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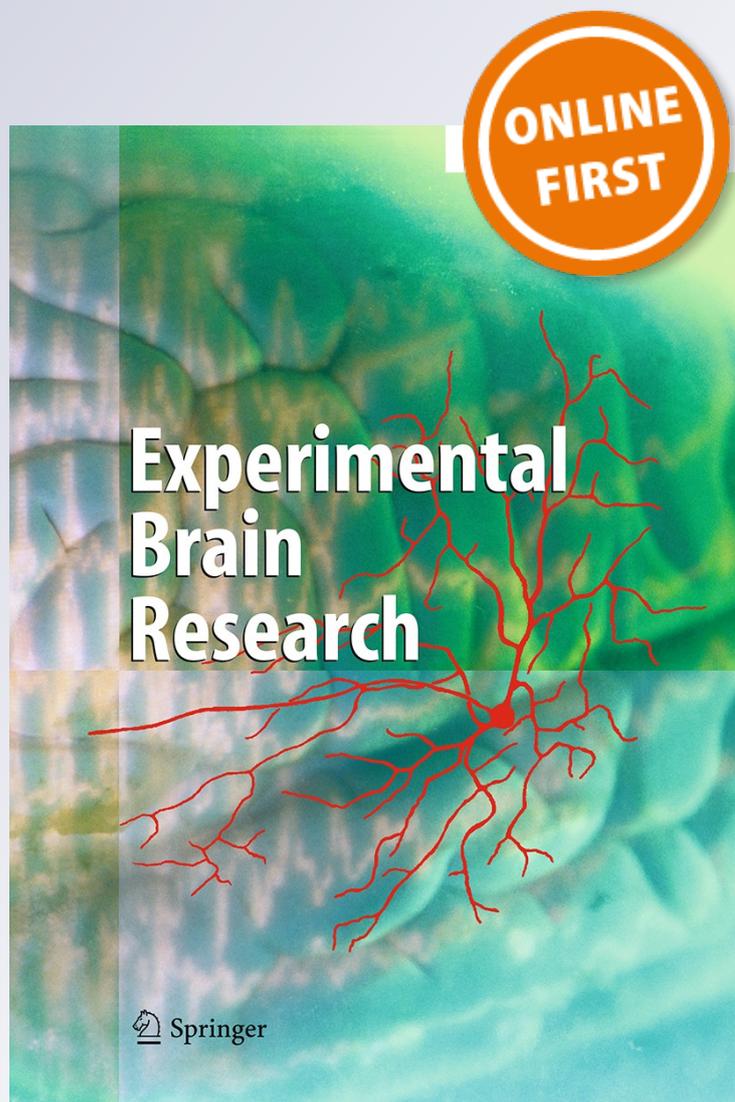
Allocation of attention for dissociated visual and motor goals

Joo-Hyun Song · Patrick Bédard

Abstract In daily life, selecting an object visually is closely intertwined with processing that object as a potential goal for action. Since visual and motor goals are typically identical, it remains unknown whether attention is primarily allocated to a visual target, a motor goal, or both. Here, we dissociated visual and motor goals using a visuomotor adaptation paradigm, in which participants reached toward a visual target using a computer mouse or a stylus pen, while the direction of the cursor was rotated 45° counter-clockwise from the direction of the hand movement. Thus, as visuomotor adaptation was accomplished, the visual target was dissociated from the movement goal. Then, we measured the locus of attention using an attention-demanding rapid serial visual presentation (RSVP) task, in which participants detected a pre-defined visual stimulus among the successive visual stimuli presented on either the visual target, the motor goal, or a neutral control location. We demonstrated that before visuomotor adaptation, participants performed better when the RSVP stream was presented at the visual target than at other locations. However, once visual and motor goals were dissociated following visuomotor adaptation, performance at the visual and motor goals was equated and better than performance at the control location. Therefore, we concluded that attentional resources are allocated both to

visual target and motor goals during goal-directed reaching movements.

Introduction

Most studies on the effects of attention have focused on sensory processing, such as how attention enhances perceptual saliency, filters out unwanted information, and increases baseline neural activity (McAdams and Maunsell 1999; Somers et al. 1999; Treue and Maunsell 1999; Palmer et al. 2000; Huang and Dobkins 2005; Reynolds and Heeger 2009). However, recent studies have established a strong link between attention and visuomotor processing. Support for this notion has first come from observations that attention and eye movements are strongly linked. For instance, behavioral studies have demonstrated that prior to the onset of a saccade, attention is directed to the goal of the upcoming movement, thereby improving perceptual discrimination at that location (Rizzolatti et al. 1994; Hoffman and Subramaniam 1995; Kowler et al. 1995; Sheliga et al. 1995; Deubel and Schneider 1996, 2003; Gersch et al. 2004; Baldauf and Deubel 2008a; Khan et al. 2011). Neuroimaging studies have shown brain activation in the fronto-parietal cortex, which controls eye movement, during attention tasks (Corbetta et al. 1998; Nobre et al. 2000; Beauchamp et al. 2001). Furthermore, stimulation studies in non-human primates have demonstrated that activation of neurons in the superior colliculus (SC), frontal eye field (FEF), and the lateral intraparietal area (LIP), which are involved in generating saccades and in the selection of a saccadic target, can change the focus of attention (Moore and Fallah 2001;

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Cutrell and Marrocco 2002; Cavanaugh and Wurtz 2004; Muller et al. 2005).

