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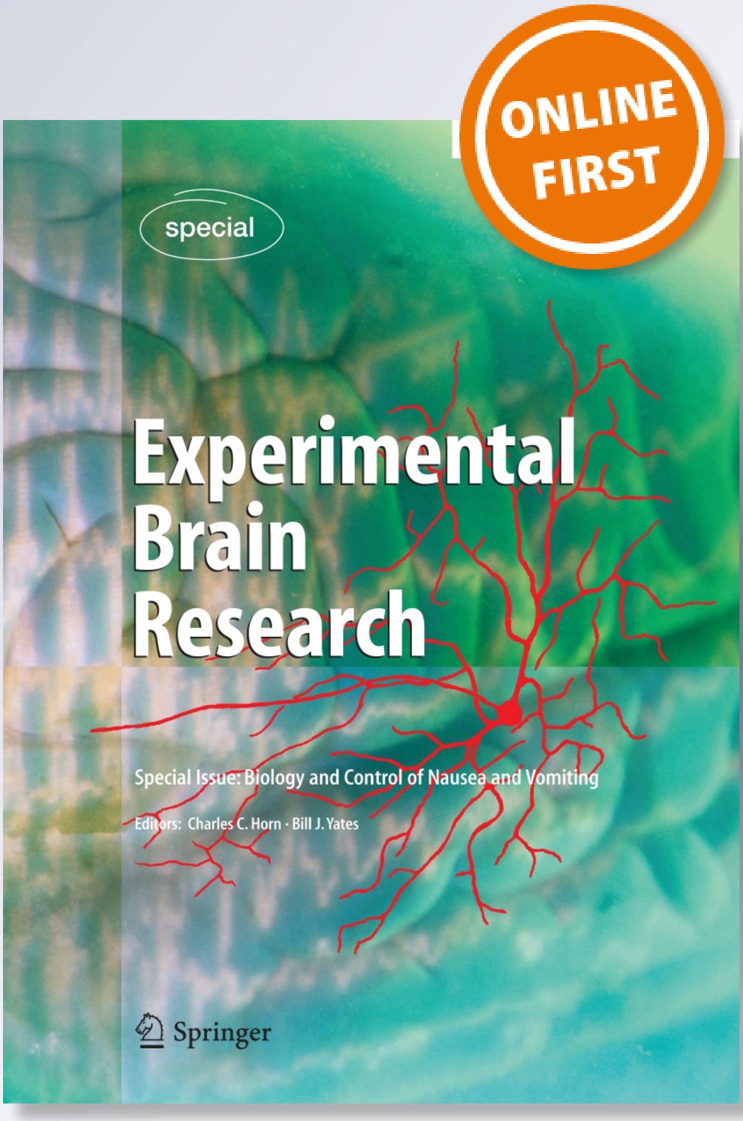

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RESEARCH ARTICLE

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Abstract The goal of this study was to elucidate the underlying mechanisms of hand and tool grasping control. We assumed that there is a single principle-governing grasping control irrespective of its effectors and that the degree of prior experience of the effector determines the smoothness of aperture control. Eight participants performed a reach-to-grasp task with four different effectors: index finger and thumb, middle finger and thumb, chopsticks, and a scissor-like tool. Although we employed different effectors with large mechanical variations and different degrees of prior use, maximum grip aperture was scaled as a function of object size and appeared at almost the same timing in all four types of grasping movements. Moreover, reaching time did not substantially differ among grasping conditions. However, plateau duration of the aperture profile differed by effector. Plateau duration was the longest in the unfamiliar scissor-like tool grasping condition. There was no difference between the unfamiliar hand-use grasp with the thumb and the middle finger and the familiar tool-grasp with chopsticks. The familiar hand-use grasp with the thumb and the index finger had the shortest plateau duration. These results supported the idea that there is an effector-independent continuity between hand-use and tool-use in motor control as a function of prior degree of use, rather than the conventionally assumed dichotomy between them.

Keywords Tool-use · Aperture · Embodiment · Motor control · Grasping

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Introduction

It is not surprising that we use our hands skillfully, but perhaps somewhat surprising that we manipulate various tools as dexterously as if they were parts of our own body. This "embodiment" of tools has been extensively investigated (see Maravita and Iriki 2004; de Vignemont and Farnè 2010); tool-use can update not only our peripersonal space but also our body representation (body schema) itself (Berti and Frassinetti 2000; Brozzoli et al. 2009, 2010; Cardinali et al. 2009; Farnè and Làdavas 2000; Kao and Goodale 2009; Maravita et al. 2002a, b). Although these findings show the remarkable plasticity of our body representation, the functional characteristics of tools embodied in the body are still unknown. Based on our assumption of continuity between hand-use and tool-use of motor control, our hand is just one of our most familiar tools. Therefore, the degree of prior experience should be the important difference between our body parts and external tools in terms of the neural representation of motor control. To test this idea, the present study investigated the temporal aspects of grasping motor control in hand-use and tool-use grasping with both familiar and unfamiliar effectors.

One body of research suggests different representations subserving motor control for tool-use grasping and natural hand-use grasping. Gentilucci et al. (2004) suggested that the two types of grasping were achieved in similar ways but with different means. In their experiment, grasp aperture in tool-use grasping developed differently from hand-use grasping, particularly in the aperture-opening phase; the aperture in tool-use grasping had a long plateau before it reached maximum grip aperture (MGA). Other studies have also reported differences in the temporal aspects of aperture control (Bongers 2010; Bouwsema et al. 2010; Wing and Fraser 1983).

