of the tool geometry. Our assumption was that such a model could be used to produce anticipatory grasping behaviours. Moreover, a visual model could be the first step towards the development of internal model. Indeed vision is needed when facing a new visuomotor transformation to link motor programmes to their 'new' outcomes (Sailer et al., 2005). If the visuomotor system relies on a visual model when the tool 'behave' like the hand (when existing models are available), it is likely that it would rely on a similar visual models when the alteration has not been experienced before. Our results however did not show compelling evidence for the presence anticipatory behaviours when using the reverse tool (little scaling of the tool-tips to object size, errors during planning and execution of the grasping movement, closure phase of the grasp only when above, or around the object, 'plateau phase'). This suggests that the visuomotor system did not develop a visual model and used a 'non-anticipatory' strategy, likely resulting in a visual 'in flight' monitoring strategy. Indeed, as proprioceptive signals would require the visuomotor system to understand the tool geometry enough to be interpreted correctly, those signals would likely be noisy and unreliable. When integrating visual and proprioceptive signals, the system would then weight more the visual signals than the proprioceptive signals, as they are more reliable (Ernst & Banks, 2002; van Beers et al., 1999, 2002). It is still possible that the visuomotor system used some sort of visual model of the tool geometry. It seems however that such a model was different from the predominantly visual model used in previous Chapters. Taken together, our results appear consistent with the idea that the grasping movement was visually controlled ‘in flight’.

A better way of capturing the development of those internal models of tools, while observing their mode of development (adaptation vs. *de novo*; Telgen et al., 2014) might reside in a perturbation study, such as in Telgen et al. (2014). That is, the design of the experiment would be similar to Experiment 2. However, on a defined proportion of trials, the perceived size of the object would be perturbed ‘in flight’. The goal of such an experiment is to examine the nature of the response to that perturbation. To respond accurately to a perturbation in object size (e.g. increasing the size of the object) the system would have to plan the same response with both tools (e.g. increasing tool-tips aperture; updating the margin-for-error), requiring opposite hand movements (larger hand opening with the normal tool vs. smaller hand opening with the reverse tool). Analysing the time required to correctly respond to the perturbation, and potential errors in the direction of correction (particularly in the early phase of the corrective movement) would be extremely informative concerning the mode of learning of internal models of tools. That is, adaptation would be characterised by a quick and adequate response to the perturbation, while skill learning (*de novo*) would be characterised by slow response and error in the response to the perturbation (as discussed in Section 1.6.5. of the General Introduction). Such an experiment would likely have to expose participants to a large number of trials with each tool, to increase the chances of observing signs of learning potential internal models of tools.

As in previous Chapters, we performed some sensitivity analysis. In both experiments, we aimed to investigate the presence of anticipatory features of grasping movements (movement velocity with object distance; grip aperture with object size). Their presence would reflect the tools being controlled ‘as body parts’. For Experiment 1, sensitivity analysis revealed that we found larger effect size than the minimal detectable effect size for both the movement velocity scaling to object distance with all effectors (mdes = 0.68; hand: d = 4.13; normal tool: d = 4.88; reverse tool: d = 5.25) and the scaling of tool-tips aperture with object size for the hand and the normal tool (mdes = 0.68; hand: d = 4.13; normal tool: d = 3.53) but not the reverse tool (d = .35). As our experiment seems to be powered sufficiently to observe the expected presence of grip scaling with the normal tool, it suggests that the effect of using the reverse tool is likely smaller than what is practically relevant. For Experiment 2, sensitivity analysis also revealed that we found larger effect size than the minimal detectable effect size for both the movement velocity scaling to object distance for conditions (mdes = 0.58; normal-tool, normal-grasping: d = 5.97; reverse-tool, normal-grasping: d = 6.86; normal-tool, reverse-grasping: d = 5.03; reverse-tool, reverse-grasping: d =5.28) and the scaling of tool-tips aperture with object size (mdes = 0.58; normal-tool, normal-grasping: d = 3.19; reverse-tool, normal-grasping: d = 1.17; normal-tool, reverse-grasping: d = 1.2; reverse-tool, reverse-grasping: d = 0.39). The reverse-tool, reverse-grasping condition is interesting as the statistically significant effect size is smaller than the minimal detectable effect size. This suggests that the effect was below the bound of what our study was set to detect ‘reliably’ but was reliable. The relevance of that effect size is low compared to the effect found in the other conditions. Taken together, the sensitivity analysis suggest that our experiments are not underpowered and are able to detect reliably the desirable effect. Further, our detected effects are practically significant.

5.10 Conclusion

To use a tool efficiently the visuomotor system must know the mapping between hand and end-effector movement, to know what hand movement needs to be produced, and develop the motor programmes that allow those hand movements to be achieved. The difficulty of using a tool that does not behave like the hand is cannot be solely explained by the requirement to produce an unusual hand movement. Thus the tool mapping itself appears to pose a problem to the visuomotor system, as no model of the reverse tool appears to have been developed.

Chapter 6 - General Discussion

6.1 What do our results mean for the 'tool as body parts' account ?

We have argued that 'tools used as body parts' implies that the same visuomotor control principles used during hand grasping could be used during tool grasping. We would then expect to observe anticipatory features of hand grasping such as scaling of movement velocity to object distance (Jeannerod, 1981, 1984) and scaling of tool-tips aperture to object size (Jeannerod, 1981, 1984; Smeets & Brenner, 1999). This idea of 'tools used as body parts' then implies that internal models of tool are developed, accounting for the tool geometry.

It could be useful to consider two extreme scenarios. In the *first* scenario, the visuomotor system does not produce anticipatory control, and rely only on 'in flight' feedback control. In that scenario, no internal model of the tool geometry was developed. Thus, interpreting proprioceptive signals is difficult, or nearly impossible. The reliance on online visual feedback would then increase. Our results are not entirely consistent with that scenario, as anticipatory features of natural grasping movement are found in tool grasping, even when visual feedback was unavailable. In the *second* scenario, the visuomotor system does not develop internal model of tools, but instead uses the existing hand model. This implies that the tool geometry would not be accounted for at all. Our results are only consistent with this scenario when visual feedback was unavailable, as we observed partial compensation for tool geometry when visual feedback was available, suggesting the use of some sort of 'visual model'. Thus, overall, our results are more consistent with the idea that the visuomotor system developed, in the time scale of our experiments, a predominantly visual model of the tool geometry, for the tools 'behaving qualitatively' like the hand. When visual feedback is not available, however, that model cannot be used, and the visuomotor system appears to revert back to using the hand model.

Why did the visuomotor system relied on a more visual model of the tool geometry? As discussed across the thesis, the development of a visual model could the first step towards the development of an internal model. It is likely that the visuomotor system would have to link the motor programme to its new (motor and sensory) consequences. As proprioceptive and haptic signals would require knowledge of the tool geometry to be interpreted, they would probably not be informative or reliable in the early stages of learning the tool geometry. In contrary, visual feedback appears reliable, and gives direct information regarding the effect of a given motor programme (Sailer et al., 2005). Even when reliable, there is even evidence that haptic information could be neglected during adaptation to a new visuomotor transformation (Heuer & Rapp, 2012), or used only if the proprioceptive signals agree with the visual signals, or provide information that was not available to the visual system (Bock & Thomas, 2011). Other studies showed that when proprioceptive signals are impoverished (Gentilucci et al., 1994, 1997, Jeannerod, 1997), a greater reliance on visual feedback is observed. Indeed, in each experiment, the presence of a 'plateau phase' indicated an increased reliance on visual signals. Taken together, a reliance on vision in the early stages of learning seem to be the expected behaviour.

The initial part of the learning of the tool geometries could be cognitively driven (Wolpert et al., 2011). That is the visuomotor system had likely developed, really early in the experiment, explicit knowledge for the different tool geometries (Taylor & Ivry, 2011; Taylor, Krakauer, & Ivry, 2014). This knowledge could have been used to develop explicit strategies (e.g. "I need to open my hand less" when using the 1.4:1 tool). As discussed already, it is likely most information about the tool alteration was visual. This step could then represent the development of an impoverished visual model, while an internal model is being updated/refined (in the 'background'; Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011). It may be that the timescale of our experiments failed to capture the development of the internal model (discussed in Section 6.3).

A predominantly visual model could be used by the visuomotor system to anticipate the visual consequences of a given motor programme. Such an visual model is consistent with the idea of a *forward* model, allowing the prediction of future visual states based on the current visual state and on the upcoming motor commands (McNamee & Wolpert, 2019; Mehta & Schaal, 2002; Miall & Wolpert, 1996; Wolpert et al., 1995; Wolpert & Kawato, 1998). It seems that a forward model could be developed quickly (Wolpert & Kawato, 1998). To operate a tool optimally, ‘as a body part’, it seems that the visuomotor system would require a forward model and an *inverse* model (Itaguchi & Fukuzawa, 2014). An inverse model allows the visuomotor system to estimate the motor commands required to produce a desired state (McNamee & Wolpert, 2019; Wolpert et al., 1995; Wolpert & Kawato, 1998). The acquisition of an inverse model is slower than that of a forward model (Wolpert & Kawato, 1998). Our results did not indicate the presence of an inverse model (no compensation for tool geometry when visual feedback was removed in Chapter 3 and 4). In the timescale of our experiments, we may have captured the acquisition of a forward model, but failed to capture the acquisition of the inverse model.

