

RESEARCH ARTICLE | *Control of Movement*

Toward natural grasping with a tool: effects of practice and required accuracy on the kinematics of tool-use grasping

 **Yoshihiro Itaguchi**^{1,2}

¹*Department of Computer Science, Shizuoka University, Hamamatsu, Japan; and* ²*Department of Psychology, Waseda University, Tokyo, Japan*

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Itaguchi Y. Toward natural grasping with a tool: effects of practice and required accuracy on the kinematics of tool-use grasping. *J Neurophysiol* 123: 2024–2036, 2020. First published April 22, 2020; doi:10.1152/jn.00384.2019.—Studies have suggested that the proficiency of an end effector is the primary factor that defines kinematics of reach-to-grasp movements across the types of effectors, such as the hand or a tool. In particular, the duration of the plateau, or the time of static open aperture (i.e., the distance between tips of effectors), is typically longer for tool use compared with natural grasping with a hand. This study investigated how improvement in the proficiency of tool use modifies the kinematics of reach-to-grasp movements. To clarify the effects of required accuracy on the kinematics in tool-use grasping, movement speed and difficulty of grasping were manipulated. The results showed that plateau duration, the length of which indicates that reaching and grasping components are temporally dissociated, shortened as tool-use practice proceeded. These results indirectly support the idea that shortened plateau duration was induced by improvement in the proficiency of tool use. Moreover, plateau duration was shortened at faster movement speeds or under conditions not requiring accurate grasping, even without any practice of tool-use grasping. Additional analyses found that plateau duration did not scale with movement time. These results suggest that the kinematic features supposed to be characteristic of tool-use grasping are not inevitable but are greatly influenced by a strategy that is not intentionally but rather automatically implemented to compensate for the lack of proficiency of end effectors, in agreement with the idea that the brain focuses on the tips of an end effector regardless of its effector type in reach-to-grasp movements.

NEW & NOTEWORTHY This study is the first reporting the relation between characteristic aperture time profile, called plateau duration, and movement time of tool-use grasping. The results suggest that improved coordination between reaching and grasping components was induced by improvement in the proficiency of tool use but not by just shortened movement time. The results also indicate the possibility that the constraints for calculations in motor planning are essentially the same between hand-use grasping and tool-use grasping.

disembodiment; embodiment of tool; motor embodiment; reach-to-grasp movement; skill learning

INTRODUCTION

We sometimes feel as if a familiar tool is incorporated in our own body. This sensation is called a sense of embodiment of tool and has been previously addressed by behavioral and

neurophysiological research (Berti and Frassinetti 2000; Brozoli et al. 2009, 2010; Cardinali et al. 2009, 2016; Farnè and Ladavas 2000; Kao and Goodale 2009; Maravita et al. 2002a, 2002b; Martel et al. 2016; Umiltà et al. 2008). According to the definition of De Vignemont and Farnè (2010) and de Vignemont (2011), embodiment refers to information processing in which external objects are processed in the same way as the properties of one's body under certain circumstances, and the sense of embodiment refers to the subjective feeling of the embodiment. For instance, it has been reported that a monkey's neurons, which have a visual receptive field specific to stimuli near the monkey's own hand, responded to visual stimuli along a tool surface only when the monkey actively used it (Iriki et al. 1996; Ishibashi et al. 2000). That is, certain cells responsible for perceiving one's own body respond to an external object through the experience of intentional voluntary use of the object (in this case, a tool). Such neural plasticity is sometimes considered evidence for neural substrates of the embodiment (for review, see Martel et al. 2016). Although the idea of embodiment of tool has been extensively investigated (e.g., Povinelli et al. 2010), the fundamental link or distinction made in the brain between body and tool has not received much attention, especially in terms of motor control.

According to the literature, reach-to-grasp movements have been used to explore the relation between body and tool. Usually, when we reach for and grasp an object, a thumb and index finger are the main contributors and the other fingers are just supplementary (Jeannerod 1984; Napier 1956). In such a "natural" reach-to-grasp movement, an aperture (i.e., the distance between tips of effectors, in this case, the thumb and index finger) does not increase quickly but gradually in the time course of the movement. The peak of the aperture opening, called the maximum grip aperture (MGA), usually appears at 60–80% of the time point of the movement (e.g., Itaguchi and Fukuzawa 2014; Jakobson and Goodale 1991; Jeannerod 1984; Marteniuk et al. 1990; Povinelli et al. 2010; Smeets and Brenner 1999; Tresilian and Stelmach 1997; Wing et al. 1986). In contrast to natural grasping, when a tool such as a pair of pliers or a prosthesis is used to grasp an object, the aperture expands quickly and maintains almost the same size before closing, which is called a "plateau" (Bongers 2010; Bongers et al. 2012; Bouwsema et al. 2010; Gentilucci et al. 2004; Itaguchi and Fukuzawa 2014; Wing and Fraser 1983; Wing et al. 1986). That is, the reaching (shoulder and elbow joint move-

Correspondence: Y. Itaguchi (itaguchi-y@inf.shizuoka.ac.jp).

ment) and grasping (finger movement) components are temporally dissociated during tool-use grasping compared with natural grasping. Although we could control a tool with greater accuracy and precision after extensive practice, these findings are also reasonable considering that we cannot usually control a novel tool skillfully without practice. The focus of the latter fact may lead one to regard body and tool as distinct entities, and most previous studies have tacitly assumed so.

One, however, can assume that body and tool are merely controlled objects not necessarily distinguished by the brain. Itaguchi and Fukuzawa (2014) investigated the possible invariance of the kinematics of reach-to-grasp movements between body and tool. They compared the time courses of changes in aperture in reach-to-grasp movements for four different effectors that differed in the proficiency of motor control: grasping with a thumb and index finger (proficient body-use grasping), grasping with a thumb and middle finger (nonproficient body-use grasping), grasping with chopsticks (proficient tool-use grasping), and grasping with a novel tool (nonproficient tool-use grasping). The study participants used chopsticks on a daily basis from their childhood and were skillful enough to use them. The study confirmed that coordination between reaching and grasping components (temporal overlap of the 2 components during the movement) was highest in proficient hand-use grasping and lowest in nonproficient tool-use grasping, by quantifying the aperture plateau as the “plateau duration.” The length of the plateau duration indicates the degree of temporal decoupling between reaching and grasping components and is therefore shorter when higher coordination is achieved. More importantly, the study found that there were no differences in plateau duration between nonproficient hand-use and proficient tool-use grasping, which were between proficient body-use grasping and nonproficient tool-use grasping in plateau duration. This result suggests that a shared principle (kinematic constraints) governs the motor control of reach-to-grasp movement (e.g., Smeets and Brenner 1999; Verheij et al. 2012) depending on proficiency regardless of end effectors (Itaguchi and Fukuzawa 2014), as opposed to the body-tool dichotomy suggested by kinematic differences between grasping using a hand and “mechanical fingers” (Gentilucci et al. 2004).

Other reports also provide evidence for the idea that proficiency of tool use predominantly affects kinematics in changes in aperture. Using a pair of pliers, Golenia et al. (2014) investigated the effect of two-day practice (200 trials of reach-to-grasp movements in total) on aperture profile. Although they found consistent decreases in movement time and plateau duration, the size of grasping aperture did not change over time. This result suggests that temporal aspects of kinematics are sensitive to proficiency of tool use. Using a different control method, Bouwsema et al. (2014) also indicated that plateau duration could be shortened by practice. In their experiment, able-bodied participants practiced using a myoelectric prosthesis that could open and close its hand by exerting forearm muscle force. Five-day practice shortened both movement time and plateau duration of reach-to-grasp movements. These studies suggested that increase in the proficiency of an end effector reduced the characteristic temporal decoupling in kinematics of tool use. However, the reason long plateau duration appears in tool-use grasping and is reduced by practice is still unclear. Furthermore, no studies have quantified the

relation between plateau duration and movement time in tool-use grasping, so it is possible that movement time and plateau duration were just correlated owing to the mechanical nature of grasping.

To further explore the relation between body and tool in terms of motor aspects and to reveal the relation between plateau and movement time, the present study conducted three experiments. *Experiment 1* tested the hypothesis that kinematic features, especially plateau duration, of tool-use grasping approach those of skilled hand-use grasping as proficiency of an end effector increases. To examine this, the present study conducted an experiment wherein participants practiced a reach-to-grasp movement with a novel tool for 10 days in 2 wk. Furthermore, this study hypothesized that low coordination in tool-use grasping is just due to a strategy to increase the probability of success in grasping, which is however not necessarily consciously adopted or controlled by the tool user. To clarify whether high coordination between reaching and grasping components as in hand-use grasping is impossible or not when tool-use proficiency is insufficient, *experiments 2* and *3* were conducted. In these experiments, the required accuracy was experimentally varied in different ways, thereby implicitly manipulating the use of possible strategies. However, in all experiments, as described above, independent variables (such as the practice period and accuracy demand) would change the movement time as well as the plateau duration. The correlation coefficients between kinematic measures and movement time were therefore calculated to dissociate these factors. If the short plateau duration during tool-use grasping is innate and solely due to the long movement time, the individual differences in movement time, which has been reported to decrease with tool-use practice (Bouwsema et al. 2014; Golenia et al. 2014), would correlate with the degree of coordination. This investigation is important because speed-accuracy tradeoff likely influences aperture profile in reach-to-grasp movement (Bootsma et al. 1994); therefore, it is plausible that the plateau evident in tool-use grasping is caused by a strategy to compensate for the tradeoff.

MATERIALS AND METHODS

Participants and tasks. In *experiment 1*, seven right-handed participants (22.8 yr old on average, 4 women) practiced reach-to-grasp movement for a wooden cylindrical object for 2 wk with a novel tool. The movement performance was evaluated before the practice (1st session) and after 1 wk (2nd session) and 2 wk (3rd session). A practice was conducted for 25 min/day excluding weekends (i.e., 5 days/wk). In the practice sessions, participants repeated reach-to-grasp movements using the same setting as in the evaluation sessions (described later). No special instructions were provided because the present study focused on the natural development of tool-use proficiency. Although the performance of hand-use grasping was also assessed in the evaluation sessions, the participants did not practice hand-use grasping but practiced tool-use grasping in the practice sessions. The first and second evaluation sessions were conducted before tool-use grasping practice in the same day. Evaluation of hand-use grasping was performed before that of tool-use grasping in the same procedure. This experiment was conducted to examine the effect of proficiency of an end effector on plateau duration.