Some neuropsychological symptoms also seem to support the existence of different representations for tool-use. For example, patients with ideomotor apraxia show a selective disorder in tool-use; they often fail to use tools, or if they can, they use them inappropriately. Previous studies have explained these symptoms in terms of disorder of the gesture engram (motor program) for tool-use (see Osiurak et al. 2011). Although these findings do not necessarily lead to the idea of effector-dependent representations for grasping control, they do suggest that tool-use and hand-use grasping could be achieved independently.

Conversely, other motor control theories do not attribute the contrast in grasping aperture between hand and tool to a difference in the control principal, but rather to a difference in the parameters of the controlled effector (e.g., proficiency). For example, Arbib and his collogues (Arbib et al. 1985; Hoff and Arbib 1993) assumed a common computational principle underlying tool control and biological hand control. Similar to this model, the constraints and calculation methods of other computational motor theories have been applied not only to hand-use, but also to tool-use (e.g., Flash and Hogan 1985; Uno et al. 1989; Harris and Wolpert 1998). Although their predictions of grasping control vary, these models predict tool grasping behavior based on the same principle as natural grasping (Jeannerod 1988; Rosenbaum et al. 2001; Smeets and Brenner 1999; Wing and Fraser 1983).

Based on this idea that the same principle governs grasping motor control irrespective of the effector, we assumed that there is continuity in grasping motor control between hand-use and tool-use and that proficiency with an effector is more important than effector type (hand vs. tool). Our hypothesis was that the degree of smoothness in motor control depends on proficiency with a particular effector. This hypothesis is in line with recent studies of how tool-use modifies perceived peripersonal space or personal space in neurotypical individuals (Cardinali et al. 2009; Maravita et al. 2002b; Witt et al. 2005), in patients (Berti and Frassinetti 2000; Farnè and Làdavas 2000; Maravita et al. 2002a), and where the same neuron fires to both hand and tool in observation (Iriki et al. 1996), and in execution (Umiltà et al. 2008). These studies also provide evidence for the compatibility of the representation between hand and tool within our brain system, supporting the idea of their continuity.

In natural grasping, hand aperture does not open quickly but gradually. Maximum hand aperture, conventionally called maximum grip aperture (MGA), usually appears about 75 % of the way through the movement and is scaled to object size (e.g., Jeannerod 1984; Meulenbroek et al. 2001; Smeets and Brenner 1999; Tresilian et al. 1997). When a tool was used to grasp an object, the aperture opened quickly, peaked in the early phase of movement, maintained almost the same size of the aperture (plateau), and finally closed to adjust to the target object (Bongers 2010; Gentilucci et al. 2004). This plateau was also observed in grasping with prosthesis (Bouwsema et al. 2010; Wing and Fraser 1983).

If there is continuity between hand-use and tool-use and if the degree of prior experience using an effector is a critical variable in grasping motor control, the characteristics of tool-use grasp should gradually vary with the degree of prior experience, but not with whether the effector is a hand or a tool. The present study employed two hand-use grasps and two types of tools-use grasps with different degrees of prior experience. We predicted that the most frequently used grasp, a typical thumb and index finger grasp, would show the finest aperture profiles followed by an atypical hand-use grasp, a typical tool-use grasp, and an atypical tool-use grasp in that order. Further, the fundamental nature of grasping control should be constant irrespective of the effectors. To test whether smoothness of aperture control varied with the types of grasping based on different degrees of prior experience, we focused on the plateau duration as one clear index of grasping control profile.

Methods

Participants

Eight right-handed student participants (24.0 ± 1.7 years old) with no visuomotor problems performed a reach-to-grasp task.

Experimental setup

The participants reached for and grasped an object on a table in front of them and transported it to a target location at a comfortable speed. The starting point and the object were placed 20 and 50 cm, respectively, away from the participants and 10 cm right of the participants' midline. The target was located 10 cm to the right of the target object as shown in Fig. 1a. The target objects were wooden cylinders 2 cm in height with three different diameters: 1.5, 2, and 2.4. The object sizes were chosen because participants would not drop them during the tool-use grasping task. In addition, target objects were wrapped with a rubber band to prevent them from falling from the tips of the fingers or tools.

Procedure

After a verbal "Go" cue from the experimenter, the participants started reaching at own timing with their fingers

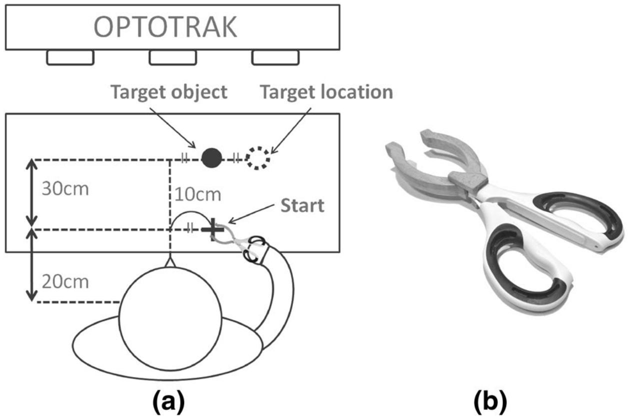

Fig. 1 **a** Experimental setting and **b** the atypical tool. Participants performed a reach-to-grasp task in the setting using four different types of effectors with their eyes open. The present study defined this scissor-like tool as an atypical tool to grasp an object

or tips of the tool closed. They performed the reach-to-grasp task under four conditions: typical hand (TH), atypical hand (AH), typical tool (TT), and atypical tool (AT) conditions. These conditions correspond to the participants grasping the object with their index finger and thumb, their middle finger and thumb, chopsticks, and a scissor-like tool, respectively. These conditions were assumed to differ by how frequently they were used for ordinary grasping. The present study used chopsticks as a typical tool for grasping because Japanese participants were accustomed to using them. In contrast, the scissor-like tool was not a common tool. None of the participants had any experience using this tool, which was designed with special mechanical characteristics for this experiment.

