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Research Article

Psychological Science
1–15
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DOI: 10.1177/0956797619859361
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Action Fluency Facilitates Perceptual Discrimination

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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.

Keywords
action fluency, action training, action, perceptual sensitivity, perception, open data, preregistered

Received: 7/6/17; Revision accepted: 6/3/19

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

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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 (Experiments 1 and 2). 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 3). 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 male; 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. 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

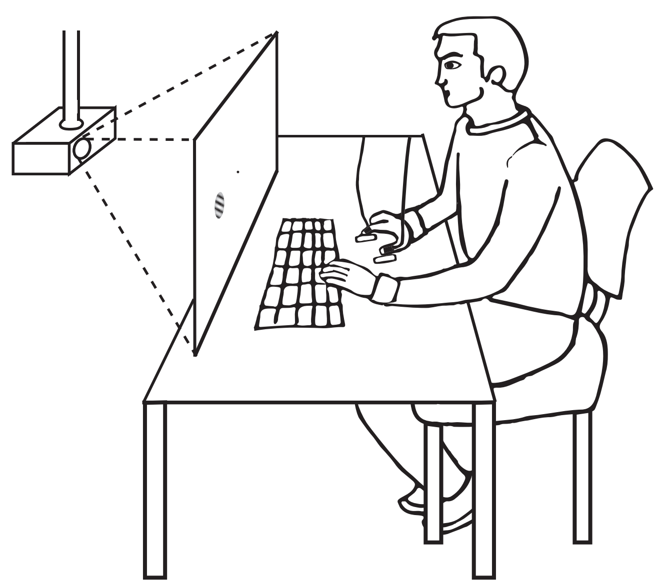

Fig. 1. Experimental set-up. In all three experiments, visual stimuli were projected onto a plexiglass screen by the projector behind it. The plexiglass screen stood upright on the table and perpendicular to the participant's line of vision. Two motion-tracking markers were secured on each participant's 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.

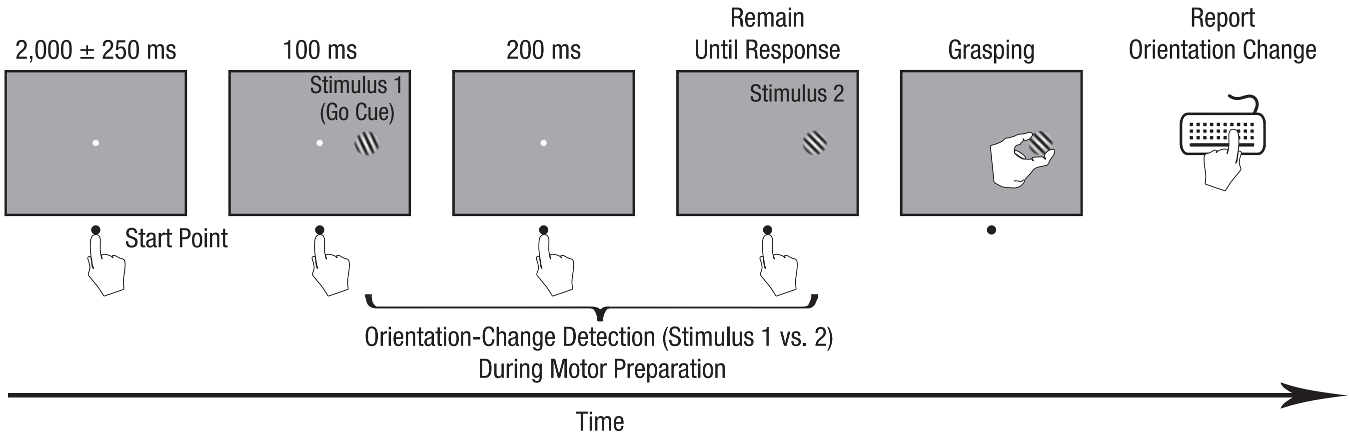

Fig. 2. Trial sequence for the main experiment in Experiment 1. Participants performed a grasping task and a perception task in each trial. The first stimulus was presented for 100 ms and disappeared (i.e., go cue), and after 200 ms, the second stimulus was presented as an action target. In the perception task, participants reported whether the orientations of the two stimuli were the same or different by pressing a button with their left hand.