We have argued that with the unreliability of proprioceptive and haptic feedback, tool use would mainly be visually controlled. Such a ‘visual strategy’ would likely disappear over time, when more ‘robust’ internal models of tool would be built. Indeed, a characteristic of natural movement is that the visuomotor system does not need to visually monitor the movement, but is instead looking ahead (Brouwer et al., 2009; Johansson et al., 2001; Land, 2006). This is rendered possible because the visuomotor system can rely on proprioceptive signals alone during most of the movement. We reasoned that, by building an internal model of tool geometry, the system could interpret proprioceptive signals. Hence, over time, the gaze pattern should change, progressively becoming more and more anticipatory, while no longer monitoring only the movement of the tool-tips. It is possible however, that even with internal models, the visuomotor system might rely more on vision during tool grasping than during hand grasping (presence of a 'plateau phase'; Golenia et al., 2014) due to the deterioration of proprioceptive and haptic signals. A way to probe the reliance on vision during tool grasping would be to monitor the gaze using an eye-tracking device during a similar experiment to those proposed in this thesis. Such an experiment would be informative in two ways. *First*, measuring eye movements during hand grasping and tool-grasping could indicate whether the visuomotor system does indeed rely more on vision to monitor the opening of the tool-tips, and to what extent. *Second*, comparing eye movements during tool use across the experiment would allow us to monitor whether the reliance on vision decreases or not, while examining the relationship between the development of the tool model and gaze pattern. In such an experiment, we would expect the gaze to follow the opening of the tool-tips in the early stages. With more practice, we would expect the reliance on vision to decrease, and the emergence of a more anticipatory gaze pattern, similar to that during hand grasping, suggesting an internal model was developed.

The alteration of the representation of the body suggested by the 'tools used as body parts' is consistent, in the internal model framework, with the adaptation of existing internal models (such as the hand internal model). Our results however are inconsistent with that idea, as we did not find compelling evidence that adaptation of felt hand size was the main mechanism behind the compensation for the different tool geometries. This suggest that a new model would likely have to be developed *de novo* (the mechanisms underlying internal model acquisition will be discussed in Section 6.2).

Although the development of predominantly visual model appears to have allowed the visuomotor system to account for the tool geometry, the brain did have a bias in the perceived tool alteration. That is, our results suggest that the brain did not have a metrically accurate perception of the alteration due to the tool geometries (for the 0.7:1 and 1.4:1 tools). We assumed that the aim of the brain was to develop a metrically accurate understanding of the alteration, to account completely for it. It might however not have been the case. We explore possible explanations, below. First, we can only infer the perception of the tool geometry from the grasping data. Grasping, however, can be defined as an optimisation problem (more on the cost of using certain mappings in Section 6.2). It is then possible that the system would not have optimised the compensation for the tool geometry. That is, the movements would reflect the 'optimised' movements, maximising the chances of success while minimising costs. Indeed, our results indicated that accounting for the tool geometry was not directly correlated to the success rates (when visual feedback was available). Second, it is possible the visuomotor system would never reach a complete compensation for the tool geometry. That is, as information about the transformation is acquired from perceptual and motor signals, both subject to noise, the visuomotor system might never be able to reach a metrically accurate perception of the tool alteration.

One of the potential limitation of the account that ‘tools are used as body parts’, by altering the representation of the body (Canzoneri et al., 2013; Cardinali et al., 2009, 2011, 2012; Martel et al., 2019; Miller et al., 2019) is that it is difficult to conceive how complex transformations of hand movements could be accounted for. That is, it must be more difficult for the visuomotor system to account for a tool geometry that does not directly map to existing body parts, or to biological movements (e.g. a bicycle). It is also possible that the representation of the body is flexible to a certain extent, allowing for more complex tools to be incorporated but that it is unlikely that the body representation can extent to incorporate *all* types of transformations. For our pliers-like tools behaving like the hand, the body representation of the thumb and index finger could ‘simply’ be altered and the brain could, in principle, adapt existing hand motor programmes to deal with the ‘gain’ alteration. In comparison, it is more difficult to image how the reverse tool would impact the body representation. The representation of the index finger and thumb would likely be altered, and the required motor programmes (closing-then-opening the hand) produce a different but existing outcomes corresponding to biological movements (opening-then-closing the end-effector). Thus it is possible that such a tool could be incorporated into the body representation (with enough practice). This maps into the distinction between adapting existing models for tools that behave like the hand, while developing new ones for tools that do not. Our results however are more consistent with the idea that new models would need to be developed for *all* tools for them to be ‘used as body parts’. Further, our results indicated that a more complex tool (reverse tool) was more difficult to learn than our normal tools. For a more complex tool, the process of using tools ‘as being part of the body may take time (and the development of a robust internal model that would be refined with practice). This resembles the phenomenological effect of ‘feeling the tool as part of the body’ (e.g. a tennis racket) that does not happen instantly, but instead requires practice. For tools that present some biologically impossible transformation, it is likely that they would never be used ‘as body parts’. It is unlikely that a car would be perceived as being part of the body. However, the system, by using internal models (refined over time) could allow the visuomotor system to use those any tool optimally, with incredible precision. Those internal models would likely be developed and refined over really long periods of time/practice

Taken together, our results are consistent with the idea that the visuomotor system developed some sort of predominantly visual model, not equivalent to the existing hand internal models, when the tools behave qualitatively like the hand. This model allowed the system to produce anticipatory behaviours observed during hand grasping. Such a model however, did not allow for the tool to be controlled ‘as a body part’. Nevertheless the idea of tools being used as body parts is still relevant, and may correctly represent how the brain deals with simple tools. For more complex tools, however, the mechanism of using ‘tools as body parts’ may be used not by adapting existing body part representations, but by acquiring new internal models, allowing for the visuomotor system to account for the tool properties.

6.2 What are the possible mechanisms behind the development of internal models of tools ?

Our results indicated the use of a predominantly visual model to account for the tool geometry. Those visual models do not appear to be equivalent to those existing for the hand. We have argued that such a model could be used to produce anticipatory behaviours. In Chapter 4, we also found encouraging signs that some participants may have developed some sort of internal model of the 1.4:1 tool, allowing them to account for the tool geometry in a perceptual task without visual feedback. In this section, we discuss potential mechanisms by which the tool alteration was accounted for, potential mode of acquisition of internal models and the potential limitations in the types of alteration that can be accounted for.

In the General Introduction, we discussed three possibilities for how a new relationship between hand movement and tool-tips movements could be implemented within the internal model framework. The *first* one is that existing models (likely the hand) would be altered to reflect, or incorporate the properties of the tools. The *second* one is that components representing the tool geometry could be added to those of the hand, linking hand movement to tool-tips movement. The *third* one is that a completely new tool model that includes the transformation due to the tool geometry could be created.

We reasoned that tools that behave like the hand (Chapter 3 and 4) could be accounted for by adaptation of existing models. In contrast, tools that did not behave like the hand could not be accounted for by adapting existing internal models. Thus, they would likely require the development of a completely new model, *de novo*. For the tools 'behaving' like the hand, our results are inconsistent with the first possibility: adaptation. It appears that adapting hand representation was not the principal mechanism by which tool geometry was accounted for (but it could still have a small effect). Moreover, adaptive processes suggest a continuous improvement of performance during a single experimental session. Our results, however, did not show compelling evidence for such an improvement of performance. Thus, for those tools, there seems to be the need for an extra-step, accounting for the tool geometry. That extra-step could be a visual model, added to the existing hand model. Or it could be that the visuomotor system has to develop a tool model *de novo*. Those two processes could act in parallel. Our results are consistent with the idea of a visual model, that could be 'added' to the existing hand model. As mentioned in Section 6.1, however, it is likely that a visual model could be the first towards building an internal model of the tool geometry. In comparison, when the tool does not behave like the hand, our results did not indicate the presence of a visual model. Thus it appears that such a tool would require the visuomotor system to develop an entirely new internal model.

Not all tool mappings of tools that behave like the hand were learned the same way. That is, Chapter 3 and 4 revealed differences in the acquisition of the visual model depending on the alteration itself. Indeed, across both experiments, we found evidence that the 0.7:1 tool was more difficult to learn than the two other tools (1:1 and 1.4:1) of the same mechanical complexity. Although during tool grasping, the 0.7:1 tool may have been difficult to use due to potential ceiling effects in hand opening, results from Chapter 4 showed that the ceiling effect cannot explain alone the difficulty to learn such a tool alteration. In Chapter 5, we showed that using a tool that did not behave like the hand presented a difficult challenge for the visuomotor system. So why are some tool transformations much harder to learn than others ?

Across the Chapters, we discussed different possibilities, such as the statistics of the world, limitations on the kinds of mapping the visuomotor can account for, and difficulty producing the appropriate movement. *First*, it is possible that the statistics of the world 'determine', across the lifespan, what mapping can be developed. That is, the visuomotor system has likely been configured through its interaction with the environment. This implies that the neural structures of the system would have been developed to account more easily for certain types of mappings, likely to be encountered. Further, there is indeed evidence that when developing a new internal model, the visuomotor system could relied on existing internal models (Gentilucci et al., 1995; Johansson, 1998; Kluzik et al., 2008) of mappings previously encountered and not start from a blank slate. In the world, tools that do not bring a clear benefice are rare, as tools are designed usually to extend the capability of the body. Thus experience with tools limiting the movement, or requiring an unusual movements are unlikely. Moreover, the visuomotor system configuration through its interaction with the environment also implies that there may be some fundamental limitations on the kind of mappings the system can internalise. We have argued that it was unlikely that our participants had previous experience with a reverse tool geometry. So, the visuomotor would have had to start from a blank slate to develop models. It may also be possible that such an tool geometry cannot be internalised (although results from Umiltà et al., 2008 suggest otherwise). In comparison, for the 0.7:1 tool, it is likely that participants had some experience with tools looking like our pliers-like tools (e.g. with a pair of scissors). It is unlikely however that participants had experienced a tool 'restricting' their movement on purpose (compared to the 'enhancement' of the movement when using the 1.4:1 tool).