The participants carried out a total of 240 trials (20 trials × 4 conditions × 3 object sizes). The presentation order of conditions and object sizes were counterbalanced among participants.

Tool mechanics

The scissor-like tool was reconstructed from a normal scissors but with wooden fingers for grasping objects (Fig. 1b). The total length was 18 cm. The fulcrum of the scissor-like tool was located at about half of the total length of the tool. Therefore, the opening distance between the tips of the tool and fingers were nearly identical.

The chopsticks were 22 cm in length with the fulcrum located very near the power point. Maximum opening ranges of the scissor-like tool and the chopsticks were 8 and 13 cm. Both of these opening ranges were wide enough to easily grasp the largest object in this study, which required only a 5 cm opening.

Data collection and preparation

Using the Optotrak system (Northern Digital Inc.), we obtained three-dimensional positions of infrared LED markers with a sampling rate at 200 Hz. Data recording started before the movement onset and stopped after the end of one trial. Three markers were attached to the tips of the effectors and the wrist. The wrist marker was used for detection of movement.

Position data were smoothed using a fourth-order Butterworth low-pass filter. We studied the reaching part of movement from onset to time of grasp, omitting the transport of the object. Trials in which participants failed to grasp the object or markers were invisible were excluded from analyses. Movement onset was determined as the first point where wrist velocity exceeded 5 cm/s, and movement end (the time of grasp) as the first point where wrist velocity fell below 5 cm/s after the peak velocity. Trials that did not satisfy these criteria for movement end were also removed from further analyses. In total, 3.39 % of the data were rejected.

The 7-mm-diameter marker could not be put on the exact tip of the effector, creating a difference between the final aperture and the actual object size. We determined where the movement ended based on tangential velocity, which could cause a slight discrepancy between the final aperture and the object size. However, this calculation was equally applied to all data, so this should not influence the main findings.

Data analysis

To examine the effects of effectors and objects size, we executed a three within-subject ANOVA on four indices: movement time, maximum grip aperture (MGA), relative timing at which MGA appears in the standardized movement time, and plateau duration of aperture profile against the standardized movement time. Multiple comparisons were carried out with Shaffer's method. We used the first three indices to confirm the classical features of grasping control, which would remain constant across the conditions. In contrast, plateau duration reflects proficiency of grasping control and was expected to vary with the condition. We conducted a paired *t* test to determine whether there was a difference in plateau duration between the AH and TT conditions, which could not be tested in the ANOVA. All measures were calculated for each trial and then averaged for one participant.

The present study defined plateau duration as the percentage of time that aperture was over 90 % of its MGA before MGA. Previous studies have also used the criterion of 90 % to distinguish aperture variation, but in a somewhat different context (Bongers et al. 2012). Bouwsema

