Action Training Facilitates Perception and Cognition

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CHAPTER 1: INTRODUCTION

A long-lasting debate for understanding human behavior is whether human actions are merely the external expressions of mental functions or they can inversely shape internal processes such as perception and cognition. Historically, the information-processing theory established a one-way information flow of acquiring perceptual input, processing the information with high-level cognition, and then planning and executing appropriate actions (Johnson-Laird, 1988; Newell & Simon, 1972; Sanders, 1980; Sternberg, 1969). This linear processing prospective from perception to action can be applied to explain many daily life examples. For example, humans perceive the size of an object to open the thumb and index fingers to grasp the object (Jeannerod, 1984; Wing, Turton, & Fraser, 1986). Previous studies showed that the maximum aperture between the thumb and index finger during the grasping is achieved before touching the object and linearly correlated with object size, suggesting maximum aperture during the action is shaped by the size information obtained during preceding perceptual processes (Jeannerod, 1984; Wing, Turton, & Fraser, 1986). In addition, extensive evidence showed that a cognitive rehearsal of a motor task in the absence of overt physical activity enhances the subsequent movement performance (for reviews, see Feltz & Landers, 1983; Driskell, Copper, & Moran, 1994). Hence, investigating how perception and cognition influence action flows logically. Investigating the inverse may seem unusual.

However, accumulated evidence has tended to show co-dependence between perception and action. For instance, planning actions affects how we perceive action-relevant features of

objects (Bekkering & Neggers, 2002; Fagioli et al., 2007; Gutteling et al., 2013, 2015). Participants enhanced their perceptual sensitivity to orientation changes between two targets when they prepared to grasp the target, which requires orientation information, rather than when pointing to it regardless its orientation (Gutteling et al., 2011). In the experiment, participants were instructed to grasp a bar to align with its orientation or point the center of the bar regardless of its orientation. While participants were preparing for the action, they were also required to detect whether two tilted bars had the same or different orientations. The results demonstrated that participants had higher sensitivity of orientation-change detection during grasping preparation than pointing preparation, suggesting that action preparation can facilitate perceptual processes of action-relevant features.

Moreover, recent evidence suggests that perception is also modulated by the action abilities of individual participants (Linkenauger et al., 2009; Witt & Proffitt, 2005). For example, Witt and Proffitt (2005) demonstrated that softball athletes with better batting averages reported perceiving a ball as bigger. Specifically, softball players who just finished a game were presented multiple circles with different diameters and were instructed to report which circle was closest to the size of a real softball. As the results, players with better batting scores chose a larger circle to match the real ball, suggesting that perception might be altered accordingly by motor skill levels. Moreover, individuals reported the apparent distance to a target as longer when they throw a heavy ball compared to a light ball (Witt, Proffitt, & Epstein, 2004). Collectively, all these studies demonstrate reciprocal interactions between perception and action.

In addition, the reciprocal interaction between perception and action is strongly implicated by the close connections between motor system and perceptual systems in the brain. For example, precise timing appears to be an important mechanism involved in both the

perception and action domains. Neural evidence has demonstrated that perceptual and motor timing tasks involve similar brain regions (Ivry & Diener, 1991; Ivry, Keele, & Diener, 1988; Schubotz et al., 2000). For instance, cerebellum legions result in deficits in both auditory time-interval discrimination tasks (Ivry & Keele, 1989) and simple finger tapping tasks (Inhoff et al., 1989).

Similarly, previous studies also demonstrated the interactions between cognitive and motor processes by their behavioral correlation or overlapping neural networks. For example, manually rotating a wheel interfered with the concurrent mental rotation of cubes (Sack, Lindner, & Linden, 2007). Neurophysiological studies revealed that mental rotation can be performed by simulating manual rotation covertly and this covert simulation activates motor cortex (Cohen et al., 1996; Kosslyn et al., 1998; Kosslyn et al., 2001). In addition, mental rotation and visuomotor rotation, a motor task that requires adaptation to rotated visual feedback of real-time hand movement, share common processing constraints and neural correlates. Pellizzer and Georgopoulos (1993) showed that processing rates of visuomotor rotation and visual mental rotation, which were revealed by the linear relation between rotated angles and response times, were positively correlated. A recent fMRI study found common brain regions underlying visuomotor adaptation and mental rotation (Anguera et al., 2010; Schlegel et al., 2016). These studies demonstrated the co-dependence between motor and mental rotation since they share a common rotation component.

Taken together, previous work has clearly demonstrated that there is a close connection between perception, cognition and action, suggesting that a more integrated approach beyond linear stage model is necessary to understand complex human behavior in our daily life. So far, a few theories have been proposed to explain the mechanisms underlying the dynamic interactions

between these mental processes. In the following section, I will introduce two mainstream theories: the theory of event coding and ecological approach.

Two mainstream theories of how action influences perception and cognition

The theory of event coding (TEC). Prinz (1990) proposed TEC to challenge the traditional information-processing view that there is sequential processing from perception to action. The basic principle of TEC is that the representations of perceived events (perception) and to-be-generated events (action) share the same coding in a common-coding system (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990, 1997; Schütz-Bosbach & Prinz, 2007). Hommel et al. (2001) further developed the theory and stated that both perceiving the environment and planning actions require equivalent cognitive processes of forming internal representations of external events. Specifically, perception is not passively receiving information from the environment but actively collecting information from the environment, which involves many sorts of action, such as eye movements during allocations of attention. Planning actions also involves many types of perceptual processes including acquiring current perceptual information in the environment and predicting the perceptual consequences of actions. Therefore, the tight co-dependence relationship between perception and action supports the core assumption that internal representations of perceptual events and action events are coded together in a common domain.

Hommel et al. (2001) explained what the concept *codes* specifically indicates in the theory. TEC assumes that both perception and action events are composites of distal features that are coded distributivity across different functional modules located in different cortical areas. According to TEC, distal features refer to abstract features of the perception and action events,

such as the *distance* or *direction* of objects. For example, in a case where participants were required to press a key with their left hand to indicate a left-tilted bar, the common distal feature *left* was shared by left-hand keypress and left-tilted bar (Müsseler & Hommel, 1997). Furthermore, the feature *left* in the common coding system was an abstract feature on the representation-level but not a concrete feature with specific neural activation patterns (Hommel et al., 2001).

Many studies have used TEC to explain their experimental results and therefore supported the theory (Kunde & Wühr, 2004; Müsseler & Hommel, 1997; Wühr & Müsseler, 2001). For instance, preparing an action enhances perceptual sensitivity of action-relevant features (Diedrichsen, Ivry, Cohen, & Danziger, 2000; Hommel & Schneider, 2002; Miall et al., 2006). Generating eye movements to a target specifically improves the spatial perception at the target location (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Neggers et al., 2007). Based on TEC (Hommel et al., 2001), planning eye movements to a location activates a code, a specific location, and further primes other events involving the same location.

Moreover, motor timing abilities involved in rhythmic movements, such as finger tapping, are closely related to perceptual sensitivity of timing (Keele, Pokorny, Corcos, & Ivry, 1985; Manning & Schutz, 2013), suggesting a common coding of timing. In Manning and Schutz's study (2013), participants heard a periodic beep sound sequence with fixed time intervals between every two beep sounds. After the periodic beep sequence, a silent period was followed and then the final probe beep would be presented. Participants were required to judge whether the final probe beep after the silent period was on the sequence track of the previous periodic beep sequence. The results showed that participants who tap their fingers along with the repeated beep sequence are better at identifying whether the final probe beep is on the track or

not compared with participants who do not tap their fingers, suggesting body movements improve perception of timing. Furthermore, fMRI studies have shown that motor timing shares a common brain basis with time perception (Schubotz, Friederici, & Cramon, 2000), which provides the possible neural evidence of TEC (Hommel et al., 2001). All the results suggest that there is a common internal timing mechanism, corresponding with the common-coding system in TEC, across perception and action domains.

There are also studies that provide neurobiological evidence for TEC (Etzel, Gazzola, & Keysers, 2008; Dayan et al., 2007; Melnik, Hairston, Ferris, & Konig, 2017). One example is that there are "mirror neurons" in monkey brains that can be activated by both executing actions and observing others performing actions (di Pellegrino et al., 1992; Gallese et al., 1996). Mirror neurons were suggested to be the possible neuronal substrate of the common coding system in TEC (Hommel et al., 2001). In an fMRI study, Etzel et al. (2008) provided further evidence on humans that perceiving actions of other people shares common codes with executing actions. In the fMRI scan, participants listened to the sound of hand actions (e.g., the sound of ripping paper) or mouth actions (e.g., the sound of crunching food) or executed these actions by themselves. The fMRI signals obtained in the listening task were used to train a classifier to separate the listened stimuli into two action categories (hand actions vs. mouth actions). The trained classifier was then applied on fMRI signals obtained in the execution tasks to separate the two types of actions. Their results show that the classifier, learned from sensory signals in the listening task, can successfully separate motor signals in the action execution task, suggesting that perceiving actions and executing actions share common neural activity patterns. Moreover, an EEG study showed that there are common EEG components involved in both perception and

motor processes (Melnik et al., 2007). The neuronal evidence describes the possible neural substrates that might be involved in the common coding system in TEC.

Ecological approach. According to Gibson (1979), animals perceive the environment based on its affordances. "Affordance" refers to the potential actions that could be provided by the environment to the animals. For example, the staircases that are 20 cm high can be perceived as "climbable" by adults but not by the crawling infants. Affordances are inherent in the object itself and can be perceived directly without any elaborate processing (Gibson, 1979). For instance, stairs have inherent stimulus characteristics that can be perceived directly by adults to inform "climbable" without further computational processing in the visual system. In sum, the ecological approach links perception and action through the affordances of environment. This approach states that there is a direct information pick-up from the environment rather than indirect perception involving inference and complicated computations (e.g., Bruggeman, Zosh, & Warren, 2007; Warren et al., 2001).

The action-specific perception theory based on Gibson's (1979) ecological approach further narrowed down the scope of action. It specifically argued that human's ability to act influences how they perceive the environment (Proffitt, 2006; Witt, 2011). There is evidence showing that action abilities can be affected by many factors, such as body size, energetic potentials, task demands and so on (Witt, 2011). Moreover, Witt (2011) demonstrated that action abilities are dynamic factors and can be improved through training.

To test the action-specific perception theory, a series of experiments have been conducted to measure the effect of action ability on different types of perception. For example, the difficulty level of the tasks impacts the perceived speed of objects (Witt & Sugovic, 2010, 2012,

2013a, 2013b). In Witt and Sugovic (2013a), participants were instructed to release a virtual net to catch a virtual fish moving with different speeds on the screen and then report the speed of the fish by keypress. The results showed that when the virtual net is bigger (i.e., task is easier), participants report the speed of the fish as slower and release the net later, which suggested that they perceived the speed of the fish slower. Moreover, the task difficulty also impacts the perceived distance of targets (Witt, Proffitt, & Epstein, 2004; Linkenauger, Witt, Stefanucci, Bakdash, & Proffitt, 2009). For example, Witt, et al. (2004) found that participants would verbally report the target to be at further distance if they were asked to throw a heavy ball, rather than a light ball, to hit the target.

Collectively, previous research and the two theories have provided evidence supporting the concept of interactions between action, cognition and perception. However, whether improvement in one process can lead to changes in the other largely remains unknown, especially how action training might influence perception and cognitive processes. A previous study has shown that past action experience altered visual perception within hand-grasping space (Thomas, 2017). Specifically, this study demonstrated that training with a power grasp (i.e., using the backs of the hands) or a precision grasp (i.e., using the tips of the fingers) selectively enhanced a subsequent motion detection task or form perception task near the hands with the same grasp training posture, respectively. In light of these findings, it is important to further test how action training influences subsequent perceptual or cognitive processes.

In this dissertation, to broaden the understanding of the dynamic interactions between perception, cognition and action, I examined the effect of action training on different types of perceptual and cognitive processes in the three following chapters. Specifically, in Chapter 2, I examined how improved or improving the precision of a simple action (e.g., grasping) impacts

early visual processing. In Chapter 3, I further investigated how action training requiring more complex movements, i.e. throwing, impacts time perception. Furthermore, Chapter 4 established the reciprocal interactions between motor learning and cognitive training.

CHAPTER 2: ACTION FLUENCY FACILITATES PERCEPTUAL DISCRIMINATION

ABSTRACT

Perception and action interact in nearly every moment of daily life. Previous studies have demonstrated not only that perceptual input shapes action but also that various factors associated with action—including individual abilities and biomechanical costs—influence perceptual decisions. However, it is unknown how action fluency affects the sensitivity of early-stage visual perception, such as orientation. To address this question, we used a dual-task paradigm: Participants prepared an action (e.g., grasping), while concurrently performing an orientation-change-detection task. We demonstrated that as actions became more fluent (e.g., as grasping errors decreased), perceptual-discrimination performance also improved. Importantly, we found that grasping training prior to discrimination enhanced subsequent perceptual sensitivity, supporting the notion of a reciprocal relation between perception and action.

Introduction

Our daily experience can be thought of as a sequence of acquiring perceptual input to make decisions, then planning and executing appropriate actions. Hence, examining the influence of perception on action flows logically. Investigating the inverse may seem unusual; however, accumulated evidence suggests codependence between action and perception. For instance, planning actions affects how we perceive action-relevant features of objects (e.g., Bekkering & Neggers, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Gutteling, Park, Kenemans, & Neggers, 2013). In addition, when participants performed the same hand action as they observed in pictures of hand images, they quickly detected an embedded oddball image that showed a different hand posture. This suggests that executing actions also assists perceptual processes in action-related tasks (Miall et al., 2006). Moreover, recent evidence has demonstrated that individual action abilities influence perception (for a review, see Witt, 2011). For example, softball players with higher batting averages reported seeing a ball as bigger (Witt & Proffitt, 2005).

Recent studies have reported that biomechanical costs associated with action outcomes affect perceptual decision-making processes. For instance, changes to perceptual decisions occurred less frequently when the physical effort associated with modifying a planned action was high (Burk, Ingram, Franklin, Shadlen, & Wolpert, 2014; Moher & Song, 2014). Hagura, Haggard, and Diedrichsen (2017) demonstrated that the cost of action could bias not only perceptual-decision thresholds but also the percept itself: Participant responses were biased away from response options associated with high resistance in a motor task. This result suggested that the ease of action can impact perceptual processes. In light of these findings, it is important to

further test whether a basic visual property processed in early visual cortex, such as orientation (Hubel & Wiesel, 1974), can also be influenced by action fluency.

Moreover, the fluency level of actions is not constant but can change with repeated practice in daily life. A previous study has shown that past action experience altered visual perception within the hand-grasping space (Thomas, 2017). Specifically, training with a power grasp (i.e., using the backs of one's hands) or a precision grasp (i.e., using the tips of one's fingers) selectively enhanced subsequent motion detection or form perception, respectively, near the hands with the same grasp-training posture. Gonzalez, Ganel, Whitwell, Morrissey, and Goodale (2008) reported that the grip aperture of an awkward right-hand grasp, which was sensitive to the size-contrast illusion at the beginning, became resistant to the illusion after practicing, suggesting that actions of different difficulty levels involve distinct visual mechanisms.

However, no one has yet examined how preparing actions with different fluency levels modulates early visual processing, such as orientation discrimination, and how enhanced action fluency through training affects later orientation discrimination. In the present study, we systematically examined the relation between action fluency and the sensitivity of orientation discrimination, with the goal of broadening the reciprocal interactions between perception and action. Specifically, we first examined how preparing grasping actions with different fluency levels impacted a simultaneously performed orientation-discrimination task using an unbiased measurement from signal detection theory (i.e., d'; Macmillan & Creelman, 2004). We established that participants increased orientation-discrimination sensitivity as their action fluency increased with their dominant hands (Experiments 1 and 2) but not with their non-dominant hands (Experiment 3). We further demonstrated that without simultaneous action

preparation, improving grasping precision through action training resulted in enhanced orientation-discrimination sensitivity in subsequent test trials (Experiment 4). Together, these experiments provide robust evidence that improved or improving action fluency can lead to enhanced perceptual-discrimination sensitivity.

Experiment 1: Effects of Action Fluency on Orientation Discrimination

To examine how the ease of action affects perceptual discrimination during grasping-movement preparation, we created four stimulus types requiring varying degrees of wrist supination, which resulted in different difficulty levels of grasping. For each participant, we also correlated the sensitivity of perceptual discrimination with grasping-angle error across four stimulus types to evaluate the effect of action fluency. We predicted that as grasping became easier (i.e., as the magnitude of grasping-angle errors decreased), orientation discrimination would be enhanced.

Method

Participants. Twenty-five Brown University students (4 males; mean age = 21.28 years) participated in a 1-hr session for course credit or monetary compensation. The sample size was determined on the basis of the effect size needed to achieve 90% statistical power ($d = 0.67$, $n = 16$) as determined with a one-sample t test on preliminary data. Participants were right-handed with normal or corrected-to-normal color vision and were naive to the aims of the experiment. All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

Apparatus. Stimuli were projected from a PJD6221 projector (60 Hz; ViewSonic, Brea, CA) positioned behind a plexiglass display (21.5 in.; 1,280 × 1,024 pixels) that was placed upright on a table perpendicular to the participant's line of vision (Fig. 2.1). The distance between the seated participant and the plexiglass display was approximately 52 cm. The size of the stimuli was adjusted relative to the viewing distance to keep the visual angle of the stimuli constant. The stimulus computer was a 2.3 GHz Dell OptiPlex 780 with a GeForce 8500GT graphics processor (256 MB of Double Data Rate 2 synchronous dynamic RAM; Nvidia, Santa Clara, CA). Three-dimensional positions of two fingers were recorded simultaneously at a rate of approximately 160 Hz using an electromagnetic position-and-orientation recording system (Polhemus Liberty 240/8, Colchester, Vermont) with a root-mean-square measurement error of 3 mm. Two motion-tracking markers were separately secured with a Velcro strap near the tip of each participant's right index finger and thumb. The participant's index finger and thumb rested on two Styrofoam blocks placed in front of him or her on the table, located 27 cm (index finger) and 33 cm (thumb) from the screen along the *z*-dimension (the axis that is bounded by the participant and the display). The two fingers were aligned with the bottom of the display along the *y*-dimension (the axis that is bounded by the top and bottom of the display). The index finger was aligned with the horizontal midline of the display along the *x*-dimension (the axis that is bounded by the left and right sides of the display). The thumb was aligned 2 cm to the left from the midline of the display along the *x*-dimension.

Stimuli. All stimuli appeared on a gray background. Participants were instructed to fixate on a white dot (0.25° of visual angle) presented at the center of the screen. Each individual Gabor element consisted of a 1-cycle-per-degree sinusoidal grating multiplied by a circular Gaussian

with a standard deviation of 1.25° of visual angle. All Gabor patches were blocked by a sharp edge and were visible within 4° of visual angle. The spatial frequency, the size, and the contrast (full) of Gabor patches were constant across the threshold-baseline test and the main experiment. In the threshold-baseline test, one Gabor patch and a dashed line (6° of visual angle) behind the patch were shown at the same time. The Gabor patch and the dashed line shared the same center. The dashed line was visible only where it extended 1° beyond the edges of the Gabor patch (Fig. 2.2). Stimulus were presented using custom software designed with MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997).

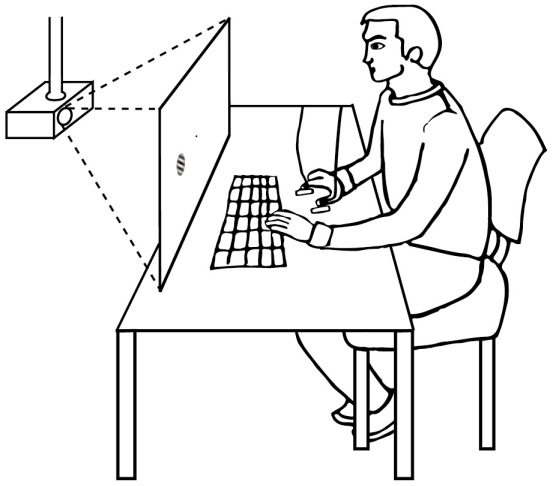


Fig. 2.1. Experimental set-up. In all three experiments, visual stimuli were projected onto a plexiglass screen by the projector behind it. The plexiglass screen stood upright on the table and perpendicular to the participant's line of vision. Two motion-tracking markers were secured on each participant's right index finger and thumb, which each rested separately on a fixed Styrofoam block as start points. The right index finger was aligned with the horizontal middle line of the screen display. The left hand rested on a keyboard to prepare for the button-press response.

Procedure. First, using double staircases (80% accuracy, three down, one up), we determined each participant's threshold of orientation-change detection with a Gabor patch (see Fig. S1 in the Supplemental Material for details). Once the threshold (*t*) was determined in the threshold-

baseline test (t = 8.56° ± 2.08°), participants simultaneously performed grasping and perception tasks in the main experiment (Fig. 2.2).

Every trial, after participants put two fingers of their right hand on the start points, a fixation dot appeared on screen and remained for 1,750 ms, 2,000 ms, or 2,250 ms. If either finger left the start point during the fixation period, the fixation time was reset. Then, as in the threshold-baseline test, the first Gabor patch was presented at 8.5° eccentricity to the left or right side of the central fixation dot for 100 ms; it then disappeared for 200 ms. As soon as the fixation dot disappeared, the second Gabor patch appeared at the same location as the first patch. The orientation of the first patch was the same (50%) or tilted either 1.5 × t (small-size condition) or 2 × t (large-size condition) from the second one (50%). Because the two patches were either identical or different only to a small degree, the first one could provide sufficient information for action preparation. Thus, participants were instructed to prepare for grasping the second Gabor patch (i.e., the target) as soon as the first patch appeared (i.e., the go cue). They were also instructed to simultaneously determine whether the orientations of the first and second Gabor patches were the same or different during grasp preparation.

Participants applied a precision grip and placed their index finger and thumb at the edge of the second Gabor patch by aligning the wrist of their right hand with the orientation of the grating. To vary levels of grasping difficulty from hard to easy, we created four types of the second Gabor patch (for the grasping condition), each having one of two tilts (135° vs. 45°) and appearing on one side of the screen (left vs. right), as shown in Figure 2.3a. The second patch stayed on screen until participants finished the trial. Auditory feedback was provided to indicate that they had completed the grasping portion of the trial. After finishing their grasp, participants

pressed a button with their left hand to report whether the orientations of the two Gabor patches were the same or different. Auditory feedback again indicated completion of the button press.

After one practice block, participants performed 12 trial blocks, consisting of 6 blocks for each tilted-size condition (small or large). Each block consisted of 32 trials—8 trials for each grasping condition. All blocks were alternated and counterbalanced across participants.

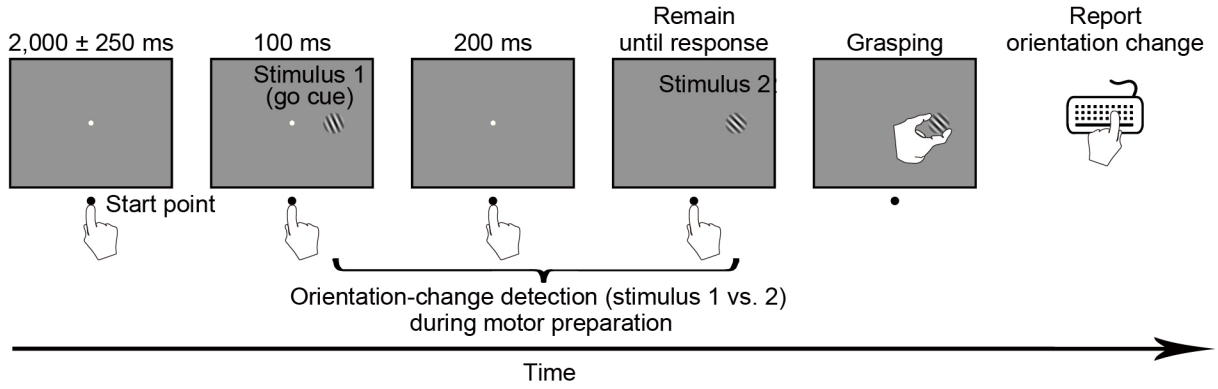


Fig. 2.2. Trial sequence for the main experiment in Experiment 1. Participants performed a grasping task and a perception task in each trial. The first stimulus was presented for 100 ms and disappeared (i.e., go cue), and after 200 ms, the second stimulus was presented as an action target. In the perception task, participants reported whether the orientations of the two stimuli were the same or different by pressing a button with their left hand.

Data analysis. In the grasping task, we differentiated the position of the marker on the index finger to obtain tangential velocity. The beginning and end of the movement were defined, respectively, as the points at which the index finger exceeded and fell below 15 cm per second. We measured initiation time as the time elapsed from the onset of the go cue (first patch) to the onset of the movement and movement time as the time elapsed between the beginning and end of the movement. Grasping-angle error was defined as the absolute angle difference between actual grasping angle and the orientation of the second Gabor patch. In the perception task, we calculated d' (Macmillan & Creelman, 2004) separately on the basis of all trials in each tilted-

size condition. We also performed a linear regression between grasping-angle error and d' for each action-fluency condition within each participant.

All data processing and statistical analyses were performed using MATLAB and Prism (Version 6.00 for Mac, GraphPad Software, La Jolla, California). We analyzed the data using repeated measures analyses of variance (ANOVAs). Greenhouse-Geisser correction (Maxwell & Delaney, 2004) was used if the assumption of sphericity was violated. All error bars were calculated as standard errors of the mean. The effect size of ANOVAs was measured by eta-squared (η^2); the effect size of *t* tests was measured by Cohen's *d*. According to Cohen (1988), η^2s of .01, .06, and .14 and Cohen's *d*s of 0.20, 0.50, and 0.80 are considered small, medium, and large, respectively.

Results

Because results from the small- and large-size conditions were similar overall, we focused on data from the large-size condition, while reporting data from the small-size condition in the Supplemental Material (see Fig. S2 in the Supplemental Material).

First, to confirm that we successfully created four grasping conditions with varying difficulties from hard to easy, we analyzed grasping-angle errors. As shown in Figure 2.3b, the four grasping movements we created from hard to easy had corresponding grasping-angle errors from large to small. A one-way repeated measures ANOVA across the four grasping conditions showed a significant main effect, $F(1.56, 37.39) = 28.24$, $p < .001$, $\eta^2 = .35$. A post hoc test for the linear trend of grasping-angle error across the four grasping conditions was significant, slope $= -2.11$, $R^2 = .33$, $p < .001$, showing that the easiest grasp produced a 40.31% reduction in grasping-angle error compared with the hardest grasp.

Of interest was whether perceptual performance across the four grasping conditions was affected by grasping fluency. Higher *d′* scores indicate better perceptual-discrimination sensitivity (Macmillan & Creelman, 2004). Figure 2.3c shows that in the easier grasping conditions, participants showed better perceptual performance. A one-way repeated measures ANOVA across the four grasping conditions showed a significant main effect, $F(2.25, 53.95) = 3.41$, $p = .035$, $\eta^2 = .03$. The post hoc test for the linear trend of *d′* scores across the four grasping conditions was also significant (slope = .07, $R^2 = .03$, $p = .003$), showing that the easiest grasp produced an 11.35% improvement in perceptual performance compared with the hardest grasp.