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 prethreshold test and the main experiment. In the prethreshold 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 (for details, see Fig. S1 in the Supplemental Material available online). Stimulus were presented using custom software designed with MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997).

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

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 ds 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 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 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]:

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

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 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 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

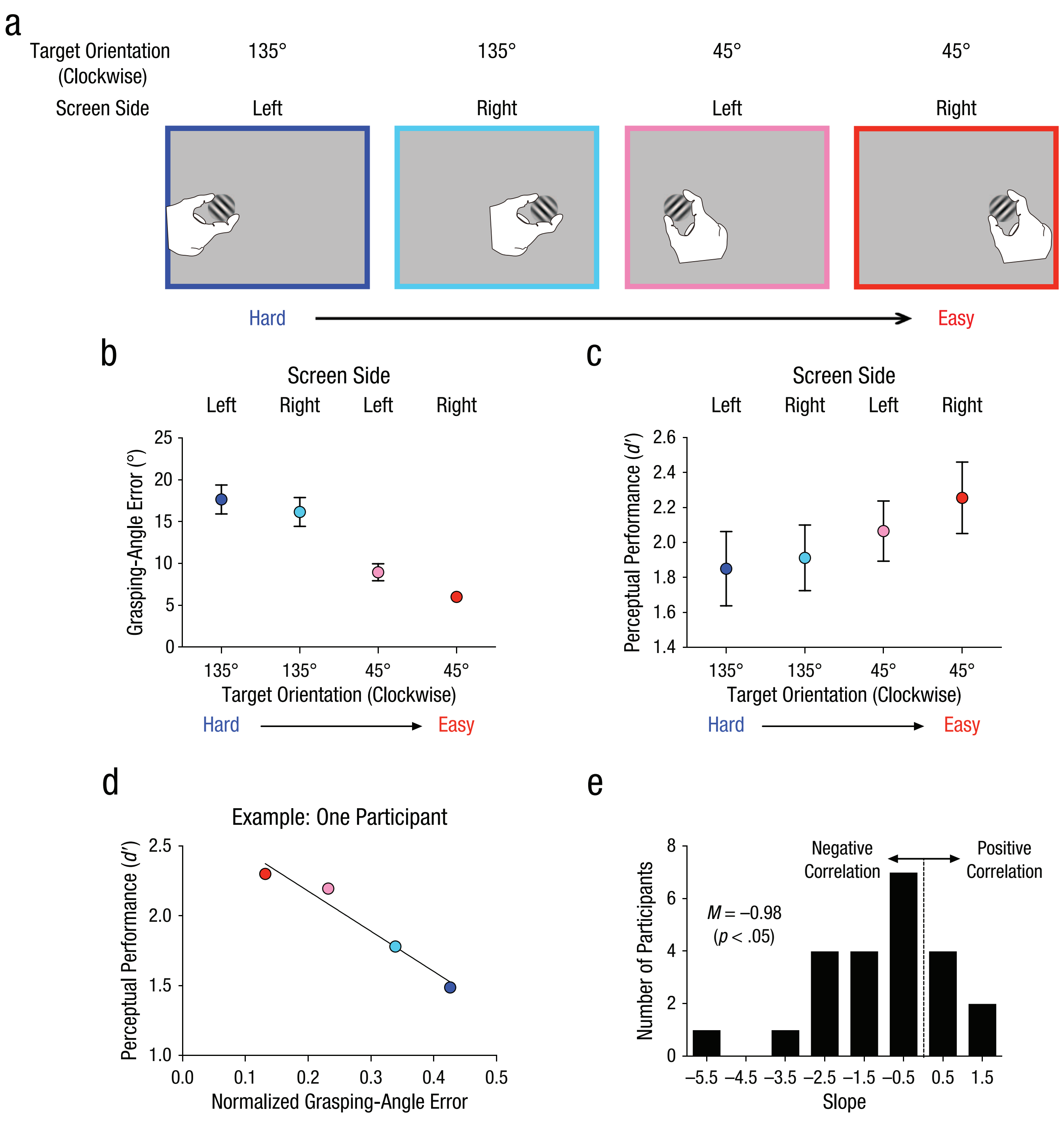

Fig. 3. Grasping conditions and results from the large-size condition in Experiment 1. The four grasping conditions created for Experiment 1 (a) varied from hard (low action fluency) to easy (high action fluency). Mean grasping-angle error (b) and perceptual performance (c) are shown as a function of 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 $y = -2.881 \times x + 2.754$. 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.