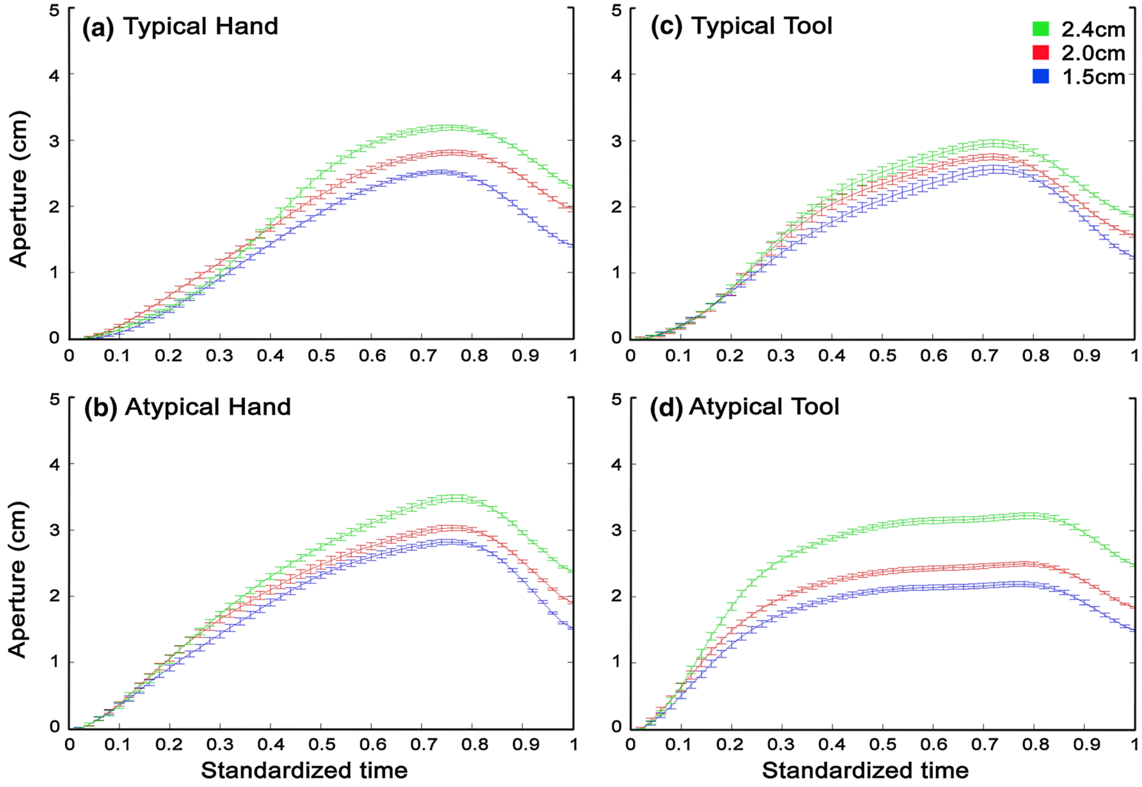

Fig. 2 Aperture profiles of the typical participants. Each *panel* corresponds to the types of effectors. The point of 0 in the abscissa indicates the onset of reaching movements and 1 indicates the time of the grasp. Aperture profile of each trial was divided into 50 points and averaged within a condition. The standard error at each time point was drawn as *error bar*

et al. (2010) defined the duration of the plateau phase as the period from the end of the finger opening to the start of finger closure, leading to the detection of only extreme aperture changes, which did not appear in the present study. Although the value of 90 % was arbitrary, we assumed that it was sufficient to distinguish characteristics of the aperture profiles between effecters.

To show averaged aperture profiles graphically, we divided the aperture profile of each trial into 50 points and computed an average and standard error within each condition (Fig. 2).

Results

The analyses of grasping control revealed four main results. (1) The plateau in the atypical tool condition was considerably longer than in the other three conditions. Typicality and effector type both related to the proficiency of effector influenced grasping control. Importantly, the atypical hand and typical tool conditions were not different in plateau duration but longer than the typical hand-use grasping. (2) Effector type affected maximum grip aperture (MGA) and movement duration. The tool-use conditions showed smaller MGA than the hand-use conditions. (3) Neither effector type nor typicality themselves influenced the timing of MGA or the variance of aperture control. (4) Object size effect on MGA was observed in the all effector conditions.

Figure 2 shows averaged aperture profiles of a single participant. Each panel corresponds to a type of effector. The point of 0 in the abscissa indicates the onset of reaching movement and 1 indicates the time of the grasp. The standard error at each time point is drawn as an error bar. The shapes of the aperture profiles of the AT condition differ from the other conditions. In the AT condition, the rising phase was shorter, and the curve before the MGA flatter. This feature, however, was not limited to the AT condition but was also seen in the AH and TT conditions, although not to such a striking degree.

We first investigated how grasping type affected plateau duration in relation to the hypothesis and then analyzed the other indices to confirm the classical features of grasping control. Generally, all the results were consistent with our hypothesis.

First, the plateau of the aperture profile, the focus of the present study, was examined. As expected, plateau duration was longest in the AT condition, followed in descending order by the TT, AH, and TH conditions (Fig. 3). The relative time of the plateaus which appeared in the aperture profiles were 19.3 ± 4.6, 24.3 ± 3.8, 24.0 ± 4.5, and 38.2 ± 5.4 % of the movement time in the TH, AH, TT, and AT conditions, respectively. ANOVA found main effects of typicality and effector ($F(1,7) = 53.95$, $p \leq .001$, $\eta^2_G = 0.204$; $F(1,7) = 92.06$, $p < .001$, $\eta^2_G = 0.193$) and an interaction effect between them ($F(1,7) = 14.51$, $p < .01$, $\eta^2_G = 0.056$). The main effect of object size was not significant ($F(2,14) = 2.83$, n.s., $\eta^2_G = 0.001$). To further examine the interaction effect between typicality and effecter, simple effect tests were conducted. They demonstrated that typicality and effector effects were significant at all levels ($p < .01$). In contrast, there was no difference between the AH and TT conditions ($t(1,7) = 0.29$, n.s., $d = 0.090$).

These statistical results indicated that plateau duration was longer either when the typicality of effector was high or when a hand was used for grasping, but one pair of tool-use and hand-use conditions was similar in grasping control. Further, the interaction effect demonstrated that plateau duration in the AT condition was considerably longer than the others. Taken together, this analysis revealed that the two factors both related to the proficiency level of the effector influenced grasping control and that the conventional distinction between hand-use and tool-use does not distinguish aperture profile in reach-to-grasp movement.

Second, movement time varied by effector type, but not by typicality and object size. As shown in Fig. 4, there seemed to be differences between the hand-use conditions and tool-use conditions. Mean and standard deviation of the movement times of each condition were 0.74 ± 0.13, 0.75 ± 0.12, 0.84 ± 0.14, and 0.81 ± 0.10 s in the TH, AH, TT, and AT conditions, respectively. ANOVA revealed a significant main effect of effector type ($F(1,7) = 9.20$, $p < .05$, $\eta^2_G = 0.047$), but there were no other significant effects ($F(1,7) = 0.53$, n.s., $\eta^2_G = 0.001$; $F(2,14) = 3.32$, n.s., $\eta^2_G = 0.002$). These results indicated that tool-use grasping prolonged reach-to-grasp movement time.