Next, we asked whether perceptual discrimination is enhanced as grasping becomes easier in each individual: Is smaller grasping-angle error (easier action) correlated with better visual performance (higher *d′* score)? To address this question, we first normalized grasping-angle error in each participant using Equation 1, leading to the range of [0, 1]:

$$\text{normalized grasping-angle error (GAE)} = \frac{\text{GAE} - \min \text{GAE}}{\max \text{GAE} - \min \text{GAE}}, \quad (1)$$

where GAE is the grasping-angle error in each trial, and min GAE and max GAE are the minimum and maximum grasping-angle errors across all four grasping conditions. We separately calculated normalized error in each tilted-size condition (small vs. large). After normalizing the grasping-angle errors, we calculated the mean value in each grasping condition; then we applied a linear regression between *d′* score and normalized grasping-angle error for each participant, as shown in Figure 2.3d. A negative slope means that as grasping errors decreased, perceptual sensitivity (*d′*) increased, indicating that easier action was associated with better perceptual

performance. Conversely, a positive slope between d' and normalized grasping-angle error means that perceptual performance was worse for the easier action. We found two outliers using the combined robust regression-and-outlier-removal (ROUT) method (Motulsky & Brown, 2006). Figure 2.3e shows the distribution of slopes for 23 participants. Overall, the majority of participants had negative slopes, suggesting that grasping-angle error was negatively correlated with perceptual performance. A one-sample t test of slopes showed that the mean of slopes was significantly smaller than 0, $t(22) = 2.72$, $p = .013$, $d = 0.57$. We also calculated velocity, initiation time, and movement time across the four grasping conditions to assure that observed correlation between action and perception was not mediated by different strategies (see Fig. S3 in the Supplemental Material for details).

In sum, we showed that as participants prepared easier grasping, they achieved better visual discrimination. Moreover, we also observed that within the majority of individuals, visual-perceptual performance was negatively correlated with action error, suggesting that easier actions increasingly enhanced visual performance.

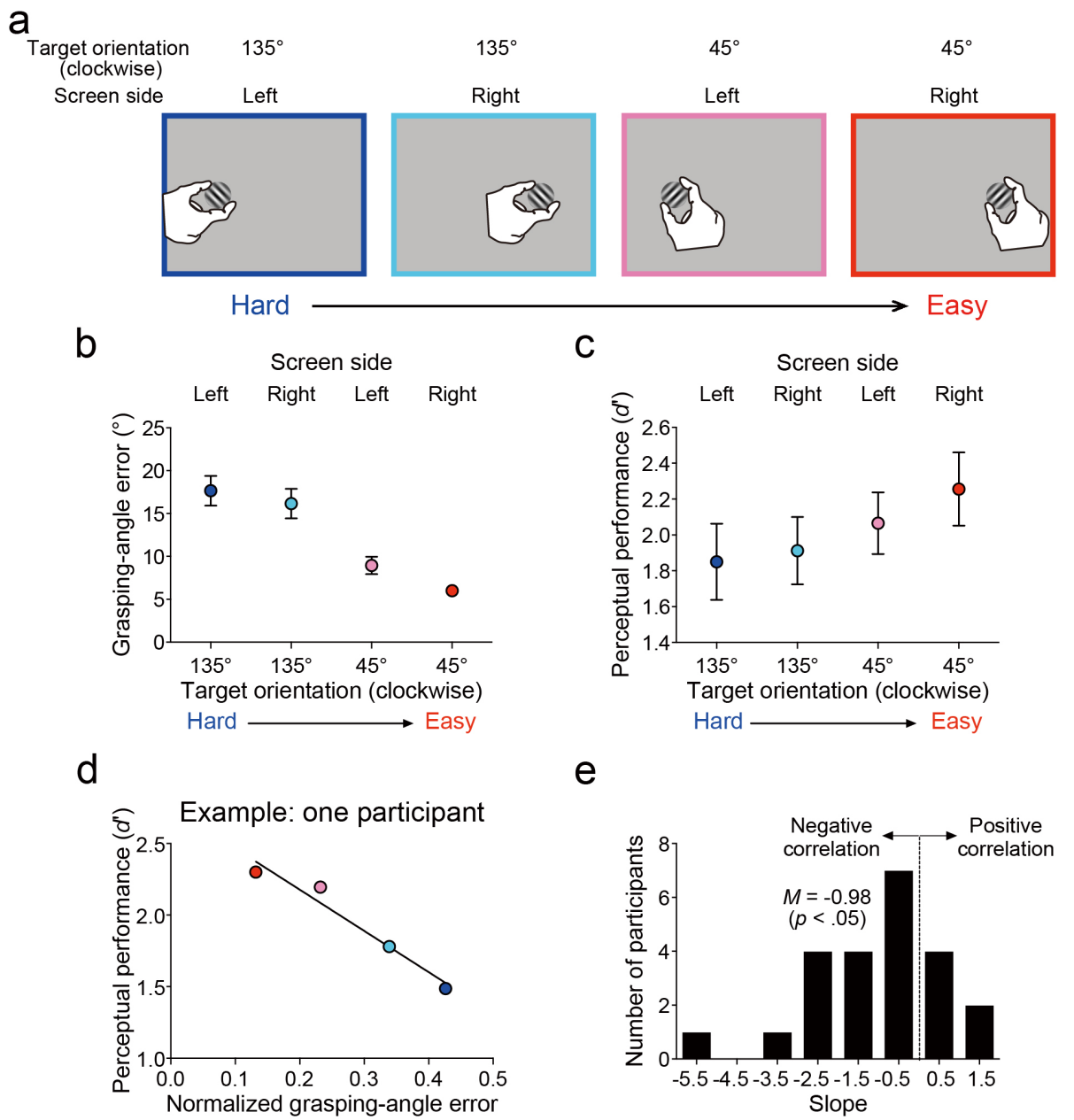


Fig. 2.3. Grasping conditions and results from the large-size condition in Experiment 1. The four grasping conditions created for Experiment 1 (**a**) varied from hard (low action fluency) to easy (high action fluency). Mean grasping-angle error (**b**) and perceptual performance (**c**) are shown as a function of target orientation and grasping condition. The four grasping conditions are sorted by action fluency (hard to easy) from left to right; the dot colors correspond to the conditions indicated by the colors of the borders in (**a**). Error bars show standard errors of the mean. An example linear regression for one participant (**d**) is shown for the relation between normalized grasping-angle error and perceptual performance in each of the four grasping conditions. The colors of the dots correspond to the conditions indicated by the colors of the borders in (**a**). The equation of the line is $y = -2.881 * x + 2.754$. The frequency distribution of slopes for 23 participants is shown in (**e**). The dashed line indicates 0 on the x-axis. Values to the left and right of the dashed line indicate whether d' scores and grasping-angle errors were negatively or positively correlated, respectively. The mean slope across participants was determined to be significantly different from zero using a one-sample t test.

Experiment 2: Effects of Different Actions on Orientation Discrimination

In Experiment 1, we found that the target orientation inducing easier grasping corresponded to better orientation-discrimination sensitivity. To further ensure that this enhanced discrimination sensitivity was primarily led by action fluency, not by some intrinsic difference of discrimination sensitivity between target orientations, we introduced pointing and no-action tasks in Experiment 2. We reasoned that different target orientations (left tilted vs. right tilted) would not affect the ease of aiming at the center of the target in the pointing task or the state in the no-action task. If action fluency were critical, we reasoned, the target orientations would modulate discrimination sensitivity only when participants prepared for grasping but not in the pointing or no-action tasks.

Method

Participants. Thirty-two Brown University students participated in an approximately 1-hr experimental session for course credit or monetary compensation. We conducted two experiments, each with 16 participants (Experiment 2a: 7 males; mean age = 21.9 years; Experiment 2b: 6 males, mean age = 20.38 years). The sample size (16 per group) was determined on the basis of the effect size needed to achieve 80% statistical power ($d = 0.85$, $n = 16$) as determined with a paired-samples t test on preliminary data. Participants were right-handed with normal or corrected-to-normal color vision and were naive to the aims of the experiment. All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki. Experiment 2b was a preregistered replication of Experiment 2a.

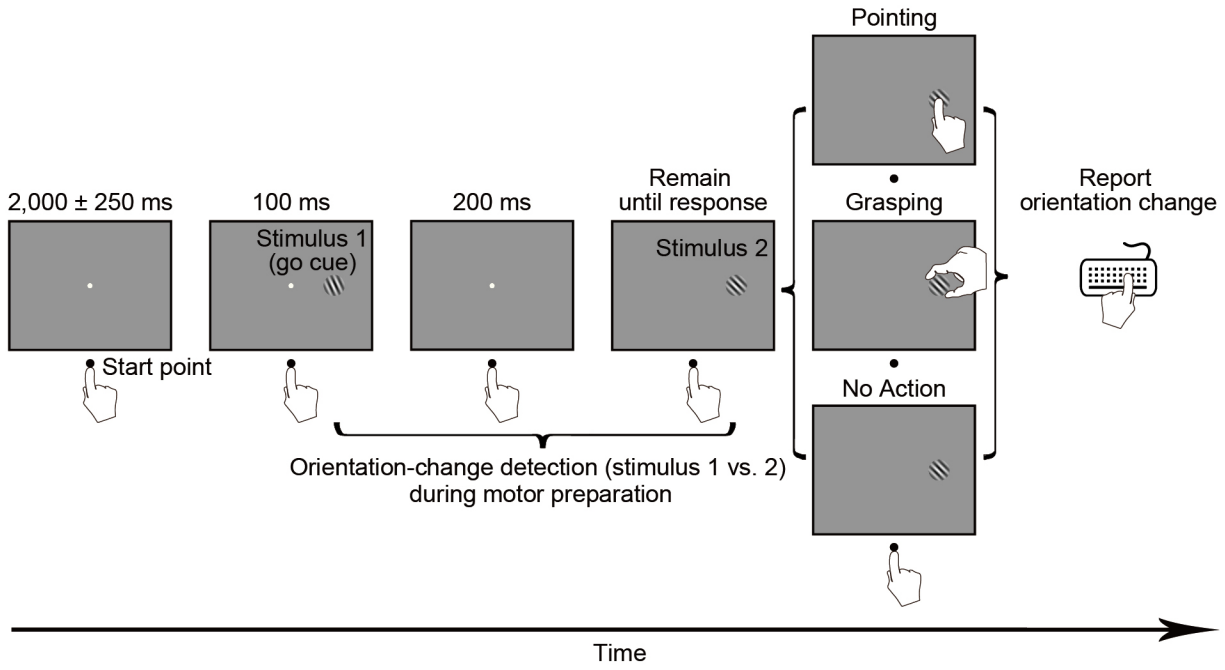


Fig. 2.4. Trial sequence in the main experiment of Experiment 2a. Participants performed a combined action task and perception task in each trial. The first stimulus was presented for 100 ms and disappeared (i.e., go cue), and after 200 ms, the second stimulus was presented as an action target. In the action task, participants performed one of three tasks: pointing to the center of the target, grasping the edge of the target by aligning their wrist with the orientation of the target, or completing no action. In the perception task, participants reported whether the orientations of the two stimuli were the same or different by pressing a button with their left hand.

Procedure. In Experiment 2a, we used almost the same procedure as in the large-size condition of Experiment 1, in which the first patch was tilted from the second one $2 \times t$ degrees ($t = 8.53° \pm 1.82°$). There were just a few modifications: Most importantly, in addition to the grasping task, we added two action tasks—pointing and no-action (Fig. 2.4). In the pointing task, participants simply pointed to the center of the second patch with the index finger of the right hand. In the no-action task, participants kept the index finger and thumb of their right hands at the start points and were allowed to press the button after the appearance of the second patch. We anticipated that the two orientations of the second Gabor patch (Fig. 2.5a) would lead to grasping with different fluency levels— hard (45° left-tilted target) versus easy (45° right-tilted target)—but that no such fluency differences would be present in the pointing and no-action tasks. Note that

to acquire sufficient trials within a 1-hr session in the pointing, grasping, and no-action tasks, we collapsed trials with Gabor patches presented on the left and right sides of the screen and categorized them on the basis of orientation (45° left-tilted or right-tilted from the vertical line; Fig. 2.5a). Participants practiced one block each of the pointing, grasping, and no-action tasks prior to the main experiment. After practice, they performed six blocks (two blocks each for pointing, grasping, and no-action), and each block consisted of 32 trials. All blocks were alternated and counterbalanced among participants. We subsequently conducted Experiment 2b to replicate key outcomes from Experiment 2a, with one modification. In addition to the large-size condition, participants also completed the small-size condition in which the first patch was tilted from the second one 1.5 × t degrees (t = 8.88° ± 1.45°).

Data analysis. In addition to the analyses used in Experiment 1, we defined pointing error as the distance between the pointing touch point and the center of the second Gabor patch. In the perception task, we calculated d' separately on the basis of all trials in each task (pointing, grasping, no action) and each tilted-size condition (small, large). We analyzed the data using repeated measures ANOVAs. For multiple post hoc comparisons, we applied Šidák correction (for comparisons between multiple treatment groups; Šidák, 1967) and Dunnett correction (for comparison of treatments with a single control group; Dunnett, 1955). Using a paired-samples t test to investigate the null hypothesis that there was no difference between results for the two stimulus types, we estimated the Jeffreys-Zellner-Siow (JZS) prior Bayes factor with a default scale (r) of 1 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). A JZS Bayes factor indicates the ratio of marginal likelihoods for given null hypothesis and alternative hypothesis. For instance, a JZS Bayes factor larger than 1 indicates that the probability density function of the

data under the null hypothesis is larger than that under the alternative hypothesis, suggesting in favor of the null hypothesis.

Results

Because results from Experiments 2a and 2b were similar overall, we focus here on Experiment 2a, reporting Experiment 2b in the Supplemental Material (Fig. S4 in the Supplemental Material).

In Experiment 2a, we confirmed that the target orientations modulated the difficulty of grasping, but not pointing, by analyzing pointing error and grasping-angle error. While pointing errors (Fig. 2.5b) were equivalent, $t(15) = 0.69$, $p > .250$, $d = 0.17$, Bayes factor = 4.23, grasping-angle errors (Fig. 2.5c) were larger toward a left-tilted than a right-tilted target, $t(15) = 2.87$, $p = .012$, $d = 0.72$.

As shown in Figure 2.5d, perceptual-discrimination sensitivity (d') was not affected by the orientation of stimuli during the pointing task, $t(30) = 0.71$, Šidák- adjusted $p > .250$, $d = 0.13$, Bayes factor = 4.17, or the no-action task, $t(30) = 1.64$, Šidák-adjusted $p > .250$, $d = 0.44$, Bayes factor = 1.61. Note that in these tasks, the difficulty of actions was not affected by the stimulus orientation.

Yet in the grasping task, in which the grasping difficulty was caused by orientation differences (left or right tilted), the outcome was different. As in Experiment 1, when participants grasped the right-tilted stimulus (Fig. 2.5d), their perceptual-discrimination sensitivity was higher compared with when they grasped the left-tilted stimulus, $t(30) = 3.60$, Šidák-adjusted $p = .003$, $d = 0.82$. This result assured us that ease of action modulated perceptual discrimination. A two-way repeated measures ANOVA with the factors task (pointing, grasping,

and no-action) and stimulus type (left-tilted and right-tilted) showed a significant main effect of task, $F(2, 30) = 3.54$, $p = .042$, $\eta 2 = .06$, and a significant interaction, $F(2, 30) = 7.81$, $p = .002$, $\eta 2 = .04$. We also confirmed that enhanced discrimination in the right-tilted condition compared with the left-tilted condition was not led by different characteristics of kinematics such as velocity, initiation time, and movement time (see Fig. S5 in the Supplemental Material for details) or by longer delays between the stimulus presentation and discrimination reaction time (see Fig. S6 in the Supplemental Material for details).

We also performed the linear correlation between action and perceptual performance in the grasping task for all participants in Experiments 2a and 2b, as in Experiment 1. We obtained the same negative correlation pattern between grasping-angle error and perceptual performance (see Fig. S7 in the Supplemental Material for details).

While comparing discrimination performance in the two action tasks with the no-action task, we made another interesting observation, which suggests an overall benefit of preparing actions for perceptual discrimination. The d' score of each orientation discrimination in the pointing task was significantly higher than the corresponding d' score in the no-action task—left tilted: $t(30) = 2.80$, Dunnett-adjusted $p = .017$, $d = 0.40$; right tilted: $t(30) = 3.73$, Dunnett-adjusted $p = .002$, $d = 0.66$. The d' score in the grasping task, however, was higher than in the no-action task only when participants performed easier grasping, $t(30) = 3.80$, Dunnett-adjusted $p = .001$, $d = 0.79$, but not harder grasping, $t(30) = 1.44$, Dunnett-adjusted $p > .250$, $d = 0.34$, Bayes factor = 2.08. This suggests that preparing for easier goal-directed actions (i.e., pointing and grasping the right-tilted stimulus) effectively enhanced perceptual sensitivity even though participants performed an additional task compared with the no-action task.

These results appear to demonstrate that the enhancement effect of pointing on orientation discrimination was similar to that of easy grasping and better than that of hard grasping. However, these results do not entirely parallel those of a previous study, in which only grasping preparation, but not pointing, enhanced orientation discrimination (Gutteling, Kenemans, & Neggers, 2011). The difference between the two studies could be driven by the different sources of orientation information—bars (Gutteling et al., 2011) versus Gabor patches (Experiment 2). Alvarez and Cavanagh (2008) showed that performance in a change-detection task is better with bars than Gabor patches because bar rotation can provide more orientation information with boundary features than Gabor-patch rotation can provide with surface features.

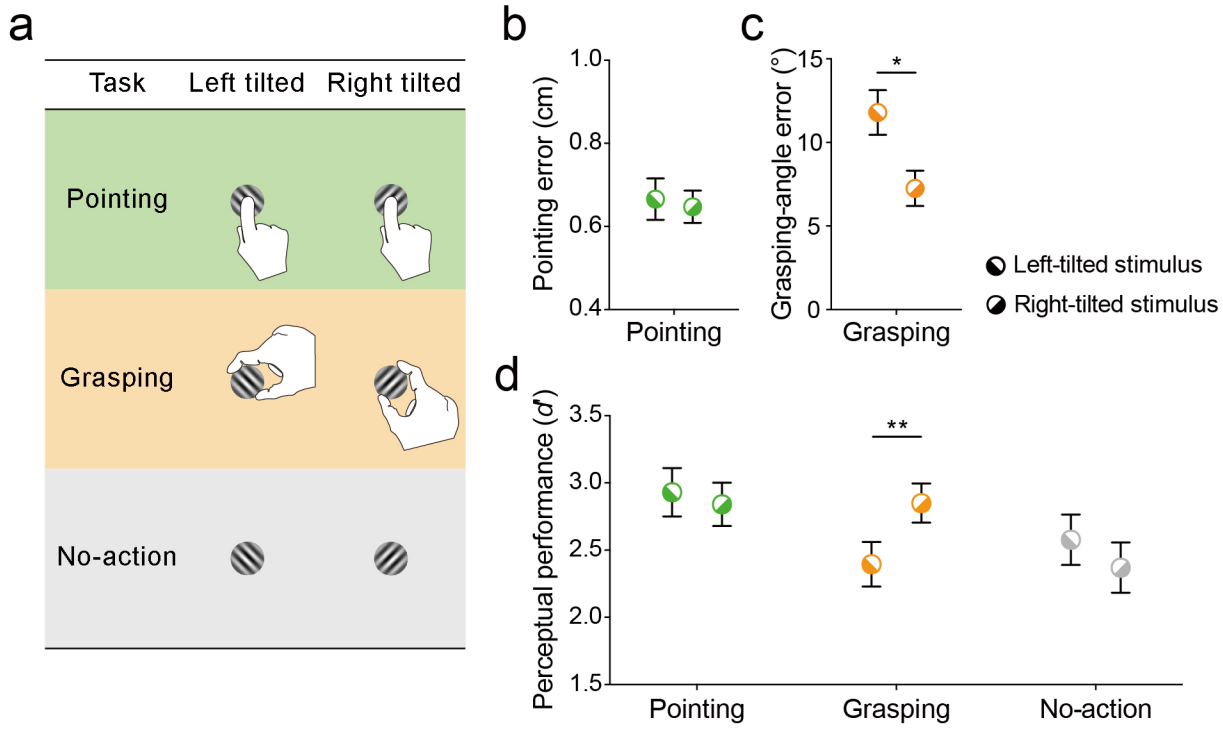


Fig. 2.5. Action and perceptual performance with the two visual stimuli in Experiment 2a. The hand postures used for the left-tilted and right-tilted stimulus across the three action tasks are shown in (**a**). Mean pointing error (**b**) and grasping-angle error (**c**) are shown for the pointing and grasping tasks, respectively, whereas mean perceptual performance (d') is shown for all three tasks; all three panels show results separately for left- and right-tilted stimuli. The dot colors correspond to the tasks indicated by the shading in (**a**). Error bars represent standard errors of the mean. Asterisks indicate significant differences between results for the two stimulus types (*$p < .05$, **$p < .01$).

Nevertheless, Experiment 2 provided further evidence that differences in discrimination sensitivity of target orientation were induced by differences in action fluency, not by other stimulus characteristics, and were consistent with what we observed in Experiment 1.

Experiment 3: Effects of Action Fluency on Orientation Discrimination with the Non-Dominant Hand

In Experiment 1 and 2, we showed that as grasping with the dominant right hand became easier, orientation discrimination also enhanced. However, Gonzalez, Ganel and Goodale (2008) showed that visual illusion had different influence on grasping with right hand and left hand for both right and left handed participants. Left hand grasping was affected by the visual illusion but right hand grasping was not. They claimed that this was because the integration of perception and action information of grasping happened at left hemisphere. Thus, in Experiment 3, we examined whether this relation between ease of action and perceptual sensitivity can be extended to the left hand.

Method

Participants. Sixteen Brown University students (8 males, mean age 20.13 years) participated in an approximately one-hour session for course credit or monetary compensation. All participants were right-handed with normal or corrected-to-normal color vision, and were naïve to the aims of the experiment. The sample size (16 per group) was determined on the basis of the effect size needed to achieve 80% statistical power ($d = 0.85$, $n = 16$) as determined with a paired-samples t test on preliminary data in Experiment 2. All procedures reported in this manuscript were

approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

Procedure. The procedure of Experiment 3 was identical to the Experiment 1. Average threshold (t) was 9.36° ± 1.30°. The difference was that participants were required to perform the grasping by their left hand and press the button by the right hand. Grasping was performed by rotating the wrist of their left hand 45° or 135° counterclockwise. The four types of Gabor patches induced grasping from hard to easy in Experiment 1 now induced grasping from easy to hard here respectively. Thus, the four levels of action fluency from hard to easy: 1) 135° counterclockwise-tilted stimuli on the right side of screen, 2) 135° counterclockwise-tilted stimuli on the left side, 3) 45° counterclockwise-tilted stimuli on the right side, and 4) 45° counterclockwise-tilted stimuli on the left side.

Data analysis and statistics. Same data analysis and statistics were performed as Experiment 1.

Results

As in Experiment 1, because results from the small- and large-size conditions were overall similar, here we focused on data from the large-size condition, while reporting those from the small-size condition in the supplementary material. In contrast to Experiment 1 with the dominant hand, in which four levels of grasping difficulty was established (Fig. 2.3a), here, we mainly observed the two levels based on the manipulation of 135° or 45° counterclockwise-tilted (Fig. 2.6a). Thus, we combined data from both left- and right-side screens and examined whether grasping-angle error (Fig. 2.6b) and perceptual performance (Fig. 2.6c) differed between 135°

vs. 45° counterclockwise-tilted conditions. A two-way repeated ANOVA with target orientation (counterclockwise-tilted 45° vs. 135°) and stimulus position on the screen (left vs. right) showed a significant main effect on the target orientation ($F(1, 15) = 8.81$, $p = .010$, $\eta^2 = .17$) but not on the stimulus position on the screen ($F(1, 15) = 0.13$, $p > .250$, $\eta^2 < .001$).

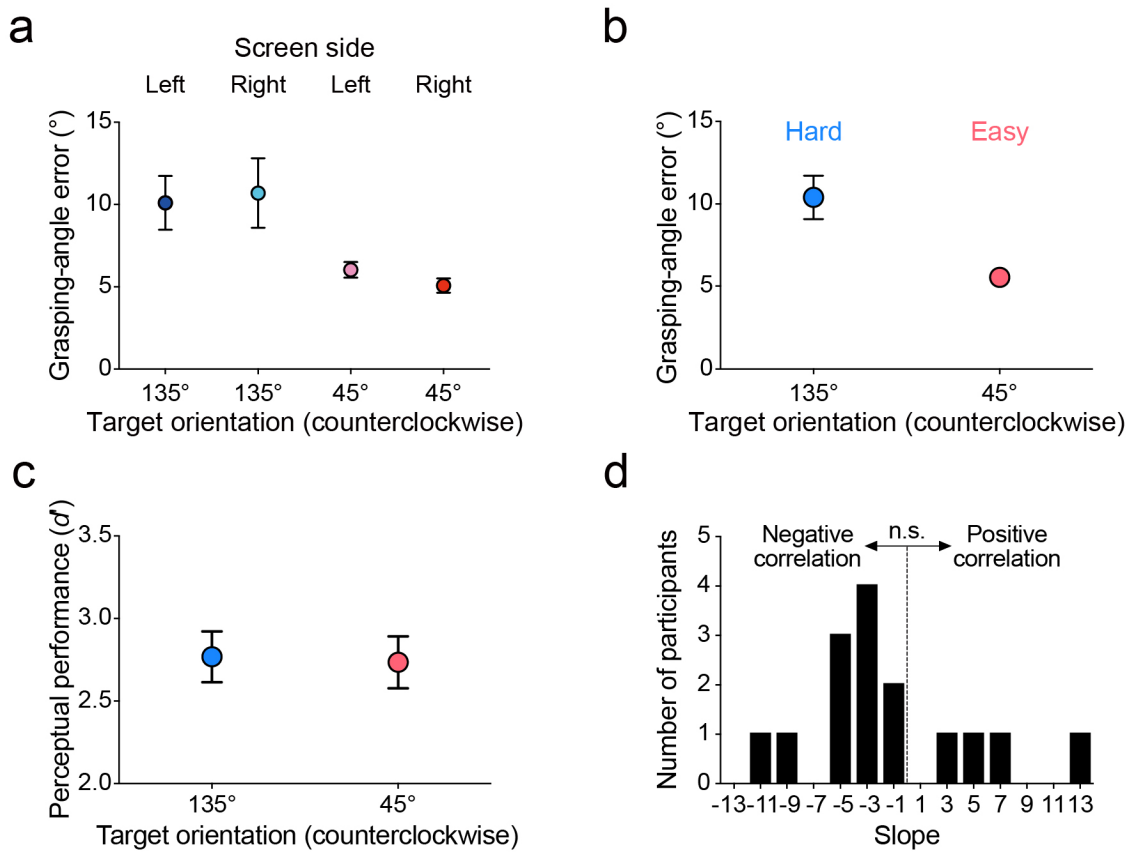


Fig. 2.6. Action and perceptual performance of large-size condition in Experiment 3. Mean grasping-angle error of four grasping conditions (**a**). Mean grasping-angle error (**b**) and perceptual performance (**c**) of two combined grasping conditions of two combined grasping conditions. Error bars show standard errors of the mean. The colors of the dots correspond to the grasping conditions. The frequency distribution of slopes for 15 participants is shown in (**d**). The dashed line indicates 0 on the *x*-axis. Values to the left and right of the dashed line indicate whether *d'* scores and grasping-angle errors were negatively or positively correlated, respectively. The mean slope across participants was determined to be not significantly different from zero using a one-sample *t* test.