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 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.

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 male, 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.

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. 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. 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. 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 $1.5 \times t$ degrees ($t = 8.88° \pm 1.45°$).

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,

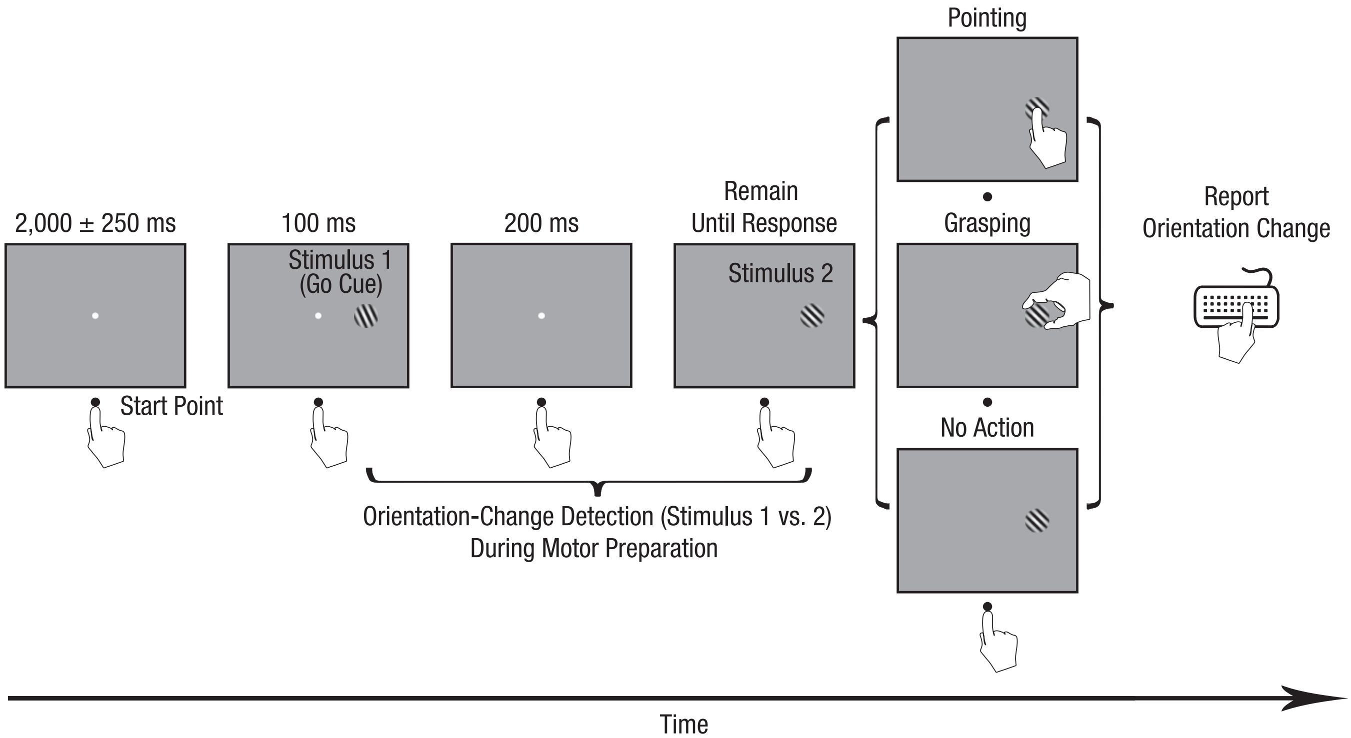

Fig. 4. Trial sequence in the main experiment of Experiment 2a. Participants performed a combined action task and perception task in each trial. The first stimulus was presented for 100 ms and disappeared (i.e., go cue), and after 200 ms, the second stimulus was presented as an action target. In the 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.