This close link between attention and visuomotor processing has also been extended to reaching movements. Behavioral and electroencephalography studies have demonstrated that spatial attention is allocated to the target before reaching, enhancing perceptual discrimination at the reach goal (Deubel and Schneider 2003; Song and Nakayama 2007; Baldauf and Deubel 2008b; Khan et al. 2011). Single-unit recording and fMRI studies have also shown that attention can modulate brain activity across the fronto-parietal cortex and sub-cortical structures (Boussaoud and Wise 1993; Snyder et al. 2000; Boussaoud 2001; Indovina and Sanes 2001; Lebedev and Wise 2001), which are involved in target selection and generating reaching movements (Cisek and Kalaska 2005; Pesaran et al. 2008; Song and McPeek 2010; Westendorff et al. 2010).

However, in these studies, both the visual target and the motor goal were usually presented at the same location (Khan et al. 2010). Furthermore, visual selection of an object is closely linked to processing that object as a potential target for action (Cisek and Kalaska 2010). Thus, it is difficult to determine whether spatial attention is allocated to the location of visual targets, motor goals, or both. One way to dissociate whether attention is directed at a visual target or at a motor goal is through sensory–motor adaptation. For instance, using saccadic adaptation, in which the amplitude and/or direction of a saccade to a visual target is gradually modified by shifting the target to another location during the saccade (McLaughlin and Webster 1967; Hopp and Fuchs 2004), Khan et al. (2010) showed that a task-irrelevant cue flashed at the saccade goal location, but not at the target location, facilitated saccades. Thus, they concluded that the influence of attention is predominantly on the motor goal of the saccade rather than on visual target.

In addition, Collins et al. (2010) measured event-related potentials (ERPs) during saccadic adaptation. ERPs have been known to be sensitive to the location of spatial attention (Mangun and Hillyard 1988; Mangun and Hillyard 1990; Heinze et al. 1994; Luck and Hillyard 1995). Collins et al. (2010) found that ERPs were amplified at visual target and saccadic goals, suggesting that both target selection and motor planning determine the focus of visual attention. Thus, prior work has addressed the relationship between attention allocation and visual/motor goals for saccades.

Here, we extended this investigation to reaching movements. We examined whether spatial visual attention is mainly allocated to the visual target, the motor goal, or both during goal-directed reaching movements. To address this question, we used a visuomotor rotational adaptation paradigm to dissociate visual and motor goals.

Participants used a computer mouse or a stylus pen to control a cursor and reached toward visual targets, while the direction of the cursor was rotated 45° counter-clockwise (CCW) from the direction of the mouse movement. Thus, this paradigm forced participants to reach to a different spatial location (motor goal) than where the target was actually located (visual target). Because the visual perturbation was introduced suddenly, large reach errors were initially committed, but these were reduced rapidly and stable performance was achieved indicating that participants had dissociated the visual from the motor goals (Krakauer et al. 2005; Shadmehr and Wise 2005; Hegele and Heuer 2010).

While visual and motor goals were dissociated by visuomotor adaptation (Fig. 1a), we assessed the focus of attention allocation using an attention-demanding rapid serial visual presentation (RSVP) task, in which participants detected pre-defined targets in a stream (Fig. 1b–d) (Raymond et al. 1992; Joseph et al. 1997). In Experiment 1, in each of the two groups, we presented the RSVP stream either at the visual target (Fig. 1b) or at the motor goal (Fig. 1c), respectively. Participants concurrently performed the visuomotor and RSVP tasks. We aimed to assess how RSVP detection accuracy changed as visuomotor adaptation progressed. In Experiment 2, we used a within-subject design, constrained eye movements, and had the location of the RSVP stream at the visual target (Fig. 1b), at the motor goal (Fig. 1c), or at a control location (Fig. 1d: 45° CCW). In the control condition, the visual target and the RSVP stream were separated as in the motor-goal condition, but the RSVP stream was at neither the motor nor the visual goal. By comparing the performance in the visual and motor conditions to the performance in the control condition, we could more precisely evaluate the allocation of attention.

In both experiments, we reasoned that if attentional resources were primarily allocated to a visual target (visual hypothesis), once visuomotor adaptation was completed, detection accuracy in the RSVP task would be higher when the visual stream was presented at the visual target than at the motor goal. In contrast, if attention resources were mainly allocated to a motor goal (motor hypothesis), detection performance would be better when the target appeared at the motor goal compared to the visual goal.

