Exp Brain Res (2017) 235:2215–2224
DOI 10.1007/s00221-017-4964-x

RESEARCH ARTICLE

Programming of left hand exploits task set but that of right hand depends on recent history

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Received: 23 July 2016 / Accepted: 20 April 2017 / Published online: 27 April 2017

Abstract There are many differences between the left hand and the right hand. But it is not clear if there is a difference in programming between left hand and right hand when the hands perform the same movement. In current study, we carried out two experiments to investigate whether the programming of two hands was equivalent or they exploited different strategies. In the first experiment, participants were required to use one hand to grasp an object with visual feedback or to point to the center of one object without visual feedback on alternate trials, or to grasp an object without visual feedback and to point the center of one object with visual feedback on alternating trials. They then performed the tasks with the other hand. The result was that previous pointing task affected current grasping when it was performed by the left hand, but not the right hand. In experiment 2, we studied if the programming of the left (or right) hand would be affected by the pointing task performed on the previous trial not only by the same hand, but also by the right (or left) hand. Participants pointed and grasped the objects alternately with two hands. The result was similar with Experiment 1, i.e., left-hand grasping was affected by right-hand pointing, whereas right-hand grasping was immune from the interference from left hand. Taken together, the results suggest that when open- and closed-loop trials are interleaved, motor programming of grasping with the right hand was affected by the nature of the online feedback on the previous trial only if it was a grasping trial, suggesting that the trial-to-trial transfer depends on sensorimotor memory and not on task set. In contrast, motor programming of grasping with the left hand can use information about the nature of the online feedback on the previous trial to specify the parameters of the movement, even when the type of movement that occurred was quite different (i.e., pointing) and was performed with the right hand. This suggests that trial-to-trial transfer with the left hand depends on some sort of carry-over of task set for dealing with the availability of visual feedback.

Keywords Programming · Grasping · Visual feedback · Trial history · Sensorimotor memory

Introduction

When people reach out to grasp an object, the opening of their grasping hand anticipates the width of that object (Jeannerod 1981). Typically, the hand opens wider than the object. Nevertheless, peak grip aperture (PGA), which is achieved about 70% of the way through the grasp, is well correlated with the width of the goal object. The presence or absence of visual feedback also plays a role in determining grip aperture.

Many studies have shown that the PGA is wider for grasps made in open loop (without visual feedback) than it is for grasps made in closed loop (with visual feedback, e.g., Fukui and Inui 2006; Jakobson and Goodale 1991; Whitwell et al. 2008; Tang et al. 2014). This difference presumably reflects the fact that grasps made in open loop cannot make use of visual feedback. In other words, the wider PGA creates a margin of error so that the hand can close around the goal object properly.

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Although the difference in the PGA between open- and closed-loop trials reflects the presence or absence of feedback on the current trial, this is not the only factor at play. The presence or absence of feedback on the previous trial also plays a role. The largest difference between the PGA on open and closed trials occurs when the two kinds of trials are blocked separately. When closed- and open loop trials are randomized or even alternated, the difference in the PGA between open- and closed-loop trials becomes much smaller, i.e., some sort of homogenization occurs (Whitwell et al. 2008). The fact that homogenization occurs when the two kinds of trials are interleaved means that performance on the current trial is affected by what happened on the previous trial. In blocked conditions, the effect of the previous trial on the current trial accumulates over trials because the feedback condition remains the same from trial to trial (Whitwell and Goodale 2009). Finally, the fact that homogenization occurs even when open- and closed-loop trials are alternated suggests that knowledge about whether or not visual feedback will be available on the upcoming trial does not play a significant role in this phenomenon. Taken together, these findings suggest that the initial programming of grip aperture on a particular trial is affected by the feedback available on that trial as well as what happened on the preceding trial—but not by explicit knowledge of what is likely to happen on the current trial.

But even though explicit knowledge does not seem to play a role, it is not clear what is being 'transferred' from one trial to the next. It has been suggested by some investigators that homogenization reflects the operation of 'task sets' (for review see Gilbert and Shallice 2002; Monsell 2003; Kiesel et al. 2010), which are associated with making sure that behavior in closed- or open-loop conditions is optimized. In closed loop, it is possible to delay the specification of the programmable parameters of the movement, such as grip aperture, until the movement is actually underway. In contrast, in open loop, it would be optimal to specify those parameters before the movement begins, since visual information would not be available during the execution of the movement. When the two kinds of feedback trials are interleaved, it would not be possible to specify an optimal task set, resulting in a reduction in the difference in grip aperture between the closed- and open-loop trials. Of course, when the two feedback conditions are each administered in separate blocks, the visuomotor system can specify grip aperture optimally.