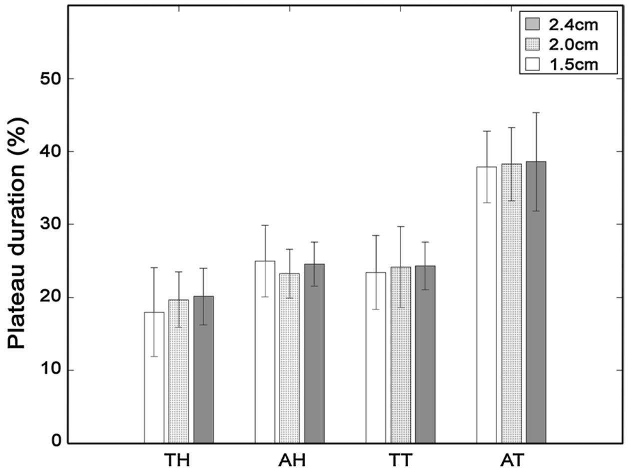

Fig. 3 Plateau duration in the four grasping conditions. *Error bar* indicates standard deviation. ANOVA found main effects of typicality and effector ($F(1,7) = 53.95$, $p < .001$, $\eta^2_G = 0.204$; $F(1,7) = 92.06$, $p < .001$, $\eta^2_G = 0.193$) and an interaction effect between them ($F(1,7) = 14.51$, $p < .01$, $\eta^2_G = 0.056$). The main effect of object size was not significant ($F(2,14) = 2.83$, n.s., $\eta^2_G = 0.001$). Simple effect tests demonstrated that typicality and effector effects were significant at all levels ($p < .01$). In contrast, there was no difference between the AH and TT conditions ($t(1,7) = 0.29$, n.s., $d = 0.090$)

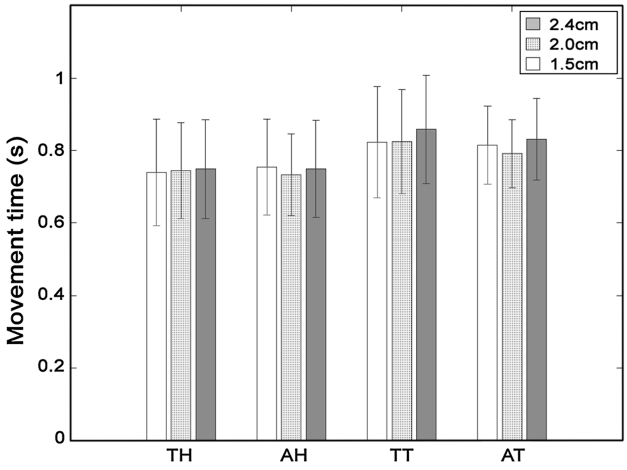

Fig. 4 Movement time in the four grasping conditions. *Error bar* indicates standard deviation. ANOVA revealed a significant main effect of effector type ($F(1,7) = 9.20$, $p < .05$, $\eta^2_G = 0.047$), but there were no other significant effects ($F(1,7) = 0.53$, n.s., $\eta^2_G = 0.001$; $F(2,14) = 3.32$, n.s., $\eta^2_G = 0.002$)

Third, all three factors affected MGA. In Fig. 2, each color corresponds to a different object size, and it shows that there was a size effect on MGA in all the grasping conditions, as also seen in Fig. 5. Indeed, ANOVA demonstrated a significant main effect of object size ($F(2,14) = 103.10$, $p < .001$, $\eta^2_G = 0.094$). In addition, there were significant main effects of typicality and effector type ($F(1,7) = 10.51$, $p < .05$, $\eta^2_G = 0.039$; $F(1,7) = 18.59$, $p < .01$, $\eta^2_G = 0.190$), but no interaction effects. MGA was 3.96 ± 0.80, 4.53 ± 0.76, 3.14 ± 0.54, and 3.39 ± 0.51 cm in the TH, AH, TT, and AT conditions, respectively. Multiple comparisons found significant differences in MGA between all pairs of objects with different sizes ($p < .05$). That is, MGA increased with object size in a linear fashion. Further, MGA in hand-use grasping was larger than in tool-use grasping, and MGA in atypical grasping was slightly larger than in typical grasping. These analyses confirmed the classical object size effect as well as showed that the opening range of the tips of the effectors was influenced both by typicality and type of effector.

Fourth, the timing of the maximum grip aperture occurred at about 75 % of the way through the movement time irrespective of the effectors. As Fig. 6 shows, MGA