Experiment 1

To compare the visual and motor hypotheses, we manipulated the position of the RSVP stream as a between-groups variable: visual-target location (Fig. 1b) versus motor-goal location (Fig. 1c: i.e., 45° CW of visual target) during the visuomotor adaptation task (Fig. 1a). We compared
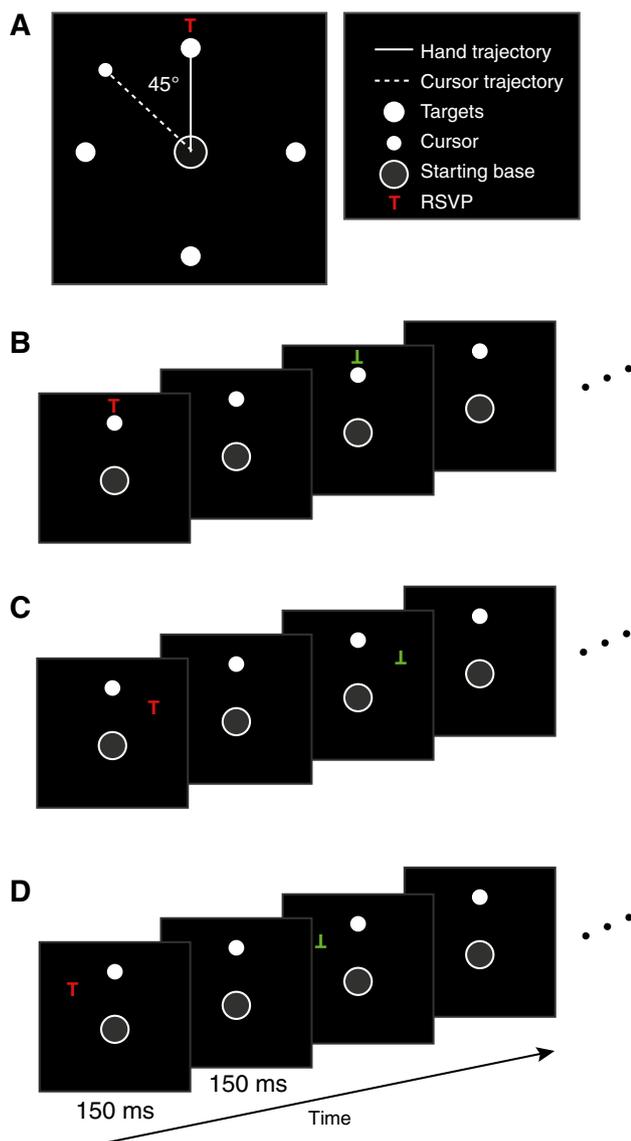
Fig. 1 Task schematic. **a** Visual targets evoking reaching movements appeared one at a time and remained visible for the whole trial. In a baseline condition, the cursor direction followed the hand trajectory normally, and during visuomotor adaptation, the cursor direction was rotated by 45° CCW from the intended hand trajectory. **b–d** In the rapid serial visual presentation (RSVP) task, a sequence of five upright or inverted 'T's (1° × 0.5°) of *red*, *white*, *green*, *purple*, or *yellow* colors were sequentially presented. Each 'T' remained onscreen for 150 ms followed by a 150-ms blank interval. Thus, a total 5 'T's were presented during the 1,500-ms trial duration. Participants reported the combined number of *upright red* 'T's and *inverted green* 'T's they had seen at the end of each trial. In the visual condition (**b**), the RSVP stream appeared 0.5° above the visual target location, in the motor condition (**c**), it appeared at the motor-goal location, which was 45° CW rotated from the visual target, and in the control condition, it appeared 45° CCW from the visual target (**d**) (color figure online)

RSVP detection accuracy between the two groups during the baseline, adaptation-training, and stable-adaptation periods.

Materials and methods

Participants

We recruited 22 participants from Brown University and the local community (ages: 18–22; 12 females). All the participants were naïve to the goal of the experiment. All participants had normal color vision and normal or corrected to normal vision. All participants provided written informed consent according to established and approved Institution Review Board guidelines for human participation in experimental procedures at Brown University. We adhered to the principles of the Declaration of Helsinki. Participants received modest monetary compensation or course credits for their participation.

Procedure

The experiment took place in a dimly illuminated room. Participants sat on a chair in front of a 21-inch Macintosh iMac computer (refresh rate of 60 Hz, spatial resolution of 1920×1080 pixels) viewed from a distance of 57 cm. They used their right (dominant) arm to perform a goal-directed reaching task with a computer mouse. The mouse rested on the table, aligned with each participant's mid-line and the center of the monitor. The mouse controlled a cursor (white dot; diameter 0.5°) viewed on the monitor. We presented visual stimuli against a black background on the monitor and recorded cursor displacement using Matlab (R2009b; MathWorks Inc., Natick MA) and functions from the PsychToolbox (Brainard 1997; Pelli 1997).

We used a dual-task paradigm in which participants concurrently performed a visuomotor adaptation task and an RSVP task. In the visuomotor adaptation task (Fig. 1a), participants had to reach from a central starting base (annulus 1° diameter) toward visual targets (white dots 1° diameter) located at 5.5° (equivalent to 5.5 cm) away from the starting base at 3, 6, 9, or 12 o'clock direction. The physical distance of the mouse motion to reach visual targets was 3.2 cm. A trial started after the participant positioned the cursor in the starting base for 500 ms, after which a visual target appeared. Each visual target appeared randomly in one of the four locations with equal probability. Participants performed one baseline block (40 trials), in which the cursor followed the mouse normally and four adaptation blocks (40 trials/block), in which the cursor direction was rotated 45° counterclockwise (CCW) to force movement adaptation (Fig. 1a). Thus, to adapt, participants had to learn to displace the cursor 45° clockwise (CW). This location was defined as the motor goal in contrast to the visual target that evoked reach onset. The cursor always remained visible to represent a current (or rotated) mouse position. Participants were instructed to make ballistic uncorrected straight

movements toward the visual target and come back to the starting position. We defined the first two adaptation blocks as the *adaptation-training* period, in which visuomotor adaptation was in progress, and the last two blocks as the *stable-adaptation* period, in which visuomotor adaptation was stably achieved.