Second, grasping can be perceived as an optimisation problem (Todorov, 2004; Todorov & Jordan, 2002; Wolpert et al., 1995), implying that the goal of the visuomotor system is to grasp the object, while minimising certain costs, such as jerk, movement, energy, … Those cost-functions could be vastly changed by the use of certain tools. That is, some tools might require more range of movement, or a more 'difficult' movement, … Thus the visuomotor system may find it difficult to build a model for a tool that keeps too 'many' costs high. For the reverse tool, our results indicated the hand movement required to operate the tool had a significant effect. That movement (closing-then-opening the hand) may have required the development of new motor programmes, and had larger 'cost' in term of jerk, movement and energy. Similarly, to produce a similar tool-tips aperture with the 0.7:1 tool than with the 1:1 tool, the visuomotor system would have to produce a larger hand opening, also having a larger cost in term of jerk, movement and energy spending. In comparison, using the 1.4:1 tool lead to opposite effects, with less movement, less energy and less jerk.

Overall, it appears that the statistics of the world, as well as the cost of using those tools may explain why certain tools might be more difficult to learn than others. Those results have direct implication for the design of tools. It appears that to make the use of a tool 'intuitive', it is best to consider the capability of the body, what sort of alteration could naturally map on existing mappings because they have likely been experienced, as well as what existing motor programmes can be used or adapted to use the tool. We need to be careful about using 'existing motor programmes', as our results with the reverse tool indicated that even when using 'normal grasping' motor programmes, the visuomotor could not produce anticipatory behaviours with the reverse tool. Nonetheless, our results indicated that making the hand movement 'easier' (less jerk, movement and energy) could fundamentally improve the speed at which a tool geometry would be accounted for. Lastly, our results indicated the importance of practice. When designing tools, we need to be aware of the potential duration of the required training for the tool to be used 'as well as the hand', and how that training could be tailored to enhance the learning of the tool (more on that in Section 6.3).

Both mode of acquisition of an internal model (adaptation vs. skill learning) suggest different pattern of performance improvement during the experiment. Adaptation is characterised by a gradual improvement in performance (Krakauer & Mazzoni, 2011) while skill learning would be characterised by a reduction in variability (Reis et al., 2009; Shmuelof et al., 2012). Moreover, between experimental session, adaptation would be characterised by a quick ‘deadaptation’ (Davidson & Wolpert, 2004; Smith et al., 2006; Telgen et al., 2014) while skill learning is characterised by offline improvement of performance (Abe et al., 2011; Telgen et al., 2014; Wright et al., 2010). Our results did not show compelling evidence for improvement of performance during experimental sessions (Chapter 4 and Chapter 5 – Experiment 2). And we did not find compelling evidence either for deterioration of performance between sessions (Chapter 3 and Chapter 5 – Experiment 2). We found, in each experiment, an increase in movement velocity across the experiments. As we found little (to none) improvement in compensation for the tool geometry, it is likely that that the increase (of movement velocity) was reflecting the learning of the task. We cannot exclude however that part of that increase in movement velocity was due to the development of some tool model. Differentiation of those mode of acquisition was not an aim of the thesis, thus we did not test it directly (we proposed a potential experiment in Chapter 5, Section 5.9 to do so). That is, we chose not to examine how individual variability evolved inside, and across experimental sessions, as our main focus was on whether the visuomotor system could account for the tool geometries. We recognize however that such statistical analysis would be extremely valuable in the optic of understanding whether skill learning could really be the principal mechanism behind the acquisition of internal models of tools.

Taken together, our results indicated that adaptation was not the principal mechanism behind the compensation for the tool geometry. It appears that the visuomotor system developed some predominantly visual models, without developing robust internal models (although we found encouraging signs that some participants may have developed such model for the 1.4:1 tool in Chapter 4). We will discussed in the next section potential reasons behind the seemingly absence of development of internal models.

6.3 Importance of the learning environment

The goal behind this thesis is to understand read world tool use. For experimental purposes, the environment had to be controlled, at the cost of ecological validity. Our experiments were designed to isolate, to the best of our abilities, components playing a central role in tool use, and the development of internal models. We are aware that our task was not representative of real world interactions. We constrained grasping movements in one direction, always starting on the same spatial position. Participants were required to wear goggles limiting their visual field. Although those choices were made for experimental purposes, we are aware that it must have had an impact on the movements produced, and on the learning of the tools' properties.

In our experiments, we used principally two sorts of 'learning environment'. *First*, in Chapter 3 and Chapter 5 (experiment 1), we respectively changed tools at every trial and randomly interleaved them. This was done to reduce the chances of seeing classical adaptation. Our results suggest that this 'learning environment' did not promote learning of the tool geometry. It is possible that the requirement to switch tools while learning different tool geometries at the same time, interfered with learning (see work on dual adaptation: Krakauer et al., 1999; Martin et al., 1996; Wada et al., 2003; Woolley et al., 2007 and on the Contextual Interference Effect: Battig, 1966; Shea & Morgan, 1979). *Second*, in Chapter 4 and Chapter 5 (experiment 2), we introduced continuous exposure to a single tool geometry, 'favouring' the use of adaptation. We reasoned that as the visuomotor system evolved from interaction in the 'real world' (as mentioned in Section 6.2), it is likely that continuous exposure could promote learning of the tool models. That is, in real life, it is likely a person would only try to learn a single tool at a time, using it over and over, practicing until reaching the desired performance. Continuous exposure has the benefit of allowing the motor system to directly correct potential errors, and update the tool model. Our results indicated that continuous exposure leads to 'better' tool model, suggesting it does improve learning. However, we still did not find compelling evidence for the development of internal models of tools.

To examine the effect of our ‘learning environments’, it is useful to look at the overall grasping profiles for the 1:1 tool across the experiments. This tool appears to be learned quickly, with good level of performance in each experiment. However, in different ‘learning environments’, we can observe different grasping profiles. Fig. 6.1 shows the overall grasping profiles at the end of the experiment for all Chapters. It can be seen that the peak tool-tips aperture is higher during Chapter 3 than the other Chapters. In Chapter 3, exposure to a single tool lasted a single trial. In comparison, in the other Chapters, the exposure to a single tool geometry was continuous (Chapter 4: block of 180 trials; Chapter 5 – Experiment 2: blocks of 40 trials). This result may be interpreted through the margin-for-error framework. That is continuous exposure may reduce uncertainty about the tool properties. Thus, when planning a movement, the visuomotor system would add less margin-for-error, as it is more confident about the tool mapping, while still ensuring the success of the grasping movement. This confidence about the tool model could be caused by the possibility of directly acting upon any error signals, allowing for constant update and refinement of the tool model.

We need to be careful about the effect of the ‘learning environment’ however, as we did not find compelling evidence for the gradual improvement of performance (as discussed in Section 6.2). This suggests that our learning environments had an effect early in the learning phase, but little to no effect on the performance afterwards. As we argued that it is likely that internal model would be acquired to skill learning, it is possible that the performance would not improve gradually, or would do so through subtle changes. This would imply that more practice would be required to observe clear signs of improvement.

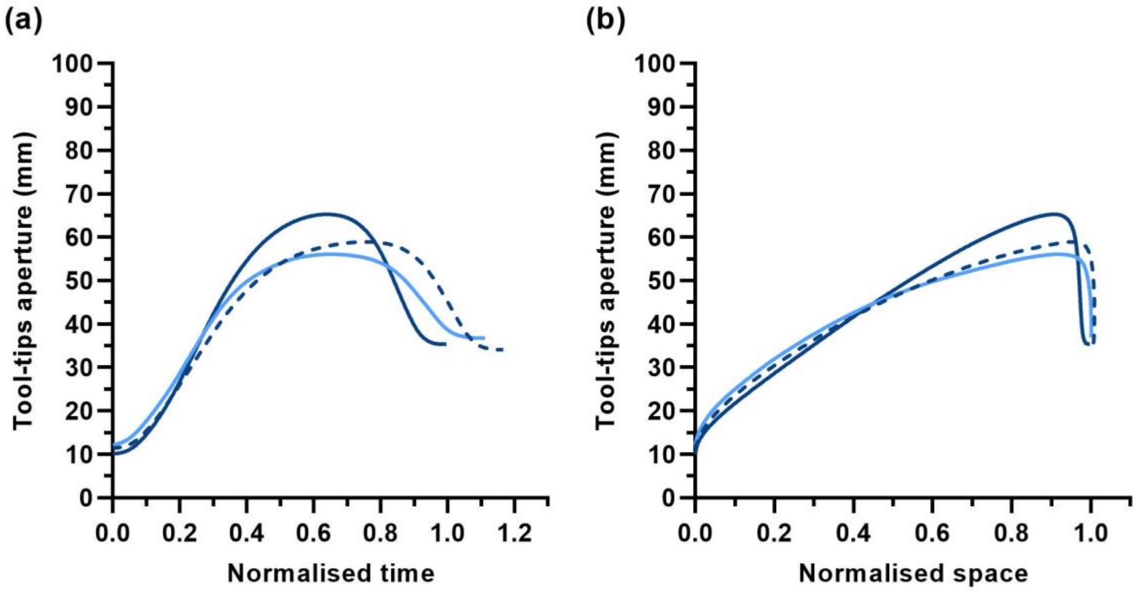


Figure 6.1. Overall grasping profiles for the different Chapters. (a) Grasping profiles with the 1:1 tool (collapsed across object size and object distance). The darker plain line represents the last 45 trials with the 1:1 in day 4 of the experiment in Chapter 3. The lighter plain line represents the last 30 trials of the training phase in the experiment in Chapter 4. The dashed line represents the last 40 trials of the experiment in Chapter 5. The profiles are normalised in time and adjusted to the movement duration of the 1:1 tool grasping in Chapter 3. (b) Same data. The profiles are normalised in space.