In *experiment 2*, another eight right-handed students (21.8 yr old on average, 5 women) participated. The participants carried out reach-to-grasp movements with the same tool used in *experiment 1* but at three different speeds: normal, faster, and fastest. Under the normal speed condition, they were required to conduct movements at a

comfortable speed for them. Under the faster speed condition, they conducted movements faster than under the normal speed condition, and under the fastest speed condition, they conducted movements at the maximum speed. Under the faster and fastest speed conditions especially, the participants were asked to prioritize speed over successful grasping. When they failed to grasp an object, the trial was not recorded and was repeated until successful. In the experiment, the participants alternated the movement speed in ascending order trial by trial and reverted to the normal-speed trial after the fastest-speed trial (i.e., normal, faster, fastest, normal...). This experiment was conducted to examine the effect of movement speed on plateau duration.

In *experiment 3*, another eight participants (21.3 yr old on average, 5 women) carried out reach-to-grasp movements for two different objects to grasp. Under the lift condition, they executed the same reach-to-grasp movements as in *experiments 1* and *2*. The participants reached for the target object and lifted it up after grasping it. Under the grasp-only condition, they reached for and grasped a hard sponge object, the width and height of which were the same as those of the target object used under the lift condition but showed different depth to reduce the accuracy demand. The front of the sponge was curved to show a round edge the same as that of the cylindrical object. In addition, unlike the cylindrical object, the sponge object was fixed on the table surface and therefore could not fall or be lifted. This grasping condition was assumed to reduce the requirement of grasping accuracy compared with the lift condition; participants did not care so much about possibilities of grasp failure, such as dropping the object, deviating from the center of the object when it was grasped, etc. This experiment was conducted to examine the effect of grasping difficulty under a more natural condition, without learning and speed constraints, on plateau duration.

All the participants gave informed written consent before participating in the experiments. This study was conducted in accordance with the Declaration of Helsinki and was approved by the Ethics Committee on Human Research of Waseda University (2012-002, 2017-031).

Experimental setup and procedure. The evaluation methods of reach-to-grasp movements followed those of Itaguchi and Fukuzawa (2014). In all the experiments, the participants were seated and reached for and grasped a cylindrical object on a table with fingers (i.e., a thumb and index finger) or a scissor-like tool. Except for the grasp-only condition in *experiment 3*, after grasping the target object, the participants transported it to a location 10 cm right of the target. The starting point and target object were 20 and 50 cm away from the

participants' midline, respectively (Fig. 1A). In a trial, after an experimenter gave a verbal cue, the participants started reaching for the object in their own time with their fingertips or the tips of the tool closed.

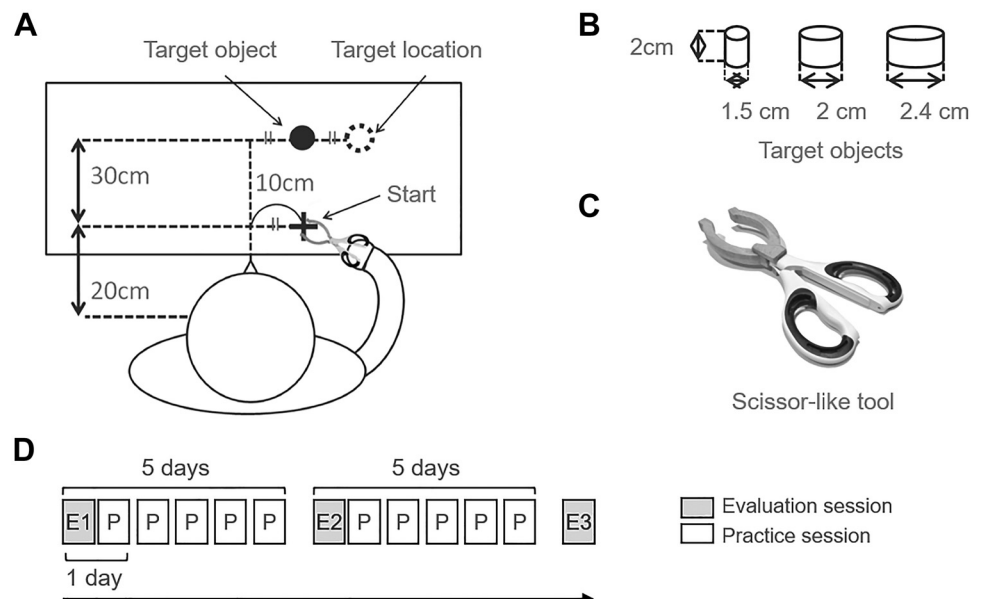
The scissor-like tool was the same as that used in the previous study (Itaguchi and Fukuzawa 2014). Three different sizes of target objects were used; their height was 2.0 cm, and their diameters were 1.5, 2.0, and 2.4 cm (Fig. 1B). The target objects were wooden but were wrapped with a rubber band to prevent them from slipping and being dropped. In *experiment 1*, 90 trials were conducted in total (30 trials \times 3 targets) in each evaluation session. In *experiment 2*, 270 trials were conducted in total (30 trials \times 3 targets \times 3 speeds). Under the lift condition of *experiment 3*, only the 1.5-cm object was used, and under the grasp-only condition, a sponge was grasped. A total of 20 trials were performed, 10 under each condition. The sponge's height, width, and depth were 2.0, 1.5, and 4 cm, respectively. The sponge was horizontally oriented and inclined 30° clockwise to the participants' midline, allowing the participants to grasp the sponge more easily with their right hand. The number of failures in reach-to-grasp movement was not recorded in the experiments.

The tool was reconstructed from a normal pair of scissors to have wooden fingers suitable for grasping objects (Fig. 1C). Its total length was 18 cm. The maximum aperture (i.e., opening distance) of the tool was 8 cm, which was sufficient to grasp the target objects used in the present study.

Kinematic analysis. The three-dimensional positions of reflective markers attached to fingertips or the tips of the tool were recorded using an optic-motion-capture system (SMARTTRACK, ART, Inc.) operated at 60 Hz with spatial resolution of 0.05 mm. We analyzed the reach-to-grasp part of the movement but not the transporting part after grasping. The onset of the reaching movement was defined as the first time point at which tangential velocity, smoothed by a 5-Hz Butterworth low-pass filter (3rd order), exceeded 1 cm/s. The offset of the reach-to-grasp movement (i.e., the time of grasp) was determined as the first time point at which tangential velocity fell below 5 cm/s after the maximum velocity and the change in aperture was terminated.

To evaluate the effects of learning, speed, and difficulty on reach-to-grasp movement, four kinematic measures from the positional data were calculated following the methods of previous studies (e.g., Bongers 2010; Itaguchi and Fukuzawa 2014): MGA, MGA timing, movement time, and plateau duration. MGA is the maximum distance between tips of effectors, MGA timing is the relative timing of MGA appearance in the movement time, movement time is the absolute time

Fig. 1. Experimental setting (A), target objects (B), scissor-like tool used for grasping (C), and task schedule (D) in *experiment 1*. In the evaluation sessions, tool-use and hand-use grasping were assessed.



duration from the onset of movement to the grasp, and plateau duration is defined as the relative time the aperture was over 90% of the MGA in the movement time. It has been reported that longer plateau duration is evident in tool-use grasping (Bongers 2010; Bouwsema et al. 2010; Gentilucci et al. 2004; Wing and Fraser 1983). This measure was expected to decrease as proficiency increased the efficiency of effectors in reach-to-grasp control (Golenia et al. 2014; Itaguchi and Fukuzawa 2014) and as the priority of accuracy decreased (Alberts et al. 2000).

In *experiment 1*, plateau duration was predicted to shorten and the other measures were not as practice proceeded. In *experiment 2*, plateau duration would shorten in movements performed at the faster speed because the capabilities of strategic and accurate grasping would decrease owing to time pressure. In *experiment 3*, plateau duration would shorten in movements for the sponge, which requires less control accuracy.

Statistical analysis. In *experiment 1*, we conducted two-factor (target size and evaluation phase) within-subject ANOVA for hand- and tool-use grasping. We conducted two separate ANOVAs because the two types of grasping were not treated in the same way; that is, the participants practiced tool-use grasping but not hand-use grasping in the experiment, and any changes in hand-use grasping in the evaluation phases were not of interest in the current study. The hand-use-grasping data are therefore considered reference data. In *experiment 2*, we conducted two-factor (effector type and movement speed) within-subject ANOVA to examine possible differences in the effect of movement speed on reach-to-grasp movement. The target size was collapsed to simplify the results and discussion. To conduct multiple comparisons as post hoc analysis, we used Holm's methods. In *experiment 3*, paired *t* tests were conducted to compare the two grasping conditions.

Furthermore, correlation analyses were conducted to reveal the relation between speed and the other kinematic measures, where plateau

duration was the particular focus of the present study. In the current statistical design, these correlation analyses can quantify the relation between variables including interindividual factors, which are qualitatively different from the results of the ANOVAs that provide information on internal changes due to practice or the experiment conditions.

RESULTS

Experiment 1: learning task. Figure 2 shows average aperture profiles obtained from one typical participant in *experiment 1*. Figure 2, A–D, indicates that the aperture was modulated by target size regardless of effectors. Aperture profiles in tool-use grasping have a long plateau but are somewhat shortened in the third session. Figure 3 shows the kinematic measures in tool-use grasping. The main focus of the present experiment was the effect of learning on the plateau duration during tool-use grasping; therefore, the other statistical results related to target effects are not entirely described.