Note that in the current study, we conventionally used the term 'visuomotor adaptation' (e.g., Krakauer et al. 2005; Bedard and Sanes 2011) since we applied a perturbation paradigm, which has been extensively used to induce the formation of a new internal model (for review Shadmehr and Wise 2005). Perturbations create movement errors, forcing the brain to learn or update new sensory–motor relationships to reestablish appropriate motor control. Thus, the visuomotor adaptation paradigm served as a tool to separate visual and motor goals, not as a subject of study per se because our primary aim is to assess where attention is allocated during goal-directed movements.

In the RSVP task (Fig. 1 b, c), five upright or inverted 'T's ($1° \times 0.5°$) of red, white, green, purple, or yellow colors appeared in sequence; each 'T' remained onscreen for 150 ms followed by a 150-ms blank interval. Thus, a total 5 'T's were presented during the 1,500 ms trial duration. Equal numbers of participants ($N = 11$) were randomly assigned to the visual or motor groups. In the visual group, the RSVP stream was presented at 0.5° above the location of the visual target (Fig. 1b), whereas in the motor group, the RSVP stream was always presented 0.5° above the 45° degrees CW location from the visual target throughout the experiment (Fig. 1c). Participants were asked to count the number of upright red 'T's and inverted green 'T's in each trial. The number of relevant 'T's varied randomly from trial to trial between one and three. Thus, the level of chance performance was 33 %. Participants reported how many 'T' they detected at the end of each trial by pressing one of three keys on a keyboard with their left hand.

Data analysis

We filtered the *x* and *y* coordinates of mouse displacements with a low-pass Butterworth filter using a 6-Hz cutoff and then calculated the cursor trajectory by taking the square root of the sum of squared *x* and *y* coordinates at each time point. We differentiated the position of the cursor to yield tangential velocity and determined the onset and end of movement when the cursor reached 5 % of peak velocity. We measured reaction time (RT) as the time elapsed from target onset to movement onset and movement time (MT) as the time elapsed between movement onset and movement end. We measured accuracy of movements by calculating the angle between the line that joined the starting base to the target with the line that joined the position of the cursor at movement onset to the position of the cursor at peak

velocity, which was defined as reach error. CCW reach errors were deemed positive and CW reach errors negative. We used repeated measures ANOVAs and *t* tests for our statistical analysis, always using participants as a random factor. All the *t* tests across phases and groups were a priori planned comparisons. We tested for sphericity of the data with Mauchly's test, which did not reveal any significant departure from sphericity.

Results

Participants in the visual and the motor groups did not differ regarding RT [mean ± s.e. 466 ± 22 ms vs. 505 ± 23 ms, $t(20) = 1.20, P = 0.25$] or MT [557 ± 22 ms vs. 636 ± 35 ms, $t(20) = 1.34, P = 0.19$].

Figure 2a shows mean reach errors by averaging across 40 trial blocks and variable reach errors as the standard deviation in those blocks for each of the visual and motor groups across all experimental phases. Regarding the mean reach error, in the baseline phase, in which the cursor followed the mouse normally, participants in both visual and motor groups accurately directed their reaching movements toward the visual targets with no group difference [$t(20) = 0.6, P = 0.56$]. During the adaptation phase, in which the cursor direction was rotated 45° CCW, both groups adapted similarly, as confirmed by a two-way ANOVA with groups (visual vs. motor) as a between-subjects factor and the four adaptation blocks as a repeated measure; there was no significant group main effect, $F(1, 20) = 0.15, P = 0.70$, but an expected significant main effect of block, $F(3, 60) = 114.6, P < 0.001$, and no significant interaction, $F(3, 60) = 0.1, P = 0.96$. Thus, reach errors in both visual [$t(20) = 4.98, P < 0.0001$] and motor groups [$t(20) = 3.79, P < 0.002$] were significantly reduced and reached asymptote in the stable-adaptation period, showing that participants successfully accomplished the dissociation between visual and motor goals, compared to the baseline period. Regarding variable reach errors, there was no difference at baseline between the two groups [$t(20) = 0.31, P = 0.76$] and during the entire adaptation blocks, the ANOVA revealed no significant main effect of groups [$F(1, 20) = 0.27, P = 0.61$], an expected significant main effect of blocks [$F(3, 60) = 8.87, P < 0.001$] and no significant interaction [$F(3, 60) = 0.38, P = 0.77$]. These results also ensure that the motor group did not use an explicit strategy of reaching to where the RSVP stream appeared, which was where they should reach to have the cursor land on the visual target. If they did, the motor group would have reduced reach error much faster than the visual group, which was not the case.