Morey, & Iverson, 2009). A JZS Bayes factor of 2 indicates that the null hypothesis is 2 times more probable than the alternative hypothesis, given the data, a JZS Bayes factor of 3 indicates that the null hypothesis is 3 times more probable, etc.

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. 5b) were equivalent, $t(15) = 0.69$, $p > .250$, $d = 0.17$, Bayes factor = 4.23, grasping-angle errors (Fig. 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 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. 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

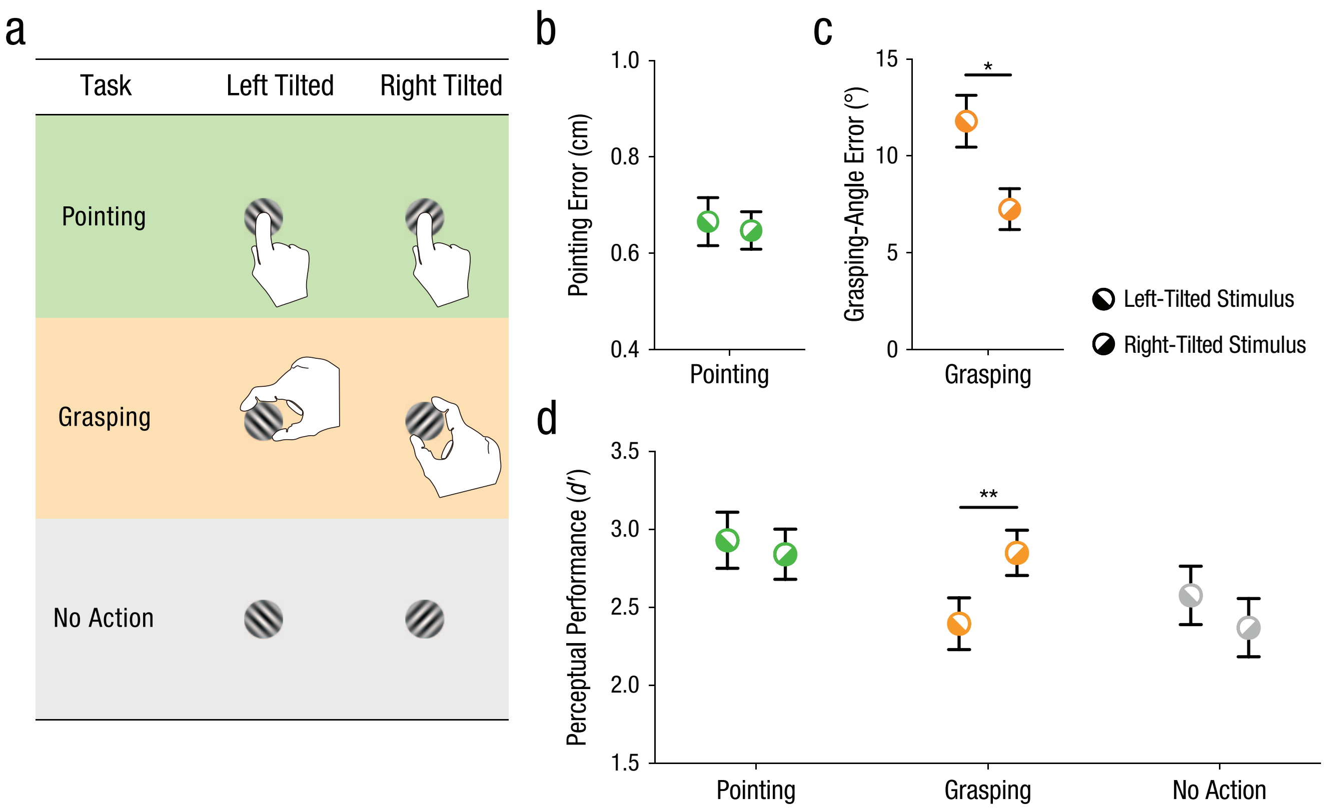

Fig. 5. Action and perceptual performance with the two visual stimuli in Experiment 2a. The hand postures used for the left-tilted and right-tilted stimulus across the three action tasks are shown in (a). Mean pointing error (b) and grasping-angle error (c) are shown for the pointing and grasping tasks, 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 (*$p < .05$, **$p < .01$).