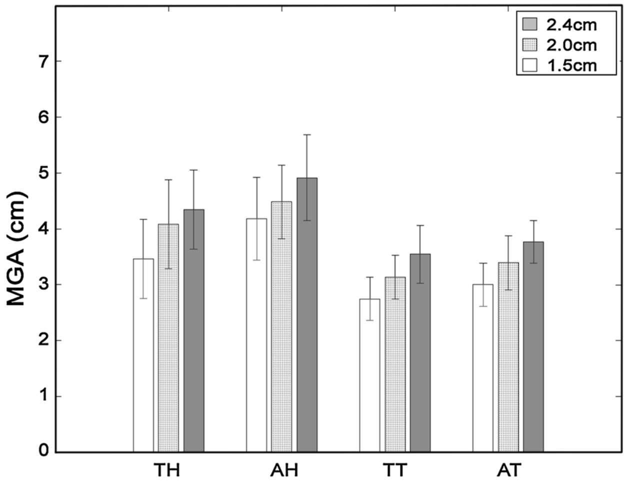

Fig. 5 Maximum grip apertures in the four grasping conditions. *Error bar* indicates standard deviation. ANOVA showed a significant main effect of object size ($F(2,14) = 103.10$, $p < .001$, $\eta^2_{\mathrm{G}} = 0.094$). In addition, there were significant main effects of typicality and effector type ($F(1,7) = 10.51$, $p < .05$, $\eta^2_{\mathrm{G}} = 0.039$; $F(1,7) = 18.59$, $p < .01$, $\eta^2_{\mathrm{G}} = 0.190$), but no interaction effects. Multiple comparisons found significant differences in MGA between all pairs of objects with different sizes ($p < .05$)

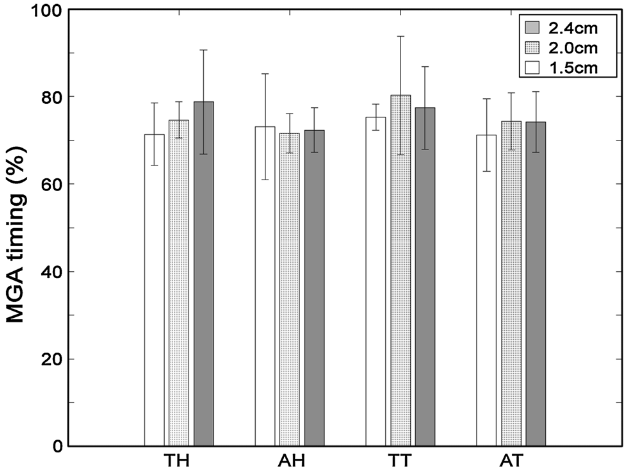

Fig. 6 MGA timing in the four grasping conditions. *Error bar* indicates standard deviation. ANOVA did not find any significant effects ($F(2,14) = 2.42$, n.s., $\eta^2_{\mathrm{G}} = 0.126$; $F(1,7) = 2.25$, n.s., $\eta^2_{\mathrm{G}} = 0.022$; $F(1,7) = 1.39$, n.s., $\eta^2_{\mathrm{G}} = 0.006$)

timing did not vary with object size or type of effector. MGA appeared at 74.9 ± 8.6, 72.3 ± 7.7, 77.7 ± 9.5, and 73.2 ± 7.1 % of the movement times in the TH, AH, TT, and AT conditions, respectively. ANOVA did not find any significant effects at all ($F(2,14) = 2.42$, n.s., $\eta^2_{\mathrm{G}} = 0.126$; $F(1,7) = 2.25$, n.s., $\eta^2_{\mathrm{G}} = 0.022$; $F(1,7) = 1.39$, n.s., $\eta^2_{\mathrm{G}} = 0.006$).

In addition to the above analyses, we examined the variance of aperture profiles within each condition to illustrate

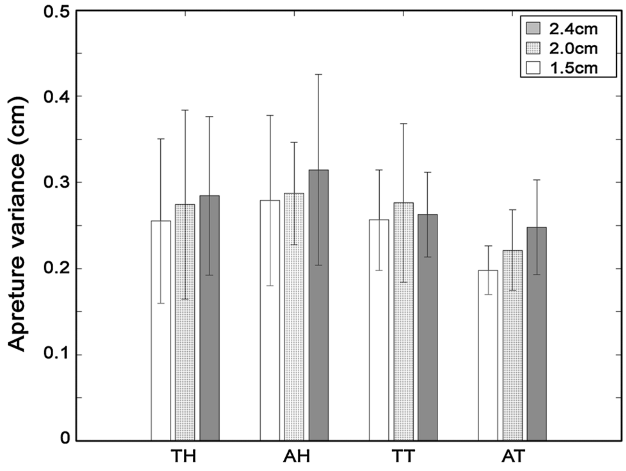

Fig. 7 Aperture variance in the four grasping conditions. *Error bar* indicates standard deviation. ANOVA on group data found no significant effects of object size, typicality, and effector type, but the interaction effect between typicality and effector type ($F(2,14) = 3.67$, n.s., $\eta^2_{\mathrm{G}} = 0.015$; $F(1,7) = 0.82$, n.s., $\eta^2_{\mathrm{G}} = 0.002$; $F(1,7) = 1.51$, n.s., $\eta^2_{\mathrm{G}} = 0.002$). A significant simple main effect of typicality was found in the atypical grasping condition ($F(1,7) = 5.79$, $p < .05.$, $\eta^2_{\mathrm{G}} = 0.083$)

the variability in grasping control (Fig. 7). ANOVA on group data found no significant effects of object size, typicality, and effector type, but the interaction effect between typicality and effector type ($F(2,14) = 3.67$, n.s., $\eta^2_{\mathrm{G}} = 0.015$; $F(1,7) = 0.82$, n.s., $\eta^2_{\mathrm{G}} = 0.002$; $F(1,7) = 1.51$, n.s., $\eta^2_{\mathrm{G}} = 0.002$). A significant simple main effect of typicality was found in the atypical grasping condition ($F(1,7) = 5.79$, $p < .05.$, $\eta^2_{\mathrm{G}} = 0.083$). These results indicate that variance of aperture control did not vary systematically with typicality or effector type. Moreover, there were no significant differences among grasping conditions except for between the AH and AT conditions.