There is also another possible explanation for the effects of trial order on grip aperture. It could be the case that sensorimotor performance on one trial is simply transferred to the next trial. In other words, some sort of sensorimotor memory could be at work. For example, if a person opened their hand wider on an open-loop trial, they might tend to open it wider on the next trial—even if that trial happened to be closed loop. Of course, there would still be some online modulation because visual feedback would be available on that closed-loop trial—but grip aperture on that trial would still be larger than if the preceding trial had been performed in closed loop. But how might one differentiate between an explanation based on sensorimotor memory and an explanation based on task sets? One way to do this would be to alternate between two kinds of motor tasks such as pointing and grasping. If task set is operating, based entirely on information about whether the last trial was open or closed loop, then pointing to the object under one feedback condition should affect performance on a subsequent grasping trial. If, however, the transfer from one trial to the next depends on sensorimotor memory, then there should be no transfer from a pointing trial to a grasping trial. In other words, the 'carry-over' of performance on trial n to performance on trial $n + 1$ should be observed only when the two trials are both grasping trials. As it turns out, we recently carried out an experiment of this kind where we simultaneously alternated pointing trials with grasping trials and open-loop trials with closed-loop trials, such that pointing was coupled with one feedback condition and grasping with the other (Tang et al. 2015). We found no transfer between pointing and grasping trials. Instead, participants behaved as if the grasping trials had been separately blocked into all open- or all closed-loop trials. These results provided strong support for the sensorimotor memory account rather than the task set account of the trial-order effects.

Almost all the work on trial-order effects, however, has focused on the right hand, which is arguably much more skilled than the left at picking up objects. In fact, many researchers have found differences in the nature of the control of right- and left-handed grasping (Boulinguez et al. 2001; Gonzalez et al. 2006, 2008). For example, the grip apertures of grasps made with the left hand are much more likely to be influenced by size-contrast illusions than the grip apertures of grasps made with the right hand (Gonzalez et al. 2006, 2008). This finding in particular has led to the suggestion that grasping with the left hand is much more likely to be influenced by perceptual/cognitive factors than grasping with the right hand, which is more automatic and encapsulated. In experiments that examined trial-order effects, Tang et al. (2014) found that when participants used their left hand to pick up the objects the difference between alternating open- and closed-loop trials was significantly larger than it was on randomized open- and closed-loop trials. This suggests that participants might have exploited knowledge about what was going to happen on an upcoming trial to program their grip aperture. Nevertheless, the PGA on closed loop trials when two visual feedbacks were alternated was still significantly smaller than it was for the separately blocked closed-loop trials. But if it were only explicit knowledge, there should have been no difference between the PGAs on the alternating trials and the blocked trials. The information that was apparently transferred from trial n to trial $n + 1$ could have been either sensorimotor memory or some sort of task set.

In the current study, we investigated which of these possible mechanisms was at work—sensorimotor memory or task set—by comparing trial-order effects in the left and right hand when the alternation of closed- and open-loop trials was coupled with alternation between pointing and grasping. In the first experiment, we examined the trial-to-trial transfer from pointing to grasping within the same hand, and in the second experiment, we examined transfer between the two hands. If task set was mediating trial-to-trial transfer in the left hand, then the left hand but not the right should show transfer between pointing and grasping trials when open- and closed-loop trials were alternated in step with the alternation with the two kind of movements. Similarly, this transfer would be observed in the left hand even when the pointing movement was performed with the right hand. If sensorimotor motor memory was at work, then trial-to-trial transfer should not occur from pointing to grasping in the left hand.

Experiment 1

Methods

Participants

Sixteen right-handed participants (6 males, 10 females, 18–40 years, mean age 22.7) with normal or corrected-to-normal vision participated this experiment. The participants provided gave informed consent before participating in the experiment. They were compensated for their time and were naive with respect to the purpose of the experiment. Their handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). The experiment was approved by the local ethics committee at the University of Western Ontario.

Design

In this experiment, we studied if the programming of grasping would be affected by a previous pointing trial performed by the same hand. Three conditions including two baseline conditions and one experimental condition were tested in this experiment (see Fig. 1). In the baseline conditions, participants always grasped the targets using their index finger and thumb. In one of two baseline conditions,