To test whether the practice of tool-use grasping decreased the plateau duration, two-way ANOVA was conducted. Target-pooled plateau duration was 46.1 (SD = 3.9), 45.1 (SD = 3.9), and 40.8% (SD = 4.0) in the first, second, and third sessions, respectively. The ANOVA indicated a significant main effect of the evaluation phase [$F(2,12) = 8.14$, $P = 0.006$, $\eta_p^2 = 0.57$], and multiple comparisons revealed that plateau duration in the third session was significantly shorter than those in the first and second sessions [$t(6) = 3.74$, $P = 0.02$; $t(6) = 3.99$, $P = 0.02$]; however, there was no statistical difference between the plateau durations in the first and second sessions [$t(6) = 0.60$, $P = 0.57$]. The main effect of the target size was

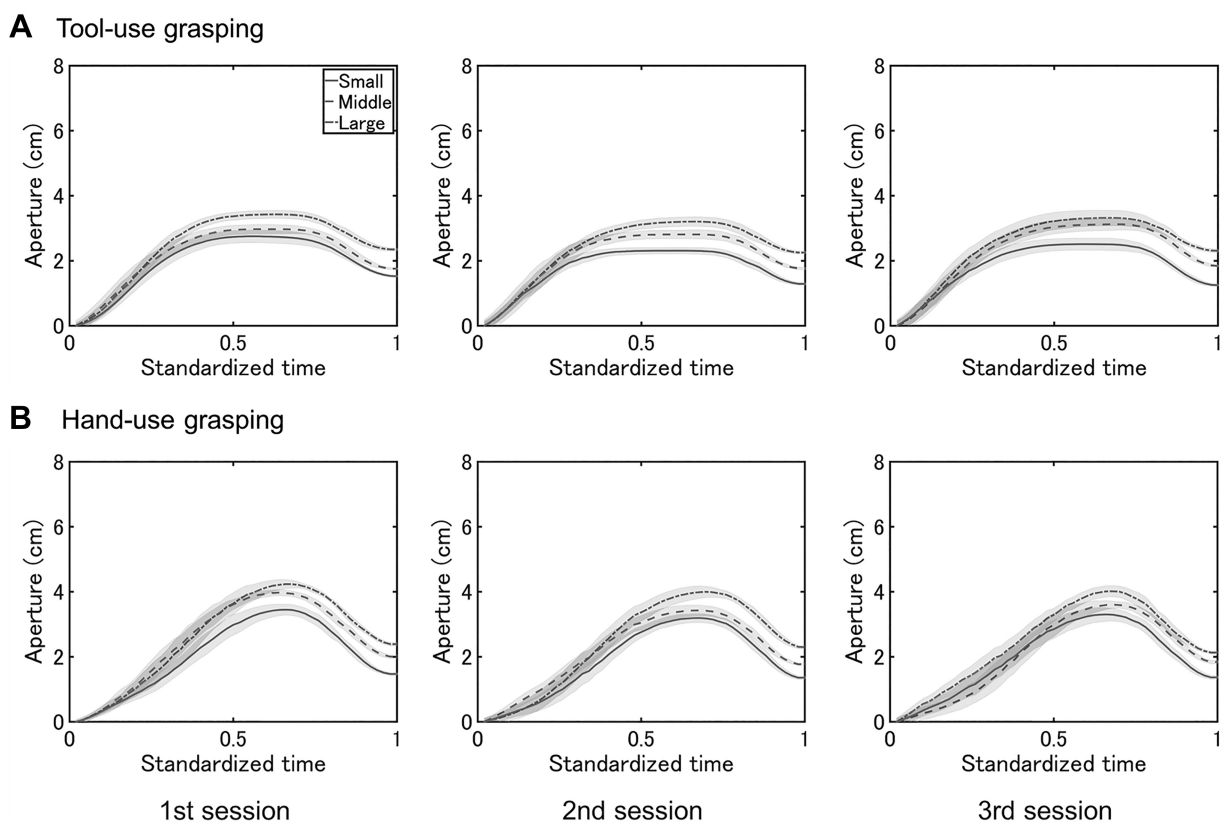


Fig. 2. Average aperture profiles of tool-use grasping (A) and hand-use grasping (B) of 1 participant in 3 evaluation sessions in *experiment 1*. The 1st session was conducted before tool-use practice, and the 2nd and 3rd sessions were conducted after 1-wk and 2-wk practices, respectively. Background shadows indicate SD.

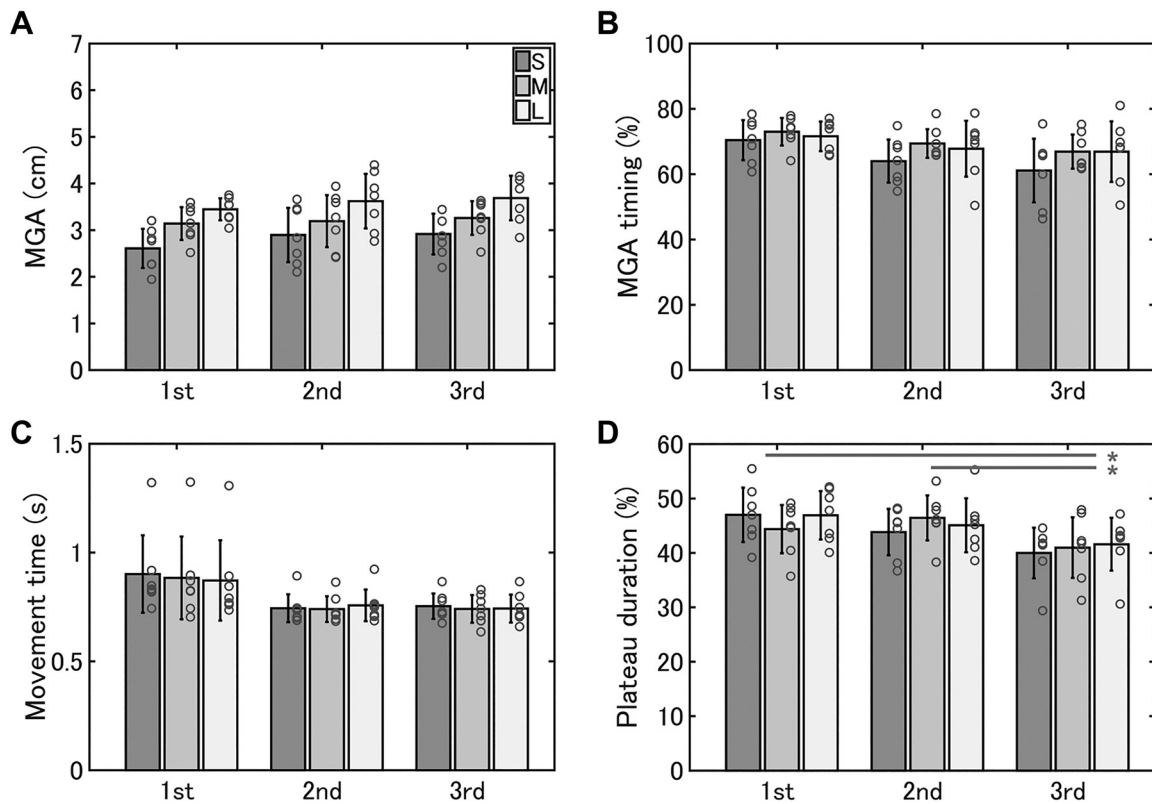


Fig. 3. Kinematic measures in tool-use grasping in *experiment 1*. *A*: maximum grip aperture (MGA). *B*: MGA timing. *C*: movement time. *D*: plateau duration. The main effect of learning was statistically significant in movement time and plateau duration. Multiple comparisons revealed plateau duration in the 3rd session was significantly shorter than those in the 1st and 2nd sessions. * $P < 0.05$, indicate significant difference between evaluation phases found in multiple comparisons. Note that although multiple comparisons did not find any statistically significant differences in movement time among the sessions, the main effect of evaluation phase was statistically significant. There were no significant interaction effects in any of the ANOVAs.

not observed in the plateau duration [$F(2,12) = 0.51$, $P = 0.61$, $\eta_p^2 = 0.08$].

ANOVAs on the other measures indicated the main effect of evaluation phase on movement time [$F(2,12) = 6.19$, $P = 0.014$, $\eta_p^2 = 0.51$] but not on MGA [$F(2,12) = 2.33$, $P = 0.13$, $\eta_p^2 = 0.28$] and MGA timing [$F(2,12) = 3.19$, $P = 0.07$, $\eta_p^2 = 0.35$]. Movement time did not show any statistical difference among the sessions [$t(6) = 2.71$, $P = 0.10$; $t(6) = 2.35$, $P = 0.10$; $t(6) = 0.12$, $P = 0.90$]. Although the main effect of target size was statistically significant in MGA [$F(2,12) = 123.15$, $P < 0.001$, $\eta_p^2 = 0.95$] and MGA timing [$F(2,12) = 5.43$, $P = 0.02$, $\eta_p^2 = 0.48$], it was not significant in movement time [$F(2,12) = 1.19$, $P = 0.34$, $\eta_p^2 = 0.16$]. None of the interaction effects was statistically significant in all the ANOVAs in tool-use grasping.

As reference data, kinematic measures in hand-use grasping were analyzed (Fig. 4). ANOVAs did not find any statistically significant main effects of evaluation phase: MGA [$F(2,12) = 0.68$, $P = 0.52$, $\eta_p^2 = 0.10$], MGA timing [$F(2,12) = 0.01$, $P = 0.93$, $\eta_p^2 = 0.01$], movement time [$F(2,12) = 1.27$, $P = 0.31$, $\eta_p^2 = 0.18$], and plateau duration [$F(2,12) = 0.63$, $P = 0.54$, $\eta_p^2 = 0.10$]. Target-pooled plateau duration was 26.0 (SD = 4.2), 23.9 (SD = 4.0), and 24.3% (SD = 3.6) in the first, second, and third sessions, respectively.

Although the main effect of target size was statistically significant in MGA [$F(2,12) = 58.74$, $P < 0.001$, $\eta_p^2 = 0.91$] and movement time [$F(2,12) = 6.51$, $P = 0.01$, $\eta_p^2 = 0.52$], it

was not statistically significant in MGA timing [$F(2,12) = 2.11$, $P = 0.16$, $\eta_p^2 = 0.26$] and plateau duration [$F(2,12) = 1.17$, $P = 0.34$, $\eta_p^2 = 0.16$]. None of the interaction effects were statistically significant in all the ANOVAs in hand-use grasping. Figure 4B also shows that one participant's MGA timing consistently deviated from those of the other participants. This participant's data were not excluded from the analysis because in the present experiment the main focus was not hand-use grasping and the main results did not change if the data were excluded.

Furthermore, correlation analyses were conducted to reveal the relation that includes interindividual factors between movement time and other kinematic measures (Fig. 5). These correlation coefficients are based on data across the participants whereas the main effect of ANOVA was based on within-participant effects. If the shortening plateau duration found in the ANOVA is exclusively induced by shortening movement time, plateau duration and movement time should be correlated over individual differences. As indicated in Fig. 5, A–C, top, however, the correlation coefficient between plateau duration and movement time was small and not significantly correlated: -0.10 [$t(19) = 0.42$, $P = 0.68$] and 0.20 [$t(19) = 0.91$, $P = 0.38$] in hand-use and tool-use grasping, respectively. The correlation coefficients for MGA and MGA timing were -0.22 [$t(19) = 0.99$, $P = 0.33$] and -0.04 [$t(19) = 0.16$, $P = 0.88$] in hand-use grasping, and -0.49 [$t(19) = 2.47$, $P = 0.02$] and 0.42 [$t(19) = 1.99$, $P = 0.06$] in tool-use grasping.