Discussion

The results supported the idea that the proficiency level of the effector produces continuity in motor control between hand-use and tool-use grasping. On the one hand, the apertures of each of the four different effectors showed the well-known invariant features of grasp aperture. On the other hand, the aperture profile shapes differed in terms of their plateau duration by effector. As expected, grasping in the atypical hand and typical tool conditions prolonged the plateau compared with the typical hand-use condition. Moreover, aperture plateau duration was considerably longer in the atypical tool condition than in the other conditions. However, there was no difference in plateau duration between the atypical hand and typical tool conditions, despite the difference in the type of grasping effector.

These findings supported the hypothesis, suggesting that there should be a principle-governing grasping control, which is not sensitive to effectors, but sensitive to the proficiency level of the effector.

In addition to supporting our hypothesis, the present results also confirmed and extended previous findings. First, in all of the grasping conditions, object size effect was observed regardless of the effector in accordance with previous reports on natural hand-use grasping (Jakobson and Goodale 1991; Jeannerod 1984; Smeets and Brenner 1999). Tool-use grasping (Gentilucci et al. 2004) and left-hand grasping (Grosskopf and Kuhtz-Buschbeck 2006) also follow this principle. To our knowledge, the present study is the first report to show that the object size effect is also observed in four different types of grasping, including the use of two different tools. Second, MGA appeared at about the 75 % point in the reaching movement in all the conditions. In natural hand-use grasping, this aperture profile feature has been repeatedly reported as well. While previous reports have failed to show consistent results of MGA in hand-use and tool-use grasping (Bongers 2010; Gentilucci et al. 2004), the present study demonstrated that aperture peak timing was almost the same, not only in hand-use but also in tool-use. In the next section, we will discuss what factors influence the length of the plateau duration.

Plateau in aperture profile

Duration of the plateau in the current study differed gradually across effectors, suggesting that the difference depended on the degree of prior use of the effector. We grasp with the index finger and the thumb most frequently, not with the middle finger and the thumb (Ingram et al. 2008; Napier 1956), although our middle finger is flexible enough to be dexterously controlled. Therefore, it is reasonable that we observed relatively little difference in aperture profiles between the typical and atypical hand-use grasping. In contrast, there was a large difference between the aperture profiles of the two types of tools; aperture control with chopsticks was much more similar to natural grasping, rather than to grasping with the scissor-like tool. This superiority of the chopsticks in smoothness of control over the scissor-like tool was not surprising as the participants used chopsticks to eat since childhood, whereas they had never used the scissor-like tool. Rather, it was surprising to find that grasp aperture with chopsticks was almost as fine as that with the two types of hand-use grasps. This similarity in aperture between the hand-use grasp and the familiar tool-use grasp is in line with the hypothesis. Accordingly, duration of the plateau in the present study suggests that aperture control is not determined solely by the type of the effector, but by the degree of prior use of the effector.

Previous studies have also observed an aperture plateau in grasping movement with tool-use. Gentilucci et al. (2004) used a tool with two mechanical fingers, which opened and closed by squeezing and releasing its handles. The aperture quickly reached a peak, gradually decreased in size during the plateau phase and closed to grasp an object. In a more extreme example of tool-use, Bongers (2010) reported that a 40-cm pliers resulted in a similar aperture profile. Studies of Wing and Fraser (1983) and Bouwsema et al. (2010), where prosthesis users grasped an object, found that reach and grasp components were decoupled. These studies reported roughly the same aperture profiles with a long plateau flanked by quick opening and closure. Although a long plateau was observed in the unfamiliar tool-use in the present study as well, it is inconsistent with the previous reports in three critical points.

First, MGA in our study did not appear as early as in previous studies. While previous studies found MGA occurred in an earlier phase than in natural grasping (Bongers 2010; Bouwsema et al. 2010; Gentilucci et al. 2004; Wing and Fraser 1983), we found that MGA timing in grasping with the scissor-like tool did not differ from the other types of grasping, even in the salient plateau phase. Second, MGA size in tool-use grasping was not larger than natural grasping with the index finger and thumb, whereas previous studies reported considerably wider MGA with tool-use grasping (Bongers 2010; Gentilucci et al. 2004). Third, the movement time in tool-use grasping did not deviate from that of the natural grasping in the present study, whereas previous studies reported much longer tool-use grasping movement times (Bongers 2010; Gentilucci et al. 2004).

Before considering the results of plateau duration, we should mention the possible effects of effector proficiency on aperture profiles. In general, proficiency level is very likely to influence not only plateau duration but other kinematics in grasping movement. First, tool-use grasping in the present study prolonged movement time but typicality had no effect. This may be because the participants may not have been cautious in grasping objects with the thumb and middle finger and the scissor-like tool. Moreover, these two types of atypical grasping may have required no special effort to *grasp* the objects without dropping them. Second, MGA was smaller in the tool-use conditions and in the typical conditions. This may be because the tools might have required much more effort to open widely due to mechanical factors. Further, participants may have opened the tips widely in atypical grasping due to the difficulty in the control. These factors related to proficiency level might be responsible for the present results. More importantly, however, the classical features of grasping (size effect, timing of MGA) were confirmed in all effector conditions, even with the wide variety of differences in the types of grasping.