We analyzed target detection accuracy in the RSVP task to examine the extent to which attention resources were allocated to the visual target or the motor goal. Figure 2b shows the RSVP target detection results for the
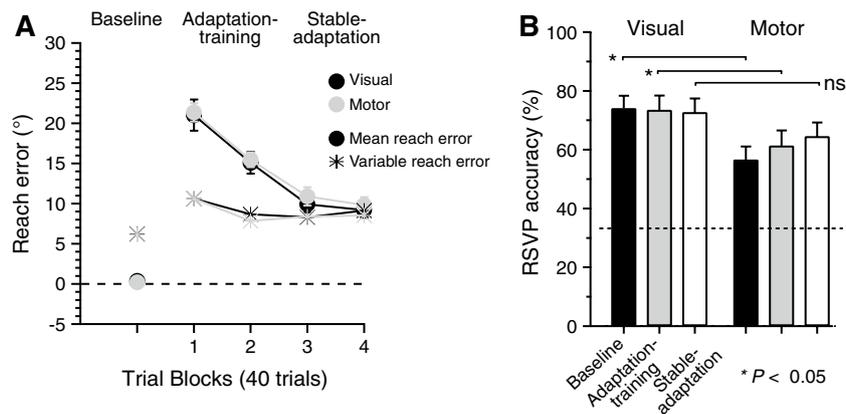
Fig. 2 Reach errors and RSVP target detection accuracy for visual and motor groups ($N = 11$ for each group) in Experiment 1. **a** Mean reach errors and variable reach errors (± 1 s.e.) across one baseline and four adaptation blocks (40 trials/block) separately plotted for the visual (*black*) and motor groups (*gray*). In both groups, reach errors are gradually reduced and attained an asymptotic level of performance in adaptation block 3 and 4 and block 2 for variable reach error. Note the *error bars* in baseline were too small to be visible. **b** Mean RSVP detection accuracy (± 1 s.e.) in the visual and motor groups is plotted during the baseline, adaptation-training, and stable-adaptation period. The visual group does not show a difference between the baseline and stable-adaptation blocks, whereas the motor group shows an improvement in detection performance. The *dotted line* represents the level of chance performance (33 %)

visual and motor groups during the baseline, adaptation-training, and stable-adaptation conditions. As can be seen, the accuracy for the visual group remained constant across the three conditions, while the accuracy of the motor group increased across the three conditions. We used a two-way ANOVA with groups (visual, motor) and conditions (baseline, adaptation-training, stable-adaptation), which revealed a main effect of groups [$F(1, 20) = 12.6$, $P < 0.002$], no significant main effect of conditions [$F(2, 40) = 1.95$, $P = 0.16$], and a significant interaction [$F(2, 40) = 8.89$, $P < 0.0006$]. Furthermore, we observed higher accuracy for the visual group compared to the motor group during the baseline and adaptation-training conditions [$t(20) = 4.85$, $P < 0.0001$, and $t(20) = 2.62$, $P < 0.02$], but no difference during the stable-adaptation condition [$t(20) = 1.24$, $P = 0.23$]. Also, the increase in accuracy across the three conditions was significant for the motor group [$F(1, 31) = 8.1$, $P < 0.05$], but not for the visual group [$F(1, 31) = 1.24$, $P = 0.28$].

These results suggest that during goal-directed reaching, attention is allocated to both visual and motor goals. However, there could be an alternative explanation for the equivalent RSVP performance during the stable-adaptation period for the visual and motor groups. For instance, the visual and motor groups had a different number of behaviorally relevant or visually salient stimulus locations. In the visual group, both the visual target and RSVP stream appeared at the same location (i.e., within 0.5° of each other), whereas in the motor group, the RSVP stream appeared at a different location, which was 45° rotated from the visual target. Thus, the motor group might have improved their performance to the same level as the visual group by practicing how to divide their attention to spatially disparate locations over time.

Furthermore, the difference in behaviorally relevant locations might also have lead to different eye movement strategies adopted by each group, which could affect attention allocation. For instance, the visual group might have gazed at the visual target before and during reaching (Neggers and Bekkering 2000), whereas the motor group might have rapidly switched gaze between the visual target and the RSVP stream.

Experiment 2

To address these concerns, we devised a new experiment using a within-subject design, in which the RSVP stream appeared at a control location (45° CW from the visual target) in addition to the locations of visual and motor goals as in Experiment 1. Furthermore, we also required participants to maintain eye fixation throughout trials, which was verified with an eye tracker.

If equated performance in the visual and motor groups during the stable-adaptation period in Experiment 1 was simply due to learning, we would expect no difference between the control and the motor conditions during the stable-adaptation period. However, if attention was allocated to both visual and motor goals, we would instead expect equal performance for the visual and motor conditions, with performance in both conditions better than performance in the control condition.

Materials and Methods

Participants

We recruited 11 participants from Brown University and the local community (ages: 18–23; 6 females). All other details were identical to Experiment 1.

Procedure

All the experimental procedures were identical to Experiment 1 except for the following modifications. To control the effect of eye movements, we required participants to always maintain gaze within a 1° radius circle around the starting position for the whole trial duration. We used an eye tracker (EyeLink II, SR Research; 250 Hz) to monitor gaze position. As soon as gaze was broken, the trial was aborted and repeated immediately in order to have the same number of trials for all participants. Less than 5 % of trials were aborted due to breaking fixation or blinking.