Although we did not find evidence for internal models, it is possible that our experiments were only snapshots of the early stages of the internal model learning process. Thus, we may have only capture part of the development of those models. It is possible that the acquisition of internal models of tools is not possible in the timescale of our experiments. It is difficult to define a number of required trials for the development of an internal model capturing the tool geometry. We explore different reasons, below. *First*, as discussed previously, our 'learning environment' could have a large impact on the required number of trials. That is, as seen in Chapter 4, we observed 'better' learning of the tool geometries than in Chapter 3 with less trials. Thus the length of the experiment might vary depending on the type of internal model acquisition favoured by the design. For example, if skill learning is promoted, the experiment should be divided in at least two sessions on two consecutive days, to use the consolidation happening during sleep (Abe et al., 2011; Telgen et al., 2014; Wright et al., 2010). *Second*, we need to account for individual variability. Evidence from Golenia et al. (2014) suggest that each individual has a particular learning curve. Indeed, in Chapter 3, our results indicated that some participants were better 'compensators', independent of the tool geometry.

Further, in Chapter 4, our results indicated that some participants may have developed internal model of the 1.4:1 tools (after ‘only’ 180 trials) while other did not.

Most principles from sensorimotor learning literature were developed from experiments using constrained movements in a highly controlled environment (Sternad, 2018). Using tool grasping allowed us to gain little insights about the application of those principles to more complex movements. Our results suggest that those principles could still be applied. Further, they bring an extremely useful framework through which we were able to review and interpret our results. Nevertheless, it appears more experimental testing is required to investigate if those principles are actually compatible with more complex movements, and to what extent they can be used with such movements.

Although using a more complex movement allows us to get a little more ecological validity, we are still not emulating real world interactions. We are aware that we are still testing in an experimental environment, still constraining the movement. This may not allow the visuomotor system to ‘explore’ the space and better understand the tool properties. A potential solution would be to run a more naturalistic experiment that would not entirely take place in an experimental setup. In the experiment, participants would be tested on their grasping performance with a tool, in a similar manner to what we did in our experiments (blocks of tool grasping, under different visual conditions). The particularity of the study is that the training would be done in the ‘real world’. Participants would be given a tool that they can bring home (and a set of objects). They would have to, as part of the study, use the tool at home, doing different ‘real world’ task (tailored to the tool properties), for a certain amount of time every day. Participants would have to report how long they used the tool for, and what they used it for. The experiment would take place across several weeks, and multiple times a week, participants would be invited to be tested in the experimental setup. This study could give us a clearer picture on the development of internal models of tools, by keeping the ‘training phase’ in a more ecologically valid environment.

Taken together, our results suggest that we need to be careful when designing the learning environment of our experiments. That is, knowing more about the mode of acquisition of internal models of tools would help to tailor experiments to promote the learning opportunities in clearly defined timescale. More research appears to be needed to investigate whether and how the sensorimotor learning principles could be applied to more complex movements.

6.4 Importance of analysing kinematic indicators in the context of the whole movement

Our 'naïve' assumption, based on Gentilucci et al. (2004) is that the goal of the visuomotor system is to produce the same movement profile with the tool-tips as with the hand, whatever the tool geometry. That is, as hand grasping should be the 'best' grasping movement the visuomotor system could produce, we assumed that the ultimate goal of using our pliers-like tools would be to produce similar grasping profiles. We are unable to confirm the validity of that assumption, as we lack of understanding of the biomechanics to know if that makes sense for all tools.

As discussed in the General Introduction, grasping can be perceived as decision-making under uncertainty as the same motor outcome can be produced by a vast number of different movements (Harris & Wolpert, 1998; Flash & Hogan, 1985; Shadmehr et al., 2016; Todorov & Jordan, 2002; Trommershäuser et al., 2003; Wolpert & Landy, 2012). Thus, selecting which movement to programme is not easy (Albert & Shadmehr, 2016; Körding & Wolpert, 2006) and need to be done while optimising some specified costs such as energy, jerk, time, muscle activation, … (Todorov, 2004; Todorov & Jordan, 2002; Wolpert et al., 1995). The optimisation of the cost-function is different for the hand and for the tools, as our tools challenge the motor system (recalibration of the relationship between visual and haptic signals, reduction of haptic sensitivity, addition of a spatial offset, mechanical constraints to the movement, …).

Our results indicated that we need to be careful when interpreting kinematic indicators. That is, similar performance could be achieved through different grasping profiles. Specifically, the comparison between grasping with the hand and the 1:1 tool is revealing. That is, by only examining kinematic indicators, performance appears similar. Deeper examination of the data, however, through overall grasping profiles, revealed important differences. That is, compared to hand grasping, tool grasping was characterised by a ‘plateau phase’, and some differences in opening and closing phase of the grasp. This is interesting, as our ‘naïve’ assumption could have led us to imagine that, as the tool ‘behaves’ like the hand, and does not alter the relationship between hand opening and tool-tips opening, the hand motor programmes could have been used (likely after being adapted to the properties of the pliers-like tool), producing similar profiles with both effectors. Our results however indicated different grasping movements. We explore potential explanations. *First*, our assumption was naïve, evidently, our tools challenged the system in numerous ways that would need to be addressed during movement planning and execution. It then appears unlikely that the visuomotor system would use the exact same motor programmes as during hand grasping when holding a tool. Those motor programmes would have to be adapted to the tool properties, leading to different movements. *Second*, there is some evidence that hand and tool grasping do not share the same underlying motor programmes (Tang et al., 2016). This implies that although the motor programmes are similar, they appear to be effector-specific. It is still possible however, that some of the hand-grasping motor primitives (‘building blocks’; Santello et al., 2016; Thoroughman & Shadmehr, 2000; Wolpert & Ghahramani, 2000) were used to build those ‘new’ motor programmes. Thus, although the motor programmes are different, they would rely on a similar ‘structure’.

Those results highlighted the importance of examining the grasping movement as a whole, and not only examining some chosen kinematic indicators. First, the overall profiles allow us to examine whether the chosen kinematic indicators are correctly representing the entire grasping movement. Second, they allow us to observe subtle details, differences in the grasping profiles that would not have been perceived otherwise. Thus those profiles can give valuable information about how grasping movements were controlled. At the moment, those profiles are only a powerful visualisation tool. In the future, it would be worthy to analyse them statistically. One way to do it could be to use a principal components analysis (Abdi & Williams, 2010; Wold, Esbensen, & Geladi, 1987) on the segmented profiles (profiles would have to be divided in multiple segments). Such an analysis has been used to identify motor primitives (Chiovetto, d'Avella, & Giese, 2016) and could allow us to investigate if the same motor primitives were indeed used in tool and hand grasping.

6.5 Tool use in the context of competing theories of grasp control

Tool use could provide insights into the underlying control mechanisms of grasping movements. Indeed, our pliers-like tools challenged the visuomotor system in a number of ways described across the thesis (recalibration of the relationship between visual and haptic signals, reduction of haptic sensitivity, addition of a spatial offset, addition of a geometrical alteration, adding mechanical constraints to the movement, …). Examining how the visuomotor system deals with those challenges could reveal some underlying mechanisms of grasping movements.

As discussed in the General Introduction, grasping movement control can be explained by two different frameworks. First, grasping can be seen as the control of two somewhat independent though coordinated components (Jeannerod, 1981, 1999; Jeannerod et al., 1995). Second, grasping can be seen as combination of two pointing movements (for the thumb and the index finger), towards selected position on the surface of the object (Smeets & Brenner, 1999). We discuss how our results from tool-grasping can fit into both frameworks, below.

We first examine the two-components framework (Jeannerod, 1981, 1999; Jeannerod et al., 1995). The *reaching* component aims to bring the hand at the object location while the *grasping* component is the preshaping of the digits to the object properties and closure of the digits to grasp the object. Tool use would likely affect the reach and grasp components differently. That is, the reaching component could be mildly affected by the tool's spatial offset (accounted for by a 'simple' calculation). In comparison, the grasping component has to account for the tool geometry (more 'complex' calculation). Both components would likely be affected by the mechanical constraints and the impoverished proprioceptive signals. If the visuomotor system was 'uncertain' about the tool geometry (due to an incomplete or impoverish model of that geometry), it could possibly adopt a strategy of decoupling the components. That is, both components would be planned in sequence, by first opening the tool-tips as wide as possible, then moving the tool-tips to the correct spatial location, before focusing on the closure phase of the grasp. That pattern somehow resembles performance with the reverse tool. When the tools behave qualitatively like the hand our results are not consistent with the use of such a strategy. This implies that both components were not entirely decoupled. Our results, however, indicated that both components were not planned and executed in complete coordination. Indeed, in all experiments, in all conditions, we found significant scaling of the movement velocity to object distance, even when there was no scaling of tool-tips aperture to object size (when using the reverse tool, or during the reverse-grasping task in Chapter 5). The contrast between the presence of object-distance movement velocity scaling and the absence of object-size grip aperture scaling in some conditions suggests that both components could indeed have been planned and executed 'separately' during tool-grasping. We assume, however, that with more robust tool models, both components of the grasp would be planned and executed in coordination.