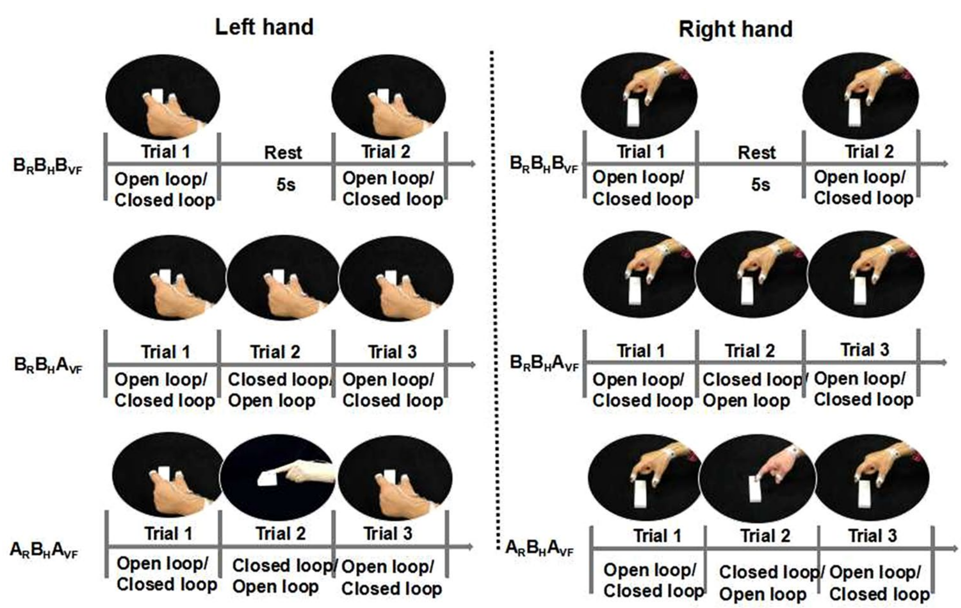

Fig. 1 The procedure of Experiment 1. There was a 5-s gap between trial n and trial $n + 1$. Participants grasped objects of three different sizes in a pseudo-random order. The panel on the *left* illustrates grasps performed with left hands, while the panel on the *right* illustrates grasps performed with right hand. $B_R B_H B_{VF}$ is the condition that the response, hand and visual feedback are all blocked. Subjects were required to grasp the object with one hand in closed loop or open loop separately. Similarly, $B_R B_H A_{VF}$ is the condition that the response and hand are blocked but closed loop and open loop are alternated. $A_R B_H A_{VF}$ is both the response and the visual feedback were alternated, but subjects still used one hand to grasp or point in one session

participants reached out with one hand to pick up any one of three rectangular objects of different widths positioned at any one of three distances (see below for details), and closed- and open-loop trials were administered in two separate blocks (i.e., blocked the response, hand and visual feedback: $B_RB_HB_{VF}$). In the other baseline condition, open-loop and closed-loop trials were alternated from one trial to the next (i.e. the response and the hand used were blocked but visual feedback was alternated: $B_RB_HA_{VF}$). The left and right hand were both tested in the $B_RB_HB_{VF}$ and the $B_RB_HA_{VF}$ conditions. In the experimental condition, both the response (grasping or pointing) and the type of visual feedback (closed loop or open loop) were alternated together (i.e., both the response and the visual feedback were alternated: $A_RB_HA_{VF}$; see Fig. 1). There were two blocks of trials in this condition. Specifically, if the grasps were executed in closed loop, then they were alternated with pointing movements that were executed in open loop. Similarly, if the grasps were executed in open loop, then they were alternated with pointing movements that were executed in closed loop. Each participant performed all the conditions, and the order of $B_RB_HB_{VF}$, $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$ condition was counterbalanced across the participants. We reasoned that if grasping was affected by previous pointing trials, then there would be transfer from pointing to precision grasping when feedback conditions (open vs. closed loop) were alternated in step with the different responses.

Apparatus and stimuli

The participants were required to reach out and pick up one of three different-sized white wooden rectangles (small: 10 cm × 1.5 cm × 2 cm; medium: 10 cm × 1.5 cm × 3.5 cm; large: 10 cm × 1.5 cm × 5 cm). On each trial, one of three objects was placed at one of three distances (near: 10 cm; middle: 20 cm; far: 30 cm) from the red start button located 5 cm from the edge of the tabletop closest to the participant. Visual feedback was controlled with liquid crystal goggles (PLATO goggles; Translucent Technologies, Toronto, ON, Canada). The default state of the PLATO goggles in the experiment was opaque. The real-time kinematic data were collected at 200 Hz with an OPTOTRAK Certus (Northern Digital, Waterloo, ON, Canada) optoelectronic recording system. Six infrared light emitting diodes (IREDs) were used in this experiment, three placed on the left hand and three on the right. The IREDs were located next to the cuticle of index fingernail, the cuticle of index thumbnail, and on the side of the wrist opposite the styloid process of the ulna. The wires corresponding to each IRED were taped to ensure complete freedom of movement. The experimenter ensured that the pads of skin on the tips of both digits were uncovered to ensure normal haptic sensory feedback from the goal objects when grasped. Data were analyzed offline with in-house software written in C.

Procedure

Participants were comfortably seated facing a table. The start button was located on a platform close to the participant. One of the three different objects was positioned at one of the three distances (near, medium, far) from the start button along an axis perpendicular to the sagittal axis of the participant. The sequence of positions and sizes was pseudo random in case participants programmed before see the objects. Participants began each trial with the thumb and index finger of one hand pressed together on top of the start button. The participants were instructed to reach out, grasp, and lift the object carefully and naturally across its width using the thumb and index finger as soon as the goggles became transparent. The goggles remained transparent for 2 s after start button was released in closed-loop condition to be sure that subjects had a full view of the object and the moving hand during grasping. On open-loop trials, the goggles closed as soon as the start button was released.

Participants were tested under three separate conditions: $B_RB_HB_{VF}$, $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$. All of the participants were informed what the upcoming condition was. The sequence of conditions was counterbalanced across subjects. Each condition consisted of 72 trials with 18 trials of closed loop and 18 trials of open loop with the right hand, and 18 trials of closed loop and 18 trials of open loop with the left hand. The three different sizes of object and the three different distances were pseudo-randomized, with each size–distance combination repeated 2 times in each condition. In $B_RB_HB_{VF}$, participants were tested in two separate blocks of closed loop and two separate blocks of open loop were carried out using the right and left hand separately for each block. The time interval between the onset of one grasping trial and the next in the $A_RB_HA_{VF}$ condition was approximately 10 s, because the two trials were separated by a pointing trial. This timing was a simple consequence of how long it took to set up and administer a single trial, approximately 5 s. Thus, to ensure that the 10-s time interval between grasping trials was the same in the blocked condition as it was in the alternating condition, the time between the end of a trial in the blocked condition and the beginning of the next was lengthened by 5 s. In between trial sets, participants removed the PLATO goggles and relaxed for 6 min before beginning the next set of trials. They were told the format of the upcoming set of trials before the commencement of each condition.