In the visuomotor adaptation task (Fig. 1a), visual targets (white dots 1° diameter) appeared at 4° (equivalent to 4 cm) away from the starting base at the 3, 6, 9, or 12 o'clock direction. We put the stimuli closer to the starting base than in Experiment 1 in order to ensure that stimuli could be perceived without eye movements. To induce more natural goal-directed reaching movements, we asked participants to use a stylus pen on a tablet touch screen (Elo touch systems) located on the table using their dominant right hand. To reach visual targets, the physical distance of the stylus movements was 3.7 cm. All stimuli appeared on the same monitor located at 57 cm from participants as in Experiment 1. After a block of 48 practice trials, participants performed three baseline blocks (60 trials/block) in which the cursor followed the reach trajectory normally, followed by six adaptation blocks (30 trials/block) with the cursor rotated by 45° CCW, followed by six additional adaptation blocks (40 trials/block) also with the cursor rotated by 45° CCW. We defined the first six adaptation blocks as the adaptation-training blocks, in which visuomotor adaptation was in progress until it attained asymptotic performance level, and the last six adaptation blocks as the stable-adaptation blocks, in which visuomotor adaptation had already attained asymptotic performance level.

Although the RSVP stream was presented on each trial, participants were required to perform the RSVP task only during the baseline blocks and the stable-adaptation blocks, and not during the adaptation-training blocks. Instead, participants made a button press in response to a visual cue at the end of each trial (i.e., 'Press button 1, 2, or 3') in the adaptation-training blocks. The RSVP stream was presented at 0.5° above the location of the visual target (Fig. 1b), 0.5° above the location of the reach goal (Fig. 1c), or 0.5° above

the location of the control position (45° CW from the visual target; Fig. 1d). The three conditions were randomized across three consecutive blocks for the baseline, adaptation-training, and stable-adaptation blocks. The order of RSVP condition blocks was also randomized across participants.

Data analysis

All the data analyses were the same as in Experiment 1.

Results

As shown in Fig. 3a (left part), during the baseline block, there were no significant difference among the visual (black), motor (dark gray), and control (light gray) conditions in both mean reach errors (dots; one-way ANOVA, $F(2, 20) = 0.27$, $P = 0.76$) and variable reach errors [star; $F(2, 20) = 1.53$, $P = 0.24$]. Note that the three conditions are plotted side by side only to allow differentiating them.

During the adaptation-training blocks (Fig. 3a, middle part), participants decreased mean reach error and variable reach error across the 6 blocks [30 trials/blocks; block 1 vs. block 6; $t(10) = 4.16$, $P < 0.05$ and $t(10) = 3.48$, $P < 0.05$, respectively] and their performance was stable by the end of the phase, that is, there was no difference across the last two blocks for mean and variable reach errors [$F(1, 10) = 0.87$, $P = 0.37$ and $F(1, 10) = 2.71$, $P = 0.13$, respectively] indicating that the visual and motor goals had been dissociated effectively.

During the stable-adaptation blocks (Fig. 3a, right part), reach error remained stable for each of the visual, motor, and control conditions. A one-way ANOVA revealed no significant differences in reach error between the three conditions [$F(2, 20) = 2.15$, $P = 0.14$]. Also, participants performed the three conditions similarly regarding RT (mean ± s.e. 675 ± 33 ms, 700 ± 38 and 694 ± 40, for the visual, motor and control conditions, respectively) and MT (mean ± s.e. 146 ± 15 ms, 132 ± 15 and 128 ± 17, for the visual, motor and control conditions, respectively). We used one-way ANOVAs which did not reveal any significant differences between the three conditions for either RT or MT [$F(2, 20) = 2.35$, $P = 0.12$ and $F(2, 20) = 2.38$, $P = 0.12$, respectively].

Figure 3b depicts the RSVP target detection accuracy for the visual, motor, and control conditions during the baseline (black) and stable-adaptation (white) blocks. We observed that the accuracy in the visual condition is higher than the other two conditions during the baseline blocks, in which visual and motor goals were still aligned. Yet, once visual and motor goals were dissociated by visuomotor adaptation, the difference between the visual and motor conditions disappeared and the performance in these two conditions was better than the performance in the control condition. Also,
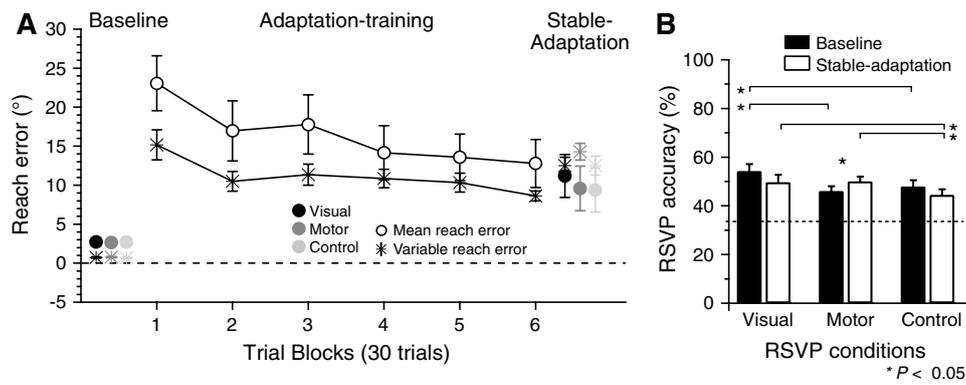
Fig. 3 Reach errors and RSVP target detection accuracy during the visual, motor, and control conditions ($N = 11$) in Experiment 2. **a** Mean reach errors and variable reach errors (± 1 s.e.) during the baseline, adaptation-training, and stable-adaptation phases (30 trials/blocks). Reach mean and variable reach errors were gradually reduced during the adaptation phase and performance was stable by the end of the phase. At the stable-adaptation phase, mean and variable reach error remained low. The motor, visual, and control conditions yielded similar performance. Note the *error bars* in the baseline were too small to be visible. **b** Mean RSVP detection accuracy (± 1 s.e.) during the baseline (*black*) and stable-adaptation (*white*) phases for the visual, motor, and control conditions. The visual condition yielded better accuracy than for the motor and control conditions during the baseline phase but during the stable-adaptation phase the visual and motor condition yielded higher accuracy than the control condition. The *dotted line* represents the level of chance performance (33 %)