We then examine the two-pointing movements framework. Tool use could be particularly challenging in this framework because our pliers-like tools 'swap' the finger and the thumb. That is, the tool-tip located spatially in front of the thumb was operated by the index finger while the tool-tip located in front of the index finger was operated by the thumb. In our tool-grasping tasks, as participants had to grasp the object front to back, they would rely on leading the tool-tip operated by the index finger to the visible part of the object, while closing the movement with the tool-tip operated by the thumb on the 'unseen' part of the object. This swapping may not be accounted for by a trivial recalibration of existing motor programmes. Our results however indicated that the normal tools were used appropriately pretty quickly. It is possible that if grasping movements were planned in end-effector units (controlling the tool-tips directly), the movements of the tool-tips would not have been planned and executed differently. Tool grasping would then be seen as two pointing movements with the tool-tips (separate from the motor programmes required to operate the tool).

6.6 Potential effect of reward/punishment

Grasping can be perceived as an optimisation problem, where the visuomotor system has to optimise a cost-function that considers the probability and value of success while minimising some costs such as energy, time, jerk, …(Scott, 2004; Todorov, 2004; Todorov & Jordan, 2002). Such a calculation must be influenced by the perceived value of success and failure. In all our experiments, failure to grasp the object, or success in grasping the object did not have any consequences. Thus, participants may have consciously chosen a strategy leading to perform 'well enough' during the task (and not at their 'best'). The presence of a reward, or a punishment may push participants to spent more energy and produce more effort in learning to use the tools.

In the sensorimotor framework, the presence of reward or punishment would likely *incentivise* the visuomotor system to perform at its best. Indeed, when the mode of acquisitions of internal models is skill learning, rewarding participants has been found to accelerate motor learning (Nikooyan & Ahmed, 2015) and even leading to the production of both faster and more accurate movement, breaking the speed-accuracy trade-off (Manohar et al., 2015). Reward could also facilitate retention of the newly acquired behaviour (Abe et al., 2011; Galea, Mallia, Rothwell, & Diedrichsen, 2015).

Although rewarding participants appears promising, we chose not to do it for two main reasons, discussed below. *First*, we wanted to observe what the visuomotor system would naturally do. We were investigating the ability of the visuomotor system to account for tool geometry. Thus, we wanted to keep the 'learning environment' simple. Moreover we were unsure about how a reward would impact participants' performance at the task. *Second*, it is difficult to define what 'level' of performance would be required for the attribution of the reward. It is indeed difficult to create a clear indicator of grasping performance. Grasping performance could be simply defined as success to grasp the desired object. Our results however have shown that performance is usually close to ceiling level when visual feedback is available (even with the reverse tool, at the end of the experiment). Moreover, accounting for the tool properties does not correlate with success rate. There may be other ways to define grasping performance through various kinematic indicators. We are still unable, however, to clearly define what constitutes a 'good' grasping movement, as all kinematic indicators are correlated (movement velocity, peak aperture, margin-for-error,…). A potential solution could be to reward the compensation for the tool geometry, producing a continuum from zero compensation to full compensation to ‘too much’ compensation. Such a reward may force the visuomotor system to explore the 'tool geometry space’, likely facilitating the development of internal models of tools. This solution is not without issues (technical and theoretical), as we are still unable to understand exactly how and by what mechanisms tool compensation is produced.

Overall, if skill learning is the principal mechanism underlying internal model acquisition, adding a reward to our experiment would be a worthy track to explore. We would expect the presence of a reward to motivate participants, likely leading to an improvement of their performance, and to the development of internal model. It is possible that the presence of an reward could also improve motivation (which can be difficult to maintain during long experiments) and trigger more conscious, cognitive effort to perform optimally at the task.

6.7 Conclusion

Tools appear not to have been ‘used as body parts’, as we found no compelling evidence for the development of internal models of tool geometries. The visuomotor system used a predominantly visual strategy to control the movements, and may have developed visual model of the tools, allowing for anticipatory behaviours to be produced, and partial compensation for the tool geometries Such models were only developed for tools behaving qualitatively like the hand. The statistics of the world, and the movement required to optimally used the tools appear to influence greatly the development of tool models.

Chapter 7 - Appendices

7.1 Chapter 3

7.1.1 Overall grasping profiles

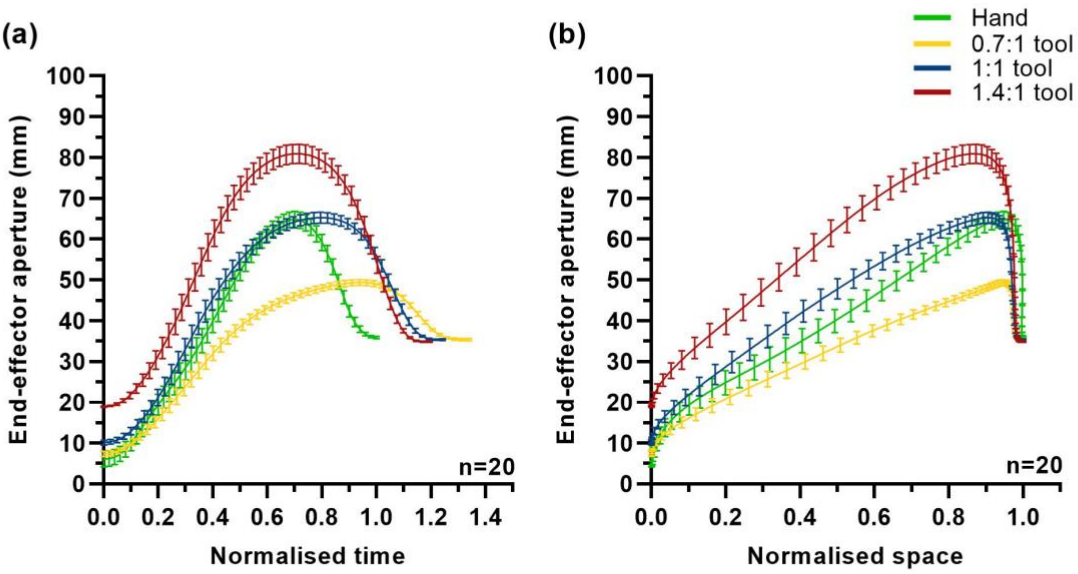


Figure 7.1. Average grasping profiles (same data as in Fig. 3.19a and c). (a) The end-effector profiles (collapsed across object distance and object size) normalised in time adjusted to the hand grasping profile (b) The end-effector profiles are normalised in space. Error bars denote the SEM.

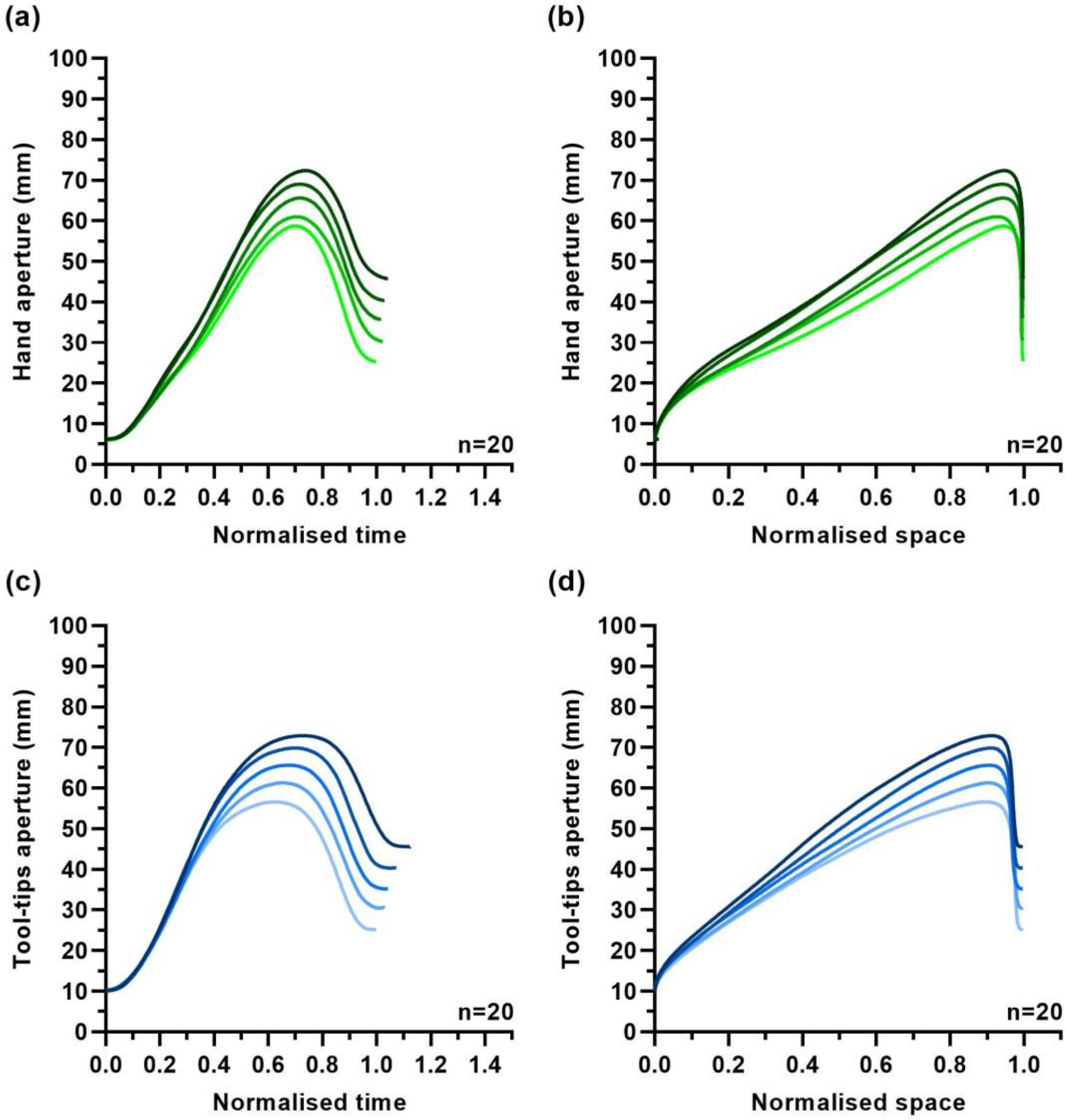


Figure 7.2. Average grasping profiles for each object size (collapsed across object distance). (a) The hand grasping profiles normalised in time adjusted to the hand grasping profile for the 25 mm object (b) Same data normalised in space. (c) The 1:1 tool grasping profiles normalised in time adjusted to the 1:1 tool grasping profile for the 25 mm object (d) Same data normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