Data collection

In this study, to assess the effect of previous trial on the programming of current trial, the peak grip aperture (PGA) and the difference between PGA on closed- and open-loop trials in different conditions (dPGA) were calculated. Movement onset was defined as the first 20 consecutive frames of IREDs on wrist above 50 mm/s, movement offset was defined as the 10 consecutive frames below 50 mm/s after onset. Thus, PGA was defined as the maximum vector distance between the index and thumb IREDs available between movement onset and initial movement offset. The difference between PGA on closed and open loop trials in different conditions (dPGA) was calculated with PGA (Open loop) minus PGA (Closed loop).

Data and statistical analysis

All the data were analyzed offline. We conducted separate 2 × 2 × 3 repeated measures ANOVAs Hand (Left, Right) × Feedback (Closed loop, Open loop) × Condition ($B_RB_HB_{VF}$, $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$) on the PGA. We also performed repeated measures ANOVA on the PGA separately for closed and open loop because three-way interactions of Hand × Condition × Feedback was significant. We conducted separate 2 × 3 rmANOVAs Hand (Left, Right) × Condition ($B_RB_HB_{VF}$, $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$) to dPGA. If the ANOVAs revealed significant differences, pairwise comparisons were performed to investigate possible differences between pairs of means. Alpha level was set at $P < 0.05$.

Results

Mean values and 95% confidence intervals (CI) of the peak grip aperture (PGA) for the left and right hands are shown in Fig. 2. The rmANOVA revealed a significant three-way interaction (Feedback × Condition × Hand), a significant two-way interaction (Feedback × Condition), and a significant main effect (Feedback). Overall, the Feedback × Condition × Hand interaction was significant ($F(2,30) = 6.422$, $P = 0.005$, $\eta^2 = 0.3$). The Feedback × Condition interaction ($F(2,30) = 19.471$, $P < 0.001$, $\eta^2 = 0.565$) reflected the fact that grasps under different conditions were differentially affected by the two kinds of feedback trials. The PGA in open loop was significantly larger than the PGA in closed loop ($F(1,15) = 62.248$, $P < 0.001$, $\eta^2 = 0.806$).

We performed rmANOVA on Feedback × Condition separately for the PGAs of the left hand and right hand. For grasps executed with the left hand, both the Feedback × Condition interaction ($F(2,30) = 13.137$, $P < 0.001$, $\eta^2 = 0.467$) and main effect of Feedback ($F(1,15) = 39.852$, $P < 0.001$, $\eta^2 = 0.727$) were significant. Pairwise comparison showed that in closed loop, the PGA for the left hand was smaller when both grasping and feedback were blocked ($B_RB_HB_{VF}$) than it was when grasping was blocked but feedback was alternated ($B_RB_HA_{VF}$), $P = 0.005$. In open loop, there were no significant effects between any two of the three conditions. For right-handed grasps, both Feedback × Condition interaction ($F(2,30) = 15.341$, $P < 0.001$, $\eta^2 = 0.506$) and main effect of Feedback ($F(1,15) = 43.984$, $P < 0.001$, $\eta^2 = 0.746$) were also significant. Comparison revealed that in closed loop, the PGA of right hand was larger when grasping was blocked but feedback was alternated ($B_RB_HA_{VF}$) than it was when grasping and feedback were blocked ($B_RB_HB_{VF}$), $P = 0.014$, and when both grasping and feedback were alternated ($A_RB_HA_{VF}$), $P = 0.004$. In open loop, there were no significant effects between any two of the three conditions. Finally, the PGAs in open loop under all conditions, whether the grasp was executed by the left or the right hand, were larger than they were in closed loop, $P_{min} = 0.001$.

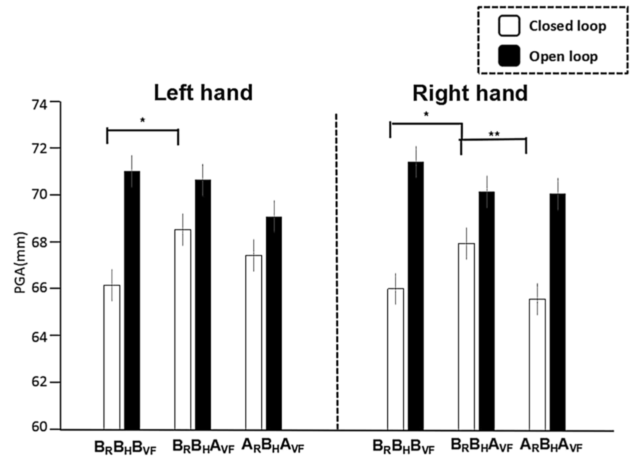

Fig. 2 Mean values and 95% confidence intervals for the peak grip aperture (PGA) in Experiment 1. *White bar* is the closed-loop condition and the *black bar* is the open-loop condition. As was the case in Fig. 1, $B_RB_HB_{VF}$ is the condition in which the response, hand, and visual feedback were all blocked. $B_RB_HA_{VF}$ is the condition in which the response and hand were blocked but closed-loop and open-loop trials were alternated. In $A_RB_HA_{VF}$ both the response and the visual feedback were alternated, but participants still used one hand to grasp or point. *Asterisk* indicates there was a significant difference between two conditions (at least $P < 0.05$)