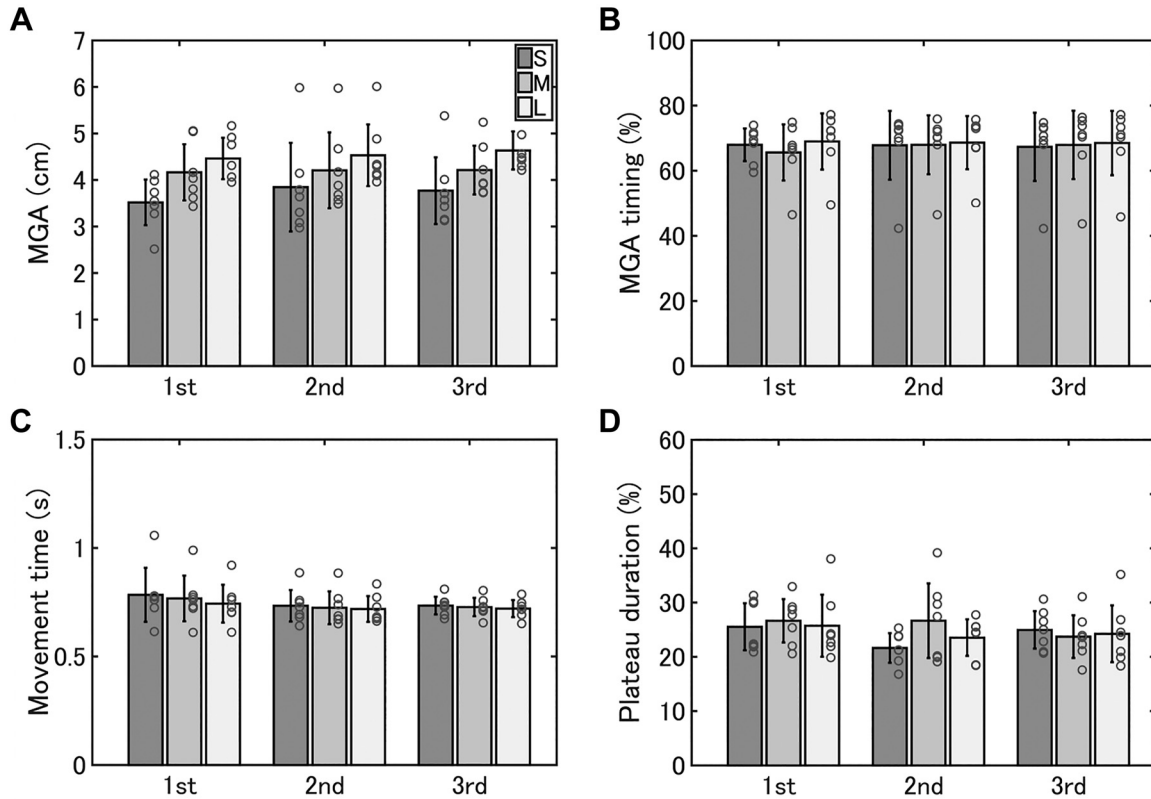


Fig. 4. Kinematic measures in hand-use grasping in *experiment 1*. Note that the participants did not practice hand-use grasping in the experiment; therefore, these data are just the result of repetition of evaluation over time, indicating reliability or replicability of the kinematic measures. A: maximum grip aperture (MGA). B: MGA timing. C: movement time. D: plateau duration. The main effect of evaluation phase was not statistically significant in all the measures.

Experiment 2: speed task. Before the speed-effect analysis, speed manipulation will be confirmed in the experiment. In tool-use grasping, the maximum tangential velocities were 86.7 (SD = 9.1), 101.1 (SD = 11.0), and 112.5 cm/s (SD = 12.9) under the normal, faster, and fastest speed conditions, respectively. In hand-use grasping, the maximum velocities were 93.6 (SD = 10.3), 110.8 (SD = 10.3), and 125.1 cm/s (SD = 13.1) in the same order, respectively. Although the two types of grasping (i.e., tool- and hand-use grasping) showed different overall maximum velocities, this result indicates that the participants controlled the movement speed well according to the instruction.

Experiment 2 was conducted to test whether plateau duration is modulated by movement speed. Figure 6 shows the average kinematic measures in *experiment 2*. In tool-use grasping, plateau duration was 40.3 (SD = 3.9), 37.3 (SD = 5.3), and 33.3% (SD = 5.7) under the normal, faster, and fastest speed conditions, respectively. In hand-use grasping, plateau duration was 19.8 (SD = 5.6), 17.8 (SD = 3.8), and 17.3% (SD = 2.9) in the same order, respectively. An ANOVA on plateau duration found statistically significant main effects of both effector type [$F(1,7) = 54.74, P < 0.001, \eta_p^2 = 0.89$] and movement speed [$F(2,14) = 11.04, P = 0.001, \eta_p^2 = 0.61$] and also a

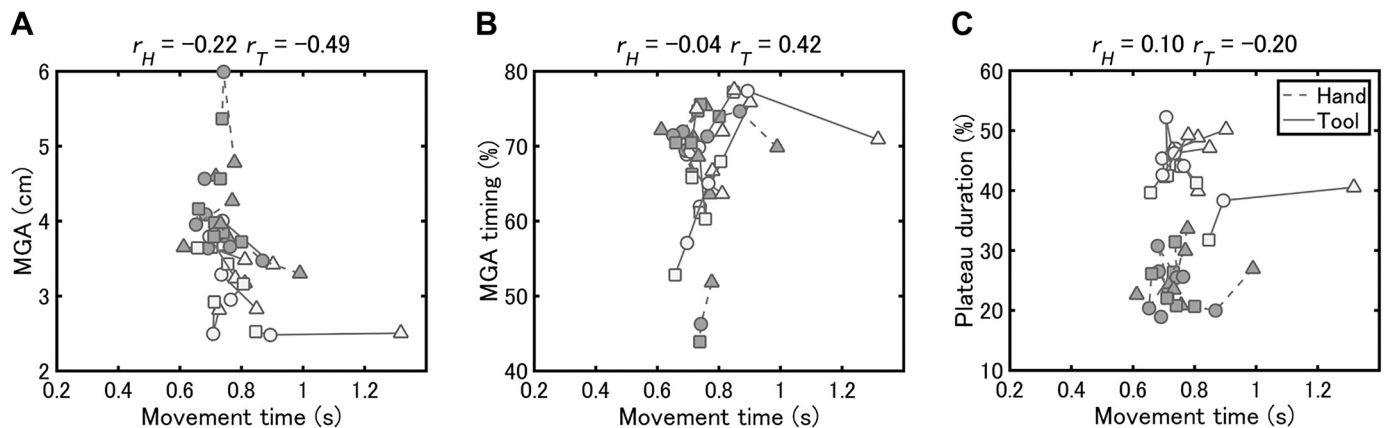


Fig. 5. Relations between movement time and the other 3 kinematic measures in *experiment 1*. The data of object sizes were collapsed. Markers connected by a line indicate data for 1 participant. A: maximum grip aperture (MGA). B: MGA timing. C: plateau duration. Correlation coefficients for each grasping movement are indicated in A–C, top. Triangles, circles, and squares indicate data obtained in the 1st, 2nd, and 3rd sessions, respectively.

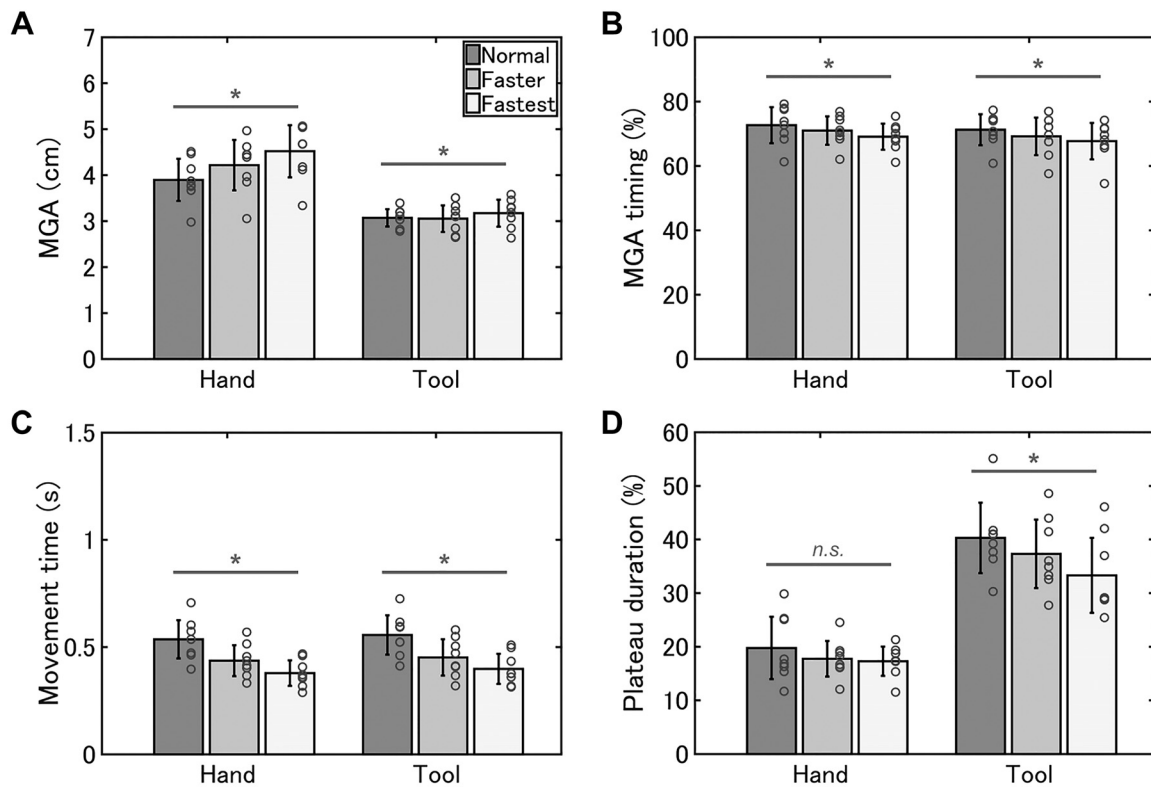


Fig. 6. Kinematic measures in tool- and hand-use grasping in *experiment 2*. The object-size data were collapsed. In plateau duration, although tool-use grasping showed a statistically significant simple main effect of speed, hand-use grasping did not. * $P < 0.05$, statistically significant main effect or a simple main effect of movement speed; n.s., effect was not statistically significant. Neither maximum grip aperture (MGA) timing nor movement time showed any statistically significant interaction effect.

statistically significant interaction effect [$F(2,14) = 11.64$, $P = 0.001$, $\eta_p^2 = 0.62$]. Although tool-use grasping showed a statistically significant simple main speed effect [$F(2,14) = 19.57$, $P < 0.001$, $\eta_p^2 = 0.74$], hand-use grasping did not [$F(2,14) = 2.74$, $P = 0.10$, $\eta_p^2 = 0.28$]. Multiple comparisons for tool-use grasping revealed that the plateau durations were all significantly different; that is, the shortest plateau duration occurred under the fastest speed condition and the longest occurred under the normal speed condition [$t(7) = 6.16$, $P < 0.05$; $t(7) = 4.80$, $P < 0.05$; $t(7) = 2.69$, $P < 0.05$]. These results indicate that plateau duration shortened as movement speed increased in tool-use grasping but not in hand-use grasping.