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.

Nevertheless, Experiment 2 provided further evidence that differences in discrimination sensitivity of target orientation were induced by differences in action

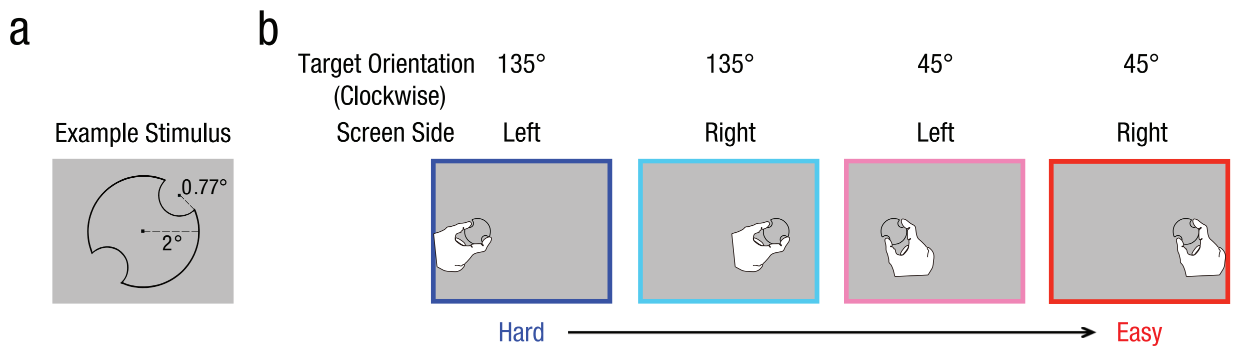

Fig. 6. Stimulus and experimental conditions in Experiment 3. The stimulus used in the training session (a) was tilted in six different orientations. Participants were instructed to grasp it (action group) or report its orientation (control group). The radius of the two large arcs was 2° of visual angle, 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 3 (b) varied from hard (low action fluency) to easy (high action fluency).

fluency, not by other stimulus characteristics, and were consistent with what we observed in Experiment 1.

Experiment 3: Perceptual Sensitivity Improved After Action Training

In Experiment 3, 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 male; mean age = 21.78 years) were included in the action group, and 22 participants (4 male; 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.

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 3 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. 6a).

Procedure. As in Experiments 1 and 2, all participants performed the prethreshold 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), 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 6a 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 orientation), 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 6b, 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. 6b), 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. 7a); then we defined grasping-performance gain as the mean difference between the early and late training periods in each condition, as shown in Figure 7b. We also assessed gain in the corresponding perceptual performance (Fig. 7c) by calculating the d' difference between the post- and preperception tests, as shown in Figure 7d. When we compared the data shown in Figures 7b and 7d, 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 7e 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.

In the control group, instead of focusing on normalized grasping-angle error, we calculated perceptual accuracy (Fig. 8a). The corresponding accuracy gain was calculated by taking the difference between accuracy in Trials 5–8 and Trials 29–32, as shown in Figure 8b. We also calculated the corresponding perceptual performance (Fig. 8c) and then calculated its gain as a d' difference between the post- and preperception tests (Fig. 8d). Comparing the data shown in Figures 8b and 8d, we found that accuracy gain was not correlated with perceptual-performance gain in the four control conditions (Fig. 8e), 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 8e 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. 8b).

In sum, Experiment 3 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 postperception 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.