Previous studies showed that the differences in the PGA between open-loop and closed-loop conditions became smaller when these two kinds of trials were interleaved (Jakobson and Goodale 1991; Whitwell et al. 2008; Tang et al. 2014). Moreover, this difference reflects how much the trials are affected by previous trials, we therefore calculated a difference score (dPGA = Open-loop PGA − Closed-loop PGA; see Fig. 3). When we analyzed differences in dPGA, the Hand × Condition interaction was

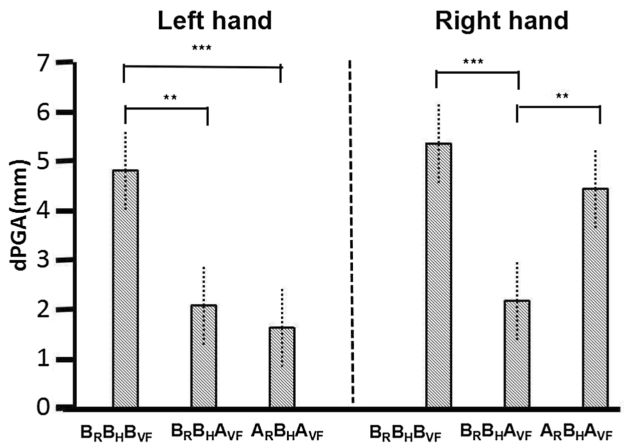

Fig. 3 Mean values and 95% confidence intervals for dPGA ($PGA_{open\text{-}loop} - PGA_{closed\text{-}loop}$). The *left panel* is the dPGA of the left hand and *right panel* is the dPGA of the right hand. $B_RB_HB_{VF}$, $B_RB_HA_{VF}$, and $A_RB_HA_{VF}$ refer to the same conditions described in previous figures. The dPGA for the left hand was smaller than the dPGA for the right hand. For the right hand, the dPGA in the $B_RB_HB_{VF}$ condition was significantly larger than it was in the A_{VF} and $A_RB_HA_{VF}$ conditions. For the left hand, dPGA in the $B_RB_HB_{VF}$ condition was significantly larger than it was in the $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$ conditions. *Asterisk* indicates there were significant differences between two conditions (at least $P < 0.05$)

significant, $F(2,30) = 6.422$, $P = 0.005$, $\eta^2 = 0.3$. The main effect of Condition was also significant, $F(2,30) = 19.471$, $P < 0.001$, $\eta^2 = 0.565$. For the left hand, pairwise comparisons revealed that dPGA of $B_RB_HB_{VF}$ was significantly larger than that of both $B_RB_HA_{VF}$ ($P = 0.003$) and $A_RB_HA_{VF}$ ($P = 0.001$). There was no difference between the last two conditions. For right hand, dPGA of $B_RB_HA_{VF}$ was significantly smaller than that of $B_RB_HB_{VF}$ ($P < 0.001$) and $A_RB_HA_{VF}$ ($P = 0.002$); again, there was no difference between $B_RB_HA_{VF}$ and $A_RB_HA_{VF}$ (Fig. 3).

Discussion

In this experiment, the PGA in open loop was larger for grasping with either hand than that it was in closed loop under all conditions which was consistent with previous research (Jakobson and Goodale 1991; Whitwell et al. 2008; Whitwell and Goodale 2009; Tang et al. 2014). The PGA in closed loop was more affected by different conditions than it was in open loop. The dPGA scores (PGA in open loop minus PGA in closed loop) reflect a homogenization that occurs when open loop trials and closed loop trials affect each other; i.e., the PGAs become more similar. Two hands were analyzed separately and the results revealed that when grasping with left hand, the dPGAs in $B_RB_HB_{VF}$ and $A_RB_HA_{VF}$ were significantly larger than they were in $B_RB_HA_{VF}$. But for right hand, the dPGA of $B_RB_HA_{VF}$ was significantly smaller than the dPGAs in $B_RB_HB_{VF}$ and $A_RB_HA_{VF}$. In other words, when subjects grasped and pointed alternately with right hand ($A_RB_HA_{VF}$), the result was virtually identical to what happened in the blocked condition ($B_RB_HB_{VF}$), indicating that in both cases the dPGA was not affected by the previous pointing task. But when they performed with left hand, PGA was affected by previous pointing task because dPGA of $A_RB_HA_{VF}$ was significantly different with dPGA in blocked condition ($B_RB_HB_{VF}$) and had no difference with $B_RB_HA_{VF}$. This result revealed that the programming of right hand was not affected by the previous pointing trial, a result which is consistent with previous findings (Tang et al. 2015). The left hand, however, was affected by pointing task. Tang et al. (2014) found that left hand but right hand could exploit the explicit knowledge of feedback. In this study, the performance of a different movement (pointing) on the previous trial also plays a role in the programming of left-hand grasping. It should be noted that we added a gap between two trials in blocked condition to rule out a possible temporal effect, which was a little different from the procedure used by Whitwell et al. (2008), Whitwell and Goodale (2009) and Tang et al. (2014). Nevertheless, there was still homogenization of the PGA when closed-loop and open-loop grasping trials were alternated in both the left and the right hand. And again, the fact that there was no transfer from pointing to grasping trials in the right hand suggests that the homogenization from grasping to grasping in alternating trials does not reflect a carry-over of task set from closed to open loop, and vice versa.