The results of ANOVAs for the other measures are as follows. In MGA, effector type and speed showed statistically significant main effects: [$F(1,7) = 14.84$, $P < 0.001$, $\eta_p^2 = 0.90$] and [$F(2,14) = 19.06$, $P < 0.001$, $\eta_p^2 = 0.73$], respectively. Although the interaction effect was statistically significant [$F(2,14) = 25.99$, $P < 0.001$, $\eta_p^2 = 0.79$], the simple main effect was statistically significant in both tool-use grasping [$F(2,14) = 4.34$, $P = 0.034$, $\eta_p^2 = 0.38$] and hand-use grasping [$F(2,14) = 25.18$, $P < 0.001$, $\eta_p^2 = 0.90$]. In MGA timing, although the main effect of speed was statistically significant [$F(2,14) = 24.24$, $P < 0.001$, $\eta_p^2 = 0.78$], the main effect of effector type was not [$F(1,7) = 0.62$, $P = 0.45$, $\eta_p^2 = 0.08$], and the interaction effect was not statistically significant [$F(2,14) = 0.15$, $P = 0.86$, $\eta_p^2 = 0.02$]. In movement time, although the main effect of speed was statistically significant

[$F(2,14) = 71.60$, $P < 0.001$, $\eta_p^2 = 0.91$], the main effect of effector type was not [$F(1,7) = 4.07$, $P = 0.08$, $\eta_p^2 = 0.36$], and the interaction effect was not statistically significant [$F(2,14) = 0.18$, $P = 0.83$, $\eta_p^2 = 0.03$].

Furthermore, to examine the relations, including interindividual factors between movement time and the other kinematic measures, the correlation coefficients were calculated (Fig. 7). As shown in *experiment 1*, the correlation coefficients between plateau duration and movement time were small and not statistically significant for both hand-use and tool-use grasping: -0.12 [$t(22) = 0.57$, $P = 0.58$] and 0.07 [$t(22) = 0.31$, $P = 0.76$], respectively. Note that Fig. 7C for plateau duration, although there seems to be a specific pattern connected by lines in tool-use grasping, the lines are caused by a within-participant factor not by an interindividual factor. In contrast to plateau duration, the correlation coefficients for MGA and MGA timing were statistically significant: -0.83 [$t(22) = 7.06$, $P < 0.001$] and 0.66 [$t(22) = 4.11$, $P < 0.001$] in hand-use grasping, and -0.58 [$t(22) = 3.37$, $P = 0.003$] and 0.68 [$t(22) = 4.34$, $P < 0.001$], in tool-use grasping.

Experiment 3: easy task. To assess the effect of required grasping accuracy on plateau duration, two types of tool-use grasping movements were compared: reach-to-grasp movement without lifting an object (i.e., grasp-only movement) and reach-to-grasp movement with lifting an object. Figure 8 shows the kinematic measures in *experiment 3*. The average plateau duration was 43.2 (SD = 4.8) and 49.1% (SD = 4.6) under the grasp-only and lift conditions, respec-

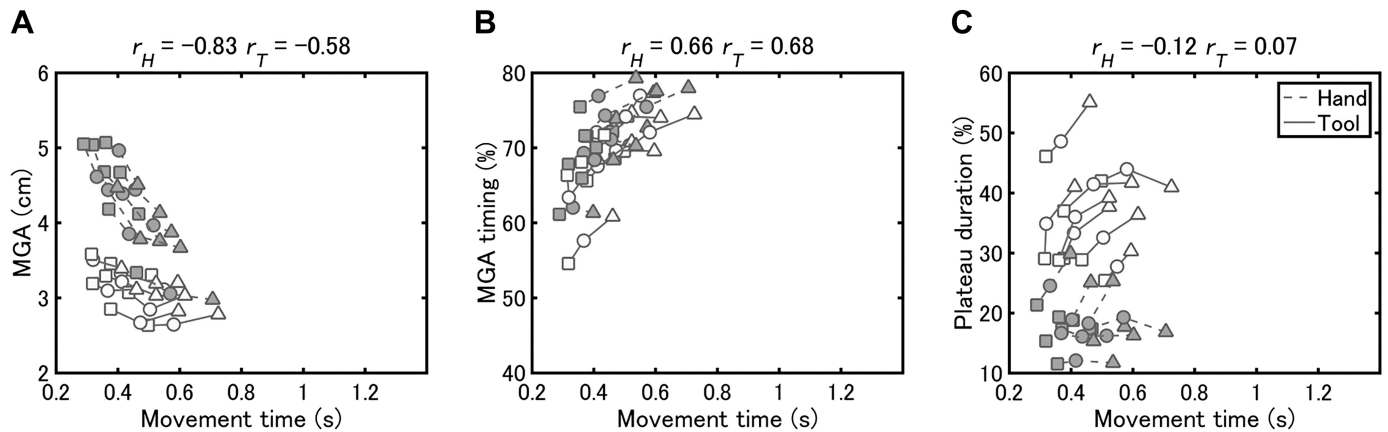


Fig. 7. Relations between movement time and the other 3 kinematic measures in *experiment 2*. The data of object sizes were collapsed. Markers connected by a line indicate the data obtained for 1 participant. *A*: maximum grip aperture (MGA). *B*: MGA timing. *C*: plateau duration. Correlation coefficients for each grasping movement are indicated in *A–C*, top. Triangles, circles, and squares indicate data obtained under the normal, faster, and fastest speed conditions, respectively.

tively, and a paired *t* test found a statistically significant difference between them [$t(7) = 2.40$, $P = 0.048$, $d = 0.85$]. The *t* tests also found significant differences in MGA timing [$t(7) = 4.28$, $P = 0.004$, $d = 1.51$] and movement time [$t(7) = 2.70$, $P = 0.03$, $d = 0.96$] but not in MGA [$t(7) = 0.56$, $P = 0.59$, $d = 0.20$].

Lastly, the relations including interindividual factors between movement time and the other kinematic measures in *experiment 3* were analyzed (Fig. 9). Correlation analysis revealed that plateau duration and movement time were not significantly correlated: 0.27 [$t(6) = 0.68$, $P = 0.52$] and 0.15 [$t(6) = 0.37$, $P = 0.72$] under the grasp-only and lift conditions, respectively. The correlation coefficients for MGA and MGA timing were -0.19 [$t(6) = 0.47$, $P = 0.66$] and 0.01 [$t(6) = 0.00$, $P = 0.99$] under the grasp-only condition and 0.24 [$t(6) = 0.60$, $P = 0.57$] and -0.03 [$t(6) = 0.07$, $P = 0.95$] under the lift condition.

DISCUSSION

The results of *experiment 1* showed that plateau duration, the length of which indicates how “tool use like” grasping movement is, decreased as tool-use practice proceeded. In addition, MGA and MGA timing were not influenced by the practice period. These results support the hypothesis that kinematics of tool-use grasping becomes similar to that of natural hand-use grasping as proficiency of tool use increases, consistent with the idea that a shared principle operates the motor control of reach-to-grasp movement depending on the proficiency of effectors regardless of effector type (Itaguchi and Fukuzawa 2014). The results of *experiments 2* and *3* showed that even without practice, shortened plateau duration similar to that of hand-use grasping was achieved if one prioritized movement speed over grasping accuracy and if there was no worry about dropping the target object. These results suggest that long

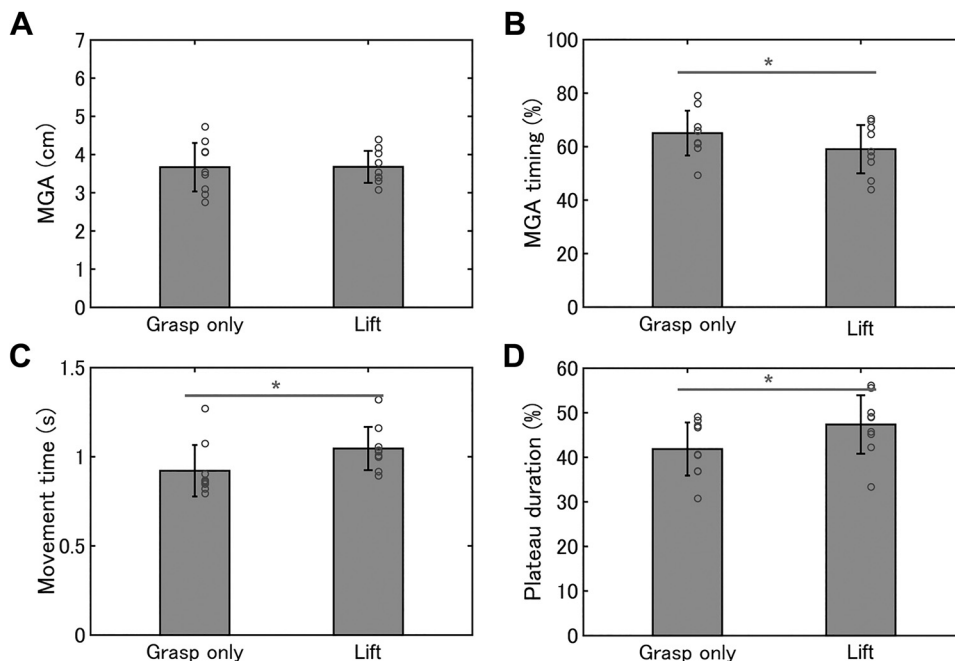


Fig. 8. Effects of type of grasping movement on kinematic measures in tool-use grasping. Only 1 size of object was used. The 4 measures did not show any statistically significant difference between the 2 types of grasping movements. * $P < 0.05$, statistically significant difference between the conditions.