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

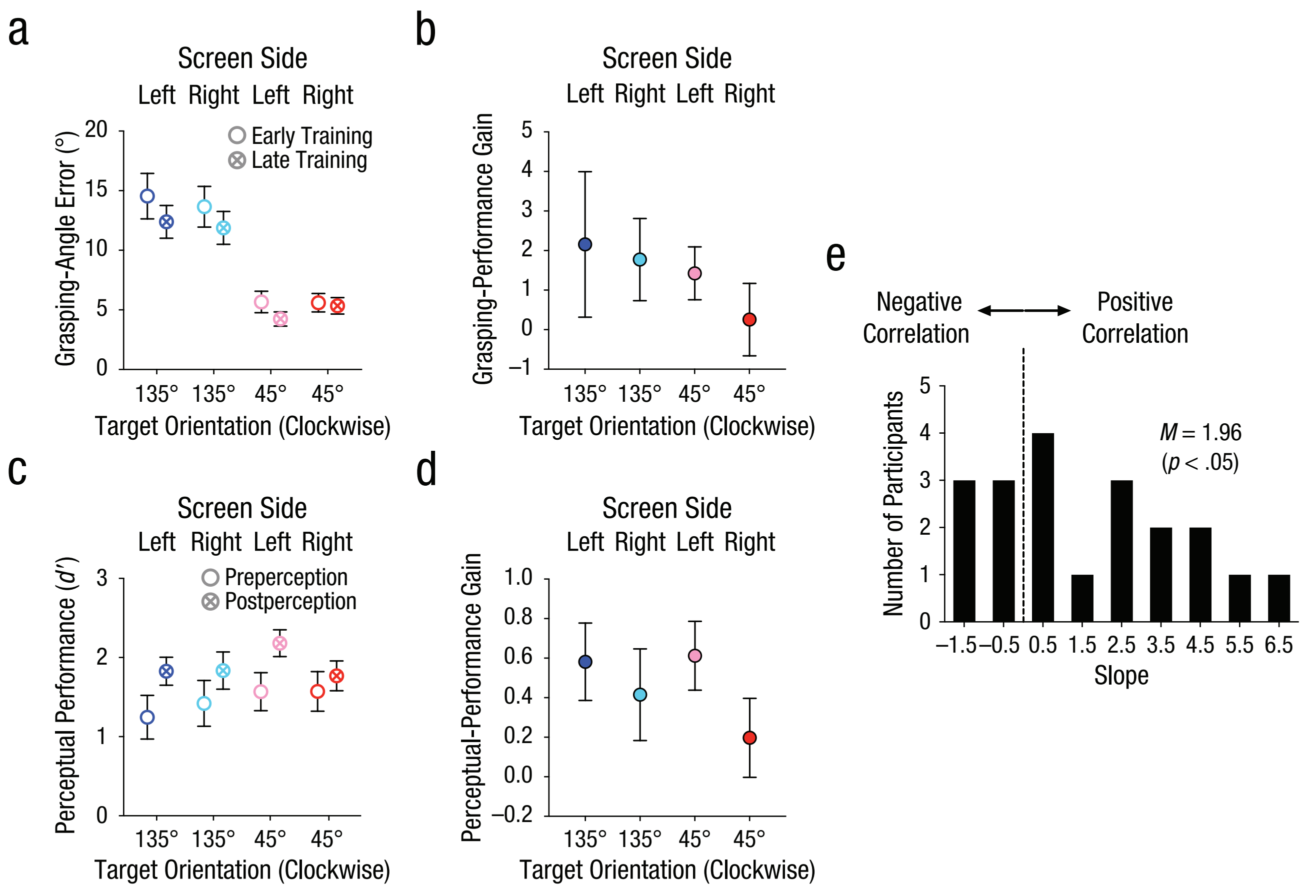

Fig. 7. Action and perceptual performance in the four grasping conditions for the action group in Experiment 3. Mean grasping-angle error (a), grasping-performance gain (b), perceptual performance (c), and perceptual-performance gain (d) are shown as a function of target orientation and screen side. 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 6b. 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.

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 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