Furthermore, we wanted to evaluate the correlation between the grasping-angle error and perceptual performance of two grasping conditions. In Experiment 1, smaller grasping-angle error (easier action) corresponded with better visual performance, implying that grasping-angle

error was negatively correlated with perceptual performance (Fig. 2.3e). However, in Experiment 3, the grasping-angle error and perceptual performance did not show any correlation. We first normalized the grasping-angle error in each participant as in Experiment 1 and applied a linear regression between *d*' score and normalized grasping-angle error of two grasping conditions for each participant. As in Exp. 1, we used ROUT method and identified one outliers in large-size condition. The distribution of all other slopes (n = 15) is shown in Fig. 2.6d. A one-sample t test of slopes showed that the mean of slopes is not significantly different from 0 ($t(14) = 0.81$, $p > .250$, $d = .22$, Bayes factor = 3.78). In sum, Experiment 3 showed that action fluency level is not correlated with visual perceptual performance for the non-dominant hand during motor preparation.

Experiment 4: Perceptual Sensitivity Improved After Action Training

In Experiment 4, we examined whether orientation-discrimination sensitivity could be further enhanced with training of precision grasping. To address this question, we compared orientation-discrimination sensitivity before and after an action-training session, in which participants were required to grasp various tilted objects, or a control training session, in which participants were instructed to report the orientation of tilted objects.

Method

Participants. Forty-four Brown University students participated in a 1-hr session for course credit or monetary compensation. Twenty-two participants (10 males; mean age = 21.78 years) were included in the action group, and 22 participants (4 males; mean age = 21.50 years) were included in the control group. The sample size (22 per group) was determined on the basis of the

effect size needed to achieve 80% statistical power ($d = 0.65$, $n = 13$) as determined with a one-sample t test on preliminary data. All participants were right-handed with normal or corrected-to-normal color vision, and all were naive to the aims of the experiment. All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

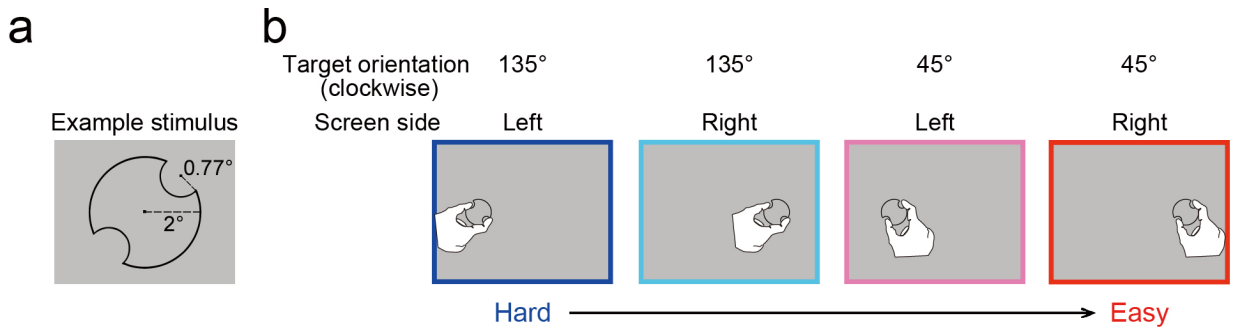


Fig. 2.7. Stimulus and experimental conditions in Experiment 4. The stimulus used in the training session (**a**) was tilted in six different orientations. Participants were instructed to grasp it (action group) or report its orientation (control group). The radius of the two large arcs was 2° of visual angle, and the radius of the two small arcs was sin (22.5°) × 2° = 0.77°. The length of the small arc was half of its perimeter. The four grasping conditions created for Experiment 4 (**b**) varied from hard (low action fluency) to easy (high action fluency).

Apparatus. The experimental setup was the same as in Experiment 1, except that we asked participants to use a chin rest to maintain the consistency of their pre- and postperception tests.

Stimuli. All stimuli used in Experiment 4 were identical to those in Experiments 1 and 2, except for the stimuli used in the training session. During the training session, we introduced a new type of stimulus (depicted in Fig. 2.7a).

Procedure. As in Experiments 1 and 2, all participants performed the threshold-baseline test (Fig. S1). In the experiment that followed, participants completed three sessions: preperception

test, training, and postperception test. During the training session, participants were randomly assigned to the action and control groups. Other sessions were identical for both groups.

In the preperception and postperception tests, participants performed the orientation-change-detection task, as in Experiments 1 and 2 (Fig. 2.2), without performing the action task. Here, we chose only the small-size condition in the perception task, because it would provide sufficient room for improvement of perception performance after action training. There were four blocks each for the pre- and postperception tests, and each block consisted of 32 trials. The orientation of the first Gabor patch was randomized within each block. The average threshold (t) for the action group was 9.60° ± 0.95° and for the control group was 9.46° ± 1.42°. An independent-samples *t* test showed that there was no significant threshold difference between the two groups, $t(42) = 0.38$, $p > .250$, $d = 0.11$.

In the training session, each trial started with a fixation dot randomly presented for 1,750 ms, 2,000 ms, or 2,250 ms. After fixation, the stimulus in Figure 2.7a appeared on the screen. The orientation of the stimulus, which was bounded by centers of two small arcs, was tilted in six different orientations, the same as in the small-size condition in Experiments 1 and 2b: 135° ± 1.5 × t (12.5% of trials for each orientation), 135° (25% of trials), 45° ± 1.5 × t (12.5% of trials for each orienta- tion), 45° (25% of trials) clockwise. The action group was instructed to apply a precision grip to the concave sides and rotate their wrists approximately 45° or 135° clockwise, as shown in Figure 2.7b, whereas the control group was instructed to report, by pressing the button, whether the stimuli was tilted clockwise approximately 45° or 135° from the vertical line. The stimulus stayed on screen until the response was completed or until 1.5 s had passed (participants in both groups heard a beep when 1.5 s had elapsed). The training session had four blocks of 32 trials each. The orientation of the stimulus was randomized within each block.

Data analysis. For both the action and control groups, we calculated d′ for the pre- and postperception tests separately, as in Experiments 1 and 2. In the training session, we calculated, respectively, grasping-angle error for the action-group participants (who performed the grasping training; Fig. 2.7b), and accuracy for the control-group participants (who reported stimulus orientation).

Results

During the training session, we discarded the first four trials to obtain a stable estimate of beginning performance in both action and control groups. In the action group, we calculated how much participants improved their grasping precision. In each condition, we defined the first four analyzed trials (Trials 5–8) as the early training period and the last four trials (Trials 29–32) as the late training period. We first calculated the grasping-angle errors of these two periods in four grasping conditions (Fig. 2.8a); then we defined grasping-performance gain as the mean difference between the early and late training periods in each condition, as shown in Figure 2.8b. We also assessed gain in the corresponding perceptual performance (Fig. 2.8c) by calculating the d′ difference between the post- and preperception tests, as shown in Figure 2.8d. When we compared the data shown in Figures 2.8b and 2.8d, it appeared that in the condition in which participants improved their grasping precision more, they also enhanced their perceptual discrimination.

To correlate grasping-performance gain with perceptual-performance gain in the four grasping conditions, we first calculated normalized grasping-angle error (Equation 1) and the gain in normalized grasping-angle error in the four grasping conditions. The gain in grasping

performance was positively correlated with perceptual-performance gain. We again used the ROUT method and identified one outlier. Figure 2.8e shows the distribution of slopes for 21 participants; the majority of participants showed positive slopes. A one-sample *t* test for slopes showed that the mean for slopes was significantly larger than 0, $t(20) = 3.32$, $p = .003$, $d = 0.72$, indicating that perceptual sensitivity improved in proportion to the improvement of action fluency in the training session.

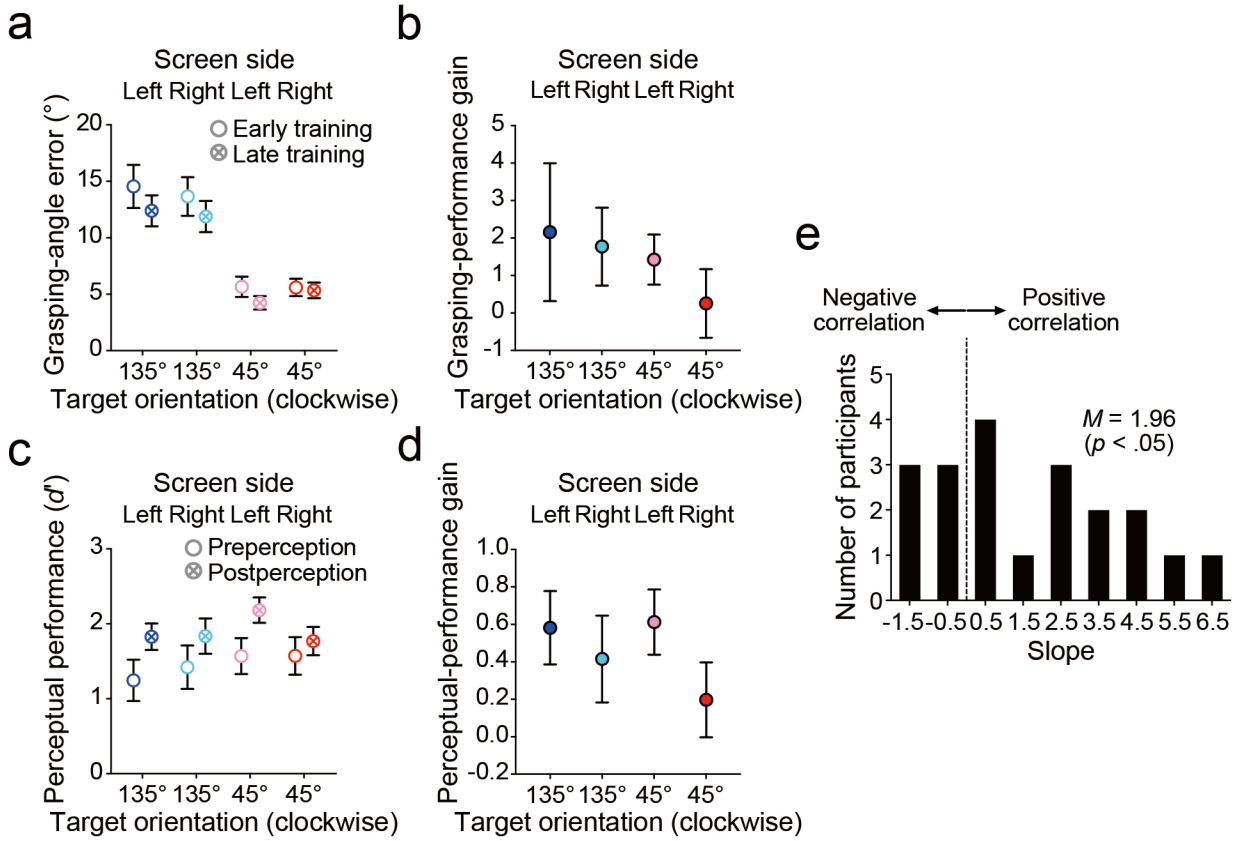


Fig. 2.8. Action and perceptual performance in the four grasping conditions for the action group in Experiment 4. Mean grasping-angle error (**a**), grasping-performance gain (**b**), perceptual performance (**c**), and perceptual-performance gain (**d**) are shown as a function of target orientation and screen side. For grasping-angle error and perceptual performance, results are also shown separately for the early and late training period (**a**) and the preperception and postperception test (**c**). Grasping-performance gain was calculated by subtracting grasping-angle error in the late training period from grasping-angle error in the early training period, whereas perceptual-performance gain was calculated by subtracting the *d*′ score in the preperception test from the *d*′ score in the postperception test. In (**a**) to (**d**), the colors of the dots correspond to the target orientations and screen sides as depicted in Figure 7b. Error bars indicate standard errors of the mean. The frequency distribution of slopes for 21 participants is shown in (**e**). The dashed line indicates 0 on the *x*-axis. Values to the left and right of the dashed line indicate whether grasping-performance gain and perceptual-performance gain were negatively or positively correlated, respectively. The mean slope across participants was determined to be significantly different from zero using a one-sample *t* test.

In the control group, instead of focusing on normalized grasping-angle error, we calculated perceptual accuracy (Fig. 2.9a). The corresponding accuracy gain was calculated by taking the difference between accuracy in Trials 5–8 and Trials 29–32, as shown in Figure 2.9b. We also calculated the corresponding perceptual performance (Fig. 2.9c) and then calculated its

gain as a d′ difference between the post- and preperception tests (Fig. 2.9d). Comparing the data shown in Figures 2.9b and 2.9d, we found that accuracy gain was not correlated with perceptual-performance gain in the four control conditions (Fig. 2.9e), implying that improvement in a control task was not correlated with perceptual improvement. Eight participants had infinite slopes because of the same accuracy gains under the four conditions and were therefore not included in the slope-distribution analysis. Figure 2.9e shows the distribution of slopes of 14 participants. A one-sample *t* test of slopes showed that the mean for slopes was not significantly different from 0, $t(13) = 0.59$, $p > .250$, $d = 0.16$, Bayes factor = 4.23. In other words, we did not find any evidence to support the notion that the enhancement of perceptual performance was improved by the control task, unlike the action task. This lack of correlation could be due to the control task being relatively easy, so there was not much room for improvement during the training period (Fig. 2.9b).

In sum, Experiment 4 extended the results from Experiments 1 and 2 by demonstrating that a short grasping training preceding postperception test trials can result in enhancement of orientation-discrimination sensitivity, although perceptual training preceding post-perception test trials cannot. Moreover, the magnitude of perceptual improvement was positively correlated with improvement during action training. Therefore, our results further bolster the close connection between action fluency and perceptual sensitivity.

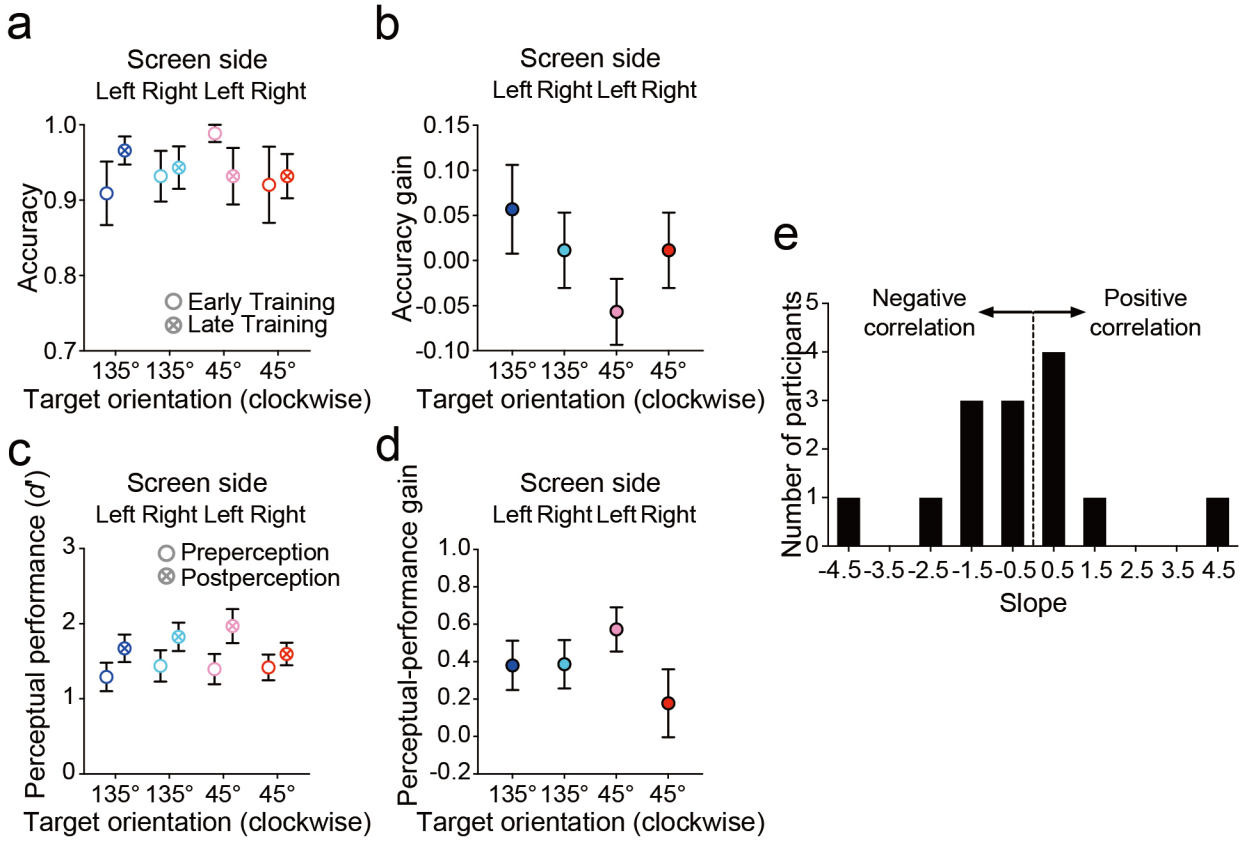


Fig. 2.9. Accuracy and perceptual performance in the four control conditions for the control group in Experiment 4. Mean accuracy (a), accuracy gain (b), perceptual performance (c), and perceptual-performance gain (d) are shown as a function of target orientation and screen side. For accuracy and perceptual performance, results are also shown separately for the early and late training period (a) and the preperception and postperception test (c). Accuracy gain was calculated by subtracting accuracy in the early training period from accuracy in the late training period, whereas perceptual-performance gain was calculated by subtracting the d′ score in the preperception test from the d′ score in the postperception test. In (a) to (d), the colors of the dots correspond to the target orientations and screen sides as depicted in Figure 7b. Error bars indicate standard errors of the mean. The frequency distribution of slopes for 14 participants is shown in (e). The dashed line indicates 0 on the *x*-axis. Values to the left and right of the dashed line indicate whether accuracy gain and perceptual-performance gain were negatively or positively correlated, respectively.

Discussion

The fluency effect extended

In the current study, we revealed that action fluency modulated the effect of action on a fundamental visual feature, orientation, in the early stages of visual processing. We demonstrated that orientation-discrimination sensitivity was enhanced by fluent actions (Experiment 1) and

that the enhancement effect was not led by other intrinsic differences among orientations (Experiment 2). The effect of action on early visual processing has been examined in a wide range of studies, including behavioral research (e.g., Bekkering & Neggers, 2002; Craighero et al., 1999), brain-imaging research (e.g., Neggers et al., 2007), and neurobiological research (for a review, see Colby, 1991). Our results clearly indicate that fluent action can indeed enhance visual sensitivity, an effect that cannot be explained by perspectives on the serial relation between perception input and action output.

It is also worth noting that although participants could experience the difference in action fluency only during the motor-execution stage, perceptual discrimination— which must occur during motor preparation—was affected. This is consistent with a prior functional MRI study (Gutteling et al., 2015) suggesting that preparation of actions, even without execution, modulates relevant neuronal populations in visual cortex as early as V1.

Our study demonstrated that with the majority of individuals, the magnitude of grasping-angle errors was negatively correlated with orientation-discrimination sensitivity (Experiment 1). Furthermore, grasping-precision enhancement by training was positively correlated with orientation discrimination afterward (Experiment 4). Yet, this enhancement is limited to grasping with the dominant hand (Experiment 3). This correlation between perceptual sensitivity and action fluency is also consistent with the action-specific perception perspective (Witt & Proffitt, 2005). For instance, Witt, Proffitt, and Epstein (2004) demonstrated that when a heavy ball was used to hit a target, the target would be perceived as farther away than when a light ball was used. We further extended their findings by systematically manipulating action-fluency levels and measuring unbiased perception, such as d'. By showing that fluent actions with a comfortable end state enhanced perceptual discrimination, we also extended prior work

demonstrating that actions with a comfortable end state, associated with high precision at the ending point of the movement, are preferred to achieve a task (Rosenbaum et al., 1990).

Moreover, we demonstrated that orientation-discrimination sensitivity could be enhanced by prior training in precision grasping (Experiment 4). This is broadly consistent with the findings of Thomas (2017), which demonstrate that short-term action training with relevant features can enhance visual processing. Whereas Thomas demonstrated that action experience modulates visual processing, particularly near the hands, we showed that after action fluency was increased by action training, the perceptual-enhancement effect could occur even though participants were resting their hands away from the visual display. This effect of action fluency on subsequent perceptual processes implies another level of interaction between action and perception systems beyond simultaneous cross talk and suggests a need for further investigation.

Potential mechanisms for the effect of action fluency on perceptual sensitivity

We contend that the availability of cognitive resources or motor effort entirely drove the effect of action fluency observed in the present study: We showed that in the easiest and least effortful no-action task, participants showed less perceptual enhancement than in the pointing or easy-grasping tasks (Experiment 2). Instead, we offer several possibilities that may explain the link between action fluency and perceptual sensitivity.

One scenario is that performing an action in itself may boost perceptual sensitivity, perhaps through attentional mechanisms. For instance, prior to the onset of a saccade or a reach, attention is directed to the goal of the upcoming movement, and perceptual discrimination is enhanced at the action-goal location (e.g., Deubel, Schneider, & Paprotta, 1998; Khan, Song, & McPeek, 2011). Furthermore, a number of studies have suggested that visual processing near the

hand is altered through spatial attention-selection mechanisms (e.g., Reed, Betz, Garza, & Roberts, 2010). Perry, Sergio, Crawford, and Fallah (2015) also demonstrated that attention deployed to near-hand space enhances orientation selectivity in early visual processing area V2 in nonhuman primates. In Experiments 1 and 2, in which action and perceptual tasks relied on visual stimuli in the same spatial location, the enhancement effect might be explained by the spatial-attention boosting effect. However, it is unclear how attentional mechanisms mediate the effect of action fluency on visual perception when action performance is separated from a perceptual task, as in Experiment 4. That said, perhaps the results of Experiment 4 suggest that spatial visual attention can be ruled out as a primary mechanism for the observed action fluency effect.

Alternatively, performance in action and no-action tasks could differ because of additional visual feedback provided while guiding the hand to the second stimulus or haptic feedback provided by grasping or pointing at the second stimulus. Previous studies have shown that the availability of visual feedback can bias perceptions and actions (e.g., Franz & Gegenfurtner, 2008; Haffenden & Goodale, 1998). For instance, Atkins, Fiser, and Jacobs (2001) demonstrated that when participants view and grasp elliptical cylinders in a virtual reality environment, they automatically compare haptic and visual percepts to determine the reliability of available visual information. However, it is unclear how this extra sensory feedback could explain the improvement of perceptual-discrimination performance in our paradigm because this extra information did not influence the more critical first visual stimulus in our perception task. Furthermore, it did not explain the perceptual differ- ence induced by easy and hard grasping.

Real-life implications

We demonstrated that action training enhances orientation-discrimination sensitivity. This is largely consistent with previous studies, in which different motor-training techniques have been utilized to ameliorate perceptual or cognitive deficits. For example, prior work with left-side-neglect patients has shown that limb-activation training, in which patients make small movements with their left limbs on the left side of space, leads to improved detection of left stimuli (for a review, see Luauté et al., 2006).

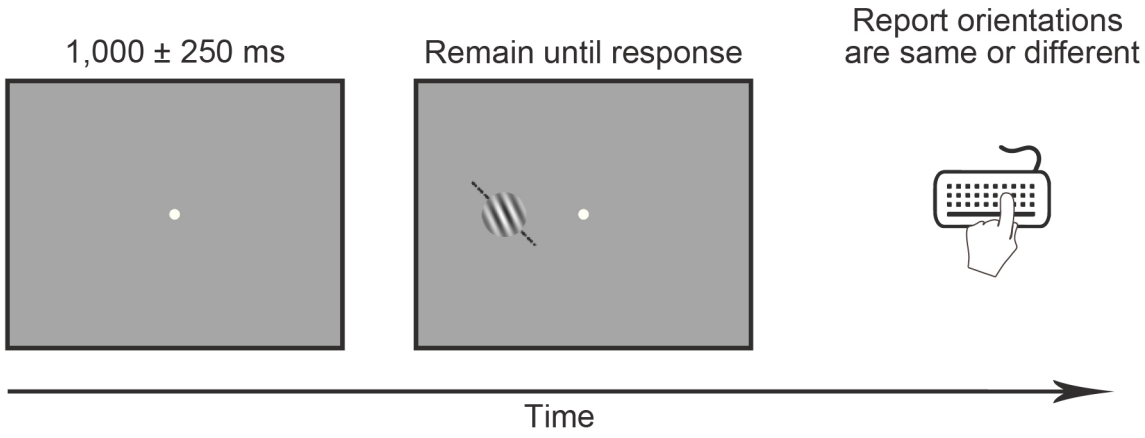
In addition, Taub and his colleagues (e.g., Taub, Mark, & Uswatte, 2014) proposed a mechanistic connection between motor deficits (e.g., stroke) and visual deficits (e.g., amblyopia). They suggested that the two deficits are commonly caused by learned nonuse after damage to the central nervous system. Thus, the rehabilitation procedures for stroke (such as constraint-induced movement therapy; Wolf et al., 2006) and those for amblyopia (such as occlusion therapy; Levi & Polat, 1996; Stewart, Fielder, Stephens, & Moseley, 2002) commonly aim to overcome learned nonuse and induce neural reorganization.

Given this close link between treatment for motor and visual deficits, it might be relevant to note that amblyopia, for instance, not only causes reduced acuity and contrast sensitivity in one eye but also causes difficulties in executing real-world actions, such as those requiring grasping, finger dexterity, and eye-hand coordination. Thus, it is important for training programs in amblyopia to include visuomotor-integrative activities (Suttle, Melmoth, Finlay, Sloper, & Grant, 2011). On the basis of our results and the aforementioned studies, which support a synergetic and reciprocal connection between perceptual and motor processes, we conjecture that combining fluent action and perceptual training might enhance visual acuity in amblyopia or other visual deficits more effectively.