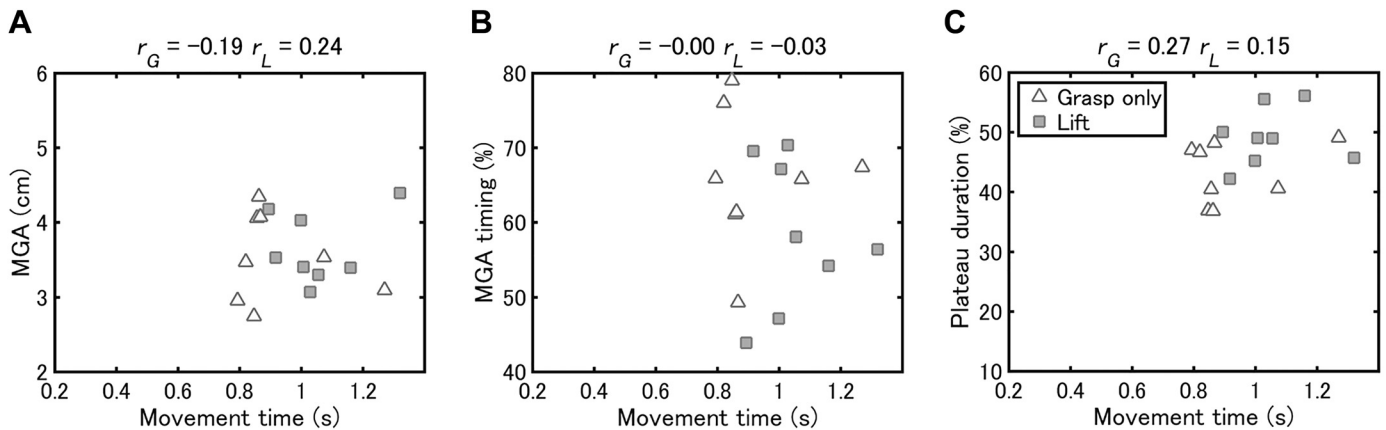


Fig. 9. Relations between movement time and the other 3 kinematic measures in *experiment 3*. *A*: maximum grip aperture (MGA). *B*: MGA timing. *C*: plateau duration. Correlation coefficients for each grasping movement are indicated in *A–C*, top. Triangles and squares indicate the data obtained under the grasp-only and lift conditions, respectively.

plateau duration is not innate in tool-use grasping but could be modulated by proficiency or required accuracy. The characteristic plateau of tool-use grasping may be caused by a strategy that might be employed to compensate for the lack of proficiency of end effectors. At the same time, the relatively small effects on plateau duration observed in all the experiments suggest that it is difficult to realize successful grasping without the characteristic plateau in the aperture, at least unless users experienced long-term practice. Furthermore, quantification of the interindividual relation between movement time and plateau duration implies the aperture plateau is not simply modulated by movement time but by the difference in the proficiency of an effector.

Practice and plateau duration. The present study provided further evidence that improvement in tool use brought about more hand-use-like kinematics in tool-use grasping, consistent with previous studies (Bouwsema et al. 2014; Golenia et al. 2014). This result strengthens the idea that low effector proficiency is involved in low-coordinated movements with longer plateaus. However, it should be noted that the effect size of practice on plateau duration of tool-use grasping was small considering the plateau duration of hand-use grasping. Although, as predicted, the length of plateau duration was shortened by the 2-wk tool-use practice, the difference was only ~5% (i.e., from 46.1% in the 1st session to 40.8% in the 3rd session), which was far from the 26.0% achieved for hand-use grasping. This may be partly because of the relatively short practice period; that is, in the present experiment, the practice period was only 25 min/day for 10 days, although this was considerably longer than those in previous studies, e.g., 2 days in Golenia et al. (2014) and 5 days in Bouwsema et al. (2014). Such training period greatly differs from that for hand-use grasping and even for grasping with chopsticks, which were used in a previous study and reportedly resulted in a more hand-use-like kinematic profile (Itaguchi and Fukuzawa 2014). The important finding in that study is that the plateau duration did not differ between the atypical hand-use and chopstick-use grasping, which is consistent with the current results. One could argue that an initial difficulty in coordinating reach and grasp components in tool-use grasping had brought shortened plateau duration by practice. This possibility is reasonable, but it is important here that plateau duration has shortened, which

was not necessarily expected; there were possibilities for plateau duration to be prolonged or unchanged by practice. Although this effect of tool-use practice was indeed consistent with the hypothesis, it still remains unclear whether extended practice will induce the same changes to further shorten plateau duration.

The shortened movement time and plateau duration by 2-wk practice may reflect improvement of the participants' skill to use the novel tool. Although we cannot escape the speed–accuracy tradeoff in conducting bodily movement (Bootsma et al. 1994; Fitts 1954), motor learning enables us to break the limit of the existing speed–accuracy function and achieve greater performance (Itaguchi and Fukuzawa 2018; Reis et al. 2009; Shmuelof et al. 2012). In addition, it has been shown that in the learning phase, speed and accuracy independently improve (Itaguchi and Fukuzawa 2018). That is, speed and accuracy may not improve together in one type of training, at least in a short practice period. In *experiment 1*, it is reasonable to assume that the participants likely always prioritized grasping the object without dropping it as instructed. Although the results found a statistically significant main effect of movement time, there were no statistical differences between any pairs of sessions. In contrast, plateau duration significantly and consistently reduced as practice proceeded. These results suggest that improvement of the motor control of tool-use grasping was reflected mainly in plateau duration, roughly maintaining the original speed–accuracy tradeoff if “accuracy” is defined as grasping success. Accordingly, it is likely that in reach-to-grasp movements, extra effort and/or strategy is reduced as controlling an end effector improves, resulting in smooth kinematics of the grasping aperture. The success rate and the number of unsuccessful trials were not counted in the present experiment, which is one of the limitations of the present study. Nevertheless, the results of *experiment 1* support that practice substantially increased the proficiency of tool-use grasping and shortened plateau duration.

The present study assumes that skillful control of a tool results in a higher level of temporal coordination between multiple joints involved in the kinematics of the tool-use grasping. It has been shown that greater multijoint coordination is observed in action with a skillful effector (e.g., Sainburg and Kalakanis 2000) and that the deceleration phase of a movement

is prolonged when accuracy demand is high (e.g., Fisk and Goodale 1989; MacKenzie et al. 1987) to improve end point accuracy by using online feedback control. In normal situations without any strategy, end point distribution of the movements was largely affected by the mechanical property of the limb (Itaguchi and Fukuzawa 2012; Lametti et al. 2007; Lametti and Ostry 2010). Increase in muscle cocontraction in the last part of the movement, however, contributes to reduced end point variability when greater target accuracy is required (Gribble et al. 2003), but it can be decreased (Osu et al. 2002; Thoroughman and Shadmehr 1999) and optimized for the task in the external space (Darainy et al. 2004; Domkin et al. 2005) after extensive practice. Based on these previous findings, the prolonged plateau duration typical in the reach-to-grasp movements with a low-proficient effector (i.e., a novel tool) or with higher accuracy demand can be interpreted as a strategy to improve the stability of the action; stiffening and fixing a joint(s) would cause decoupling of temporal coordination and slowing but stabilize the action.

Speed, accuracy, and plateau duration. In *experiments 2* and *3*, on the other hand, varying movement speed and grasping difficulty showed that improvement of proficiency was not necessarily required to just shorten aperture plateau in tool-use grasping. In *experiment 2*, time pressure of the movement significantly shortened plateau duration without any practice. This result disagrees with the idea that we “cannot” execute well-coordinated reach-to-grasp movements, which have shorter plateau duration, with an unfamiliar tool. It rather supports the idea that we do not execute coordinated movements with an unfamiliar tool, consciously or unconsciously, to prioritize grasping accuracy, owing to lack of proficiency with the tool. One of the possible reasons for these strategies might be careful attention under novel motor control conditions. In accordance with the result of *experiment 2*, *experiment 3* found that decreasing the required grasping accuracy shortened plateau duration. These findings together indicate that manipulation of required grasping accuracy can alter the method of grasping, thereby suggesting that plateau duration in unskillful tool-use grasping is due to a strategy to achieve successful grasping. However, this idea was not directly justified by the present experiment, and it is possible that aperture plateau is merely related to movement time.

Nevertheless, the correlation analyses including interindividual factors may refute the possibility that shortened plateau duration was caused simply by shortened movement time. In the three experiments, the correlation coefficients between movement time and plateau duration were calculated, and none of them showed any reliable correlation. Whereas the ANOVA used in the current study investigated internal changes induced by a specific factor and within-participant noise from motor planning and execution, the correlation analyses on data including both within-participant and interindividual factors provide integrative information on the relation between variables; that is, more fundamental and innate characteristics that may govern the grasping motion. If shortening plateau duration is exclusively induced by shortening movement time, they should be correlated over individual differences. However, they were not correlated at all in any of the experiments. On the contrary, MGA and MGA timing in *experiment 2* were consistently correlated with movement time regardless of the type of effector, suggesting that they are strongly influenced by move-

ment time, whereas plateau duration is not. Note that this modulation of MGA and MGA timing by movement speed was observed both in the ANOVAs and correlation analyses. Although the correlation between MGA and movement time was for tool-use grasping in the current study, this finding is consistent with those of previous studies investigating hand-use grasping (Bootsma et al. 1994; Grosskopf and Kuhtz-Buschbeck 2006; Mason and Carnahan 1999; Wing et al. 1986), suggesting that those relations are innate. Furthermore, this study is the first reporting the relation between plateau duration and movement time. In addition to the correlation analysis, the results of *experiment 1* support that plateau duration is not affected only by movement time. Although there was no statistically significant change in movement time between *sessions 2* and *3*, plateau duration was shortened between the sessions. Taken together with the overall results, it is reasonable to consider that longer plateau duration is primarily relevant to the strategy to increase grasping accuracy, which varies according to task requirement or proficiency of the effector rather than according to time period, wherein movement is executed, even though speed-accuracy tradeoff is inevitable.