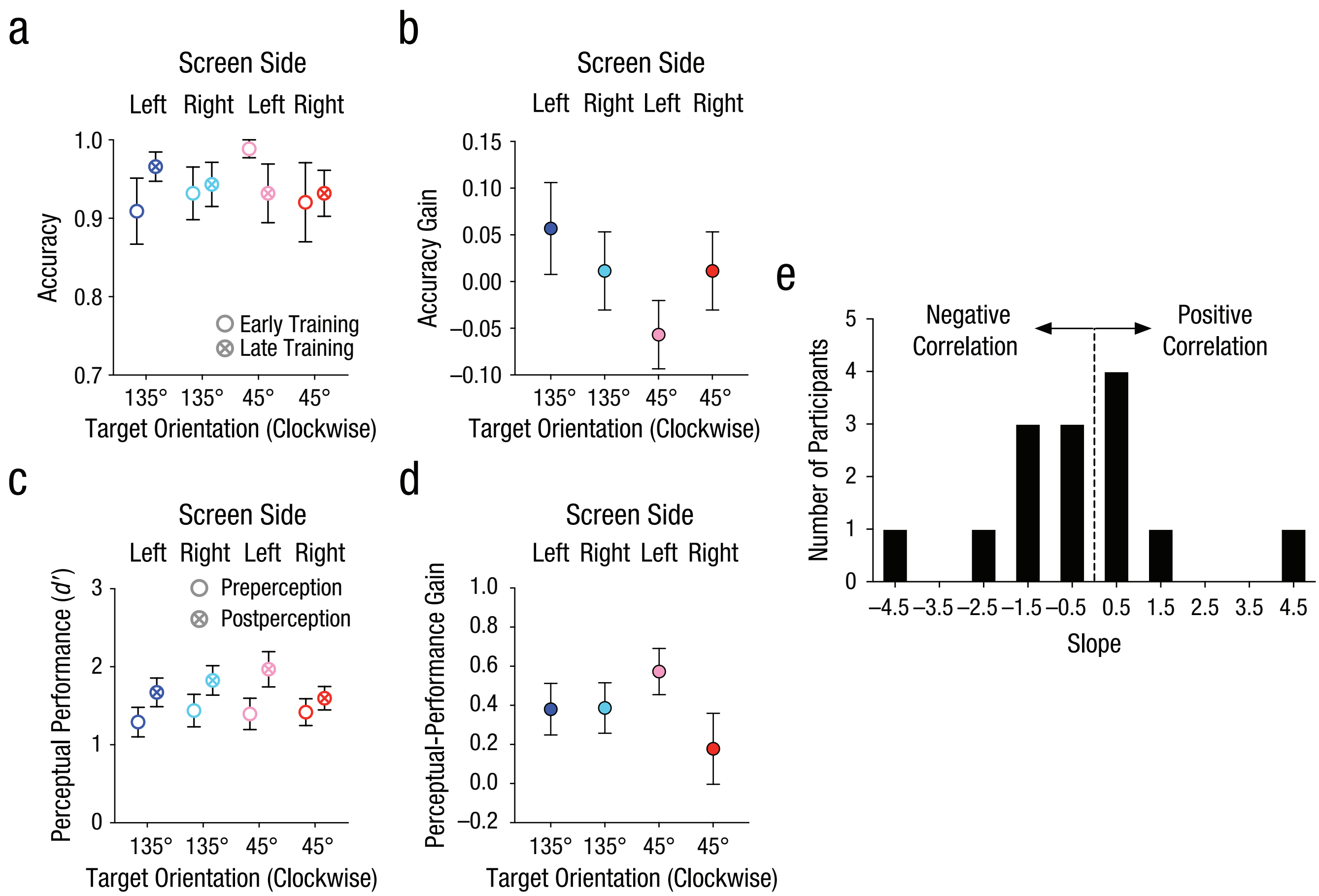

Fig. 8. Accuracy and perceptual performance in the four control conditions for the control group in Experiment 3. Mean accuracy (a), accuracy gain (b), perceptual performance (c), and perceptual-performance gain (d) are shown as a function of target orientation and screen side. For accuracy and perceptual 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 6b. 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.

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 3). 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 3. That said, perhaps the results of Experiment 3 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 difference 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.

Action Editor

Edward S. Awh served as action editor for this article.

Author Contributions

J. Guo and J.-H. Song designed the tasks. J. Guo collected the data. J. Guo and J.-H. Song analyzed the data. J. Guo and J.-H. Song wrote the manuscript and approved the final version for submission.

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Acknowledgments

We thank J. D. McCarthy for helpful discussion.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

Funding

This work is supported by National Science Foundation CAREER Award (BCS 1555006) to J.-H. Song.

Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797619859361

Open Practices

All data have been made publicly available via the Open Science Framework and can be accessed at https://osf.io/vgmjs/. The design and analysis plans for Experiment 2b were preregistered at https://osf.io/dtm7j. The complete Open Practices Disclosure for this article can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797619859361. This article has received the badges for Open Data and Preregistration. More information about the Open Practices badges can be found at http://www.psychologicalscience.org/publications/badges.

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