The mechanical features of the particular tools used may have influenced handleability, causing the discrepancies of aperture profile shape between the studies. That is, the reason previous studies had long plateaus flanked by quick opening and closure may have been due to the type of tools used. The two tools used in the present study were easily manageable, whereas the tools used in Gentilucci et al. (2004) and Bongers (2010) seem relatively hard to operate due to their mechanical properties. Gentilucci et al. (2004) used a tool with a handle and spring, and Bongers (2010) used extremely long pliers. These tools may have been hard to control due to the force and coordination required to use them; they required force to hold or compress as well as coordination of biological hand motion with the distant tips of the tool. In addition, the orientation of the tool's fingers was not aligned to the biological hand, but was vertical to the participants' arm. In contrast, although our scissor-like tool was a new object for participants, its mechanical fingers were light and easy to control. Chopsticks, of course, are a simple and good tool for grasping objects. Difficulty or lack of proficiency in using a tool may cause a deviation in the aperture profile. With such a variety of tool types, it is reasonable that differences in the aperture plateau between the previous studies and the present study exist.

Movement factors other than the degree of prior use of the effector may also cause a plateau in specific situations. Bongers et al. (2012) found that participants sometimes showed plateau patterns with natural hand-use grasping, which the mechanism assumed in the present study did not predict. However, the reach-to-grasp movements in Bongers's study differed considerably from those of the present study. In Bongers's study, hand movements started at a rightmost position or a position behind the body, which necessitated trunk rotation. Hand movements in the present study always occurred in front of the body without requiring trunk motion. Previous studies have reported that a simple reaching movement with trunk motion yields almost the same trajectory and velocity profile as arm-only reaching movement (Adamovich et al. 2001; Kaminski et al. 1995) and that reach-to-grasp movement with trunk motion maintains invariant kinematic components related to grasping (Wang and Stelmach 1998). These studies used a relatively small space in front of the body compared with Bongers et al. (2012). Therefore, plateau trials observed in Bongers et al. (2012) were likely to have been caused by the extreme range of movement requiring large joint rotations of the elbow, shoulder, and trunk. The present study observed an evident plateau pattern only in the AT condition, where joint rotation ranges of the elbow and shoulder were almost the same among the four conditions. Accordingly, movement factors seem to also cause a plateau in aperture profile, which may be independent of those factors responsible for the plateau in unfamiliar grasping.

Continuity in grasping control

Our results supporting the assumption of continuity between hand-use grasping and tool-use grasping also accord with neurophysiological studies. Using macaque monkeys, Umiltà et al. (2008) also demonstrated that the neurons in F5 were able to code the concept of "grasp" through long-term training regardless of how the tool was controlled. This neural plasticity may be a common substrate for both hand-use and tool-use behaviors in primates. This finding implies that tool-use and hand-use could be governed by the same principle of motor control. Although the present study provided only evidence of behavioral similarity of aperture profiles between various types of grasping, it extends the idea of goal-directed motor control and suggests that there might not be a simple dichotomy between a hand and a tool in grasping control. Rather, continuity due to the influence of one control principle should prevail, without denying the possibility that an effector-dependent representation of the tool may play some role in grasping control.

The concept of the continuity between hand and tool may also be in accord with the framework of forward and inverse models in computational motor control. If the hypothesis of the present study is true, tool-use grasp would be implemented differently from hand-use grasp before the tool is completely embodied. Perceptual aspects of tool embodiment (Iriki et al. 1996; Maravita et al. 2002a, b) and motor embodiment (Umiltà et al. 2008) could be achieved by tool-use. These embodiments may be realized by neural substrates where the goal of action (i.e., "grasp" in this context) is substantiated. In the computational view, a forward model realizes such a representation of the goal of action. Completing a goal of action requires calculating how to achieve it using a particular set of effectors based on an inverse model. Previous studies have shown that acquisition of an inverse model is much slower than a forward model (Bhushan and Shadmehr 1999; Flanagan and Johansson 2003; Gentili et al. 2010; Kawato and Wolpert 1998). To master a new tool requires a new inverse model, which is not effector-independent but effector-specific (Malfait and Ostry 2004; Williams and Gribble 2012). One could speculate that an effector-independent representation of a forward model operates in an early phase of tool-use. After long practice, an effector-specific controller of the inverse model might then allow skillful tool-use similar to hand-use. Thus, the proposed idea of continuity of proficiency in grasping control based on one principle may correspond to the computational framework, which consists of a fast-acquired, effector-independent forward model and slow-acquired, effector-specific inverse model. This correspondence between our results and computational motor theory may help explain grasping control but requires further investigation.

To confirm the idea that a relatively unused effector is subject to the same principle of motor control and acquires efficient control through experience, further research should investigate the practice-dependent variance of grasping aperture. If aperture profiles in grasping control with any type of effector are subject to the same principle, long-term training with the tool should improve aperture profiles and decrease their plateaus. Further, if once the embodiment of the tool is completed, stiffness control of the upper limb and its position perception would adjust to the new environment, that is, the updated upper limb (Burdet et al. 2001; Franklin and Milner 2003; Darainy et al. 2004; Itaguchi and Fukuzawa 2012a, b). These experiments remain as the subject for future study.

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