Concluding remarks

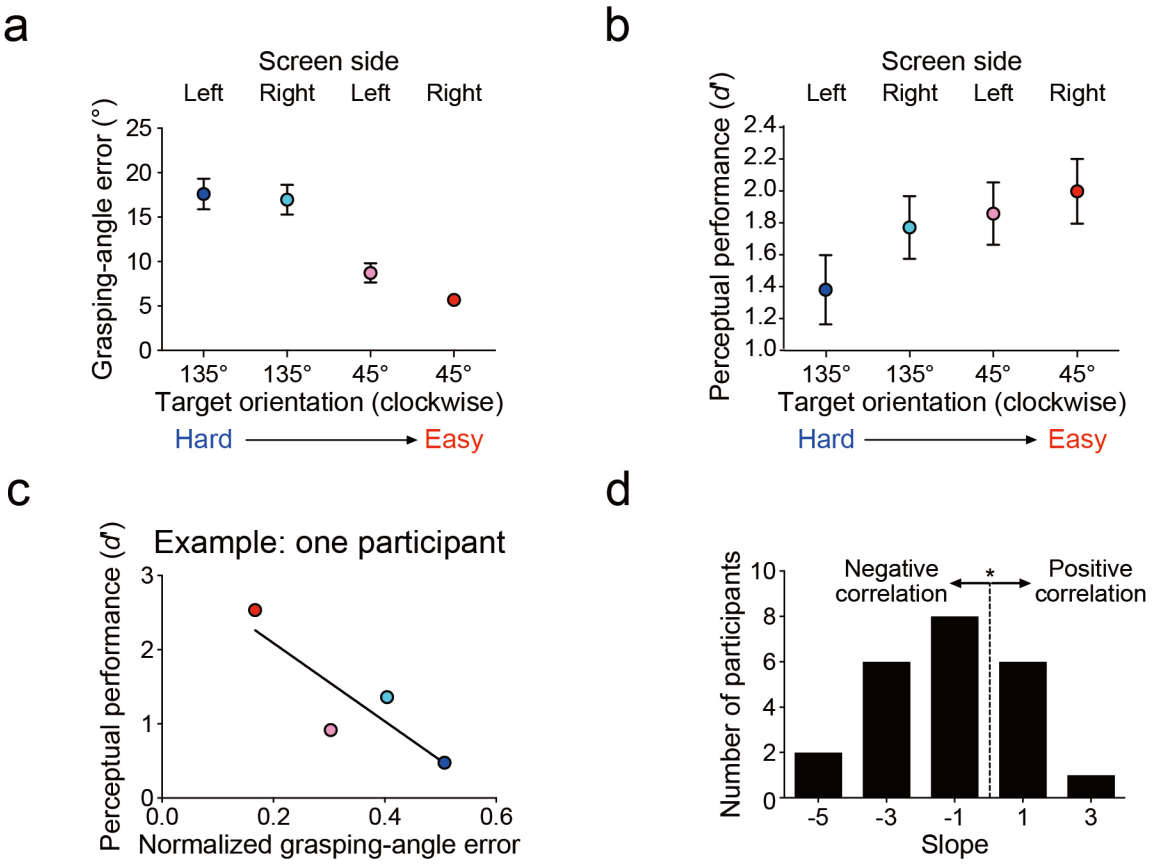
Here, we reported that perceptual orientation can be enhanced by simultaneous easy-action preparation or even by prior action training. This newly observed modulation of visual perception by action fluency could not be explained by the traditional sequence of information-processing stages (Cover & Thomas, 1991). Rather, it highlights the necessity of an integrated approach to understanding adaptive behavior in a complex environment. Future studies should examine the interplay between the action system and perception. Such research would allow us to investigate a range of broader questions that cannot be resolved by studying the motor system alone or vision alone.

Supplemental Material



sFig. 1. Trial sequence of the threshold-baseline test in all Experiments. To determine each participant's threshold of orientation-change-detection, we first asked participants to perform a threshold-baseline test. Every trial started from a fixation dot (randomly presented for 750, 1,000 or 1,250 ms), then the dashed-line and the Gabor patch appeared simultaneously. The Gabor patch and the dashed-line were both shown on the left side or right side randomly of the fixation dot at 8.5° eccentricity along the horizontal meridian. The dashed-line was tilted 45° from the vertical line either clockwise (50%) or counterclockwise (50%), whereas the orientation of the Gabor patch was the same as the dashed-line (40%) or tilted from the dashed-line (60%) to left or right direction randomly. We used double staircases (80% accuracy, 3 down, 1 up): one staircase ascending from 3° tilt and the other descending from 12°.

Participants were instructed to report if a dashed-line and a Gabor patch have the same or different orientations by pressing a button with the left hand. All stimuli stayed on the screen until participants responded. Participants received auditory feedback regarding their accuracy. The prethreshold test stopped when either staircase had more than 100 trials or both of them had more than 10 direction reversals. The threshold, *t*, was the mean of two staircases.



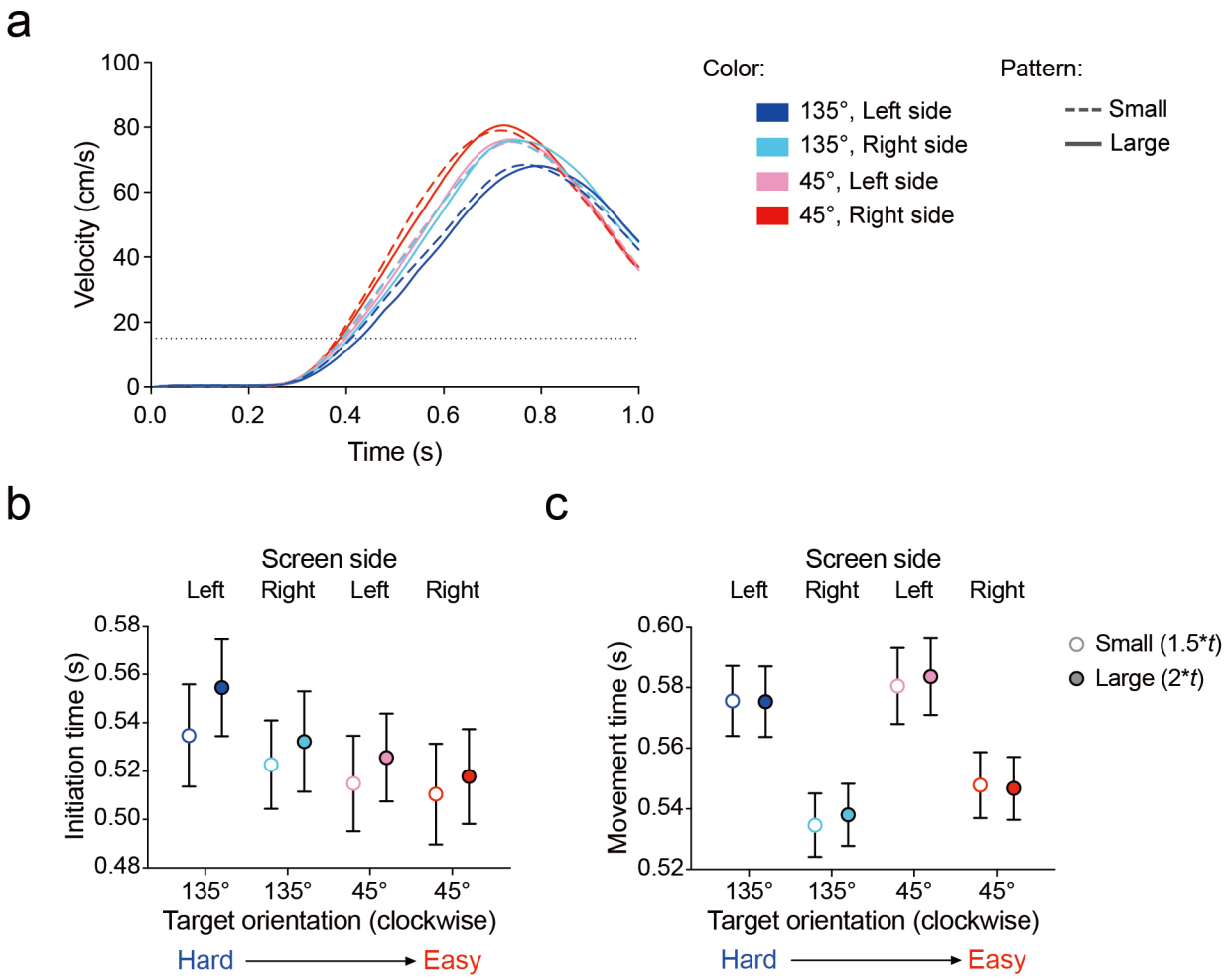
sFig. 2. Results of the small-size condition in Experiment 1. (a) Grasping-angle error. (b) Perceptual performance (d'). In both (a) and (b), represented mean performance across the four grasping conditions sorted by the action fluency (hard to easy). (c) Example of linear regression in one participant between action and perceptual performance. The equation of the line is: Y = -5.27 * X + 3.14, showing a linear decrease in perceptual performance with successive increases in action difficulty. In (a) – (c), the colors of dots indicate four grasping conditions with four difficulty levels (blue = 1st hard, cyan =2nd hard, pink = 3rd hard, red=4th hard). (d) Frequency distribution of slopes of 23 participants. The dashed-line indicates x = 0. The negative slopes on the left side of the dashed-line indicate the d' and grasping-angle error are negatively correlated. The positive slopes on the right side of the dashed-line indicate the *d*' and grasping-angle error are positively correlated. An asterisk indicates significance in a one-sample *t* test comparing slopes to zero across participants (*$p < .05$).

To confirm that we successfully created the four grasping conditions with varying difficulties from hard to easy, we analyzed grasping-angle errors. As shown in sFig. 2a, the four grasping movements we created from hard to easy had corresponding grasping-angle error from large to small. A one-way repeated measures ANOVA across the four grasping conditions showed a significant main effect, $F(1.55, 37.31) = 34.42$, $p < .001$, $\eta^2 = .38$. A post hoc test for linear trend of grasping-angle error across the four grasping conditions was significant, slope = -2.20, $R^2 = .35$, $p < .001$, showing that the easiest grasping produced a 37.46% reduction in grasping-angle error compared to the hardest grasping.

Of interest was whether the perceptual performance across the four grasping conditions is affected by fluency of grasping. sFig. 2b shows that in the easier grasping conditions, participants showed better perceptual performance. A one-way repeated measures ANOVA across the four grasping conditions showed significant main effect, $F(2.23, 53.62) = 7.18$, $p = .001$, $\eta^2 = .05$. A post hoc test for linear trend of *d'* across four grasping conditions was significant, slope = 0.10, $R^2 = .04$, $p < .001$, showing that the easiest grasping produced a 21.72% improvement in perceptual performance compared to the hardest grasping.

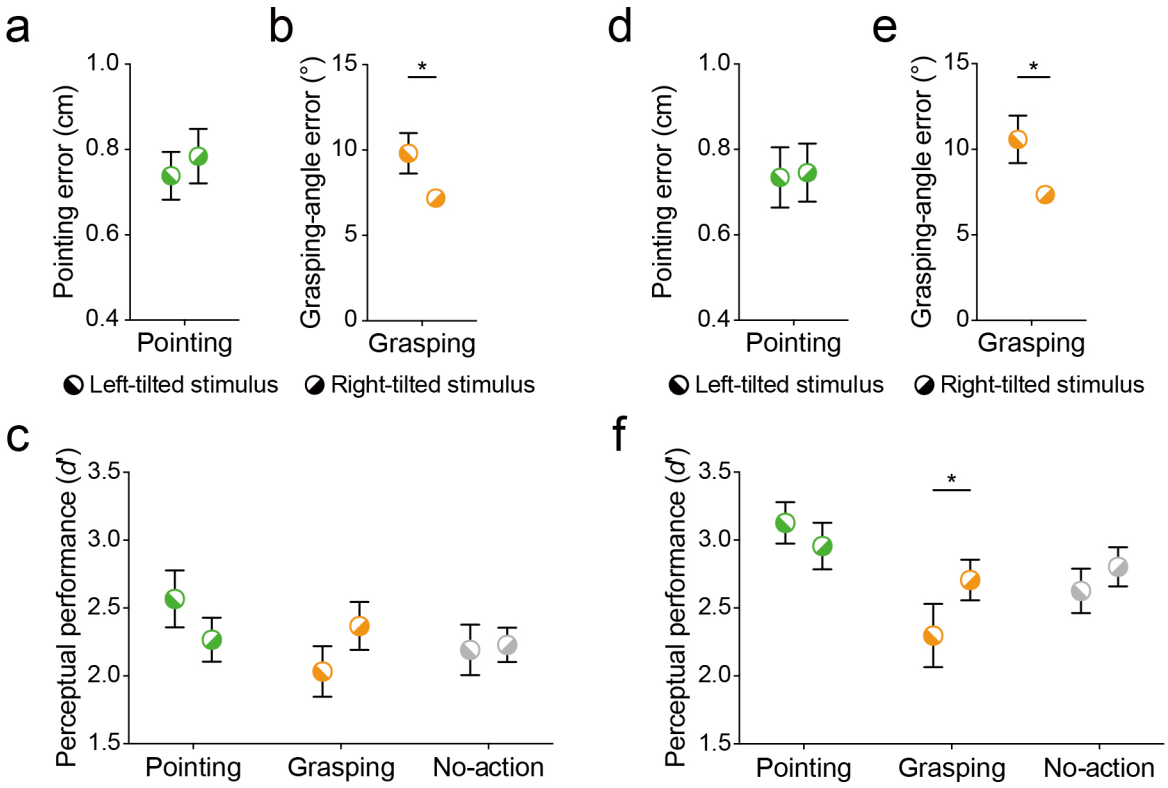
After normalizing grasping errors (Eq. 1), we calculated the mean value in each grasping condition. Then, we applied a linear regression between *d'* and normalized grasping-angle error in each participant as shown in sFig. 2c. We used ROUT method to identify the outliers, and two outliers were identified. sFig. 2d shows the distribution of slopes for 23 participants. Overall, it shows that the majority of participants show the negative slopes. It suggested that the grasping-angle error is negatively correlated with perceptual performance consistent with the results of the large-size condition. A one-sample *t* test of slopes showed that the mean of slopes is significantly

smaller than 0, $t(22) = 2.82$, $p = .010$, $d = 0.59$. We also calculated velocity, initiation time and movement time across the four grasping conditions to assure that observed correlation between action and perception is not mediated by different strategies (see sFig. 3 for details).



sFig. 3. Action performed in the four grasping conditions in Experiment 1. (a) Velocity curve. The colors of lines indicate the four grasping conditions with four difficulty levels and the patterns of lines indicate two tilted size conditions (Color: blue = 1st hardest, cyan =2nd hardest, pink = 3rd hardest, red = 4th hardest; Pattern: dashed-line = small-size, solid-line = large-size). The horizontal dashed-line indicates the threshold of the movement onset: 15 cm/s. (b) Initiation time. (c) Movement time. In both (b) and (c), the colors of dots indicate the four grasping conditions with four difficulty levels and the patterns of dots indicate two tilted size conditions (Color: blue = 1st hardest, cyan = 2nd hardest, pink = 3rd hardest, red = 4th hardest; Pattern: clear dot = small-size, solid dot = large-size).

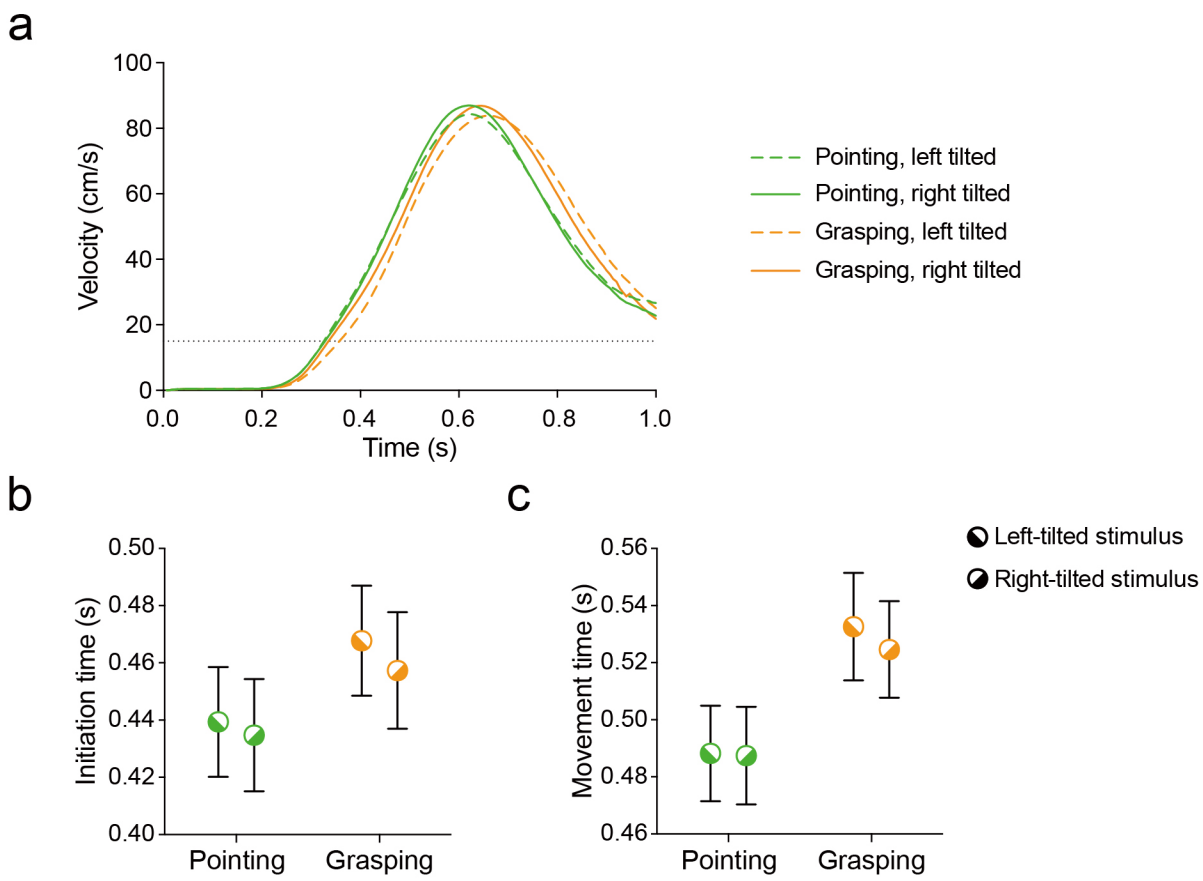
We also calculated velocity, initiation time and movement time across the four grasping conditions to assure that observed correlation between action and perception is not mediated by different strategies. The velocity curves under four situations were similar (sFig. 3a). In addition, initiation time (sFig. 3b) and movement time in both size conditions (sFig. 3c) showed linear patterns like the grasping-angle error. We further compared initiation time and movement time. Although a linear trend for both initiation time and movement time across four grasping conditions from hard to easy, grasping a stimulus on the right side of the screen had shorter initiation time and movement time than grasping a stimulus on the left side of the screen. One-way repeated measures ANOVAs for both initiation time and movement time across four grasping conditions in each tilted size condition showed significant main effect (initiation time: small, $F(1.65, 39.69) = 3.73$, $p = .041$, $\eta^2 = .01$; large, $F(2.54, 60.95) = 10.16$, $p < .001$, $\eta^2 = .02$; movement time: small, $F(2.14, 51.43) = 25.85$, $p < .001$, $\eta^2 = .10$; large, $F(1.86, 44.68) = 33.79$, $p < .001$, $\eta^2 = .10$). The post hoc tests for linear trend of initiation time and movement time in both tilted size conditions across four grasping conditions were significant (initiation time: small, slope = - .004, $R^2 = .01$, $p = .002$; large, slope = - .005, $R^2 = .02$, $p < .001$; movement time: small, slope = - .002, $R^2 = .007$, $p = .019$; large, slope = - .002, $R^2 = .01$, $p = .010$). We also ran a two-way repeated measures ANOVA with target orientation (clockwise-tilted 45° vs. 135°) and stimulus position on the screen (left vs. right) for initiation time and movement time. There was a significant main effect of the stimulus position on the screen for initiation time in the large size condition (small: $F(1, 24) = 1.81$, $p = .191$, $\eta^2 = .001$; large: $F(1, 24) = 14.97$, $p < .001$, $\eta^2 = .01$) and movement time in both size conditions (small: $F(1, 24) = 75.46$, $p < .001$, $\eta^2 = .10$; large: $F(1, 24) = 128.60$, $p < .001$, $\eta^2 = .10$).



sFig. 4. Action and perceptual performance with the two visual stimuli in Experiment 2b. (a) – (c) Results of the small-size condition. (a) Pointing error. (b) Grasping-angle error. (c) Perceptual performance (*d'*). (d) – (f) Results of the large-size condition. (d) Pointing error. (e) Grasping-angle error. (f) Perceptual performance (*d'*). In (a) - (f), the green, orange, and gray dots represent performance in the pointing, grasping, and no-action tasks, respectively. The left-tilted and right-tilted dot patterns represent performance in trials with the left- and right-tilted stimuli, respectively. In the pointing task, action errors (a and d) and associated perceptual performance (c and f: green) are not affected by the stimulus orientations as in the no-action task (c and f: gray). However, in the grasping task of the large size condition, action error (e) increases and perceptual performance (f: orange) decreases when the left-tilted target is presented compared to the right-tilted one. Error bars represent standard error of the mean (SEM). An asterisk indicates significant differences between results for the two stimulus types (*$p < .05$).

First, to confirm that two types of target orientation led to different grasping difficulty but same pointing, we analyzed grasping-angle error and pointing error. In both small- and large-size conditions, while pointing errors (sFigs. 4a and 4d) were equivalent (small: $t(15) = 1.26$, $p = .227$, $d = 0.32$, Bayes factor = 2.56; large: $t(15) = .39$, $p > .250$, $d = 0.10$, Bayes factor = 4.92), grasping-angle errors (sFigs. 4b and 4e) were larger towards a left-tilted than a right-tilted target (small: $t(15) = 3.01$, $p = .009$, $d = 0.75$; large: $t(15) = 2.71$, $p = .016$, $d = 0.68$).

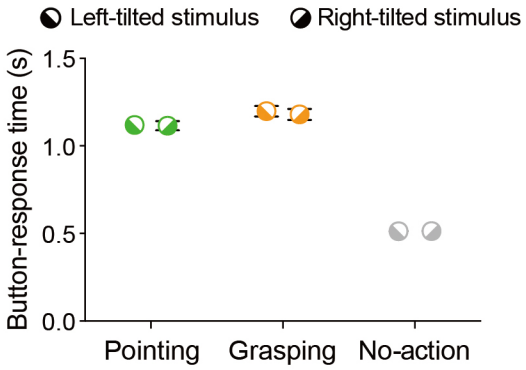
How did the grasping difficulty induced by orientation differences (left- or right-tilted) influence perceptual performance? For both tilted size conditions, as shown in sFigs. 4c and 4f, we observed that perceptual discrimination sensitivity (*d'*) during point planning (sFigs. 4c and 4f: green) or no-action (sFigs. 4c and 4f: gray) was not affected by the orientation of stimuli. Yet, grasping right-tilted (sFigs. 4c and 4f: right-tilted orange) stimulus improved perceptual discrimination sensitivity comparing to grasping left-tilted stimulus (sFigs. 4c and 4f: left-tilted orange). This result suggests that ease of action enhances perceptual discrimination in both tilted size conditions, which is consistent with Experiment 2a. For both size conditions, a two-way repeated measures ANOVA with tasks (pointing, grasping and no -action) and stimulus-type (left-tilted and right-tilted) showed significant interaction effect (small: $F(2, 30) = 4.36$, $p = .022$, $\eta^2 = .03$; large: $F(2, 30) = 4.02$, $p = .029$, $\eta^2 = .03$). Post hoc analyses confirmed that *d'* did not differ between two types of stimulus in pointing and no-action tasks of both size conditions (pointing: small, $t(30) = 1.97$, Sidak adjusted $p = .164$, $d = 0.40$, Bayes factor = 1.01; large, $t(30) = 1.17$, Sidak adjusted $p > .250$, $d = 0.51$, Bayes factor = 2.82; no-action: small, $t(30) = .25$, adjusted $p > .250$, $d = 0.07$, Bayes factor = 5.14; large, $t(30) = 1.22$, Sidak adjusted $p = .232$, $d = 0.23$, Bayes factor = 2.68). For the grasping task of the small-size condition, Bayes analysis was in favor of the alternative hypothesis that the *d'* was different between two types of stimulus, while Sidak-adjusted post hoc analysis showed no significant difference between the two, $t(30) = 2.20$, Sidak adjusted $p = .103$, $d = 0.46$, Bayes factor = .71. For the grasping task of the large-size condition, the right-tilted stimulus had a higher *d'* than left-tilted stimulus, $t(30) = 2.81$, Sidak adjusted $p = .026$, $d = 0.54$.



sFig. 5. Action performed toward two types of stimulus in Experiment 2a. (a) Velocity curve. The colors of lines indicate two action tasks (green = pointing, orange = grasping). The patterns of lines indicate movements toward different stimuli (dashed-line = left-tilted, solid-line = right-tilted). The horizontal dashed-line indicates the threshold of the movement onset: 15 cm/s. (b) Initiation time. (c) Movement time. In both (b) and (c), the green, orange dots represent performance in the pointing and grasping tasks, respectively. The left-tilted and right-tilted dot patterns represent performance in trials with the left- and right-tilted stimuli, respectively.

We further examined kinematics of grasping and pointing movements to assure that observed difference in the left- vs. right-tilted stimuli in the grasping task is not led by different strategies. sFig. 5a shows the mean velocity curves were very similar when the two types of stimulus in pointing (green) and grasping (orange) tasks are presented respectively. We further compared the initiation time (sFig. 5b) and movement time (sFig. 5c). Pointing (green) had shorter initiation time and movement time than grasping (orange), but there was no significant difference between two types of stimulus in pointing and grasping tasks. We did a two-way

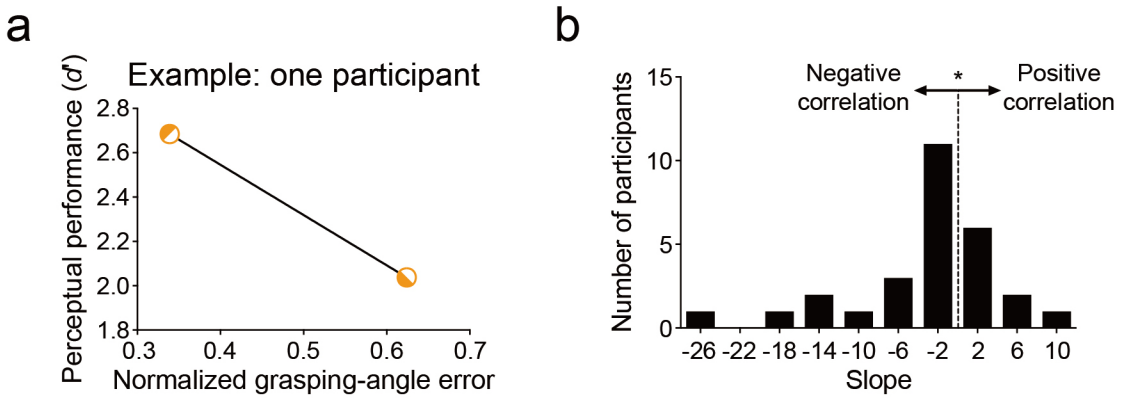
repeated measures ANOVA with tasks (pointing and grasping) and stimulus-type (left-tilted and right-tilted) for initiation time and movement time. There was a significant main effect of tasks for both initiation time, $F(1, 15) = 9.42$, $p = .008$, $\eta^2 = .03$, and movement time, $F(1, 15) = 23.05$, $p < .001$, $\eta^2 = .08$. In the post hoc t test, the initiation time in pointing and movement time in both pointing and grasping tasks didn't show significant difference between two types of stimulus (initiation time: pointing: $t(15) = 1.05$, Sidak adjusted $p > .250$, $d = 0.30$; grasping: $t(15) = 2.34$, Sidak adjusted $p = .066$, $d = 0.60$; movement time: pointing: $t(15) = 0.23$, Sidak adjusted $p > .250$, $d = 0.09$; grasping: $t(15) = 2.39$, Sidak adjusted $p = .061$, $d = 0.44$).



sFig. 6. The button-response time of two types of stimulus in three action tasks in Experiment 2a. Comparison of time between the appearance of the first patch and button-press as a function of action tasks (pointing, grasping, and no-action) and stimulus type (left-tilted and right-tilted). The green, orange, and gray dots represent performance in the pointing, grasping, and no-action tasks, respectively. The left-tilted and right-tilted dot patterns represent performance in trials with the left- and right-tilted stimuli, respectively.