note the improvement for the motor condition from baseline to stable-adaptation.

To confirm our observation, we conducted a two-way ANOVA with the three RSVP conditions and two phases (baseline and stable-adaptation), which revealed a significant main effect of condition [$F(2, 20) = 7.24$, $P < 0.005$], no significant effect of phase [$F(1, 10) = 0.87$, $P = 0.37$], and a significant interaction [$F(2, 20) = 7.51$, $P < 0.01$]. We also confirmed that during the baseline, accuracy was higher for the visual condition than the motor [$t(10) = 4.64$, $P < 0.0001$] and control conditions [$t(10) = 3.63$, $P < 0.005$]; the motor and control conditions did not differ from each other [$t(10) = 0.84$, $P = 0.4$]. Thus, in accord with Experiment 1, we showed that attention was primarily allocated to the aligned visual and motor goals in the visual condition, in contrast to irrelevant locations used in the motor and control conditions. After visuomotor adaptation, i.e., in the stable-adaptation phase, we confirmed that accuracy was higher for the visual [$t(10) = 2.62$, $P < 0.03$] and motor conditions [$t(10) = 3.08$, $P < 0.02$] than for the control condition and the difference between the visual and motor conditions disappeared [$t(10) = 0.15$, $P = 0.88$]. Finally, there was a significant increase in accuracy from the baseline to the stable-adaptation phase in the motor condition [$t(10) = 2.65$, $P < 0.02$], a marginally significant decrease in accuracy in the visual condition [$t(10) = 1.99$, $P = 0.07$], and no significant difference in the control condition [$t(10) = 1.59$, $P = 0.14$].

To sum up, in accordance with Experiment 1, we found equivalent RSVP detection performance in the visual and motor conditions following visuomotor adaptation, which was significantly better than detection performance in the control group. This result could not be explained by a difference in the number of task-relevant locations or improvement of divided-attention in the motor condition because these were equated between the motor and control conditions. Furthermore, results were not due to different eye movement strategies because eye movements were prevented with continuous eye-monitoring.

Discussion

In contrast to the classical view assuming serial information processing stages, a recent view of interactive behavior suggests that processes that specify potential motor actions and select between them occur in parallel (Cisek and Kalaska 2010). From this perspective, visual target selection and planning a movement toward that object are closely connected. Visual and action targets are typically identical in daily life. In the present study, however, we examined how visual and motor targets attract spatial attention by dissociating them using a visuomotor adaptation paradigm. In this task, visually perceived reach movement direction was rotated 45° CCW from actual hand movement direction. Thus, to acquire the visual target with the cursor, reach programming should be adaptively modified to direct the hand toward the motor goal, which is 45° CW from the visual target.

While visual and motor goals were dissociated by visuomotor adaptation, we measured the locus of allocated attentional resources using the RSVP task. We predicted that if attentional resources were allocated to a given location, performance in the RSVP task would be subsequently

improved. In two experiments, we compared RSVP target detection performance when the visual stream was presented at the location of the visual target, the motor goal, or a control location, which was neither a visual nor a motor goal. We observed that visual detection is equivalently better at the visual and motor goals compared to the control location. Thus, we concluded that attention is allocated to both visual and motor goals during visually guided reaching movements.

Attention allocation during visuomotor adaptation

We demonstrated that participants in the visual and motor groups reduced reach errors to a similar level after adaptation was completed in both experiments. This result indicates that visual and motor goals were dissociated regardless of the locations of the RSVP stream. The converging result from the within-subject design including the control location (Experiment 2) demonstrated that this result is not caused by distinctive explicit strategies for visuomotor adaptation induced by different locations of the RSVP stream. This is in accord with previous studies showing that visuomotor adaptation is mainly governed by implicit processes (Gabrieli et al. 1993; Tranel et al. 1994; Shadmehr et al. 1998; Mazzoni and Krakauer 2006; Krakauer 2009).