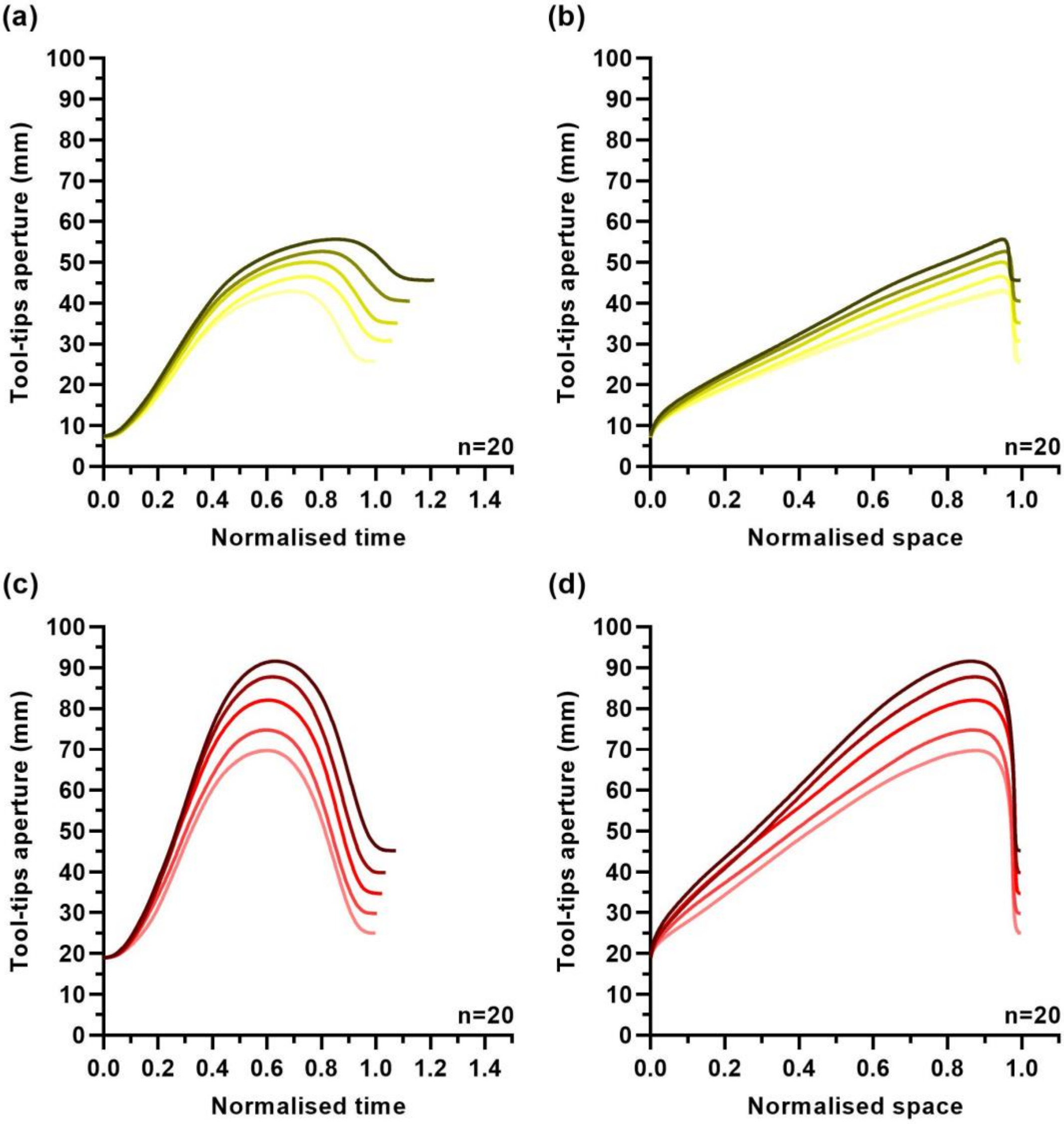


Figure 7.3. Average grasping profiles for each object size (collapsed across object distance). (a) The 0.7:1 tool grasping profiles normalised in time adjusted to the 0.7:1 tool grasping profile for the 25 mm object (b) Same data normalised in space. (c) The 1.4:1 tool grasping profiles normalised in time adjusted to the 1.4:1 tool grasping profile for the 25 mm object (d) Same data normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

7.2 Chapter 4

7.2.1 Overall grasping profiles

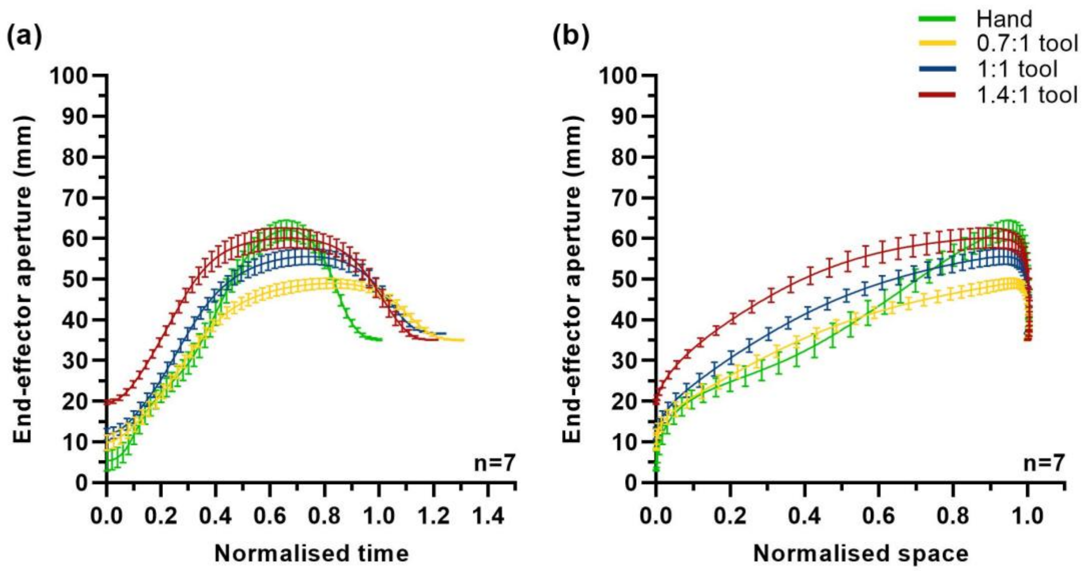


Figure 7.4. Average grasping profiles (same data as in Fig. 4.10 a and c).(a) The end-effector profiles (collapsed across object distance and object size) normalised in time adjusted to the hand grasping profile (b) The end-effector profiles are normalised in space. Error bars denote the SEM.