We then analyzed the button-response time to assure that the difference between left vs. right-tilted grasping was not because of decay of the orientation memory. The easy grasping (sFig. 6: right-tilted orange) showed shorter button-response time than hard grasping (sFig. 6: left-tilted orange). However, the no-action task (sFig. 6: gray) showed the shortest button-response time among three tasks, which implied that shorter button-response time is not

correlated to better perceptual performance. A two-way repeated measures ANOVA with tasks (pointing, grasping, and no-action) and stimulus-type (left-tilted and right-tilted) showed significant main effect of tasks, $F(2, 30) = 405.6$, $p < .001$, $\eta^2 = .92$. There was a significant main effect of stimulus type, $F(1, 15) = 6.71$, $p = .021$, $\eta^2 < .001$ and a significant interaction effect, $F(2, 30) = 5.64$, $p = .008$, $\eta^2 < .001$. In the post hoc t test, there was a significant difference between two types of stimulus in the grasping task, $t(30) = 4.37$, Sidak adjusted $p < .001$, $d = 0.68$.



sFig. 7. Correlation results in the grasping task of the large-size condition in Experiment 2a and 2b. (a) Example of linear regression in one participant between action and perceptual performance. The equation of the line is: Y = -2.27 * X + 3.45, showing a linear decrease in perceptual performance with successive increases in action difficulty. The left-tilted and right-tilted orange dots represent performance in trials with the left- and right-tilted stimuli, respectively. (b) Frequency distribution of slopes of 28 participants in Experiment 2a and 2b. The dashed-line indicates x = 0. The negative slopes on the left side of the dashed-line indicate the *d'* and grasping-angle error are negatively correlated. The positive slopes on the right side of the dashed-line indicate the *d'* and grasping-angle error are positively correlated. An asterisk indicates significance in a one-sample *t* test comparing slopes to zero across participants (*$p < .05$).

Of interest was whether the perceptual performance across the two grasping conditions is affected by fluency of grasping. We performed the linear correlation between action and perceptual performance for all participants in Experiment 2a and 2b the same as in Experiment 1. After normalizing grasping errors (Eq. 1), we calculated the mean value in each grasping condition. Then, we applied a linear regression between *d'* and normalized grasping-angle error

in each participant as shown in sFig. 7a. We used ROUT method to identify the outliers, and four outliers were identified. sFig. 7b shows the distribution of slopes for 28 participants. Overall, it shows that the majority of participants show the negative slopes. It suggested that the grasping-angle error is negatively correlated with perceptual performance consistent with the results of Experiment 1. A one-sample *t* test of slopes showed that the mean of slopes is significantly smaller than 0, $t(27) = 2.34$, $p = .027$, $d = 0.33$.

CHAPTER 3: IMPROVED MOTOR TIMING ENHANCES TIME PERCEPTION

ABSTRACT

Previous studies demonstrated that motor timing and time perception share common mechanisms and brain processes. For instance, participants who displayed larger timing variability in single-finger rhythmic tapping also demonstrated lower acuity in time perception (Keele et al., 1985). However, these studies examined simple movements, i.e. finger or foot tapping, performed in an explicitly rhythmic fashion. It is unclear whether the inherent timing of more complex movements without explicit periodicity also affected time perception. Here, we examined whether practicing a sequence of controlled throwing movements enhances the sensitivity of time-interval discrimination and, if so, whether this enhanced sensitivity is selectively linked to the timing of the trained movement. We found that with throwing practice, they enhanced the sensitivity of time discrimination selectively for the interval close to the release time, but not for others. Importantly, we found that the learned motor skills and perceptual discrimination can be retained for a long-term. These results demonstrated that improvement of motor timing enhances the sensitivity of time perception, even for timing patterns inherent to a more complex motor task. We interpret these finding that there is a shared temporal mechanism between perception and movement regardless of rhythmicity or complexity of the motor tasks.

Introduction

Historically, complex human behaviors are composed of perceptual, cognitive and motor systems, each consisting of function-related submodules (Hurley, 2001). One traditional view is that we acquire information in the environment through sensory input, process the information in cognition, and then utilize the cognition outcomes to guide action, in which perception and action do not contact with each other (Johnson-Laird, 1988; Newell & Simon, 1972; Sanders, 1980; Sternberg, 1969). However, this one-way causal flow between perception and action leaves behind the fact that in everyday behaviors motor circuits act closely in concert with perceptual systems. For instance, in Chapter 2 we demonstrated that a prior action training enhanced subsequent early visual processing (Guo & Song, 2019), suggesting that improving action precision can result in better perceptual sensitivity. In addition, the precise timing of behavior stretches all the way across the two domains. For instance, we determine when to move with remarkably accurate temporal estimation of events in the environment (Rosenbaum, 2009). Perceived duration of visual stimulus is distorted by the length of a concurrent movement (Yokosaka, Kuroki, Nishida, & Watanabe, 2015). In light of these findings, it is important to further understand adaptive behavior in a complex environment through an integrated perspective but not studying perception or action alone.

Precise timing is a critical feature of almost all ecologically valid behaviors in complex dynamic environment (Rijn, 2018), such as synchronizing dance movements to auditory beats imbedded in music (for a review, see Maes et al., 2014). Inaccurate timing result in consequences ranging from inconveniences in everyday activity to fatal accidents. Thus, being able to understand how humans acquire the ability to precisely estimate the length of intervals is crucial to explain how successful behavior in complex tasks can be achieved. Recently, a

growing body of research has tended to show correlation between motor timing and time perception. For instance, the temporal consistency on time perception and simple motor tasks are positively correlated. Individuals who displayed larger timing variability in single-finger rhythmic tapping also demonstrated lower acuity in time perception (Keele et al., 1985). Performance declines similarly at increasing temporal intervals for perception and production tasks (Ivry, & Hazeltine, 1995). In addition, hand reaching movements led to a better performance in a simultaneous time reproduction task (Wiener et al., 2019), suggesting executing actions assists perceptual processes of timing. Moreover, neural evidence demonstrated that time perception and motor timing tasks have similar brain regions involved in (Ivry & Diener, 1991; Ivry, Keele, & Diener, 1988; Schubotz et al., 1999). For instance, cerebellum legions result in dysfunctions in both duration discrimination tasks (Ivry & Keele, 1989) and finger tapping movements (Inhoff et al., 1989). Collectively, these findings demonstrated that the precisely timed interactions between perceptual and motor processes are at the root of all effective goal-directed behaviors.

Such correlational evidence has left open the possibility that sensory and motor systems merely represent time in a similar fashion, rather than sharing a common mechanism. To evaluate the common mechanism much directly, in this chapter we estimated whether plastic modifications of motor temporal properties can automatically affect corresponding sensory temporal representations. Specifically, we examined whether practicing a sequence of controlled throwing movements enhances the sensitivity of time-interval discrimination and, if so, whether this enhanced sensitivity is selectively linked to the timing of the trained movement. In Experiment 1 and 2 we examined whether times that emerge in a motor training task without any explicit emphasis on timing can improve auditory time-interval discrimination. We established

that with throwing practice, participants enhance the sensitivity of time-interval discrimination, and this enhanced sensitivity is selectively linked to the timing of the trained movement. In Experiment 3 we further demonstrated that such improved sensitivity of perceptual discrimination associated with motor training can persist in the long-term. Together, these experiments provide robust evidence that improved motor timing can lead to enhanced time-interval discrimination sensitivity.

Experiment 1: Training in Motor Timing Enhances Time Perception

Here, we examined whether throwing practice facilitates the sensitivity of time-interval discrimination and, if so, whether this enhancement effect is selectively linked to the timing of the practiced movement. Participants practiced throwing a ball to hit a target in a virtual environment in multiple days (Fig. 3.1a, 3.1b). Following each throwing session, participants also performed a time-interval discrimination task. We predicted that with throwing practice, the sensitivity of time discrimination would be enhanced selectively for the interval linked to the improved motor timing.

Method

Participants. Twenty-five participants (13 females; mean age = 22.56 years) were recruited and compensated with $10/h after completing the 5 experimental sessions on 5 separate days. The sample size was determined on the basis of the effect size needed to achieve 90% statistical power ($d = 0.69$, $n = 15$) as determined with a one-sample t test on preliminary data. Participants had normal or corrected-to-normal color vision and were naive to the aim of the experiment. All procedures were approved by the Northeastern University Institutional Review Board.

Motor training task ("Skittles"). Skittles is a target-oriented throwing action similar to the American playground game tetherball (Fig. 3.1a). In the game, the players throw a ball that is attached to a vertical post via a string to hit one or more target skittles on the far side (Cohen & Sternad, 2012; Hasson et al., 2016; Zhang, Guo, Huber, Park, & Sternad, 2018; Zhang & Sternad, 2019). The experimental version of the task simplified the movement to a single-joint forearm rotation in the horizontal plane where the throw is triggered by extending the index finger from a contact sensor to simulate the opening of the hand to release the ball. This task is implemented as a virtual game where the target and the workspace are shown to the participant as a top down view (Fig. 3.1b). The participants see their own arm movements as a rotating purple bar (40 cm) and the virtual white ball (10 cm diameter) as it traverses around the red post (50 cm diameter) after the release hitting or missing the yellow target (10 cm diameter).

Participants stand 1.5 m in front of a large backprojection screen (2 x 2 m) and rest their forearm on a lever arm and perform forearm flexion-extension movements in the horizontal plane. The height of the lever arm is individually adjusted so that the subject's upper arm has a 45° angle with respect to the trunk. Angular displacements of the lever arm are measured by an optical encoder with a sampling rate of 700 Hz. The participant grasps a wooden ball that is fixed at the distal end of the lever to 'throw' the ball to hit a target. A contact sensor (Interlink Electronics, Camarillo, CA), attached to the ball, is closed when pressing the index finger onto it; finger extension opens the contact and triggers the release of a virtual ball on the screen. The angular position and angular velocity of the arm movement at the moment of ball release is used to compute the ball trajectory. Using these as initial conditions, the ball traverses around the post in an elliptic trajectory towards the target at the opposite side (Fig. 3.1b).

The ball's trajectory is generated by a simple 2D model where the ball is attached to two orthogonal springs that hold the ball in its equilibrium position at the center of the workspace, the center post, defined as $x = y = 0$. At time t the equations for the ball position in x- (Eq. 1) and y-direction (Eq. 2) are:

$$x(t) = A_x \sin(\omega t + \varphi_x) e^{-\frac{t}{\tau}}, \text{ Eq (1)}$$

$$y(t) = A_y \sin(\omega t + \varphi_y) e^{-\frac{t}{\tau}}, \text{ Eq (2)}$$

ω represents the natural frequency of the springs. The amplitudes Ax and Ay, as well as the phase φ_x and φ_y of the springs result from the ball's release angle and angular velocity. The ball motions are lightly damped by the exponential term to approximate realistic motion, where τ denotes the relaxation time of the decay.

Figure 3.1c illustrates the x-y coordinates of the workspace and three exemplary ball trajectories traversing around the red post; the target is the small yellow circle at the top left. The two larger insets show the definition of the angle of the lever arm and the error as the minimal distance between target and trajectory. The delay between data collection and display are within the refresh rate of the computer, which is 13 ms. Importantly, the throwing action has redundancy: mathematically infinitely many combinations of angle and velocity at ball release can achieve zero error. This feature is summarized in the solution space (Fig. 3.1d: green band): a successful hit can be achieved with infinite combinations of release angle and velocity. Spanned by angle and velocity, the green U-shaped line is the set of all angle-velocity combinations that hit the target successfully with errors < 1.1 cm. The yellow band comprises those solutions that touch the target with errors < 2.5 cm. The orange shades encode the error that the ball trajectory would have achieved. The black area encodes the errors > 40 cm or hitting the center post. The geometry of the solution manifold is determined by the target location in the

workspace. Small changes in target location can generate qualitatively different solution manifolds, i.e. different throwing strategies.

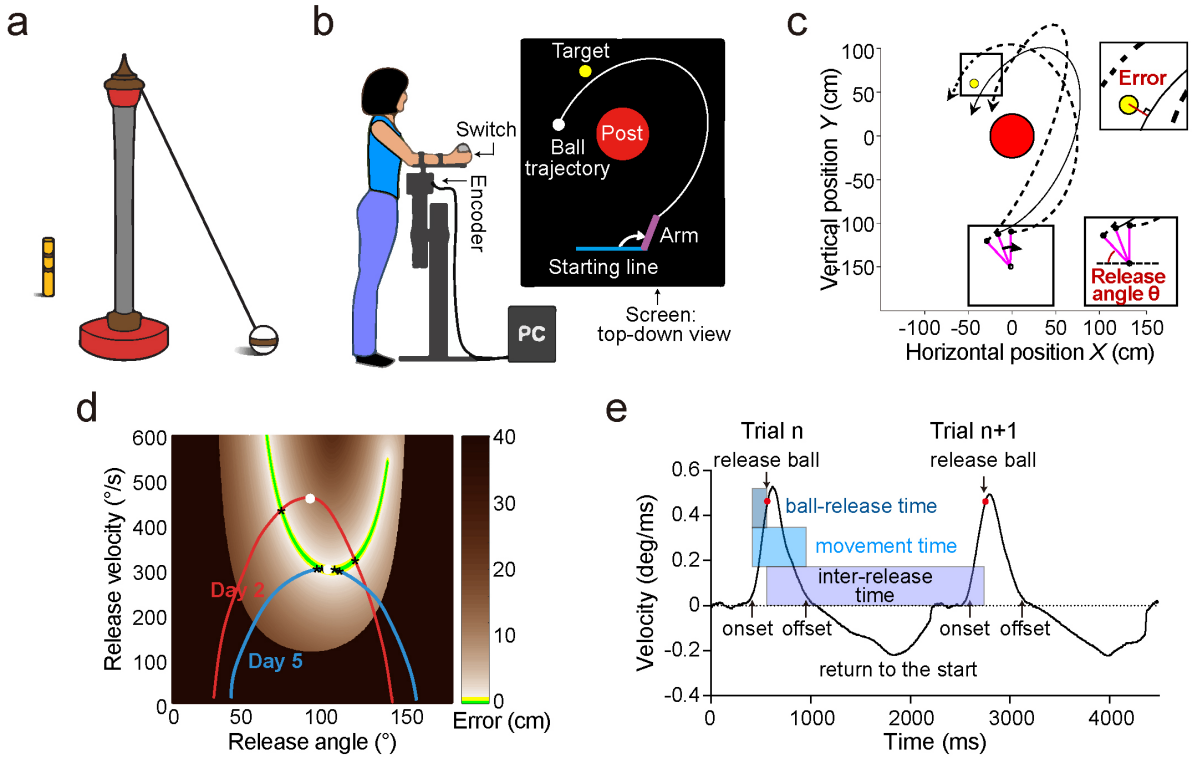


Fig. 3.1. The motor training task and three types of motor timing in Experiment 1. (**a**) Real skittles throwing game that was modeled as motor training task. In the game, players aimed to hit a skittle target at the other side of the post by throwing a tethered ball around the post. (**b**) Experimental setup of the virtual throwing task. The participant grasps a real ball that is fixed at the distal end of the lever to 'throw' a virtual ball to towards a target. Angular displacements of the lever arm are measured at 700 Hz by an optical encoder. (**c**) Top down view of the skittles workspace. The red circle is the post, the green circle is the target, and the purple bar is the lever arm. The solid ball trajectory passes within the 1.1 cm error threshold and is a successful hit; the two dashed ball trajectories are unsuccessful throws. The two insets illustrate the definition of the target error (top) and the release angle (bottom). (**d**) The execution space of the Skittles task. The green band denotes the solution manifold, where the error is zero or sub-threshold. Two representative arm trajectories and their ball releases from Exp.1-1 are plotted. The red trajectory is from Day 2; the blue trajectory is from Day 5; the white dots represent ball releases. The release point on the red trajectory resulted in a large error while the release point on the blue trajectory was a successful hit. (**e**) Three types of motor timing: ball-release time, movement time and inter-release time. The red dot indicates the ball release moment at trail n and trial n+1.

To determine how timing of movement can influence perceptual timing, the time series of the arm velocity is analyzed. Figure 3.1e shows two successive throws revealing a relatively

invariant temporal pattern: timing of the onset of movement, followed by the ball release and the re-setting of the arm, ready for the next throw. The movement onset and offset were defined as the points when the velocity exceeded and fell below 10 degree per second, respectively. This time profile can be parsed into three intervals: 1) ball-release time, defined as the interval between the movement onset and ball release; 2) movement time, defined as the interval between movement onset and offset, and 3) inter-release time, defined as the interval between two successive ball-releases in trials n and n+1 (Fig. 3.1e).

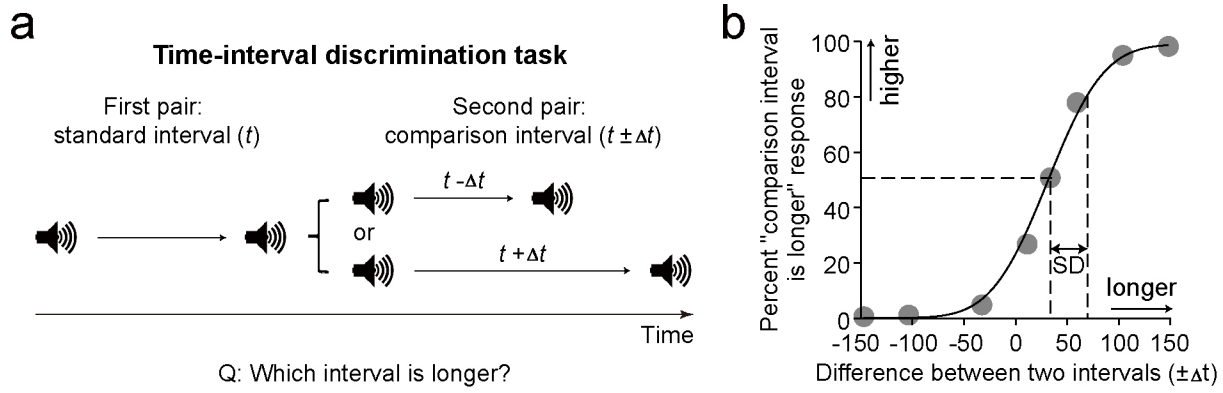


Fig. 3.2. The time-interval discrimination task in Experiment 1. (**a**) Trial structure. Participants compared the time-intervals of two pairs of beep sounds and reported whether the comparison interval was 'short' or 'longer' than the standard interval. The discrimination threshold (Δt) under every standard-interval (t) condition was measured separately by QUEST+. (**b**) Estimation of auditory time duration discrimination threshold. Threshold = standard deviation (SD) of the fitted psychometric function.

Time-interval discrimination task. Participants compared the time-intervals of two pairs of tones: a standard and a comparison interval (Fig. 3.2a). The first standard interval (t) was always fixed in one block, whereas the second comparison interval was either shorter or longer than the standard interval ($t \pm \Delta t$). Two pairs of tones are separated by t x 1.25 ($t \leq 1000$) or t x 0.75 ($t > 1000$). Participants reported which pair of tones has longer interval by button-press without accuracy feedback (Keele et al., 1985). The threshold of each standard interval was estimated by a Bayesian adaptive procedure called QUEST+ (Watson, 2017). QUEST+ selected the difference

between two intervals (± Δt) in each trial based on the keypress responses in all past trials. The probability of the keypress response given the ± Δt was assumed as a cumulative normal distribution (Fig. 3.2b). After each keypress, ± Δt of next trial is computed by maximizing the posterior density of responses obtained in all previous trials. The comparison interval was then determined as $t \pm \Delta t$. After all trials, a subsequent maximum likelihood (ML) fitting was applied based on all responses. The time-interval discrimination threshold is the estimated standard deviation of the ML-fitted psychometric function.

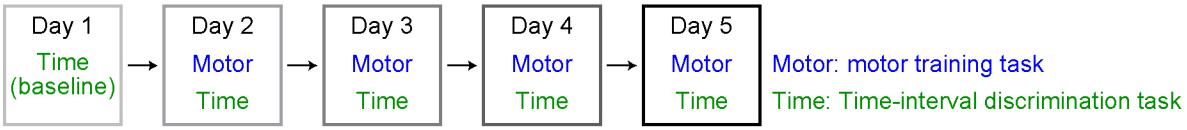


Fig. 3.3. Timeline of the two tasks in the five daily sessions in Experiment 1. In day 1, the threshold baseline of time-interval discrimination was measured. In day 2 to day 5, participants performed the motor training task first and then the time-interval discrimination task. The word colors represent the two different tasks. The border colors of each box represent the daily sessions.

Procedure. All participants performed 5 daily sessions (Fig. 3.3). They performed the time-interval discrimination task on day 1 as the baseline measurement. This perceptual task was composed of 4 standard intervals associated with three movement intervals extracted from motor timing involved in skittles (Fig. 3.1e) and one unrelated control interval. Matching the standard intervals and movement intervals were through pilot test for potential manifold in skittles with a separate group of participants. According to our pilot results, the standard intervals were set to 300 ms (linked to the ball-release time), 600 ms (linked to the movement time), 1000 ms (unrelated time) and 3000 ms (linked to the inter-release time). On days 2 - 5, participants first practiced throwing with 320 trials per day. Note that to reduce the individual movement variability, we ask participants to start their throwing movement from the identical position (Fig. 3.1b: starting line). Over practice, they are expected to stabilize motor timing including the ball-

release time (Fig. 3.1e). Following each throwing session, they continued with the perceptual time task with the same interval as on day 1. The QUEST+ procedure for each standard interval in each day included 70 trials. A prior 10-trial QUEST+ procedure with a unrelated 500 ms standard interval was used as the practice block in day 1.

Data analysis. In the skittles task, we calculated the duration for each motor timing: ball-release time, movement time, and inter-release time (Fig. 3.1e). We also calculated the motor-timing variability, defined as the standard deviation of the durations divided by the mean duration, operated as a normalized measure of temporal variability (Spencer et al., 2003). It was separately calculated for each motor-timing as well. Motor learning has been gauged by the reduction in timing variability throughout training (Fig. 3.4b, Meegan et al., 2000; Wing & Kristofferson, 1973).

In the perceptual task, to compare discrimination performance across different standard intervals, the Weber fraction (Grondin, 2010) was calculated as the ratio between the estimated threshold and the standard interval (Eq. 3):

$$Weber\ fraction = \frac{\text{threshold}}{\text{standard interval}}, \text{Eq (3)}$$

A smaller Weber fraction corresponds to better discrimination. We also evaluated the relation between the reduction of motor timing variability and the threshold of auditory duration discrimination using linear regression.

All data processing and statistical analyses were performed using MATLAB and GraphPad Prism version 8.0. We analyzed the data using a mixed-effects model. For multiple post hoc comparisons, we applied Dunnett correction for comparison of treatments with a single control

Group (Dunnett, 1955). We identified outliers using the combined robust regression-and-outlier-removal (ROUT) method (Motulsky & Brown, 2006). All error bars represented standard error of the mean (SEM). The effect size of mixed-effects model will be measured by eta-squared (η^2) and *t* tests will be measured Cohen's *d*, respectively. η^2 s of .01, .06, and .14 and Cohen's *d*s of .02, .013, and .26 refer to small, medium and large (Cohen, 1988).

Results

As we expected, participants stabilized each motor-timing segment over throwing practice. In accord, we showed that participants shortened their motor timing across days 2-5 (Fig. 3.4a): ball-release time ($F(3, 72) = 5.54$, $p = .002$, $\eta^2 = .03$), movement time ($F(3, 72) = 3.41$, $p = .022$, $\eta^2 = .04$), and inter-release time ($F(3, 72) = 42.97$, $p < .001$, $\eta^2 = .20$). It is also captured by the reduction of motor timing variability, our index of motor improvement (Fig. 3.4b): ball-release time ($F(3, 72) = 45.13$, $p < .001$, $\eta^2 = .50$), movement time ($F(3, 72) = 32.34$, $p < .001$, $\eta^2 = .40$), and inter-release time ($F(3, 72) = 35.04$, $p < .001$, $\eta^2 = .47$).

Of primary interest is how the reduction of motor timing affected the threshold of time duration discrimination. We showed that participants enhanced the sensitivity of time discrimination selectively for the interval of 300 ms associated with their ball release time, but not other time-intervals (Fig. 3.4c). To quantify this observation, we performed a linear regression between the discrimination threshold of each standard interval as a function of elapsed days for each participant. A negative slope means that as time elapsed, the discrimination threshold decreases, indicating that the sensitivity of time perception gets better with training. The regression slopes across participants for each standard interval were averaged and shown as in Fig. 3.4d. Only the averaged slope of 300 ms standard interval was significant different from 0

($t(19) = 4.36$, $p < .001$, $d = .98$). A one-way mixed-effect model across four standard intervals showed a significant main effect ($F(3, 63) = 10.28$, $p < .001$, $\eta^2 = .33$). The post hoc test showed that the averaged slope of 300 ms standard interval was different from the slopes of other three standard intervals (300 v. 600 ms: $t(63) = 2.93$, Dunnett-adjusted $p = .013$, $d = .61$; 300 vs. 1000 ms: $t(63) = 4.81$, Dunnett-adjusted $p < .001$, $d = .95$; 300 vs. 3000 ms: $t(63) = 4.93$, Dunnett-adjusted $p < .001$, $d = .80$).