In both experiments, we showed that RSVP detection accuracy remained constant from baseline throughout adaptation blocks when the RSVP stream was presented at the visual goal. This suggests that attentional resources remained allocated to the visual target location while reaches needed to be directed to the visual target (baseline) or to the motor goal (i.e., 45°CW stable-adaptation). In contrast, as the motor goal was separated from the visual target by adaptation, RSVP detection accuracy was improved at the location of the motor goal. This suggests that attentional resources were also allocated to the adapted motor goal during reach programming, resulting in equally divided attentional resources between the visual and motor goals. Thus, we conclude that the locus of attentional allocation for reaching movements is determined by both visual target and motor goal.

However, it is yet to be examined whether this represents separate foci of attention at the two locations or a single extended focus of attention encompassing both visual and motor target locations (Collins et al. 2010). Previous studies have shown that allocation of attentional resources is tightly centered on target locations for actions such as saccades and reaches without spreading to distractors located between targets. This result can be also extended to several target locations when sequential movements are required (Baldauf et al. 2006; Baldauf and Deubel 2009; Khan et al. 2011). In addition, when the visual target and the motor goal were dissociated by using a triangular hand-held tool,

Collins et al. (2008) demonstrated that perceptual performance was enhanced in parallel at both spatial locations, but not at nearby and intermediate locations. These results suggest that both action goal selection and motor planning contribute to attention allocation for action, and attentional selection for action can occur at multiple foci.

In the present study, we used a sudden adaptation paradigm, in which the visual perturbation appeared suddenly yielding large reach error. Because participants often become aware of such a perturbation, they may have implemented some explicit cognitive strategies to adapt, which in turn could have affected RSVP performance. Adaptation could also occur via a gradual schedule of perturbation (e.g., perturbation increases 1° per trial), which leaves participants unaware of the perturbation but yields similar learning, after-effects, and recall performance as sudden adaptation (Ingram et al. 2000; Kagerer et al. 1997; Klassen et al. 2005) though transfer across arms is impaired (Malfait and Ostry 2004). Using a gradual adaptation schedule would probably yield better RSVP performance early during adaptation because large reach errors would be absent and explicit processes would not be required. However, note that in the present study, when the RSVP stream appeared at the motor goal during the stable-adaptation phase, performance was undistinguishable from when the RSVP stream appeared at the visual goal. This result suggests that gradual adaptation would have likely yielded similar RSVP performance at the stable-adaptation phase.

Attention allocation and target selection for actions

We demonstrated that when visual and motor goals for reaches were dissociated by visuomotor adaptation, attentional resources were evenly allocated to both goals. A similar result has been also reported during saccadic adaptation. For instance, Collins et al. (2010) recorded ERPs at the visual target location and the upcoming motor endpoint during saccadic adaptation. They found that ERPs as early as 130–170 ms were modulated by attention at both the visual target and motor endpoint locations. These results indicate that spatial attention is simultaneously allocated to both the visual and motor goals while preparing saccades, resulting in enhanced perceptual processing of stimuli. This result implies that different types of goal-directed actions, such as saccades and reaches, might share common mechanisms to allocate attention to selected goals.

Previous studies, in which visual and motor goals were aligned, have shown that target selection mechanisms are coupled for saccade and reach as well as attention. For instance, distractor number, color priming, and fixation offset have similar effects on target selection in visual search for saccades, reaches, and shifts of attention (Bravo and Nakayama 1992; Maljkovic and Nakayama 1994; Bichot

and Schall 1999;McSorley and Findlay 2003; Song and Nakayama 2006; Song and Nakayama 2007; Song et al. 2008). Song and McPeek (2009) have also shown that when saccades and reaches were simultaneously coordinated in visual search, target selection for reaching and saccades was highly correlated. Furthermore, Khan et al. (2011) suggested that shared attentional resources are used for planning eye and hand movements.

Previous neurophysiological studies in non-human primates have demonstrated that LIP and parietal reach region (PRR) in posterior parietal cortex are commonly modulated by an effector non-specific response, presumably reflecting attentional modulation at stimulus-onset. However, neurons in these same regions show effector-specific responses involved in planning saccades and reaches, respectively (Snyder et al. 2000). Furthermore, temporary inactivation or stimulation of superior colliculus (SC), an area involved in selecting saccadic targets and executing saccades, can influence covert attention, leading to changes in performance for difficult perceptual tasks (Basso and Wurtz 1998; Horwitz and Newsome 1999; Krauzlis and Dill 2002; Carello and Krauzlis 2004; Cavanaugh and Wurtz 2004; McPeek and Keller 2004; Muller et al. 2005; Kim and Basso 2008; Lovejoy and Krauzlis 2010; Nummela and Krauzlis 2010). Song et al. (2011) have further demonstrated that temporary focal inactivation of the primate SC causes target selection deficits for reaching movements. Thus, activity in SC contributes to target selection for both saccades and reaches. Taken together, results from these studies show a close congruence among reaches, saccades, and attention, suggesting that target selection for all three modalities may be based on shared mechanisms.

Conclusions

We demonstrated that both visual target selection and motor planning processes are involved in allocating visual attention when goal-directed reaching is required. This result is also in accord with what has been found in saccade studies (Collins et al. 2010). Thus, we conjecture that attention allocation mechanisms might be shared across different effectors such as the eye and the hand.

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