Experiment 2

In Experiment 1, trial-to-trial transfer from pointing to grasping within the same hand was studied. The result revealed that programming of right-hand grasping was not affected by previous pointing task, whereas the programming of left-hand grasping was. In Experiment 2, we investigated if this kind of trial-to-trial transfer happens between two hands. If task set is exploited by left hand, then it would not be limited to the same hand since the transfer of task set should transcend which hand was used on the previous trial. In other words, pointing to the object under one feedback condition with right or left hand should affect performance on a subsequent grasping trial executed with left hand.

Methods

Participants

Twenty right-handed participants (6 males, 14 females, aged 19–42, mean age 24.8) with normal or corrected-to-normal vision participated this experiment. One subject did not complete the experiment, so 19 subjects' data were analyzed. The participants provided written and informed consent before participating in the experiment. They were naive with respect to the purpose of the experiment. Their handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). The experiment was approved by the local ethics committee.

Apparatus

The experimental apparatus was identical to Experiment 1. Three sizes of wooden rectangles (small: 10 cm × 1.5 cm × 2 cm; medium: 10 cm × 1.5 cm × 3.5 cm; large: 10 cm × 1.5 cm × 5 cm) were also used in this experiment. But the difference with Experiment 1 was one of three objects was placed at one of two distances (near: 10 cm; far: 30 cm) from the red start button.

Procedure

The procedure of this experiment was similar to that used in Experiment 1. Participants sat comfortably facing a platform with a start button on it. One of three objects was positioned at one of two distances (near, far). Participants began each trial with thumb and index finger of one hand pressed together on top of the starting button. Participants were required to reach to grasp and lift the object or point to the center of object as soon as the goggles became transparent. The goggles were transparent for 2 s after the start button was released in closed-loop condition. In open loop, the goggles closed as soon as the start button was released.

There were two conditions in this experiment (See Fig. 4): blocked the response, hand and visual feedback ($B_RB_HB_{VF}$) and alternated the response, hand and visual feedback ($A_RA_HA_{VF}$). The sequence of conditions was balanced across subjects. $B_RB_HB_{VF}$ consisted of 24 trials (closed loop: 12 trials, open loop: 12 trials) with the left hand and 24 trials with the right hand. $A_RA_HA_{VF}$ consisted of 24 trials for grasping with right hand in closed loop and pointing with left hand in open loop alternately, and 24 trials for grasping with right hand in open loop and pointing with left hand in closed loop alternately. There were also 48 trials for grasping with left hand and pointing with right hand. The total trials were 144 trials ($B_RB_HB_{VF}$: 48 trials plus $A_RA_HA_{VF}$: 96 trials). Between sessions, participants removed the PLATO goggles and relaxed for 5 min before beginning the next session. Subjects were told the format of the upcoming set of trials before the commencement of each condition.

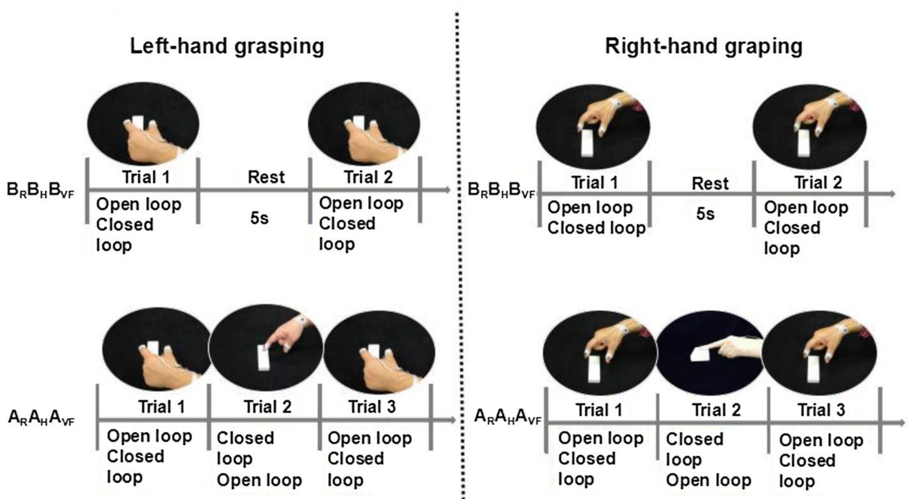

Fig. 4 The procedure of Experiment 2. Similarly with experiment 1, there was a 5-s gap between trial n and trial $n + 1$. Participants grasped objects of three different sizes in a pseudo-random order. Left/right hand means participants reached to grasp with their left hand and pointed with their right hand. Right/left hand means participants reached to grasp with right hand but pointed with left hand. $B_RB_HB_{VF}$ is the condition that the response, hand, and visual feedback were all blocked. However, in the $A_RA_HA_{VF}$ conditions, the left hand pointed or the right hand pointed. That is, both the response and the visual feedback were alternated, but participants grasped with one hand and pointed with other hand alternately in step with closed loop and open loop

Data collection

It is the same with Experiment 1, the peak grip aperture (PGA) and the difference between PGA (dPGA = PGA in open loop-PGA in closed loop) were calculated.