The cause of longer plateau duration in tool-use grasping would be complex. It is natural to assume, for the primary factor, that participants open and close the tool fingers quickly to securely grasp the object. First, quick opening offers participants sufficient time to wait before closing the tool fingers; therefore, it is easy to grasp the object because participants are required only to close the tool fingers at the appropriate time. Second, the quick closing at late timing renders the pincer movement straighter and more perpendicular to the object. It is also beneficial that the reaching movement becomes slow close to the target. Although studies so far cannot determine whether this strategy is employed consciously or unconsciously, it might require extra muscle effort. In addition to this strategy, changes in perception are possibly involved in the characteristic kinematics. Smeets and colleagues (Smeets and Brenner 2008; Smeets et al. 2002) proposed that grasping action is controlled by object position (location). If perception of peripersonal space or body length is changed by tool use (e.g., Cardinali et al. 2009; Farnè and Ladavas 2000), position perception of the tool fingers and/or target object location are/is also subject to the illusion. This might be one of the causes of the disturbed coordination between reaching and grasping movements and might explain why reduced plateau duration accompanied tool-use practice.

In *experiment 3*, movement time and MGA timing were modulated by the experimental condition as well as plateau duration. When assuming speed-accuracy tradeoff, the shortened movement time in the grasp-only condition, which requires less accuracy, is reasonable. The earlier MGA timing in the grasp-only condition compared with the lift condition was, however, opposite to the effect observed in *experiment 2*, where MGA was observed at earlier timing in faster conditions. In *experiment 2*, earlier MGA timing in relative time is explained by assuming that the time for closing fingers is fixed to achieve successful grasping. In *experiment 3*, if the finger closing movement speeds up due to less required grasping accuracy, MGA timing in relative time would be delayed. Further studies are needed to test these possibilities for under-

standing of the relation among characteristic components of grasping kinematics.

Tool-use practice and motor embodiment. The present results agree with the idea that one shared principle operates motor control of reach-to-grasp movement depending on the proficiency of effectors. Active tool use has been known to induce phenomena relevant to the idea called “embodiment of tool” not only in motor terms (Umiltà et al. 2008) but also in perceptual ones (Iriki et al. 1996; Maravita et al. 2002a; Maravita and Iriki 2004). From a computational view, perceptual embodiment can be regarded as a state wherein a forward model of an action has been generalized to an external object (i.e., a tool), and motor embodiment, the state in which a tool is processed in the same way as a part of one’s body for motor tasks (de Vignemont 2011), can be regarded as a state wherein an effector-dependent inverse model of the action has been acquired (Grafton 2010; Itaguchi and Fukuzawa 2014). These two models are suggested to be stored in different brain areas, each of which is separate from the areas responsible for functional knowledge of tools (Fogassi and Luppino 2005; Goldenberg and Spatt 2009; Imamizu and Kawato 2008; Imamizu et al. 2000; Ramayya et al. 2010; Yoo et al. 2013). Acquisition of an inverse model usually takes longer than that of a forward model (Flanagan and Johansson 2003; Gentili et al. 2010), which is consistent with the small effect of tool-use practice observed in the present study. The hypothesis of the present study is consistent with the computational theory that a single constraint is shared between simple reaching and reach-to-grasp movements (Verheij et al. 2012).

It is, however, still debatable that the hand-use and tool-use grasping share a common motor control principle, because the current study does not offer direct evidence for the idea. It would be advantageous to define the level of the shared principle. This study presumes that the kinematics of the tips of an effector were the focus of the motor control in the brain, which is a rather common idea in the literature (Hoff and Arbib 1993; Smeets and Brenner 1999; Verheij et al. 2012) and supported by several consistent characteristics of aperture profiles in grasping movement under various conditions (e.g., Jakobson and Goodale 1991; Jeannerod 1984; Wing et al. 1986). Although there are not as many studies of tool-use grasping as of natural grasping, characteristic features of aperture profiles such as MGA scaled by target size and relative timing of MGA have been observed even for tools without practice (Bootsma et al. 1994; Gentilucci et al. 2004). Practice induced shortened plateau duration (Golenia et al. 2014), the length of which is the largest difference in the kinematics between the two types of grasping. The time course of aperture changes including plateau duration of hand grasping with thumb and middle finger did not differ from that of proficient tool-use grasping (Itaguchi and Fukuzawa 2014). To clarify the possibility that the two types of grasping share a control principle at the level of aperture kinematics, more convincing evidence is required by studying the use of tools with various mechanics and proficiency.

The small effects of practice and experimental conditions observed in the current study indicate that it may be difficult to achieve “natural” grasping movement with a novel tool without long-term practice. However, the present results suggest that reduction of the required accuracy of multijoint movements would contribute to achievement of more coordinated move-

ment. In daily practice (such as playing musical instruments and sports) and in clinical rehabilitation, improvement in multijoint coordination is of particular interest. Stroke patients suffering sensorimotor deficits are also in need of improving motor coordination. With the aim of application toward such people, further studies are expected to reveal the efficacy of tool-use learning requiring less grasping accuracy to develop more efficient technique.

Conclusion. This study addressed plateau duration of tool-use grasping by three different experimental tasks. Consistent with the findings of previous studies (Bouwsema et al. 2014; Golenia et al. 2014), the results of *experiment 1* confirmed that the practice of tool-use grasping reduced the length of plateau duration, the effect size of which remained small compared with the effect size of natural grasping. *Experiments 2* and *3* showed that reduced required accuracy induced shorter plateau duration without practice. Further analyses revealed that shortened plateau duration was not due to shortened movement time but was induced by practice, which has not been examined in previous studies. These results also suggested that characteristic kinematics in tool-use grasping are caused by a strategy that could be unconsciously employed for successful grasping movement. One of the limitations of this study is the small number of participants. However, if the number of participants was increased, the main results would remain the same because the results were stable (the effect size was considerable: $\eta_p^2 = 0.57$). Another limitation is that in *experiment 3*, both the type of action (lift versus grasp-only) and the object (cylindrical object versus sponge object) were modified, which could be a confounding factor when considering the differences between the two conditions (normal versus easy). The present study focused on the motor aspects of tool-use grasping and did not investigate the perceptual and neural changes accompanied by long-term tool-use practice (e.g., Rochat et al. 2010; Yoo et al. 2013). As Martel et al. (2016) argue, the tool-use paradigm provides us with many insights into body representation. Accordingly, future studies must systematically clarify the relation among tool-use-induced motor, perceptual, and neural changes, thereby establishing a theory that explains not only embodiment of tool but also brain-damage-induced “disembodiment” and distinction of self from other.

GRANTS

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Y.I. conceived and designed research; Y.I. performed experiments; Y.I. analyzed data; Y.I. interpreted results of experiments; Y.I. prepared figures; Y.I. drafted manuscript; Y.I. edited and revised manuscript; Y.I. approved final version of manuscript.

REFERENCES

Alberts JL, Saling M, Adler CH, Stelmach GE. Disruptions in the reach-to-grasp actions of Parkinson’s patients. *Exp Brain Res* 134: 353–362, 2000. doi:10.1007/s002210000468.