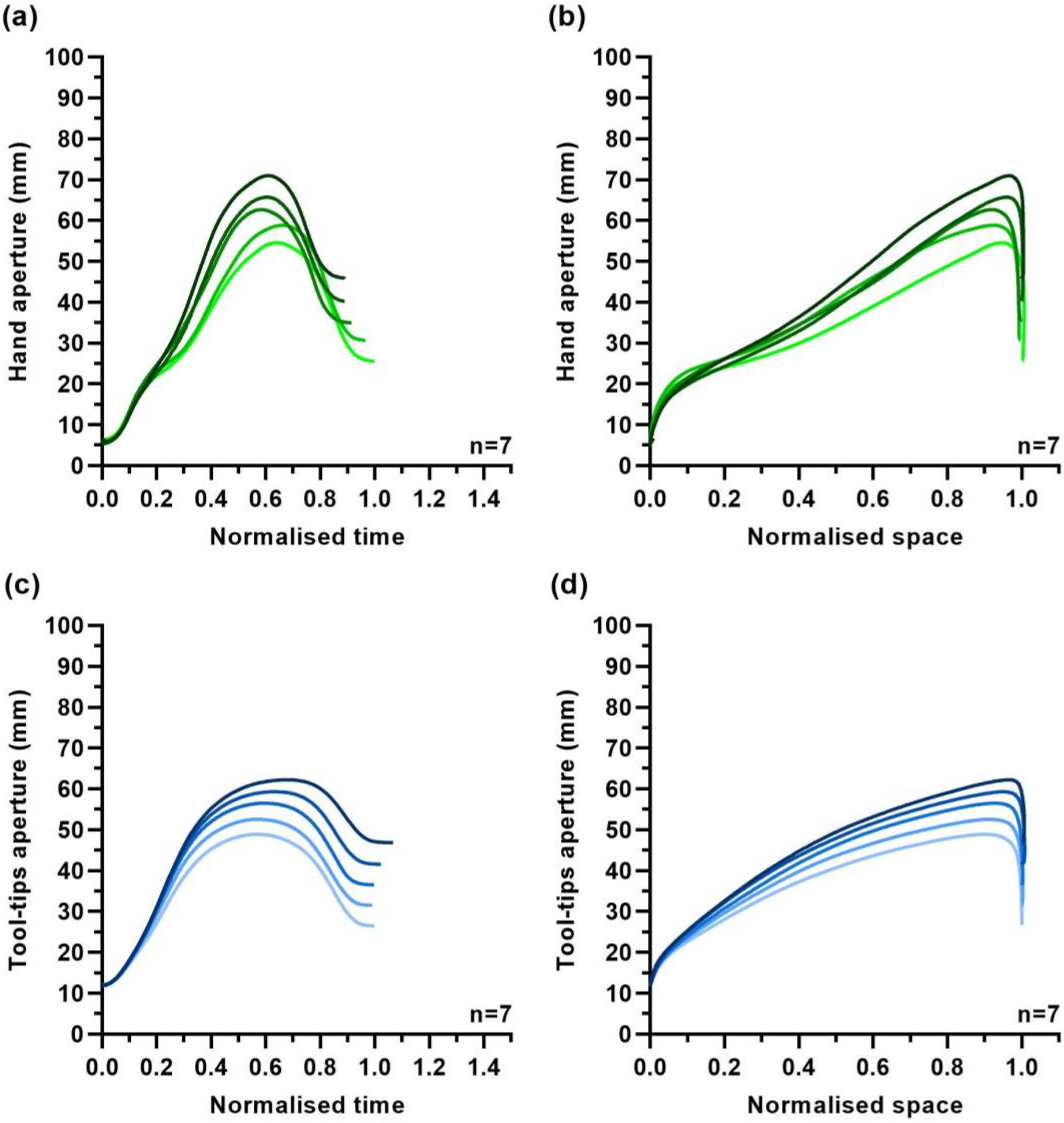


Figure 7.5. Average grasping profiles for each object size (collapsed across object distance). (a) The hand grasping profiles normalised in time adjusted to the hand grasping profile for the 25 mm object (b) Same data normalised in space. (c) The 1:1 tool grasping profiles normalised in time adjusted to the 1:1 tool grasping profile for the 25 mm object (d) Same data normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

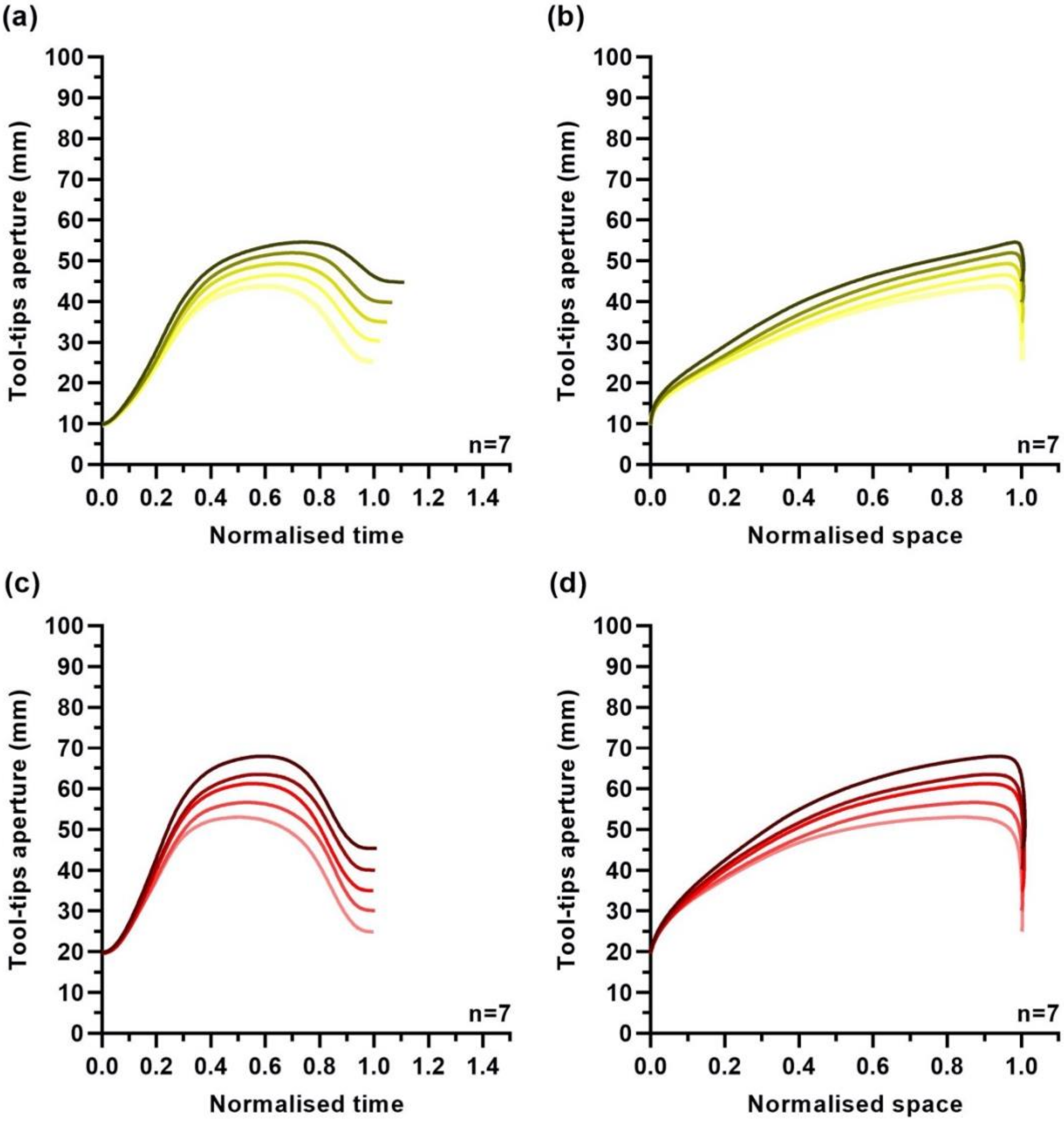


Figure 7.6. Average grasping profiles for each object size (collapsed across object distance). (a) The 0.7:1 tool grasping profiles normalised in time adjusted to the 0.7:1 tool grasping profile for the 25 mm object (b) Same data normalised in space. (c) The 1.4:1 tool grasping profiles normalised in time adjusted to the 1.4:1 tool grasping profile for the 25 mm object (d) Same data normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

7.3 Chapter 5

7.3.1 Overall grasping profiles

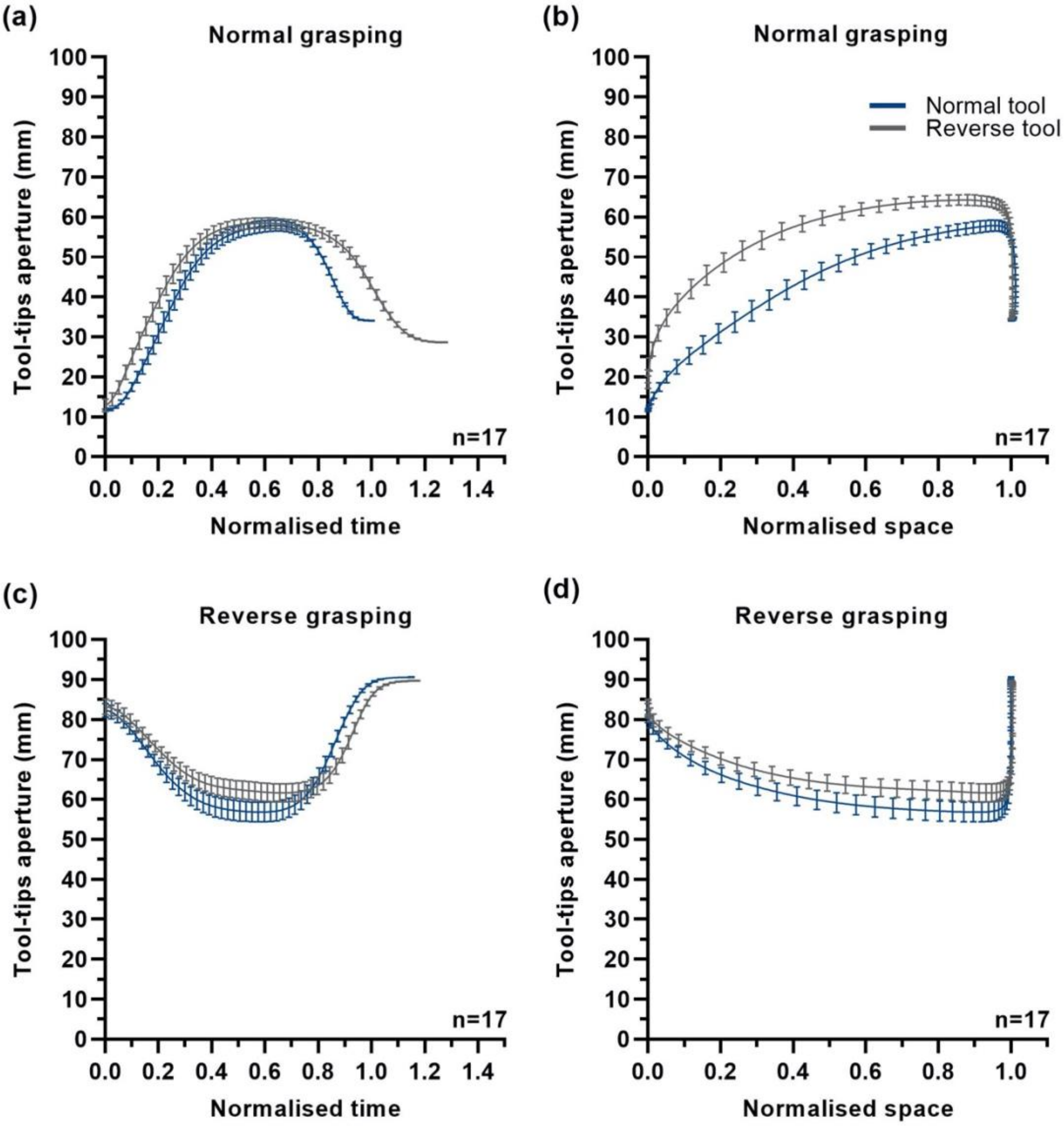


Figure 7.7. Average grasping profiles (collapsed across object distance and object size) (same data as in Fig. 5.12). (a) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the normal grasping task (b) The tool-tips profiles (a) normalised in space. (c) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the reverse grasping task (d) The tool-tips profiles (c) are normalised in space. Error bars denote the SEM.