Data and statistical analysis

All the data were analyzed offline. We conducted separate repeated measured ANOVA 2 × 2 × 2 Hand (Left, Right) × Feedback (Closed loop, Open loop) × Condition ($B_RB_HB_{VF}$, $A_RA_HA_{VF}$) for the PGA. Because the three-way interaction of 2 × 2 × 2 was significant, we analyzed Feedback × Condition separately for the left and right hand with repeated measure ANOVA. Then we compared different conditions with paired *t* tests. We also performed an rmANOVA 2 × 2 Hand (Left, Right) × Feedback (Closed loop, Open loop) × Condition ($B_RB_HB_{VF}$,$A_RA_HA_{VF}$) on the dPGA. Alpha level was set at $P < 0.05$.

Results

One participant did not perform the alternating condition correctly, and therefore data from nineteen subjects were analyzed. Figure 5 showed mean values and 95% CI for the peak grip aperture (PGA) for both hands. The peak grip aperture (PGA) was analyzed using 2 × 2 × 2 Hand (Left, Right) × Feedback (Closed loop, Open loop) × Condition ($B_RB_HB_{VF}$, $A_RA_HA_{VF}$) repeated measures ANOVA. Mean effect of Feedback was significant, $F(1,18) = 19.979$, $P < 0.001$, $\eta^2 = 0.526$. This indicated that PGA in open loop was larger than PGA in closed loop. The three-way interaction of Hand × Feedback × Condition was also significant, $F(1,18) = 4.633$, $P = 0.045$, $\eta^2 = 0.205$. We performed a Feedback × Condition repeated measures ANOVA separately for right hand and left hand. For the left hand, the Feedback × Condition interaction, $F(1,18) = 5.613$, $P = 0.029$, $\eta^2 = 0.238$ and the main effect of Feedback, $F(1,18) = 11.46$, $P = 0.003$, $\eta^2 = 0.389$ were significant. Pairwise comparison revealed no significant effect between two Conditions whether in closed loop or open loop, $P_{min} = 0.081$. Nevertheless, the main effect of Feedback, $F(1,18) = 25.876$, $P < 0.001$, $\eta^2 = 0.59$ was significant for the right hand. Pairwise comparisons were run to compare $B_RB_HB_{VF}$ with $A_RA_HA_{VF}$ in closed loop and open loop. There was no significant effect, $P_{min} = 0.638$. In addition, the PGAs in open loop were bigger than PGAs in closed loop under all conditions performed by left hand and right hand.

We also analyzed dPGA scores using 2 × 2 Hand (Left, Right) × Condition ($B_RB_HB_{VF}$, $A_RA_HA_{VF}$) repeated measures ANOVA. There was significant difference for 2 × 2 interaction effect, $F(1,18) = 4.633$, $P = 0.045$, $\eta^2 = 0.205$. A Pairwise comparison indicated that the dPGA score in $B_RB_HB_{VF}$ was larger than in $A_RA_HA_{VF}$ in the left hand, $P = 0.029$. But there was no significant difference between these two conditions for right hand, $P = 0.865$. Figure 5 showed Mean values of dPGA and 95% CI with two hands.

Discussion

In this experiment, we investigated if previous pointing task of one hand affected current grasping task performed by the other hand. The fact that the PGA on open-loop trials was