- Berti A, Frassinetti F.** When far becomes near: remapping of space by tool use. *J Cogn Neurosci* 12: 415–420, 2000. doi:10.1162/089892900562237.
- Bongers RM.** Do changes in movements after tool use depend on body schema or motor learning? In: *International Conference on Human Haptic Sensing and Touch Enabled Computer Applications*. New York: Springer, 2010, p. 271–276.
- Bongers RM, Zaai FT, Jeannerod M.** Hand aperture patterns in prehension. *Hum Mov Sci* 31: 487–501, 2012. doi:10.1016/j.humov.2011.07.014.
- Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaai FT.** The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. *Exp Brain Res* 98: 535–541, 1994. doi:10.1007/BF00233990.
- Bouwsema H, van der Sluis CK, Bongers RM.** Movement characteristics of upper extremity prostheses during basic goal-directed tasks. *Clin Biomech (Bristol, Avon)* 25: 523–529, 2010. doi:10.1016/j.clinbiomech.2010.02.011.
- Bouwsema H, van der Sluis CK, Bongers RM.** Changes in performance over time while learning to use a myoelectric prosthesis. *J Neuroeng Rehabil* 11: 16, 2014. doi:10.1186/1743-0003-11-16.
- Brozzoli C, Cardinali L, Pavani F, Farnè A.** Action-specific remapping of peripersonal space. *Neuropsychologia* 48: 796–802, 2010. doi:10.1016/j.neuropsychologia.2009.10.009.
- Brozzoli C, Pavani F, Urquizar C, Cardinali L, Farnè A.** Grasping actions remap peripersonal space. *Neuroreport* 20: 913–917, 2009. doi:10.1097/WNR.0b013e32832c0b9b.
- Cardinali L, Brozzoli C, Finos L, Roy AC, Farnè A.** The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition* 149: 1–5, 2016. doi:10.1016/j.cognition.2016.01.001.
- Cardinali L, Frassinetti F, Brozzoli C, Urquizar C, Roy AC, Farnè A.** Tool-use induces morphological updating of the body schema. *Curr Biol* 19: R478–R479, 2009. doi:10.1016/j.cub.2009.05.009.
- Darainy M, Malfait N, Gribble PL, Towhidkhan F, Ostry DJ.** Learning to control arm stiffness under static conditions. *J Neurophysiol* 92: 3344–3350, 2004. doi:10.1152/jn.00596.2004.
- de Vignemont F.** Embodiment, ownership and disownership. *Conscious Cogn* 20: 82–93, 2011. doi:10.1016/j.concog.2010.09.004.
- de Vignemont F, Farnè A.** Widening the body to rubber hands and tools: what's the difference? *Rev Neuropsychol* 2: 203–211, 2010. doi:10.3917/me.023.0203.
- Domkin D, Laczko J, Djupsjöbacka M, Jaric S, Latash ML.** Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Exp Brain Res* 163: 44–57, 2005. doi:10.1007/s00221-004-2137-1.
- Farnè A, Làdavas E.** Dynamic size-change of hand peripersonal space following tool use. *Neuroreport* 11: 1645–1649, 2000. doi:10.1097/00001756-200006050-00010.
- Fisk JD, Goodale MA.** The effects of instructions to subjects on the programming of visually directed reaching movements. *J Mot Behav* 21: 5–19, 1989. doi:10.1080/00222895.1989.10735461.
- Fitts PM.** The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47: 381–391, 1954. doi:10.1037/h0055392.
- Flanagan JR, Johansson RS.** Action plans used in action observation. *Nature* 424: 769–771, 2003. doi:10.1038/nature01861.
- Fogassi L, Luppino G.** Motor functions of the parietal lobe. *Curr Opin Neurobiol* 15: 626–631, 2005. doi:10.1016/j.conb.2005.10.015.
- Gentili R, Han CE, Schweighofer N, Papaxanthis C.** Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *J Neurophysiol* 104: 774–783, 2010. doi:10.1152/jn.00257.2010.
- Gentilucci M, Roy AC, Stefanini S.** Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? *Exp Brain Res* 157: 496–506, 2004. doi:10.1007/s00221-004-1863-8.
- Goldenberg G, Spatt J.** The neural basis of tool use. *Brain* 132: 1645–1655, 2009. doi:10.1093/brain/awp080.
- Golenia L, Schoemaker MM, Mouton LJ, Bongers RM.** Individual differences in learning a novel discrete motor task. *PLoS One* 9: e112806, 2014. doi:10.1371/journal.pone.0112806.
- Grafton ST.** The cognitive neuroscience of prehension: recent developments. *Exp Brain Res* 204: 475–491, 2010. doi:10.1007/s00221-010-2315-2.
- Gribble PL, Mullin LI, Cothros N, Mattar A.** Role of cocontraction in arm movement accuracy. *J Neurophysiol* 89: 2396–2405, 2003. doi:10.1152/jn.01020.2002.
- Grosskopf A, Kultz-Buschbeck JP.** Grasping with the left and right hand: a kinematic study. *Exp Brain Res* 168: 230–240, 2006. doi:10.1007/s00221-005-0083-1.
- Hoff B, Arbib MA.** Models of trajectory formation and temporal interaction of reach and grasp. *J Mot Behav* 25: 175–192, 1993. doi:10.1080/00222895.1993.9942048.
- Imamizu H, Kawato M.** Neural correlates of predictive and postdictive switching mechanisms for internal models. *J Neurosci* 28: 10751–10765, 2008. doi:10.1523/JNEUROSCI.1106-08.2008.
- Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Pütz B, Yoshioka T, Kawato M.** Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* 403: 192–195, 2000. doi:10.1038/35003194.
- Iriki A, Tanaka M, Iwamura Y.** Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport* 7: 2325–2330, 1996. doi:10.1097/00001756-199610020-00010.
- Ishibashi H, Hihara S, Iriki A.** Acquisition and development of monkey tool-use: behavioral and kinematic analyses. *Can J Physiol Pharmacol* 78: 958–966, 2000. doi:10.1139/y00-063.
- Itaguchi Y, Fukuzawa K.** The influence of the indicator arm on end point distribution in proprioceptive localization with multi-joint arms. *Exp Brain Res* 222: 77–88, 2012. doi:10.1007/s00221-012-3196-3.
- Itaguchi Y, Fukuzawa K.** Hand-use and tool-use in grasping control. *Exp Brain Res* 232: 3613–3622, 2014. doi:10.1007/s00221-014-4053-3.
- Itaguchi Y, Fukuzawa K.** Influence of speed and accuracy constraints on motor learning for a trajectory-based movement. *J Mot Behav* 50: 653–663, 2018. doi:10.1080/00222895.2017.1400946.
- Jakobson LS, Goodale MA.** Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res* 86: 199–208, 1991. doi:10.1007/BF00231054.
- Jeannerod M.** The timing of natural prehension movements. *J Mot Behav* 16: 235–254, 1984. doi:10.1080/00222895.1984.10735319.
- Kao KL, Goodale MA.** Enhanced detection of visual targets on the hand and familiar tools. *Neuropsychologia* 47: 2454–2463, 2009. doi:10.1016/j.neuropsychologia.2009.04.016.
- Lametti DR, Houle G, Ostry DJ.** Control of movement variability and the regulation of limb impedance. *J Neurophysiol* 98: 3516–3524, 2007. doi:10.1152/jn.00970.2007.
- Lametti DR, Ostry DJ.** Postural constraints on movement variability. *J Neurophysiol* 104: 1061–1067, 2010. doi:10.1152/jn.00306.2010.
- MacKenzie CL, Marteniuk R, Dugas C, Liske D, Eickmeier B.** Three-dimensional movement trajectories in Fitts' task: implications for control. *Q J Exp Psychol* 39: 629–647, 1987. doi:10.1080/14640748708401806.
- Maravita A, Clarke K, Husain M, Driver J.** Active tool use with the contralesional hand can reduce cross-modal extinction of touch on that hand. *Neurocase* 8: 411–416, 2002a. doi:10.1076/neur.8.5.411.16177.
- Maravita A, Iriki A.** Tools for the body (schema). *Trends Cogn Sci* 8: 79–86, 2004. doi:10.1016/j.tics.2003.12.008.
- Maravita A, Spence C, Kennett S, Driver J.** Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83: B25–B34, 2002b. doi:10.1016/S0010-0277(02)00003-3.
- Martel M, Cardinali L, Roy AC, Farnè A.** Tool-use: an open window into body representation and its plasticity. *Cogn Neuropsychol* 33: 82–101, 2016. doi:10.1080/02643294.2016.1167678.
- Marteniuk RG, Leavitt JL, MacKenzie CL, Athenes S.** Functional relationships between grasp and transport components in a prehension task. *Hum Mov Sci* 9: 149–176, 1990. doi:10.1016/0167-9457(90)90025-9.
- Mason AH, Carnahan H.** Target viewing time and velocity effects on prehension. *Exp Brain Res* 127: 83–94, 1999. doi:10.1007/s002210050776.
- Napier JR.** The prehensile movements of the human hand. *J Bone Joint Surg Br* 38-B: 902–913, 1956. doi:10.1302/0301-620X.38B4.902.
- Osu R, Franklin DW, Kato H, Gomi H, Domen K, Yoshioka T, Kawato M.** Short- and long-term changes in joint co-contraction associated with motor learning as revealed from surface EMG. *J Neurophysiol* 88: 991–1004, 2002. doi:10.1152/jn.2002.88.2.991.
- Povinelli DJ, Reaux JE, Frey SH.** Chimpanzees' context-dependent tool use provides evidence for separable representations of hand and tool even during active use within peripersonal space. *Neuropsychologia* 48: 243–247, 2010. doi:10.1016/j.neuropsychologia.2009.09.010.
- Ramaya AG, Glasser MF, Rilling JK.** A DTI investigation of neural substrates supporting tool use. *Cereb Cortex* 20: 507–516, 2010. doi:10.1093/cercor/bhp141.
- Reis J, Schambra HM, Cohen LG, Buch ER, Fritsch B, Zarahn E, Celnik PA, Krakauer JW.** Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proc Natl Acad Sci USA* 106: 1590–1595, 2009. doi:10.1073/pnas.0805413106.
- Rochat MJ, Caruana F, Jezzini A, Escola L, Intskirveli I, Grammont F, Gallese V, Rizzolatti G, Umiltà MA.** Responses of mirror neurons in area

- F5 to hand and tool grasping observation. *Exp Brain Res* 204: 605–616, 2010. doi:[10.1007/s00221-010-2329-9](https://doi.org/10.1007/s00221-010-2329-9).
- Sainburg RL, Kalakanis D.** Differences in control of limb dynamics during dominant and nondominant arm reaching. *J Neurophysiol* 83: 2661–2675, 2000. doi:[10.1152/jn.2000.83.5.2661](https://doi.org/10.1152/jn.2000.83.5.2661).
- Shmuelof L, Krakauer JW, Mazzoni P.** How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *J Neurophysiol* 108: 578–594, 2012. doi:[10.1152/jn.00856.2011](https://doi.org/10.1152/jn.00856.2011).
- Smeets JB, Brenner E.** A new view on grasping. *Mot Contr* 3: 237–271, 1999. doi:[10.1123/mcj.3.3.237](https://doi.org/10.1123/mcj.3.3.237).
- Smeets JB, Brenner E.** Grasping Weber's law. *Curr Biol* 18: R1089–R1090, 2008. doi:[10.1016/j.cub.2008.10.008](https://doi.org/10.1016/j.cub.2008.10.008).
- Smeets JB, Brenner E, Biegstraaten M.** Independent control of the digits predicts an apparent hierarchy of visuomotor channels in grasping. *Behav Brain Res* 136: 427–432, 2002. doi:[10.1016/S0166-4328\(02\)00189-4](https://doi.org/10.1016/S0166-4328(02)00189-4).
- Thoroughman KA, Shadmehr R.** Electromyographic correlates of learning an internal model of reaching movements. *J Neurosci* 19: 8573–8588, 1999. doi:[10.1523/JNEUROSCI.19-19-08573.1999](https://doi.org/10.1523/JNEUROSCI.19-19-08573.1999).
- Tresilian JR, Stelmach GE.** Common organization for unimanual and bimanual reach-to-grasp tasks. *Exp Brain Res* 115: 283–299, 1997. doi:[10.1007/PL00005697](https://doi.org/10.1007/PL00005697).
- Umiltà MA, Escola L, Intskirveli I, Grammont F, Rochat M, Caruana F, Jezzini A, Gallese V, Rizzolatti G.** When pliers become fingers in the monkey motor system. *Proc Natl Acad Sci USA* 105: 2209–2213, 2008. doi:[10.1073/pnas.0705985105](https://doi.org/10.1073/pnas.0705985105).
- Verheij R, Brenner E, Smeets JB.** Grasping kinematics from the perspective of the individual digits: a modelling study. *PLoS One* 7: e33150, 2012. doi:[10.1371/journal.pone.0033150](https://doi.org/10.1371/journal.pone.0033150).
- Wing AM, Fraser C.** The contribution of the thumb to reaching movements. *Q J Exp Psychol A* 35: 297–309, 1983. doi:[10.1080/14640748308402135](https://doi.org/10.1080/14640748308402135).
- Wing AM, Turton A, Fraser C.** Grasp size and accuracy of approach in reaching. *J Mot Behav* 18: 245–260, 1986. doi:[10.1080/00222895.1986.10735380](https://doi.org/10.1080/00222895.1986.10735380).
- Yoo K, Sohn WS, Jeong Y.** Tool-use practice induces changes in intrinsic functional connectivity of parietal areas. *Front Hum Neurosci* 7: 49, 2013. doi:[10.3389/fnhum.2013.00049](https://doi.org/10.3389/fnhum.2013.00049).