We then asked whether the reduction of ball-release time variability is correlated with the improvement of discrimination threshold of 300 ms within each individual. We performed a linear regression between discrimination threshold of 300 ms and release-ball variability for each participant (Fig. 3.4e). A positive slope means that as ball-release time variability increased, discrimination threshold increased, indicating that worse motor timing was associated with worse perceptual performance. The distribution of regression slopes was shown in Fig. 3.4f (3 outliers removed using the ROUT method). The majority of participants have positive correlation between improvement of ball-release timing and time perception around 300ms ($t(21) = 3.77$, $p = .001$, $d = .80$). These results revealed plastic modifications induced by motor-training could also affect perceptual timing.

In sum, we found that with throwing practice, participants enhanced the sensitivity of time discrimination selectively for the interval of 300 ms close to the ball-release time, but not for others. In addition, within the majority of individuals, the magnitude of motor timing improvement is positively correlated with the enhancement of time-interval discrimination, suggesting that improvement of motor timing enhances the sensitivity of time perception.

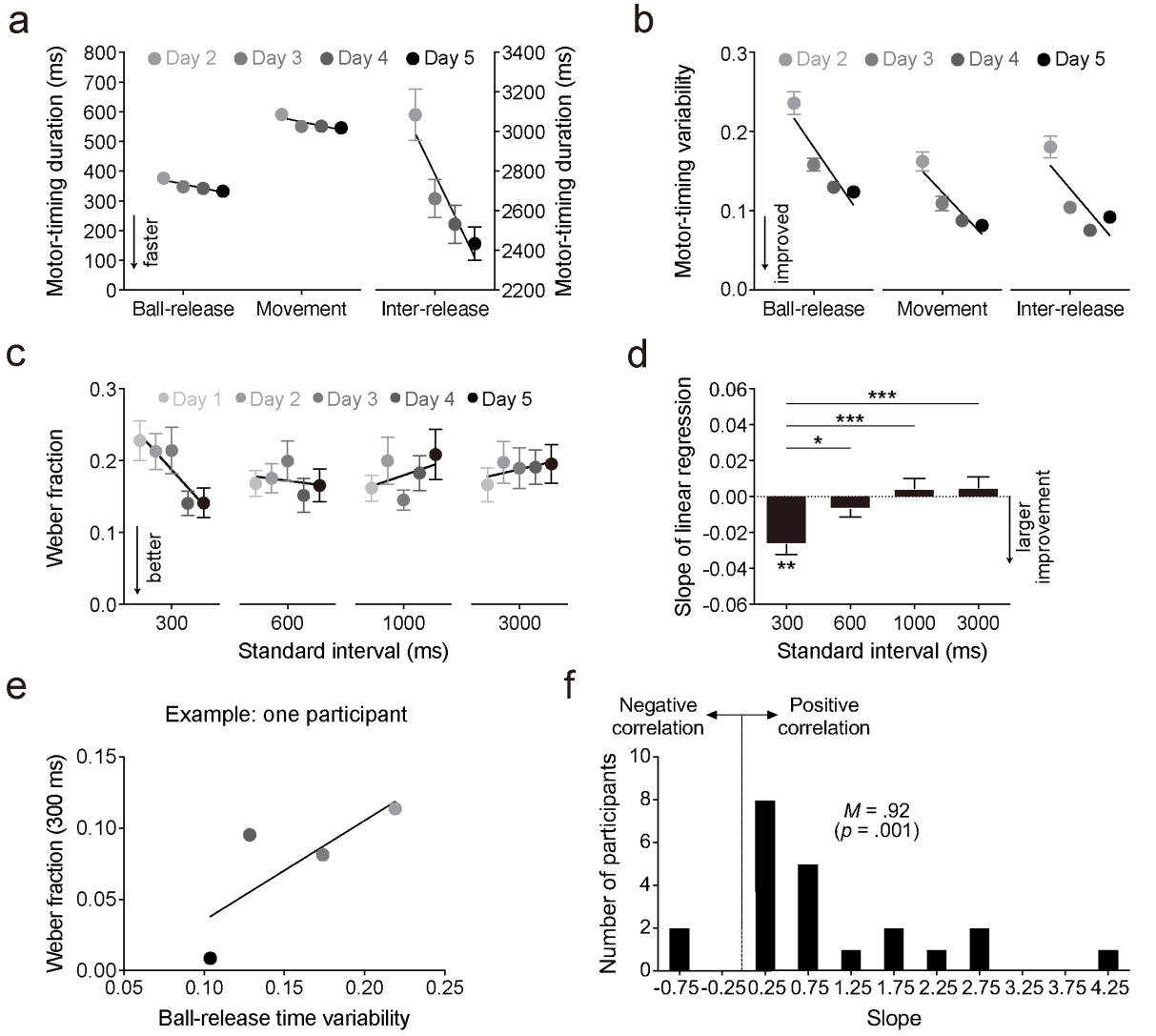


Fig. 3.4. Motor and perceptual performance in Experiment 1. All three types of motor timing showed shortened durations (**a**) and reduced variability (**b**). The linear regression line for each motor-timing was averaged based on regression lines across all participants. (**c**) Weber fraction for the time-interval discrimination threshold of each standard interval across days 1 - 5. Smaller Weber fraction indicates better perceptual performance. The linear regression line for each standard interval was averaged based on regression lines across all participants. In (**a**) - (**c**), the colors of the dots correspond to the daily sessions. (**d**) Averaged regression slope for each standard interval across all participants. A negative slope indicates time perception gets better with training. (**e**) An example linear regression for one participant is shown for the relation between ball-release time variability and threshold of 300 ms standard interval in days 2 – 5. The equation of the example regression line is $y = .70 * x - .03$. The colors of the dots correspond to the daily sessions indicated by the colors of the dots in (**a**) - (**c**). (**f**) The frequency distribution of linear regression slopes of 22 participants. The dashed line indicates 0 on the *x*-axis. Values to the left and right of the dashed line indicate whether ball-release time variability and threshold of 300 ms standard interval were negatively or positively correlated, respectively. The mean slope across participants was determined to be significantly different from zero using a one-sample *t* test.

Experiment 2: The Effect of Perceptual-based Learning on Time Perception

In Experiment 1, we found that practicing a sequence of throwing movements enhances the sensitivity of time-interval discrimination and this enhanced sensitivity is selectively linked to the ball-release time. To further ensure that this enhanced time-interval discrimination sensitivity was primarily led by motor training, not by the perceptual-based learning effect of the time task per se, we asked another group of participants to only perform the time-interval discrimination task without throwing in Experiment 2. We predicted that without motor practicing, time-interval discrimination sensitivity under all standard intervals would not show improvement after five days.

Method

Participants. Fifteen participants (8 females; mean age = 23.00 years) were recruited and compensated with $10/h after completing the 5 experimental sessions on 5 separate days. The sample size was determined on the basis of the effect size needed to achieve 80% statistical power (d = 0.70, n = 13) as determined with a one-sample t test on preliminary data. Participants had normal or corrected-to-normal color vision and were naive to the aim of the experiment. All procedures were approved by the Northeastern University Institutional Review Board.

Procedure. All tasks and procedures were identical to those in Experiment 1, except in day 2 - 5, all participants only performed the time-interval discrimination task as day 1 without the prior motor training task. The four standard intervals in the time-interval discrimination task are also the same as in Experiment 1.

Data analysis. All data analysis and statistics were performed as Experiment 1. In addition, using a paired-samples *t* test or a one-sample *t* test to investigate the null hypothesis that there was no difference between means, we estimated the Jeffreys-Zellner-Siow (JZS) prior Bayes factor with a default scale (*r*) of 1 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). A JZS Bayes factor indicates the ratio of marginal likelihoods for given null hypothesis and alternative hypothesis. For instance, a JZS Bayes factor larger than 1 indicates that the probability density function of the data under the null hypothesis is larger than that under the alternative hypothesis, suggesting in favor of the null hypothesis.

Results

Participants did not show any improvement in the sensitivity of time discrimination for the 300 ms standard interval as in Experiment 1, whereas the discrimination sensitivity for other standard intervals are the same as in Experiment 1 (Fig. 3.5a). We performed a linear regression between the discrimination threshold of each standard interval as a function of elapsed days for each participant. A negative slope means that as time elapsed, the discrimination threshold decreases, indicating that the sensitivity of time perception gets better with training sessions. The regression slopes across participants for each standard interval were averaged and shown as in Fig. 3.5b. The averaged slope of 300 ms was not significant different from 0 ($t(12) = .10$, $p > .250$, $d = .03$, Bayes factor = 4.80), but was different from the averaged slope of 300 ms in Experiment 1 ($t(31) = 3.15$, $p = .004$, $d = 1.19$). We also compared the averaged slopes of 600, 1000, 3000 ms with those in Experiment 1, and they were all equivalent (600: $t(34) = .33$, $p > .250$, $d = .11$, Bayes factor = 3.84; 1000: $t(36) = .01$, $p > .250$, $d = .004$, Bayes factor = 4.08; 3000: $t(38) = .87$, $p > .250$, $d = .29$, Bayes factor = 3.02).

In sum, we found that without throwing practice, participants did not show any improvement in the sensitivity of time discrimination for all time-intervals. The results further evidence that the improvement of discrimination sensitivity of 300 ms time interval was induced by motor training but not by the pure perceptual-based learning.

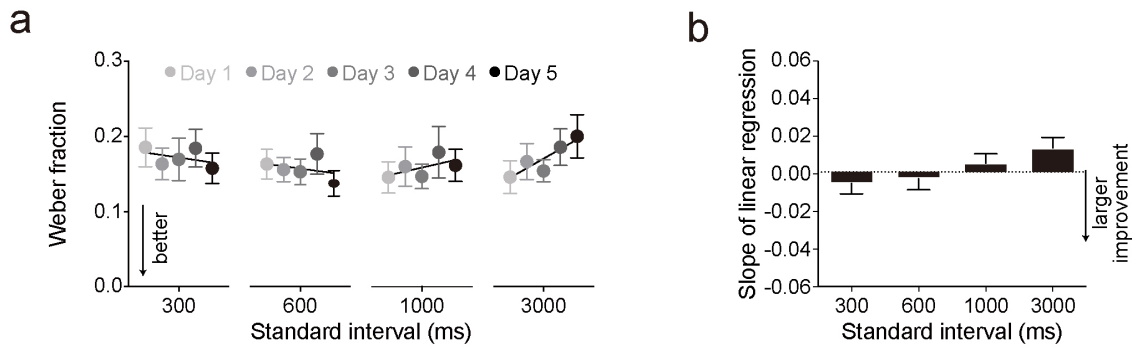


Fig. 3.5. Results in Experiment 2. (**a**) Weber fraction for the time-interval discrimination threshold of each standard interval across days 1 - 5. Smaller Weber fraction indicates better perceptual performance. The dot colors indicate experimental days. The linear regression line for each standard interval was averaged based on regression lines across all participants. (**b**) Averaged regression slope for each standard interval across all participants. A negative slope indicates time perception gets better with training.

Experiment 3: Improved Time Perception Persists in the Long Term

In Experiment 3, we examined whether such improved sensitivity of perceptual discrimination associated with ball-release time can persist in the long-term. In motor control, it has been shown that temporal patterns in movement skills have remarkable persistence. Previous work showed how individuals develop idiosyncratic temporal patterns in a bimanual polyrhythmic task that persist 6 months after the end of practice (Park & Sternad, 2015; Park et al, 2013). We reasoned that 1) the discrete time primitive formed by throwing practice can be encoded into the long-term memory; 2) while the retention of motor timing is maintained, the improved perceptual time duration discrimination ability persists together.

Method

Participants. Eleven participants (7 females; mean age = 22.64 years) who have accomplished Experiment 1 were recalled and compensated with $10/h. The sample size was determined on the basis of the effect size needed to achieve 80% statistical power (d = 1.07, n = 11) as determined with a one-sample t test on preliminary data. Participants had normal or corrected-to-normal color vision and were naive to the aim of the experiment. All procedures were approved by the Northeastern University Institutional Review Board.

Procedures. After participants finished all five sessions in Experiment 1, we asked them to return for a retention session after a period of time, in the range of 6 – 91 days. On average, participants returned from Experiment 1 after 22.9 ± 7.69 s.e. days. The time period between Experiment 1 and the retention session was determined based on the availability of each participant. Upon return, they performed one session of the identical skittles task followed by the time-interval discrimination task, which are the same as days 2 – 5 in Experiment 1.

Data analysis. We calculated the motor-timing variability and Weber fraction of the discrimination threshold on the retention day as in Experiment 1.

Results

We first calculated how much participants maintain the learned throwing skill. For each participant, we performed linear regressions on the ball-release time variability as a function of each motor training session in Experiment 1 (day 2 – 5). Then, we used the derived regression equation to conversely determine performance on which day equates with the retention day's

performance (Fig. 3.6a) and defined that day as the retained days of motor skill learning. A retained day of 5 indicates that the learned motor skill was fully maintained on the retention day without loss. Larger retained days indicated longer persistence of the improved motor skills. The retained days of ball-release time variability were averaged across participants (Fig. 3.6b). We observed that the motor performance on the retention day was almost equivalent to the last training session (retained days = 4.75 ± 0.26 s.e.), indicating the learned throwing skill almost fully persisted on the retention day. A one-sample *t* test of retained days showed that the mean of retained days was significantly different from 0, $t(10) = 14.88$, $p < .001$, d = 4.49.

Furthermore, we calculated how much participants maintain the improved time perception of 300 ms. For each participant, we performed linear regressions on Weber fraction of the time-interval discrimination threshold in 300 ms as a function of each daily session in Experiment 1 (day 1 – 5). Then, we used the derived regression equation to conversely determine performance on which day equates with the retention day's performance and defined that day as the retained days of the improved time perception. A retained day of 5 indicates that the improved time perception was fully maintained on the retention day without loss. Larger retained days indicated longer persistence of the improved time perception. The retained days of Weber fraction in 300 ms standard interval were averaged across participants (Fig. 3.6c). We observed that the time perception performance on the retention day was equated with the one before the last session (retained days = 3.89 ± 1.21 s.e.), indicating the improved time perception persisted most on the retention day. A one-sample *t* test of retained days showed that the mean of retained days was significantly different from 0, $t(8) = 3.20$, $p = .013$, d = 1.07.

In sum, Experiment 3 extend the results from Experiment 1 and 2 by demonstrating that the improved ball-release time variability can be encoded into the long-term memory. Moreover,

while the retention of motor timing is maintained, the improved time perception ability persists together.

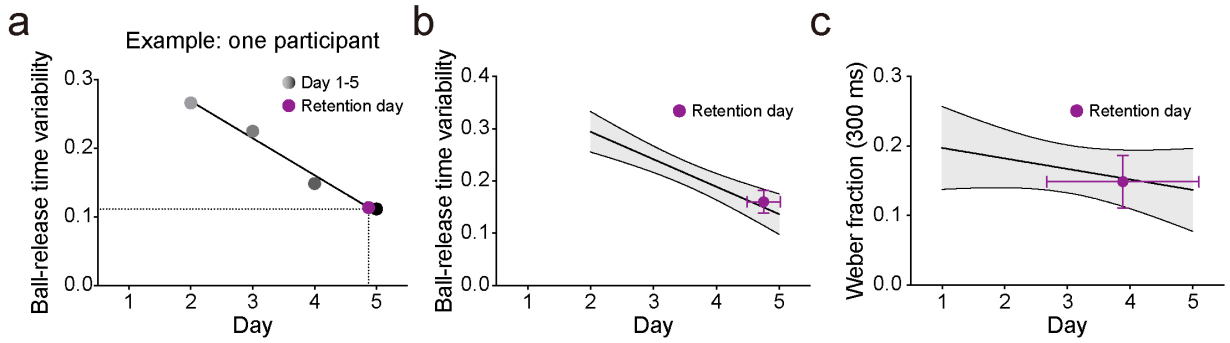


Fig. 3.6. Retention performance in Experiment 3. (**a**) Within each individual, linear regressions were performed on ball-release time variability across day 2 - 5 to determine which day's performance is equated with the motor performance on the retention day. The equation of the example regression line is $y = -.05 * x + .38$. The dot colors represent the days. (**b**) The averaged regression line ($y = -.05 * x + .40$) and retained day (4.75 ± 0.26 s.e.) of ball-release time variability. (**c**) The averaged regression line ($y = -.02 * x + .2$) and retained day (3.89 ± 1.21 s.e.) of Weber fraction of 300 ms discrimination sensitivity. In (**b**) and (**c**), the gray area represents the 95% confidence interval of the best-fit line.

Discussion

Complex movement practice facilitates time perception

In the current study, we discovered that improvement of motor timing enhances the sensitivity of time perception, even for timing patterns inherent to a more complex motor task. First, we observed that time-interval discrimination sensitivity was enhanced by 4-day throwing practice (Experiment 1) and that the enhancement effect was not resulted from perceptual-based learning of the time perception task per se (Experiment 2). The effect of action on time perception has been examined in a wide range of studies, including behavior research (Hagura, Kanai, Orgs, & Haggard, 2012; Manning & Schutz, 2013; Press et al., 2014; Tomassini et al., 2012, 2014, 2017; Wiener, Zhou, Bader, & Joiner, 2019), brain-imaging research (Schubotz, Friederici, & Cramon, 2000; Treisman, Faulkner, & Naish, 1992), and neurobiological research (Ivry & Spencer, 2004). Beyond the modulation effect of action on time perception, our findings provide strong evidence

that time perception is indeed enhanced after practicing complex movements without explicit periodicity.

It is also worth noting that only the ball-release time, but not other motor timings involved in the motor training task improve corresponding perceptual timing (Experiment 1). The results suggest that 1) only improvement in the specific motor timing, i.e., ball-release time, can impact corresponding time-interval discrimination, and 2) the transfer from motor timing to perceptual discrimination is temporal specific and would not be generalized to other time-intervals in the time perception task. Furthermore, with the majority of individuals, the selective enhancement in time perception was positively correlated with the improvement in ball-release time variability (Experiment 1). This correlation between motor-timing variability and perceptual discrimination suggested that there is a shared temporal mechanism between perception and movement regardless of rhythmicity or complexity of the motor tasks.

In addition, we observed that while retention of motor timing is maintained, the improved time-interval discrimination ability persists together. Furthermore, the performance decay in perceptual timing retention is faster than that of motor timing (Experiment 3). The remarkable persistence of motor timing is consistent with a prior longitudinal case study demonstrating that temporal patterns in a bimanual polyrhythmic task can be retained even for 8 years after the end of 2-month practice (Park et al, 2013). The results are also in accord with a previous study showing that visuomotor learning and its arbitrary association with external sensory stimuli persists in the long-term (Im et al., 2016). We further extended their findings by showing that perceptual discrimination on the trained time-interval can persist with the retention of motor timing in a long-term.

Potential mechanisms for the effect of motor training on time perception

One long-standing debate in understanding the timing of real-life behavior is whether there is one centralized representation of time or multiple timing mechanisms underlying different tasks. To address this question, previous studies compared the abilities to precisely perceive and produce temporal durations, reasoning that a common timing mechanism should drive similar performance variance among different time tasks (Gibbon, 1977; Keele, et al., 1985, Wearden & McShane, 1988). For example, Ivry and Hazeltine (1995) companied the timing mechanisms underlying a perception and a repetitive finger tapping task. Participants showed similar linear relationships between performance variance and squared interval duration in both tapping and perception tasks, suggesting a common internal representation of temporal duration for both perceptual and motor timing. This conclusion was also supported by a prior functional MRI study (Schubotz et al., 2000) suggesting that motor timing and time perception involve similar brain areas and neural network. Our results demonstrated that improvement of motor timing enhances the sensitivity of time perception, even for timing patterns inherent to a more complex motor task. We interpret these finding that there is a shared temporal mechanism between perception and movement regardless of rhythmicity or complexity of the motor tasks.

Alternative, participants enhanced time discrimination selectively for the interval of 300 ms associated with their ball-release time but not for other intervals, suggesting that different timing mechanisms might be involved in distinct temporal durations. Previous studies demonstrated that temporal perceptual learning is temporally specific (Bartolo & Merchant, 2009). For instance, Wright et al. (1997) demonstrated that training in interval of 100 ms can only improve perceptual discrimination of the trained one but not for other intervals of 50, 200, and 500 ms, suggesting that each specific time interval consists of their

own timing mechanisms. Moreover, only the ball-release time but no other motor timings improve corresponding perceptual timing, suggesting that the ball-release time is more crucial in the direct talk between perceptual and motor timing. However, the specific underlying mechanism is still unknown and need future exploration. We speculate that it might because only the ball-release time is critically linked to the success of target acquisition or the agency of movement control.

Concluding remarks

Here, we reported that duration discrimination sensitivity can be enhanced by prior motor training, and this enhancement effect is selectively to the trained interval in the motor task. This newly observed modulation of time perception by complex motor training could not be explained by the traditional one-way information flow from perception and action (Cover & Thomas, 1991). Rather, it highlights that perceptual and motor systems operate closely in concert with each other in the complex real-life environment. The study also suggested that there is a shared temporal mechanism between perception and movement regardless of rhythmicity or complexity of the motor tasks.

CHAPTER 4: RECIPROCAL FACILITATION BETWEEN MENTAL ROTATION AND VISUOMOTOR ROTATION

ABSTRACT

Cognition and action are deeply grounded in our bodily interactions with the environment. Yet, to date, evidence for common processing for mental rotation and visuomotor rotation has been only indirect and correlational. For instance, mental rotation and visuomotor rotation have similar processing rates and involve similar brain regions. Such correlational evidence has left open the possibility whether cognitive and motor systems merely process rotation in a similar fashion or whether they are tightly coupled, sharing a common mechanism. The present study explicitly juxtaposes mental rotation and visuomotor rotation tasks to induce direct effects from one to the other. Specifically, we investigated whether training in visuomotor rotation task, where participants reached to a target, while the cursor feedback was rotated 45º to force movement adaptation, can improve performance in a visual mental rotation task, where they decided whether a letter (e.g., 'R') or a map in different rotation angles was normal or mirror-reversed, and vice versa. We observed the bidirectional transfer: participants performed visual mental rotation faster after the visuomotor rotation training, and their learning rate for visuomotor adaptation improved after their mental rotation training. Therefore, this remarkable reciprocal plasticity achieved through the two widely different tasks provides strong evidence for close reciprocal connections between visual cognition and action. It may also imply that the operation of "rotation" itself could be a common primitive.

Introduction

A fundamental question for understanding human behaviors is whether human actions are merely the expressions of internal mental functions or if they can actually shape cognitive processes. Historically, the field of cognitive science assumed a unidirectional information flow of acquiring sensory input, processing the information with high-level cognition, and then planning and executing appropriate actions (Johnson-Laird, 1988; Newell & Simon, 1972; Sanders, 1980; Sternberg, 1969). The linear processing prospective can be applied to explain many daily life examples, such as humans perceive and mentally represent an object to open the thumb and index fingers to grasp it (Goodale, Jakobson, & Keillor, 1994; Johansson, 1991). In addition, extensive evidence showed that prior mental practice of a motor task in the absence of overt physical activity enhances the movement performance (for reviews, see Feltz & Landers, 1983; Driskell, Copper, & Moran, 1994). In spite of the wealth of literature on linear-order information processing, there is little work investing the interactions between mental activities and motor performance, especially the potential effect of action on cognition. However, accumulated evidence suggests a codependence between perception and action. For instance, the action-specific perception theory states that humans' ability to act influences how they perceive the environment (Proffitt, 2006; Witt, 2011). In Chapter 2, we demonstrated that a prior grasping training enhanced subsequent perceptual discrimination (Guo & Song, 2019).

Recently, a growing body of research has shown connections between mental and manual operations. For instance, manually rotating a wheel interfered with the concurrent mental rotation of cubes (Sack, Lindner, & Linden, 2007). Neurophysiological studies revealed that mental rotation can be performed by simulating manual rotation covertly and this covert simulation activates motor cortex (Cohen et al., 1996; Kosslyn et al., 1998; Kosslyn et al., 2001). In

addition, there are suggestive parallels between mental rotation and visuomotor rotation, a simple motor task that requires participants to adapt to rotated visual feedback of hand reaching movements. For instance, processing rates of visuomotor rotation and visual mental rotation, the linear relationship between rotated angle and response time, were positively correlated (Pellizzer & Georgopoulos, 1993). Moreover, neural evidence showed that visuomotor rotation activates the corresponding rotation of neuronal population vectors in the motor cortex as mental rotation does (Georgopoulos et al., 1989). Also, a recent fMRI study found common brain regions underlying visuomotor adaptation and mental rotation (Anguera et al., 2010; Schlegel et al., 2016). Collectively, these findings implied that a common operation of rotation can bridge the mental and motor processing in distinct tasks.

However, as correlational studies, the aforementioned evidence cannot fully determine whether a common mechanism drives motor and mental rotation. We reasoned that more direct evidence supporting a common mechanism can be obtained by examining whether improvement in one process can lead to changes in the other when they both involve a rotation operation. If so, we predict that 1) training in visuomotor rotation will facilitate mental rotation but other motor tasks without rotation operation will not; reversely, 2) mental rotation training will enhance visuomotor rotation but other cognitive tasks without a rotation judgment will not. If we only see transfer from visuomotor rotation training to mental rotation but not transfer in the opposite direction, it could indicate that 1) rotation transfer is unidirectional from motor to cognition, or alternatively, 2) visuomotor rotation requires more complex movement control beyond a rotational operation, and mental rotation training is not sufficient to modify the adaptative performance required for visuomotor rotation. If there is a bidirectional transfer between

visuomotor rotation and mental rotation, this could indicate a common mechanism between cognition and action.

In Experiment 1, to determine the impact of visuomotor rotation training on mental rotation, we compared response times (RTs) for a mental rotation task before and after a visuomotor rotation training session. In the visuomotor rotation task, participants were required to reach to a target, while the cursor feedback was rotated 45º to force movement adaptation. We demonstrated that training on visuomotor rotation adaptation resulted in significantly larger improvement in a mental rotation task compared to training on other motor tasks without a rotational component, such as a direct reach task and a sequential reaction time (SRT) task. In Experiment 2, we provided converging evidence by extending Experiment 1 to a more ecologically relevant task, mental rotation of maps. We consistently observed that the visuomotor rotation training resulted in larger reaction time improvement in mental map rotation than a direct reach task. In Experiment 3, we reversely examined the effect of mental rotation training on visuomotor rotation learning. We observed that the learning rate of visuomotor adaptation was improved after training on a mental rotation but not after a control task that did not require a rotation judgment. Taken together, we provide evidence for reciprocal facilitations between visuomotor rotation and mental rotation.

Experiment 1: Learning Visuomotor Rotation Enhances Mental Rotation

To examine how visuomotor training affects mental rotation, we compared RT for a mental rotation task before and after a visuomotor training session. In the training session, participants were required to perform a visuomotor rotation task, a control direct reach task, or a control sequential reaction time (SRT) task.