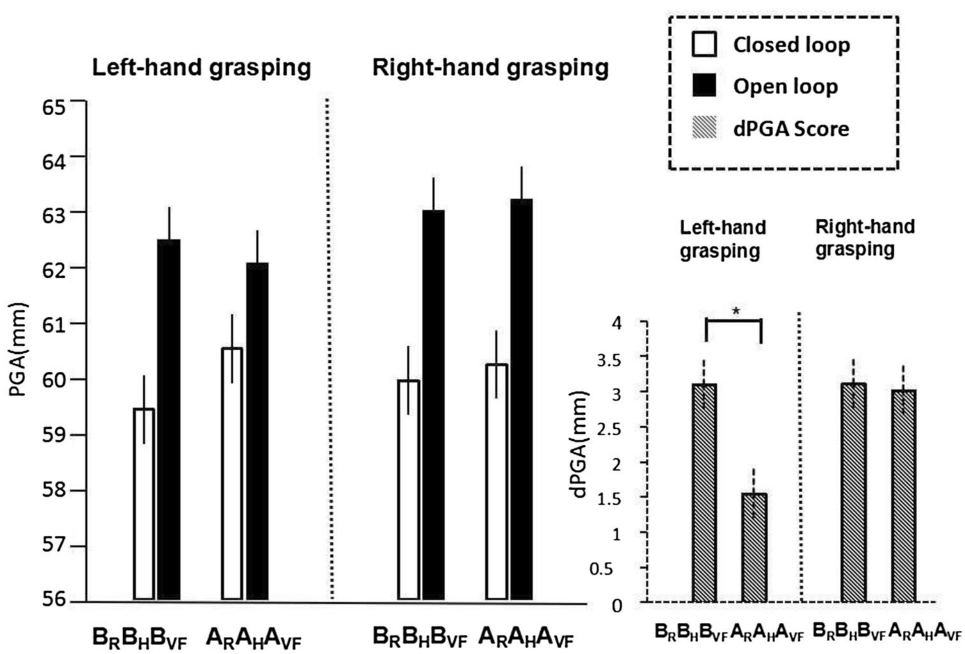

Fig. 5 Mean values and 95 % confidence intervals for the peak grip aperture (PGA) and dPGA ($PGA_{open\text{-}loop} - PGA_{closed\text{-}loop}$) in Experiment 2. Left-hand grasping refers to left-hand grasping alternated with right-hand pointing. Right-hand grasping refers to right-hand grasping alternated with left-hand pointing. $B_RB_HB_{VF}$ and $A_RA_HA_{VF}$ conditions are the same as in Fig. 4. For left-hand grasping, dPGA scores in $B_RB_HB_{VF}$ was significantly larger than in $A_RA_HA_{VF}$. But for right-hand grasping, there was no difference between $B_RB_HB_{VF}$ and $A_RA_HA_{VF}$. *Asterisk* indicates there are significant difference between two conditions (at least $P < 0.05$)

larger than that on closed-loop trials was consistent with Experiment 1. The difference between closed- and open-loop trials (dPGA) between the two hands was not significant, but there was a significant interaction between hand and condition (alternating vs. blocked). Follow-up analyses revealed that the dPGA of the left hand was greater in the alternating condition ($A_R A_H A_{VF}$) than it was in the blocked condition ($B_R B_H B_{VF}$), but there was no difference in dPGA for the right hand across conditions. These results indicated that the PGA of right hand on a grasping trial was not affected by a previous pointing trial by the left hand, but the PGA of the left hand was affected by a previous pointing trial by the right hand. In short, the results suggest that performance on a pointing trial with the right hand can affect grasping with the left hand, but such transfer cannot occur from the left hand to the right.

General discussion

Previous studies have shown that programming of grip aperture performed by right hand is affected by trial-to-trial experience of feedback but not by explicit knowledge of the availability of feedback on the upcoming trial (Whitwell et al. 2008), but left-hand grasping is influenced by such explicit knowledge (Tang et al. 2014). Nevertheless, there was some suggestion that, in addition to explicit knowledge, some other kind of trial-to-trial transfer of information occurred in the left hand. It was not clear, however, if this transfer was due to sensorimotor memory or a carry-over of task set. In this study, we used a task in which pointing was alternated with grasping in step with alternating open- and closed-loop feedback both within and between hands to determine which of these two mechanisms was at work.

We found that unlike what occurs in right-hand grasping, the programming of left-hand grasping is affected by a previous pointing trial performed by either the left or the right hand. These results make it clear that trial-to-trial transfer of information that affects the programming of grasping with the left hand is due to task set not to sensorimotor memory. In other words, it seems that grasping with the left hand (in right handers at least) is mediated by visuomotor networks that are quite different from those mediating grasping with the right hand in which trial-to-trial transfer depends entirely on sensorimotor memory.

Previous work showed that explicit knowledge also plays a role in trial-to-trial transfer on the left hand: there was a bigger difference in PGA between open- and closed-loop trials when they were alternated than when they were randomized (Tang et al. 2014). In this study, however, we found that the difference in the PGA for the left hand between open and closed loop was larger in the condition in which the hand, the response and the visual feedback were all blocked ($B_R B_H B_{VF}$) than when grasping with the left hand was alternated with pointing in step with visual feedback whether or not the participants always performed the movements with the left hand ($A_R B_H A_{VF}$) or whether they alternated between the left and the right hand ($A_R A_H A_{VF}$). This was true even though participants knew what the trial order was in all the conditions, i.e., they could predict with 100% certainty what visual feedback would be available on an upcoming trial. In other words, it appears that the left hand carries over some sort of task set when programming grasping movements, even though explicit knowledge may also play some sort of role.

The fact that task set can be transferred from pointing movements with the right hand to grasping with the left (non-preferred) hand suggests that whatever mechanisms are responsible are operating at some high level beyond programming the particular movements of the hand. Earlier work has shown that grasping with the left hand can be interfered with by high-level perceptual/cognitive factors. For example, Gonzalez et al. (2008) have shown that pictorial illusions affect left-handed grasping more than right-handed grasping. Perhaps then, it is not surprising that task set can be transferred from the movements made with the right hand, even pointing, when people grasp objects with their left hand.

Gonzalez et al. (2008) has shown that even left-handers prefer to use the right hand when grasping small objects. In addition, chimpanzees tend to use their right hand rather than their left to pick up small food items (Hopkins et al. 2002, 2006, 2007). As the current experiments have shown, grasping with the left hand but not the right is affected by task set. In addition, there is evidence that explicit knowledge (Tang et al. 2014) and other high-level cognitive factors such as illusions (Gonzalez et al. 2006) can affect grasping with the left but not the right hand. It would appear that grasping with the right hand is insulated from all these factors. The fact that right hand is more "automatic" and less sensitive to cognitive factors may contribute to the accurate control of movement and motor learning in this hand.

In summary, our results suggest that the programming of left hand exploits task set in a grasping task while the programming of right hand is influenced only by sensorimotor memory of performance on a previous trial. This difference in programming between two hands provides new evidence for a specialization of the right hand (and thus the left hemisphere) in the performance of skilled prehension movements.

Acknowledgements Thank Dr. Melvyn A. Goodale for the comments on the manuscript and help on writing. This study was supported by grants from National Natural Science Foundation of China (Grant #31571131) to R.T.

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