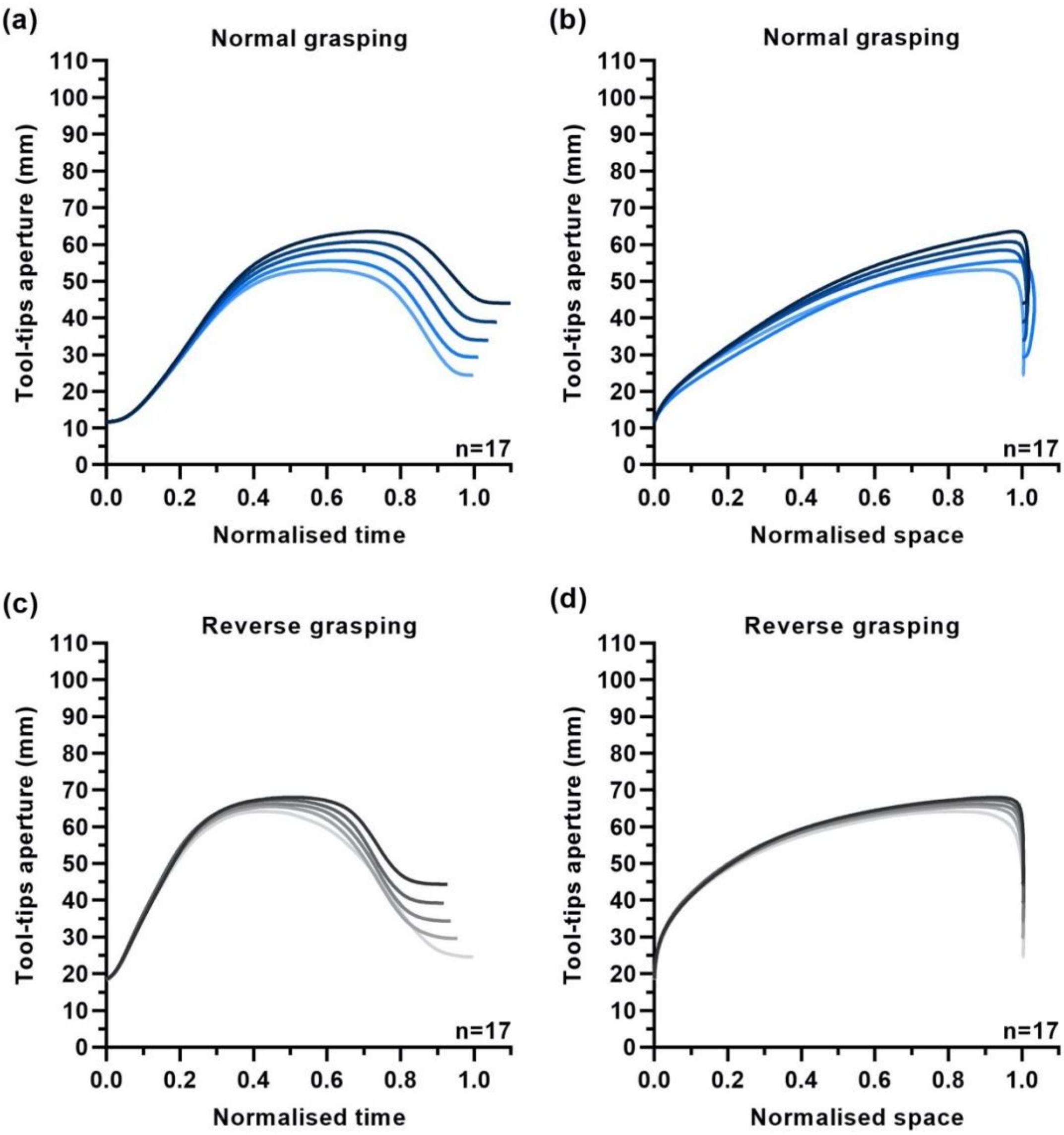


Figure 7.8. Average grasping profiles for the normal grasping task (collapsed across object distance) (a) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the 25 mm object (b) The tool-tips profiles (a) normalised in space. (c) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the 25 mm object (d) The tool-tips profiles (c) are normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

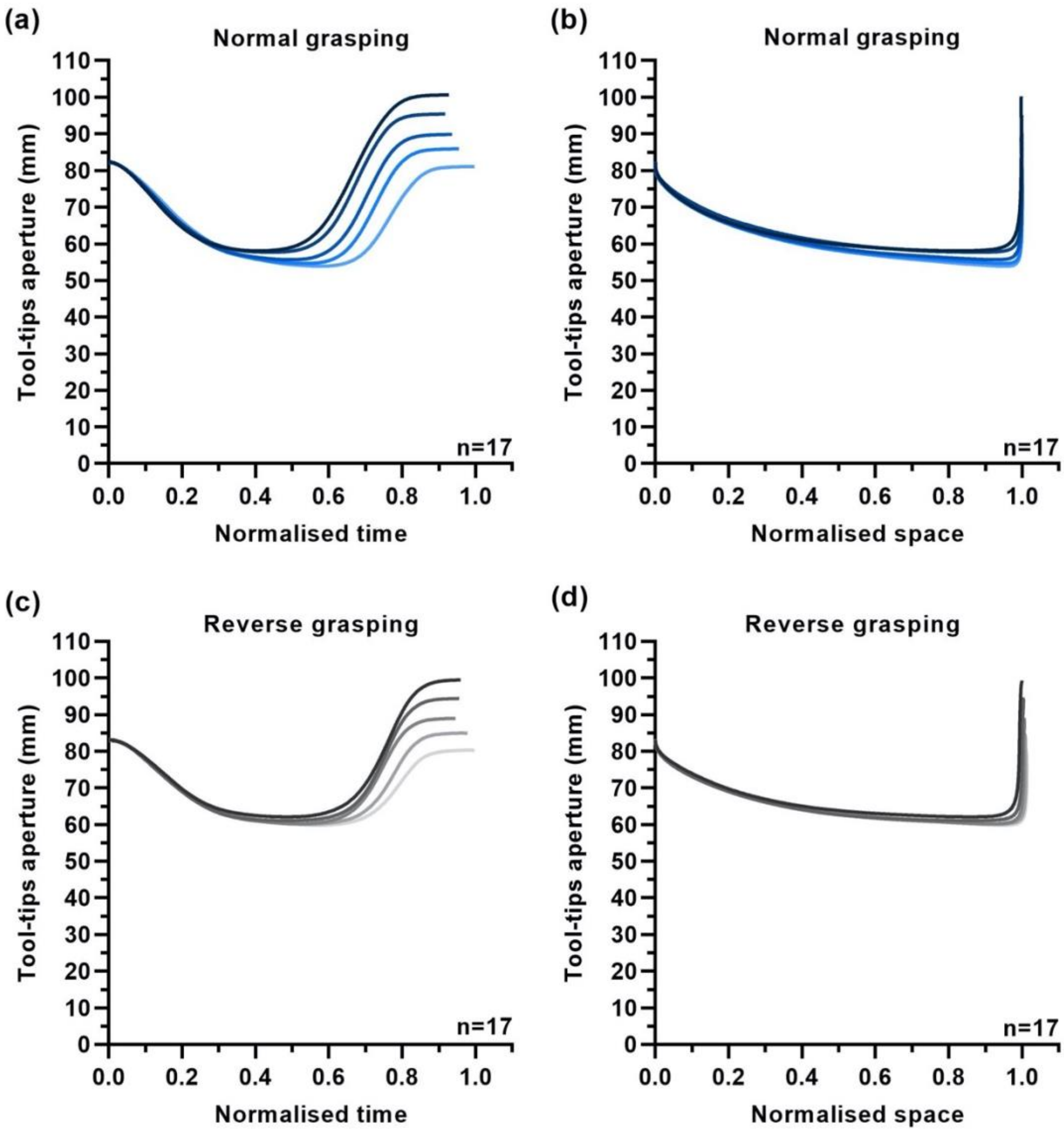


Figure 7.9. Average grasping profiles for the reverse grasping task (collapsed across object distance) (a) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the 25 mm object (b) The tool-tips profiles (a) normalised in space. (c) The tool-tips profiles normalised in time adjusted to the normal tool grasping profile for the 25 mm object (d) The tool-tips profiles (c) are normalised in space. The different object sizes are represented by the colour gradient, with the smallest object size represented by the lightest colour and the largest object size represented by the darkest colour.

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