Method

Participants. A total of 57 right-handed Brown University students participated in the one-hour study for course credit or monetary compensation, reported normal or corrected-to-normal color vision and were naïve to the aims of the experiment. Nineteen participants (15 females, mean age 21.26 years) were included in the visuomotor rotation group, 19 participants (19 females, mean age 19.58 years) were included in the direct reaching group, and 19 participants (16 females, mean age 21.05 years) were included in the SRT group. The sample size (19 per group) was determined on the basis of the effect size needed to achieve 75% statistical power ($\eta^2 = 0.13$, $n = 18$) as determined with an ordinary one-way ANOVA on preliminary data. All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

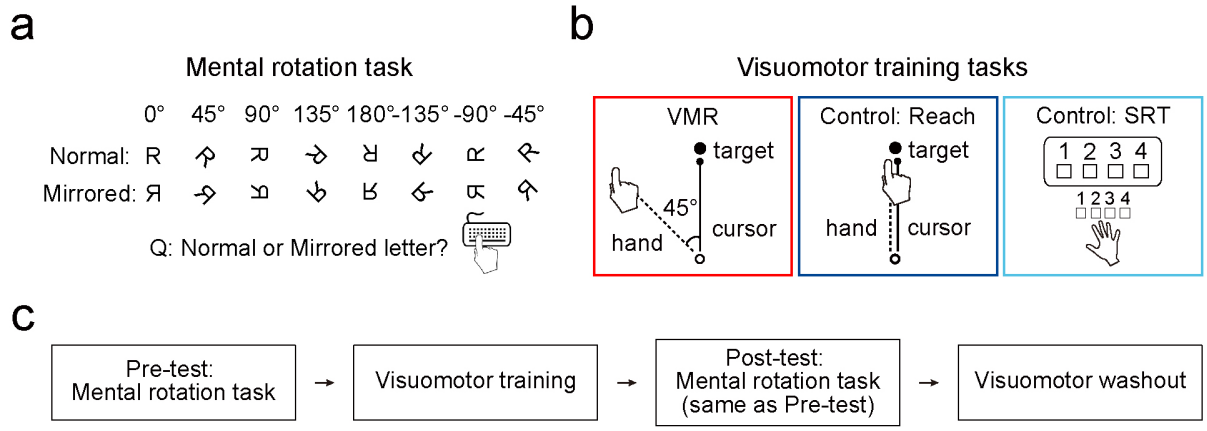


Fig. 4.1. Schematics of Experiment 1. (**a**) In the mental rotation task, participants were asked to respond whether a tilted letter (e.g., R) was a normal or a mirrored image. Four asymmetric letters (F, G, J, R) were presented as targets randomly in the tasks. (**b**) In the visuomotor training session, participants performed a visuomotor rotation (VMR; red border) task, or one of the two control tasks: a direct reach task (blue border) or a sequential reaction time (SRT; cyan border) task. In the VMR and control reach task: participants moved the cursor (small black dot) from the starting base (open circle) toward the target (big black dot), and the cursor direction (solid line) was rotated 45° clockwise from (VMR) or normally followed the hand trajectory (dotted line). In the SRT task, participants pressed a button to indicate the corresponding target location. (**c**) The experimental procedure.

Apparatus. All sessions are conducted in a dimly illuminated room. Participants sat in front of a 21.5-inch Apple iMac computer, and all stimuli were presented with 60Hz refresh rate and 1920 x 1080 pixel resolution. In the visuomotor rotation and direct reach tasks, participants held a stylus pen with their right hand and moved the pen across the surface of a touch screen (Magic Touch; Keytec, Garland TX), which lay flat on a table and aligned with the midlines of participants and the computer screen. The stylus movement controlled a corresponding cursor on the computer screen. Stimulus presentation and recording of cursor displacement were conducted using custom software designed with MATLAB (2011a, Mathworks) and Psychtoolbox (Brainard, 1997).

Mental rotation task. Four asymmetric upper-case letters (F, G, J, R) and their horizontally-flipped (mirrored) images were used as stimuli, for a total of eight characters (font: Courier New, height: 2.82 cm, color: white). Each stimulus was rotated in 45° increments from -135° (counterclockwise from upright) to 135° (clockwise from upright), for a total of eight angles (Fig. 4.1a). On each trial a white fixation dot (0.24 cm diameter) appeared at the center of the screen (black) and stayed for 1,000 ms. Then, the stimuli were presented at the same location as the fixation dot. Participants were instructed to determine whether each stimulus was a normal letter or a mirrored image by pressing a button with their right hand and were required to respond as accurately and as quickly as possible. The stimuli stayed on the screen until a button was pressed, but no longer than 5,000 ms. Distinct auditory feedback was presented to inform the accuracy of button-press responses. After one practice block of 64 trials, all participants performed 4 blocks in both the pre-test and post-test sessions, and each block consisted of 64 trials (8 stimuli x 8 angles) in random order.

Visuomotor rotation (VMR) task. Participants were instructed to move a cursor on the screen from the starting base in the center of the screen toward a reach target, in which the cursor motion was rotated 45° clockwise from the hand trajectory (rotation trials) (Fig. 4.1b, red border). The starting base was a white circle with a diameter of 1 cm, and the reach target was a solid white dot with a diameter of 1 cm and located 5.5 cm from the starting base. At the beginning of each trial, the initial location of the cursor was outside the starting base. Participants moved the cursor into the starting base to trigger the appearance of the target, which stayed on the screen for 1,500 ms. Each target direction was located in 45° increments from 0° (12 o'clock) to 315°, for a total of eight possible target locations. Participants were asked to move the cursor toward the target as fast and as linear as possible and move it back to the starting base immediately after they reached the target.

Control direct reach task. Everything was the same as the VMR task except the cursor direction followed the hand trajectory normally without rotation (no-rotation trials) (Fig. 4.1b, blue).

Control sequential reaction time (SRT) task. Four white open squares were arranged horizontally on the screen to indicate four possible target locations, designated 1 - 4, which corresponded to four horizontally arranged buttons (V, B, N, and M) on the keyboard (Fig. 4.1b, cyan). The four squares, with 2.43 cm sides and a 0.15 cm border width, were presented along the horizontal meridian with 4.05 cm gaps between them. On each trial a white dot target (2.03 cm diameter) appeared at one of the four locations. Participants were instructed to press the corresponding button as accurately and as quickly as possible and were not given accuracy

feedback. Targets appeared either at random locations (random trials) or at a target location within a 12-item repeating sequence ([2, 3, 1, 4, 3, 2, 4, 1, 3, 4, 2, 1]) (repeated trials).

Procedure. All participants performed four sessions: pre-test of mental rotation, visuomotor training, post-test of mental rotation, and visuomotor washout. The two mental-rotation sessions were identical for all participants regardless of group. During the visuomotor training session, participants were randomly assigned to the visuomotor rotation group or the other two control groups: direct reach and SRT (Fig. 4.1c). The visuomotor washout session was designed to measure how much the visuomotor training effects were maintained after post-test of mental rotation.

Visuomotor rotation (VMR) group. The visuomotor training session included 3 phases: 1) 1 practice block (24 no-rotation trials), 2) 1 baseline block (80 no-rotation trials), and 3) 4 training blocks (4 x 80 rotation trials, 10 trials for each of the 8 reach targets). The baseline block measured for inherent bias in the hand reaching movement toward each target. After the mental rotation post-test, a visuomotor washout block (80 no-rotation trials) followed. Eight target locations were presented randomly within every 8 trials in each block.

Control reach group. The visuomotor training session included 3 phases: 1) 1 practice block (24 no-rotation trials), 2) 1 baseline block (80 no-rotation trials), and 3) 4 reach blocks (4 x 80 no-rotation trials, 10 trials for each of the 8 reach targets). After the mental rotation post-test, a visuomotor washout block (80 no-rotation trials) followed. Eight target locations were presented randomly within every 8 trials in each block.

Control sequential reaction time (SRT) group. The visuomotor training session included 2 phases: 1) 1 practice block (12 random trials), 2) 1 baseline block (80 random trials), and 3) 5

training blocks (5 x 120 repeated trials). The baseline block measured any inherent bias in the reaction time toward each target location. After the mental rotation post-test, a washout block followed, including 48 repeated trials and 80 random trials.

***Data analysis*.** Performance for the mental rotation task was measured by reaction time, the duration between the letter onset and button response, of all correct trials in each test session. Data analysis procedures of VMR and control direct reach tasks generally followed our previous studies (Song & Bédard 2015). We differentiated the position of the cursor to obtain tangential velocity. The onset and offset of the movement were defined as when the cursor speed exceeded and fell below 5% of peak velocity, respectively. The reach error was defined as the angle difference between the line joining the starting base to the target and the line jointing the cursor locations at movement onset and at peak velocity. The reach error was averaged across 8 successive trials as a trial block covering all target locations. For the SRT task, the performance was measured by reaction times, the duration between the target onset and button response, of correct trials. The reaction times were averaged in each block in the visuomotor training session. For the washout block, the reaction times were averaged for first 48 repeated trials and following 80 random trials, respectively.

We used MATLAB (2015b, Mathworks) and Prism (Version 6.00 for Mac, GraphPad Software, La Jolla California USA, www.graphpad.com) to perform all data processing and statistical analysis. We used parametric ANOVA to analyze the data. If multiple post hoc comparisons followed, we used Šidák correction for comparisons between multiple treatment groups (Šidák, 1967) and Dunnett correction for comparison of treatments with a single experiment group (Dunnett, 1955). Greenhouse-Geisser correction (Maxwell &

Delaney, 2004) was applied when the assumption of sphericity was violated. In addition, using a paired-samples *t* test to investigate the null hypothesis that there was no difference between two means, we estimated the Jeffreys-Zellner-Siow (JZS) prior Bayes factor with a default scale (*r*) of 1 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). A JZS Bayes factor indicates the ratio of marginal likelihoods for a given null hypothesis and alternative hypothesis. For instance, a JZS Bayes factor larger than 1 indicates that the probability density function of the data under the null hypothesis is larger than that under the alternative hypothesis, suggesting in favor of the null hypothesis. All error bars represented standard error of the mean (SEM). The effect size of ANOVAs and *t* tests were measured by eta-squared (η^2) and Cohen's *d*, respectively. According to Cohen (1988), η^2s of .01, .06, and .14 and Cohen's *d*s of 0.20, 0.50, and 0.80 are considered small, medium, and large effect sizes, respectively.

Results

We first compared the motor performance of three groups in the visuomotor training session. In the visuomotor rotation (VMR) group, reach error was reduced across trial blocks in the visuomotor training (Fig. 4.2a: red), suggesting enhancement in visuomotor rotation. As a control, the direct reach task without the rotated visual feedback showed uniformly small reach error (Fig. 4.2a: dark blue). In the control SRT group, reaction time was reduced across blocks in the training session (Fig. 4.2b), which indicates learning of the sequential motor skills. We conducted a one-way repeated measures ANOVA of reach error across trial blocks in the visuomotor training session for the VMR and control reach group. There is a significant effect of trial block for the VMR group ($F(5.524, 99.43) = 40.72$, $p < .001$, $\eta^2 = .55$) but not for the control reach group ($F(6.595, 118.7) = 0.7506$, $p > .25$). We conducted a one-way repeated measures

ANOVA of reaction time across blocks in the visuomotor training session for the SRT group, which shows a significant effect of trial block ($F(2.551, 45.92) = 7.175$, $p < .001$, $\eta^2 = .07$). A post-hoc linear trend analysis of reaction time across blocks is significant (slope = -9.37, $R^2 = .96$, $p < .001$).

Of interest was whether the mental rotation performance was differentially affected by the three visuomotor training tasks. We calculated the mean reaction times of the mental rotation task in the pre- and post-test sessions (Fig. 4.2c) and the RT reduction as a RT difference between the two test sessions (Fig. 4.2d). Larger RT reduction indicates larger mental rotation improvement. The visuomotor rotation group shows a significantly larger mental rotation improvement than the other two groups. A two-way group x test session ANOVA shows a significant main effect of test session ($F(1, 54) = 121.4$, $p < .001$, $\eta^2 = .09$) and an interaction effect ($F(2, 54) = 3.618$, $p = .034$, $\eta^2 = .12$), but no main effect of group ($F(2, 54) = 1.171$, $p > .250$). A one-way ANOVA of RT reduction across the three groups shows a significant main effect ($F(2, 54) = 3.618$, $p = .034$, $\eta^2 = .12$). Post-hoc independent t-tests show that the VMR group showed significantly more RT reduction than the control reach ($t(54) = 2.33$, Dunnett-adjusted $p = .043$, $d = .67$) and SRT ($t(54) = 2.33$, Dunnett-adjusted $p = .044$, $d = .72$) groups.

Finally, we compared the motor performance of the three groups in the visuomotor washout session. In the VMR group, the mean reach error of first trial block in visuomotor washout was 25.77° ± 7.76° s.e., indicating that participants still maintained partial adaptation to the 45° tilted visual feedback until the end of the mental rotation post-test. In the control reach group, the reach error of first trial block was 0.30° ± 2.04° s.e., which was not significantly different from the reach error of last trial block (-0.17° ± 1.76° s.e.) in the visuomotor training session ($t(18) = 1.00$, $p > .025$, Bayes factor = 3.59). This indicates that the control reach group

maintained the same performance as in the visuomotor training session. In the SRT task, the averaged RTs for the repeated trials in visuomotor washout was 307.9 ± 62.03 s.e., which was significantly shorter than the averaged RTs for the last training block (334.5 ± 58.73 s.e.) in the visuomotor training session ($t(18) = 2.81$, $p = .006$, $d = .66$). This indicates that the learning in the SRT task was maintained until the end of mental rotation post-test.

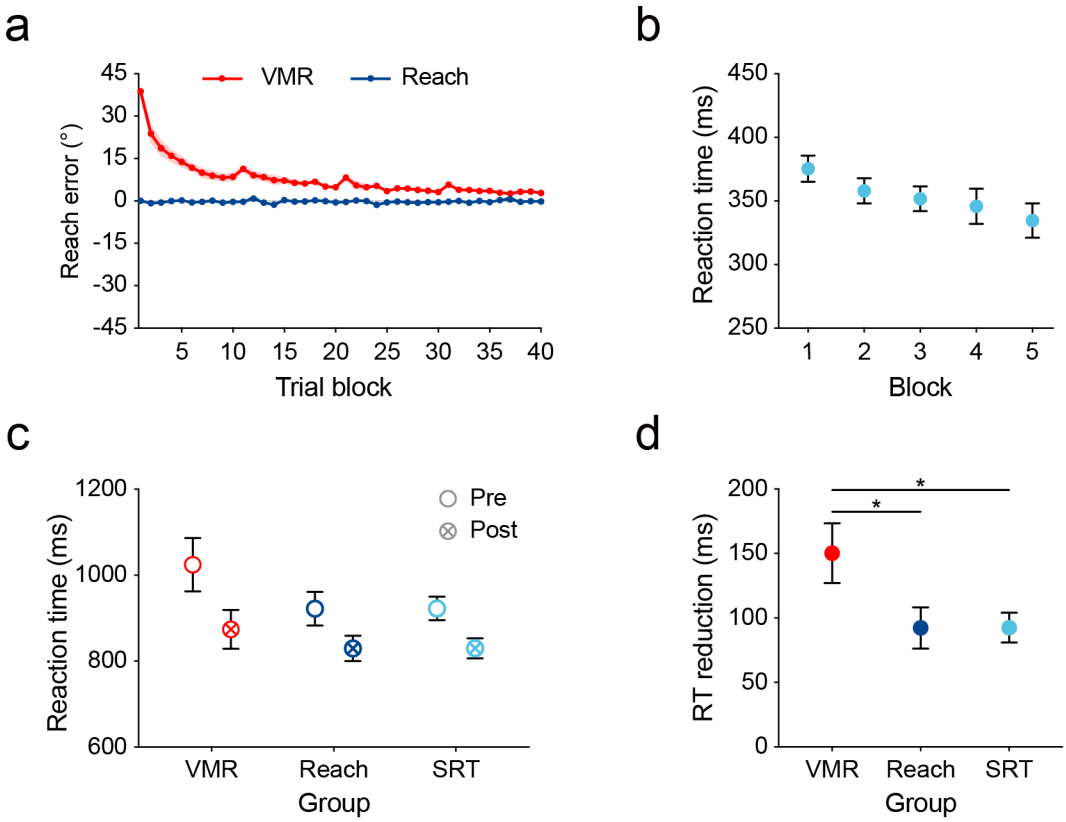


Fig. 4.2. Results in Experiment 1. Reach error of VMR (**a**, red) and Control reach (**a**, dark blue) groups and reaction time of SRT (**b**) group in visuomotor training session. (**c**) Reaction time (RT) of mental rotation tasks. The patterns of dots indicate test session (clear dot = pre-test, crossed dot = post-test). (**d**) RT reduction calculated by subtracting RT in the post-test period from RT in the pre-test period. In (**a**) to (**d**), the colors of the dots correspond to visuomotor training groups as depicted in Figure 1c. Error bars indicate standard errors of the mean. Asterisks indicate significant difference between results for the two training groups (*$p < .05$).

In sum, we observed that after a short session of visuomotor rotation training, participants became faster in the mental rotation task compared to before, whereas training on the two control motor tasks without the operation of rotation resulted in significantly weaker transfer to the

mental rotation task. Thus, Experiment 1 uncovered that training on visuomotor rotation can be transferred to mental rotation.

Experiment 2: Learning Visuomotor Rotation Enhances Mental Rotation of Maps

In Experiment 2, we sought to find converging evidence by extending our work to a more ecologically relevant task such as the mental rotation of maps. To address this question, we compared reaction times of mental map rotation tasks before and after a visuomotor training session, where the visual cursor feedback of reach was given with or without 45˚rotation (VMR vs. control reach group). In the mental map rotation task, participants were asked to determine whether a 2D target map was consistent or not compared to a 2D or a 3D reference map (2D vs. 3D condition). When the reference map was a 2D image, participants performed mental rotation in the 2D image-plane, whereas when it was a 3D image, they further rotated the 2D map in depth (Aretz & Wickens, 1992). If VMR training enhanced mental rotation in the both 2D image-plane and 3D in-depth direction, the 3D condition would show larger improvement than the 2D condition, otherwise the mental rotation in 3D conditions would not benefit more from the VMR training session compared to the 2D condition.

Method

***Participants*.** A total of 30 right-handed Brown University students participated in the one-hour study for course credit or monetary compensation, reported normal or corrected-to-normal color vision and were naïve to the aims of the experiment. Fifteen participants (8 females, mean age 21.6 years) were included in the visuomotor rotation group, and 15 participants (9 females, mean age 20.7 years) were included in the direct reaching group. The sample size (15 per group) was

determined on the basis of the effect size needed to achieve 80% statistical power as determined with an independent-samples *t* test on preliminary data ($d = 1.06$, $n = 9$). All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

Stimuli. All stimuli used in visuomotor training session in Experiment 2 were identical to those in Experiment 1. For the mental rotation sessions, we introduced 2D maps and their corresponding 3D forward-view as new stimuli (Fig. 4.3). In the 2D condition, two grey solid circle tangent to each other were arranged along the horizontal meridian on the screen to represent the make-believe world, with a 24.33 cm diameter. Each solid circle contained a 2D square-shaped map and a dot (black or white, 0.68 cm diameter) at the center. The 2D maps were 10.14 x 10.14 cm and located 5.95 cm from the center of the circle. In the 3D condition, a solid grey circle was located 4.45 cm below the screen center, the same size as in the 2D condition. The 3D forward-view of the 2D map was 6.42 x 12.84 cm and located 8.91 cm above the screen center. All maps were adopted and modified in Google SketchUp.

Procedure. As in Experiment 1, all participants performed four sessions: pre-test of mental rotation, visuomotor training, post-test of mental rotation, visuomotor washout (Fig. 4.1c). During the visuomotor training and washout sessions, participants were randomly assigned to the visuomotor rotation (Fig. 4.1b, red) and control reach (Fig. 4.1b, blue) groups. Other sessions were identical for both groups.

In the pre- and post-tests of mental rotation on maps, participants were asked to determine whether a 2D target map was consistent or not compared to a 2D or 3D reference

stimulus (2D vs. 3D condition) shown at the same time. In the 2D condition, four 2D maps in the standard up-right position were used as reference stimuli. In addition, these four reference maps and their horizontal-flipped (mirrored) maps were used as target stimuli, for a total of eight images. Each target stimulus was rotated in 45° increments from -135° (counterclockwise from upright) to 135° (clockwise from upright), for a total of eight angles. Every trial started with a fixation dot (0.24 cm diameter) presented for 1,000 s at the screen center. After fixation, two grey solid circles appeared on the screen and were located horizontally (Fig. 4.3a). The solid circle with a black center dot contained the reference stimulus (4 images), and the other one with a white center dot contained the corresponding 2D target map that was either the same or mirrored from the reference stimulus (8 images x 8 angles).

In the 3D condition, the 3D reference stimuli were the forward-view of the four reference maps in the 2D condition, and the target stimuli were the same as in the 2D condition (Fig. 4.3b). After fixation, a 3D reference stimulus was shown on the top, and the grey solid circle containing the corresponding 2D target map was shown below at the same time. In both conditions, the reference stimuli were fixed at either the left side (left-reference) or right side (right-reference) on the screen across each block. Participants were instructed to determine whether the target map was a normal or a mirrored image compared to the reference stimuli by pressing a button with their right hand and were required to respond as accurately and as quickly as possible. The stimuli stayed on the screen until a button was pressed, but no longer than 8,000 ms. Distinct auditory feedback was presented to signal the accuracy of button-press responses.

Participants practiced 16 trials each of the 2D (8 trials each of the left- and right-reference) and 3D condition prior to the main experiment. After practice, they performed 4 blocks including 2 blocks each for 2D (1 block each of the left- and right-reference) and 3D

conditions in the pre- and post-test sessions, respectively. Each block consisted of 64 trials (8 images x 8 angles) arranged randomly. All blocks were alternated and counterbalanced among participants.

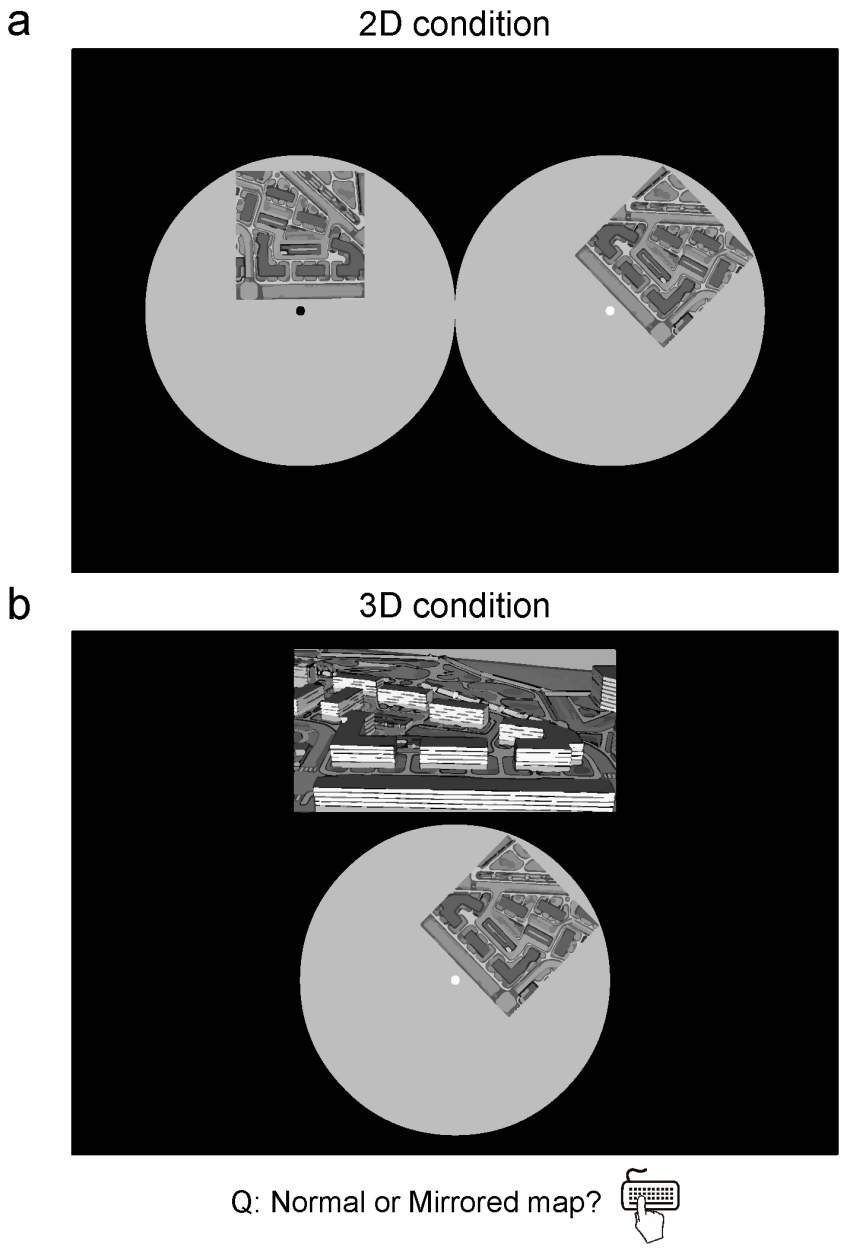


Fig. 4.3. Examples of map stimuli used in Experiment 2. In the 2D condition (**a**), two grey solid circles representing the make-believe world were presented horizontally at the same time. The circle with the black center dot contained the standard up-right reference map, and the other one with the white center dot contained the tilted comparison map. In the 3D condition (**b**), the 3D forward-view reference and its corresponding 2D comparison map were presented vertically at the same time. In both conditions, participants were instructed to report whether the comparison map was a normal or a mirrored map compared to the reference map by pressing a button with their right hand.

Data analysis. In each mental rotation session, we calculated the reaction time of mental rotation under 2D and 3D conditions. All other data analysis and statistics were performed as in Experiment 1.

Results

In the visuomotor rotation (VMR) group, reach error was reduced across trial blocks in the visuomotor training, suggesting improvement in visuomotor rotation. As a control, the direct reach task without the rotational adaptation did not show any change in performance. We conducted a one-way repeated measures ANOVA of reach error across trial blocks in the visuomotor training session for the VMR and control reach group. There is a significant main effect for VMR group ($F(5.03, 70.39) = 12.29$, $p < .001$, $\eta^2 = .35$) but not for control reach group ($F(5.11, 71.48) = 091$, $p > .25$).

Of interests was whether the performance of mental map rotation is differentially affected by the two visuomotor training tasks. We first calculated the reaction time of mental rotation tasks in the pre- and post-test sessions under 2D (Fig. 4.4a) and 3D (Fig. 4.4b) map rotation conditions. Then we calculated RT reduction as the RT difference between the two test sessions (Fig. 4.4c). A larger RT reduction indicates a larger mental rotation improvement. The visuomotor rotation group shows significantly larger mental rotation improvement than the control reach group across the two conditions. In both conditions, the two-way group x test session ANOVAs show significant main effects of test session (2D: $F(1, 28) = 89.00$, $p < .001$, $\eta^2 = .19$, 3D: $F(1, 28) = 198.00$, $p < .001$, $\eta^2 = .37$) and an interaction effect (2D: $F(1, 28) = 4.92$, $p = .035$, $\eta^2 = .01$, 3D: $F(1, 28) = 4.34$, $p = .046$, $\eta^2 = .01$), but no main effect of group

(2D: $F(1, 28) = .008$, $p > .250$, 3D: $F(1, 28) = .07$, $p > .250$). A two-way condition x group ANOVA of RT reduction shows a significant main effect of group ($F(1, 28) = 6.01$, $p = .021$, $\eta^2 = .11$) and a main effect of condition ($F(1, 28) = 42.55$, $p < .001$, $\eta^2 = .24$).

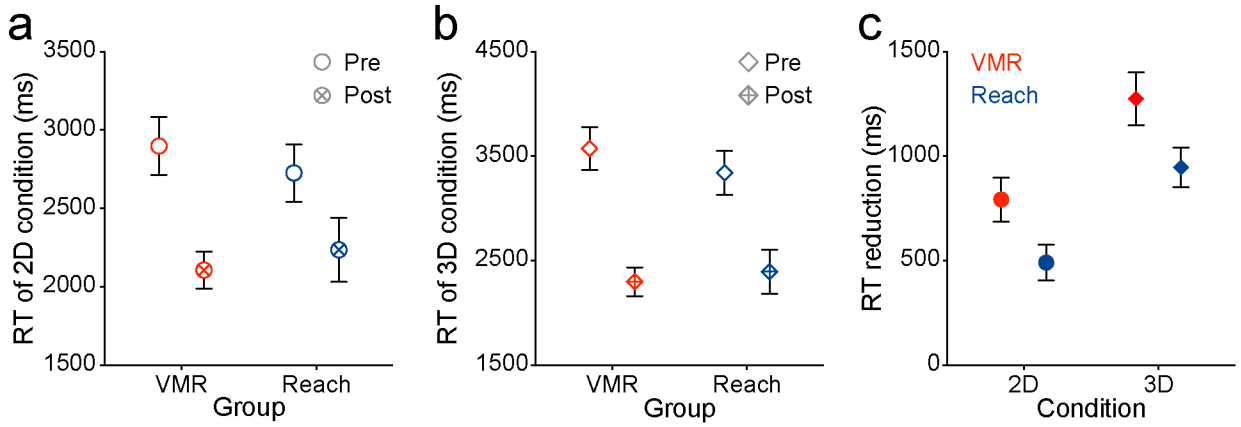


Fig. 4.4. Results in Experiment 2. Reaction time (RT) of mental rotation tasks under 2D (**a**) and 3D (**b**) conditions. The patterns of dots/diamonds indicate test session (clear dot/diamond = pre-test, crossed dot/diamond = post-test). (**c**) RT reduction calculated by subtracting RT in the post-test period from RT in the pre-test period under 2D and 3D conditions. In (**a**) to (**c**), the shapes indicate condition (dot = 2D, diamond = 3D). The colors of the dots/diamonds correspond to visuomotor training groups as depicted in Figure 1c. Error bars indicate standard errors of the mean.

In sum, we observed that a short training in visuomotor rotation training resulted in faster 2D plane rotation and 3D depth rotation compared to previous performance, whereas training on the control reach task without the rotational operation resulted in a significantly weaker transfer to the mental rotation. Thus, Experiment 2 extended the key findings from Experiment 1 that training on visuomotor rotation can be transferred to mental rotation.

Experiment 3: Learning Mental Rotation Enhances Visuomotor Rotation

In Experiments 1 and 2, we have demonstrated that training in visuomotor rotation can transfer to mental rotation. However, it is unknown whether training in mental rotation can also affect visuomotor rotation. To address this question, we compared the learning rate (LR) of visuomotor

rotation before and after a visual training session, in which participants were required to perform a mental rotation task, or a control color discrimination task.

Method

Participants. A total of 36 right-handed Brown University students participated in the one-hour study for course credit or monetary compensation. Each reported normal or corrected-to-normal color vision and were naïve to the aims of the experiment. Eighteen participants (9 females, mean age 20.78 years) were included in the mental rotation group, and 18 participants (12 females, mean age 19.33 years) were included in the control color group. The sample size (18 per group) was determined on the basis of the effect size needed to achieve 80% statistical power ($\eta^2 = 0.12$, $n = 15$) as determined with a one-way ANOVA on preliminary data. All procedures were approved by the Brown University Institutional Review Board and followed the guidelines of the Declaration of Helsinki.

Stimuli. The stimuli were almost same as those in Experiment 1, except for the stimuli used in the visual training session. During the training session, the same four letters and their mirrored images were used as in Experiment 1 but were presented in two colors: pink (RGB: 255, 240, 255) and purple (RGB: 240, 255, 255).

Procedure. The VMR task was the same as in Experiment 1. All participants performed four sessions: pre-test of VMR, visuomotor washout, visual training, and post-test of VMR. The two VMR sessions and visuomotor washout were identical for the two participant groups. The washout session was designed to remove the adaptation to the 45° tilted visual feedback. During

the visual training session, participants were randomly assigned to the mental rotation group or the control color-discrimination group.

The two VMR sessions included 3 phases: 1) 1 practice block (24 no-rotation trials), 2) 1 baseline block (80 no-rotation trials), and 3) 4 testing blocks (4 x 80 rotation trials). After the VMR pre-test, a visuomotor washout block (80 no-rotation trials) followed. Eight target locations were arranged randomly within every 8 trials in each block.

In the visual training session, each trial started with a white fixation dot (0.24 cm diameter) appeared at the center of the screen (black) and stayed for 1000 ms. Then, the letter stimulus in either pink or purple was presented at the same location as the fixation dot. The mental rotation group was instructed to indicate whether the stimulus was a normal letter or a mirrored image regardless of its color, whereas the control color-discrimination group was instructed to indicate whether the stimulus was pink or purple regardless its rotation angles. Both groups reported their answers by pressing a button with their right hand and were required to respond as accurately and as quickly as possible. The stimuli stayed on the screen until a button was pressed, but no longer than 5,000 ms. Distinct auditory feedback was presented to signal the accuracy of the button-press responses. After one practice block, all participants performed 4 blocks in the training session, and each block consisted of 64 trials arranged randomly. The color of the stimulus was randomized within each block.

***Data analysis*.** In additional to the analyses used in Experiment 1, we further calculated the learning rate (LR) in the VMR tasks to indicate the learning performance. The LR is quantified based on the reach errors in the first block of each session, using Equation 2.

$$y = \mathrm{a} + \mathrm{b} * \mathrm{e}^{(\mathrm{c}* - \mathrm{x})} \quad , (2)$$

Where *y* is the averaged reach error of each trial block in the first block; *a* is the level of performance at the end of the block; *b* is the initial performance; *c* is the learning rate, representing the rate of visuomotor adaptation; *x* is the trial block index from 1 to 10, representing the time course of the visuomotor adaptation. The initial values of *a* and *b* for the model-fitting is the reach error in trial block 10 and 1, respectively. The learning rate *c* was fitted from .5 leading to the range of [0, 1].

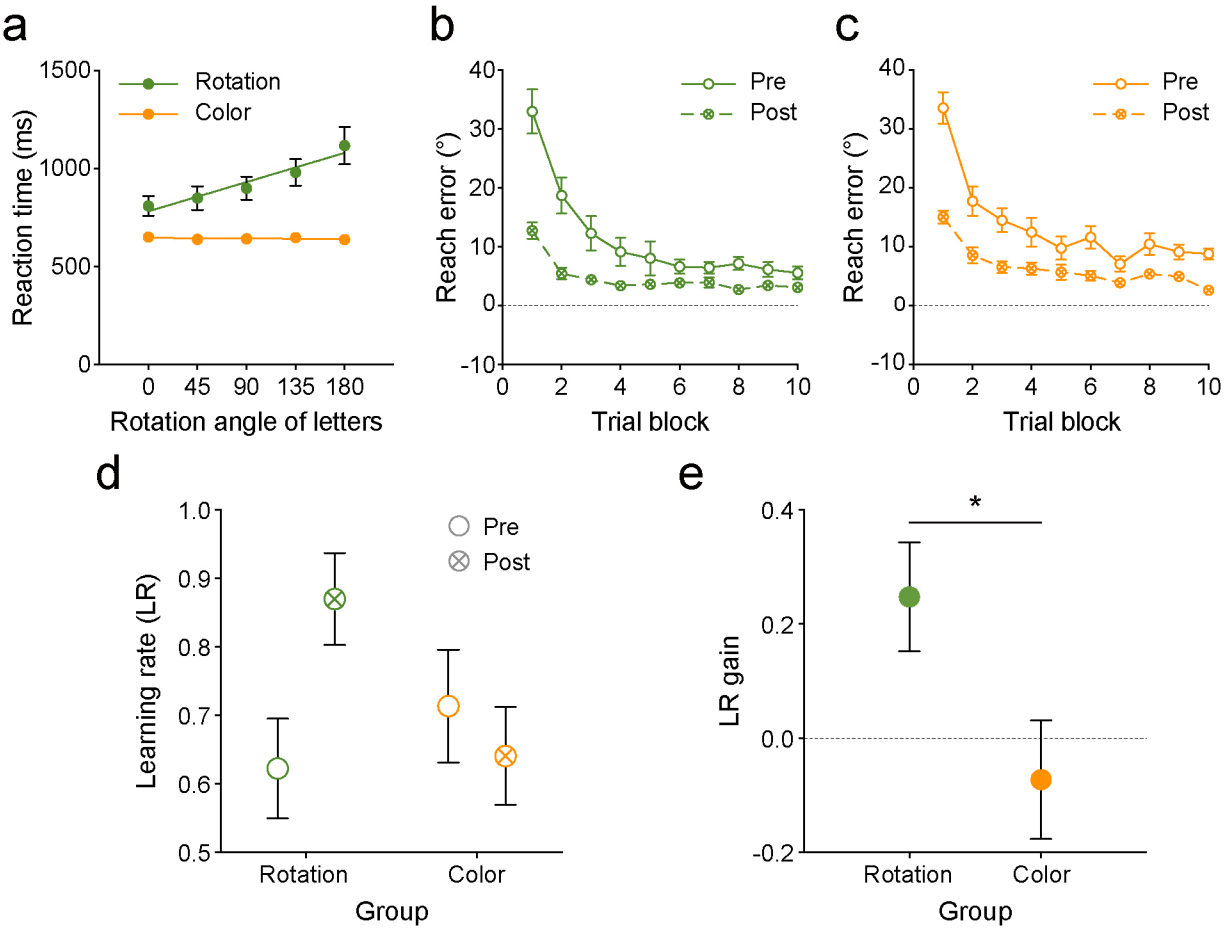


Fig. 4.5. Results in Experiment 3. (**a**) RTs of mental rotation and control color tasks. The linear regression line for each group was averaged based on regression lines across all participants in each group. Reach error of VMR for the rotation group (**b**) and control color group (**c**) in trial blocks 1-10 in the VMR pre-test and post-test. The pattern of lines indicates test sessions (solid line = pre-test, dotted line = post-test). (**d**) Learning rate (LR) of VMR tasks. In (**b**) to (**d**), the patterns of dots indicate test session (clear dot/solid line = pre-test, crossed dot/ dotted line = post-test). (**e**) LR gain calculated by subtracting LR in the pre-test period from LR in the post-test period. In (**a**) to (**e**), the colors of the dots correspond to visual training groups (orange = mental rotation, green = control color). Error bars indicate standard errors of the mean. An asterisk indicates significant difference between results for the two training groups (*$p < .05$).

Results

First, we confirmed that only the mental rotation task but not the control color task involved mental rotation processes (Fig. 4.5a). In the mental rotation group, the RTs increased linearly with the rotation angles, suggesting that participants mentally rotated the letters from the rotation angle to upright. However, the RTs of the control color task were the same across all letter angles, indicating that the task did not involve the mental rotation process. We performed a linear regression on the averaged RT across the absolute letter-rotation angles regardless of the rotation directions (clockwise vs. counterclockwise) for the mental rotation and control color group, respectively. The linear regression slope is significantly different from zero in the mental rotation group (slope = 1.65, $R^2 = .12$, $p < .001$) but not in the control color group (slope = -.04, $R^2 < .001$, $p > .025$).

Of interest was whether VMR performance is differentially affected by the two visual training tasks. Based on our previous work, the learning process of visuomotor rotation mainly happened in the first 10 trial blocks. We first calculated the reach errors of this period for the mental rotation group (Fig. 4.5b) and the control color group (Fig. 4.5c) in the pre- and post-test sessions. Then we calculated the learning rate (LR) based on the reach errors in the pre- and post-test sessions (Fig. 4.5d) and the LR gain as a LR difference between the two test sessions (Fig. 4.5e). Larger LR gain indicates larger VMR improvement. The mental rotation group showed significantly larger LR gain than the control color group. A two-way group x test session ANOVA shows a significant interaction effect ($F(1, 34) = 4.41$, $p = .043$, $\eta^2 = .06$), but no main effect of group ($F(1, 34) = 1.51$, $p = .227$) or test session ($F(1, 34) = .82$, $p > .25$). An

independent t-test of LR gain showed that the mental rotation group had a significant higher LR gain than the control color group ($t(34) = 2.27$, $p = .030$, $d = .39$).

In sum, we observed that after a short mental rotation training, participants became faster in visuomotor adaptation compared to before, whereas training on the control color-discrimination task without the rotation operation did not facilitate the learning rate of visuomotor rotation. Thus, Experiment 3 revealed that training on mental rotation can be transferred to visuomotor rotation.

Discussion

Reciprocal facilitation between visuomotor rotation and mental rotation

In the current study, we discovered the bidirectional transfer between visuomotor rotation and mental rotation. First, we observed a significantly larger improvement in mental rotation after training in visuomotor rotation versus in control motor tasks without the rotation operation (Experiment 1). We then successfully replicated the results by introducing new 2D- and 3D-map stimuli in a mental rotation task that provided converging evidence and extended the findings to a more ecological context (Experiment 2). Similarly, we showed that training in mental rotation also improved the learning rate of visuomotor rotation, wheareas the control visual task did not (Experiment 3). The correlation between manual rotation and mental rotation has been examined in a number of studies, including behavior research (McDougle & Taylor, 2019; Sack, Lindner, & Linden, 2007; Wohlschläger & Wohlschläger, 1998), brain-imaging research (Richter et al., 2000; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002) and neurobiological research (Georgopoulos et al., 1989). Our findings provide strong evidence for close reciprocal

connections between visual cognition and action by showing that learning in one process can improve the other one when the tasks involve a common rotation component.

In addition, we observed that the improvements in 2D- and 3D-map rotation after visuomotor rotation training was not different from each other (Experiment 2). Previous work demonstrated that comparing a tilted 2D-map image with the 3D real-world, similar to our 3D condition, involves two successive steps: 1) participants mentally rotated the tilted 2D image to the upright position in the 2D image-plane, similar to our 2D condition; 2) they further rotate the upright 2D image in depth to compare with the 3D world (Aretz & Wickens, 1992; Levine, Jankovic, & Palil, 1982; R. N. Shepard & Hurwitz, 1984). Therefore, our findings suggested that the training in visuomotor rotation mainly enhanced the mental rotation in the 2D image-plane rather than the 3D forward-rotation in depth. Otherwise, the 3D condition would show larger improvement than the 2D condition.

Possible mechanisms for the reciprocal facilitation between the two rotational processes

One scenario is that mental rotation training facilitates motor performance through mental practice on the rotational movement. Mental practice refers to a training method by which an imagined motor act is mentally rehearsed multiple times in the absence of real movement execution (Driskell, Copper, & Moran, 1994; Jackson et al., 2001). Previous studies have demonstrated that mental practice can improve motor skill performance (Feltz & Landers, 1983; Hinshaw, 1991; Yágüez, Nagel, Hoffman, Canavan, Wist, & Hömberg, 1998) and multiple theories have been proposed to explain the enhancement process (Jackson et al., 2001). For instance, symbolic learning theory (Sackett, 1934) stated that mental practice leads to rehearsal of the cognitive components of a motor task. Mackay (1981) proposed that mental practice

primes the specific movement patterns required by the movement execution. In Experiment 3, training in mental rotation might induce a cognitive rehearsal of the rotational movement, and in turn, facilitate visuomotor rotation. However, the imagined movement associated with mental rotation on tilted objects is manually rotating the object, which is not same as the rotational movement involved in VMR. Therefore, it is unclear that how mental practice on rotating tilted letters can benefit VMR learning process. Similarly, mental practice does not explain the effect of VMR training on mental rotation.

Alternatively, the bidirectional transfer between visuomotor rotation and mental rotation might depend on a common rotation operation on spatially mapped representations of stimuli. In the mental rotation tasks, participants rotated the internal representations of tilted visual stimuli (Cooper, 1975). For instance, Zacks (2008) demonstrated that mental rotation modulates neuronal activity in brain regions that consist of spatially mapped representations. In VMR tasks, participants learn how to rotate the internal representation of tilted visual feedback to determine the appropriate direction of hand movements (Imamizu, Uno, & Kawato, 1995). Therefore, we could speculate that training in either process would benefit the rotational processing of internal representations, and in turn, enhance the other process.

Concluding remarks

To summarize, we reported the bidirectional transfer between visuomotor rotation and mental rotation. This newly observed reciprocal enhancement between the cognitive and motor processes cannot be explained by a unidirectional sequence of information processing (Johnson-Laird, 1988; Cover & Thomas, 1991). Rather, it highlights that human actions are not merely the outcomes of internal mental functions, but in fact they can influence cognitive processes. The

study also suggested that the operation of rotation itself might be a primitive for cognition and action that has yet to be fully identified or understood.

CHAPTER 5: DISCUSSION

In this dissertation, we revealed that improving motor performance through training can indeed enhance perceptual sensitivity and mental processing. In Chapter 2, we showed that improving action precision facilitates early visual processing. In Chapter 3, we extended the action training effect from simple hand-reaching movements to a more complex motor skill: throwing a ball to hit a target. We showed that practicing ball-throwing movements enhanced auditory duration discrimination, and the enhanced perception was selectively linked to the timing of the ball-throwing practice, suggesting a shared timing mechanism between perception and motor systems even though the motor task was complex. Importantly, we found the action training effects on time perception extended over a long time. In Chapter 4, we expanded the motor training effect from perception to a more integrative cognitive process by showing the reciprocal facilitation between visuomotor rotation and mental rotation. While mental rotation of visual stimuli is typically considered a perceptual-like process, recent studies have suggested that mental rotation is a more general cognitive process involving higher-level mental operation (Georgopoulos & Massey 1987; Georgopoulos et al., 1989; Lurito et al., 1991). To summarize, our results suggest that action training can facilitate mental processes when they share relevant components.

However, substantial work is needed in the future to fully understand the mechanisms underlying this newly observed modulation of mental functions by motor learning. Our studies showed three sets of transfer from action training to perception and cognition, but it remains to be studied if such training effects are a general phenomenon across broader human behavior.

Besides, the shared components that bridge different mental processes need further investigation. Therefore, in this chapter, we propose a hypothetical model of how action training facilitates other processes through a common component. This model provides a potential explanation to our key experimental observations and brings up important questions that need to be addressed moving forward.

We hypothesize that there are three critical steps in how action training affects perception and cognition:

1) **Action training activates representations of action-relevant components.** During motor learning, many perceptual and cognitive components are critically linked to the success of the motor task. Training in action precision activates the representations of these crucial components.
2) **Mental functions requiring the activated representations become better.** If a perceptual or cognitive task requires the representations activated by the preceding motor training, the task would benefit from the action training.
3) **The activation of representations is modulated by higher-level cognitive factors**. The magnitude of an action training effect relies on the activation level of representations, which can be modulated by other cognitive processes, such as attention and memory.

For instance, in chapter 2 the visual representation of orientation is crucial to a precise grasp toward a tilted stimulus. Hence, training in grasping precision activated the representation of corresponding orientations, step 1, and in turn, led to the better performance in the orientation discrimination task that requires the representation of trained orientations (step 2). Similarly, throwing practice, chapter 3, activated the representation of the crucial ball-release time and subsequently enhanced the temporal processing of the

activated duration representation. The retention of learned motor skills and time perception can be modulated by memory (step 3). Importantly, training in visuomotor rotation did not merely activate the spatially mapped representation of hand reaching movement but rather facilitated the rotational processing of the visual representations of hand reaching movements. As a result, mental rotation that requires rotational processing of an object representation was enhanced after the training in visuomotor rotation.

This model shares many common features with the theory of event coding (TEC, Hommel et al., 2001). First, the two models both challenge the classical information-processing view that information flows linearly from perception to action (Sanders, 1983). TEC proposed that there is a common coding system consisting of features that can be activated by both perception and action events (Hommel et al., 2001). Secondly, the two models both propose that action can influence perception by activating the shared components. According to TEC, preparing a button-press with the *left* hand activates the feature *left* in the common code system and then interferes with perceiving a *left*-tilted bar that requires the same *left* feature (Müsseler & Hommel, 1997).

However, the scope of our model is different from TEC, since TEC mainly depictes the relation between simultaneous motor preparation and perception, whereas our model is proposed to explain the action training effect on a wide range of subsequent mental processes. In TEC, preparing an action interferes with a perceptual event since the shared feature is occupied by the action event and cannot be further utilized by the perception event. However, in our model, the representations activated through motor training are not simultaneously involved in another task. Instead, we speculate that the representations activated in motor training task are maintained in memory and available for subsequent mental processes.

Therefore, we speculate that memory, such as working memory capacities, would modulate the transfer from action training to other processes as a step 3 in the model. Previous studies have shown that visual working memory is necessary for active maintenance of specific features of visual stimuli no longer in view (Baddeley, 2003; Harrison & Tong, 2019; Luck & Vogel, 1997). Practicing a sequence of throwing movements might allocate more working memory resource to the crucial activated *ball-release time*, and then facilitated perceptual discrimination of the same duration. Moreover, the retention of learned motor skills and time perception in a long-term scale also provided evidence suggesting the formation of long-term memory. In the future, more studies can be conducted to further estimate how working memory is involved in the activation of representations in the action training phase (step 1) and maintenance of representations in the subsequent transfer phase (step 2).

In addition, previous studies demonstrated that higher spatial working memory capacity correlated with faster learning rate for visuomotor rotation between individuals (for a review, see Seidler, Bo, & Anguera, 2012). Kaufman (2007) demonstrated that mental rotation performance is correlated with working memory ability, whereas Hyun and Luck (2007) showed that mental rotation only interfered with performance in working memory tasks requiring the storage of object features but not spatial working memory tasks requiring remembering object locations. Moreover, motor sequence learning (e.g., control SRT task) is also correlated with spatial working memory capacity (for a review, see Seidler, Bo, & Anguera, 2012). In chapter 4, the SRT task resulted in much weaker enhancement in mental rotation compared to visuomotor rotation. Therefore, in the future, more studies can be conducted to further estimate how different types of working memory are involved in the transfer between visuomotor rotation and mental rotation.

Another speculation is that attentional mechanisms might also modulate the action training effects on other processes (Desimone, Wessinger, Thomas, & Schneider, 1990). The pre-motor theory of attention argues that action influences perception through attentional mechanisms involved in the motor processes (Rizzolatti, Riggio, Dascola, & Umilta, 1987). A wide range of studies have demonstrated that preparing an action would orientate attention to the action-goal location, and in turn, facilitate the perceptual processes in the attended spatial location (e.g., Craighero et al., 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Posner, 1980; Poster, Snyder, & Davidson, 1980; Rensink, O'Regan, & Clark, 1997). We speculate that attention mainly involves step 1, activation of representations during an action training phase. Action training might allocate more attentional resource to the crucial components, which can facilitate the activation of representations of these components.

Future directions

One direction is estimating whether the action training effect on perception is limited to the orientations and durations we observed here or is a more general process. If there is a general mechanism underlying the interactions between sensory and motor systems, we reason that action training could impact perception as long as they share a component regardless of tasks. However, there is little work investigating how action impacts other fundamental elements in visual processing, such as spatial frequency, contrast, size, etc. Gutteling et al. (2011) demonstrated that preparing a grasp did not facilitate perceptual discrimination of luminance changes compared to pointing preparation, however it might merely because luminance is not relevant for grasping. Meanwhile, there is less work investigating how action training might influence other perception modules, such as the auditory system. Therefore, more work could be

done on different types of perception and action tasks, to broaden our knowledge of the dynamic interactions between different stages of mental processes.

Another interesting question is whether perceptual training can result in action improvement, and if so, whether perceptual training can lead to stronger or weaker transfer to action compared to the transfer from action training to perception. A previous study demonstrated that training in an auditory duration discrimination task showed transfer to a motor task. However, this motor task was successive finger taps, which is extremely simple and explicitly focuses on producing a temporal interval bounded by two taps (Meegan & Aslin, 2000). It is unknown whether training in time perception can also affect more complex movements in daily life. If perceptual training does not facilitate complex motor skill learning, multiple explanations are possible. First, it could indicate the transfer of timing is one-way from motor to perception. Alternatively, throwing requires more complex movement control beyond motor timing, and perceptual timing training alone is not sufficient to modify the temporal pattern in movement performance that is implicitly acquired. It could indicate that the transfer only occurs when the action task is simple. In Chapter 4, we discovered the bidirectional transfer between motor learning and cognitive training. The motor task was VMR and the cognitive task was mental rotation. However, the two learning processes are quantified by two different parameters: one is the fitted learning rate of visuomotor adaptation, and one is the reaction times of mental rotation, which cannot be compared directly to determine which process has larger magnitude of improvement. In the future, new data analysis methods could be developed to directly compare the transfer in both directions.

Another interesting direction is exploring the brain mechanisms involved in the action training effect. For instance, we speculate that hand actions facilitate perception of action-

relevant features through neuronal feedback connections from cortical motor areas to early visual cortex. To test this hypothesis, a functional neuroimaging (fMRI) study could be conducted to examine whether better orientation discrimination after action training is associated with changes in the BOLD activity of early visual cortex such as V1. One prediction in accord with our results in Chapter 2 is that the action training group shows enhanced orientation discrimination sensitivity. Meanwhile, this behavioral improvement in the action-training group would be associated with BOLD signal changes in early visual cortex such as V1. Alternatively, action training could result in representation changes without the change in the BOLD level, which could be detected by multi-voxel pattern analysis (MVPA, Gutteling et al., 2015).

Concluding remarks

This dissertation critically examined how action training facilitates various perceptual and cognitive functions, which could not be explained by the traditional one-way causal flow of information processing stages (Cover & Thomas, 1991). Rather, it highlights the dynamic interactions underlying adaptive behaviors in a complex environment. Our findings also suggested that there might be common mechanisms bridging perception, cognition and action regardless of the dissimilarities of tasks. Deciphering the interactions between perception, cognition and action have broad relevance for a better understanding of many visual disorders led not only by visual deficits but also by motor deficits. Outcomes of this dissertation will interest practitioners who seek new training methods of improving perceptual and cognitive deficits in rehabilitation settings, and ultimately improve the quality of life. It will also facilitate interdisciplinary collaboration and unified theoretical frames of integrated perception and motor control mechanisms.

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