Impaired visuomotor generalization by inconsistent attentional contexts

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Abstract

In daily life, people are constantly presented with situations to learn and acquire new motor skills in complex environments, where attention is often distracted by other events. Being able to generalize and perform the acquired motor action in different environments is a crucial part of visuomotor learning. The current study examined whether attentional distraction impairs generalization of visuomotor adaptation or whether consistent distraction can operate as an internal cue to facilitate generalization. Using a dual-task paradigm combining visuomotor rotational adaptation and an attention-demanding secondary task, we showed that switching the attentional context from training (dual-task) to generalization (single-task) reduced the range of transfer of visuomotor adaptation to untrained directions. However, when consistent distraction was present throughout training and generalization, visuomotor generalization was equivalent to without distractions at all. Furthermore, this attentional-context dependent generalization was evident even when sensory modality of distractions differed between training and generalization. Therefore, the general nature of the dual tasks, rather than the specific stimuli, is associated with visuomotor memory and serves as a critical cue for generalization. Taken together, we demonstrated that attention plays a critical role during sensorimotor adaptation in selecting and associating multisensory signals with motor memory. This finding provides insight into developing learning programs that are generalizable in complex daily environments.

New & Noteworthy

Learning novel motor actions in complex environments with attentional distraction is a critical function. Successful motor learning involves the ability to transfer the acquired skill from the trained to novel environments. Here, we demonstrate attentional distraction does not impair visuomotor adaptation. Rather, consistency in the attentional context from training to generalization modulates the degree of transfer to untrained locations. The role of attention and memory must therefore be incorporated into existing models of visuomotor learning.

The ability to learn and perform motor skills, such as driving a car, is a fundamental aspect of human behavior and is often critical for daily function. The example of driving under different traffic conditions illustrates how motor skills must be performed in different environmental conditions. The ability to transfer and extrapolate motor skills to novel and different contexts is an important function of motor learning, which possibly reveals the underlying representational changes in motor memory (Poggio & Bizzi, 2004; Thoroughman & Shadmehr, 2000; Taylor et al., 2013; Thoroughman & Taylor, 2005). For instance, people can extend and generalize acquired motor behaviors to other directions (Krakauer et al., 2000), hand positions (Shadmehr & Moussavi, 2000), and even movements of the other arm (Criscimagna-Hemminger et al., 2003; Wang & Sainburg, 2004; 2006).

Learning is often localized such that the transfer of motor learning to untrained spatial regions is limited (Krakauer et al., 2000). For instance, generalization of the visuomotor adaptation to untrained directions generally decreases as a function of increased angular distance from the trained direction and it is often confined to target directions within 45° either side of the trained direction (Ghahramani et al., 1996; Krakauer et al., 2000; Taylor & Ivry, 2013a). A neural network model readily accounts for these findings (Tanaka et al., 2009; 2012; Donchin et al., 2003; Thoroughman & Taylor, 2005) by assuming that adaptation updates neural populations, with each neuron being represented by a tuning function corresponding to separate spatial directions. Adaptation training to one spatial direction tunes neurons to preferably respond to that movement. Importantly, the width of the tuning function determines the range with which this movement generalizes to untrained directions.

Transfer of motor actions can be also affected by changes in the environmental cue (Lee & Schweighofer, 2009; Shea & Morgan, 1979). Learning under certain contexts also constrains the transfer of motor behavior to novel contexts (Hommel, 1993; Mechsener et al., 2001; Ivry et al. 2004; Dionne & Henriques, 2008; Ayala, Hart, & Henriques, 2015). In a sequential motor learning paradigm for example, Ruitenberg et al. (2012) trained participants to make one of four key presses on the keyboard that corresponded to one of four positions on the computer screen. They learned two six-key sequences and each sequence was associated with either a blue or yellow training cue. For one group, the mapping between training cue color and key sequence was reversed between training and test. It resulted in longer mean response times (RT) compared to a group that retained the original cue-sequence mapping. Therefore, the ability to reproduce the learned sequence was dependent on the color of training cue.

Similar external constraints on generalization of visuomotor adaptation have also been observed. For instance, Criscimagna-Hemminger (2003; see also Wang & Sainburg, 2004; 2006) showed that participants could transfer visuomotor adaptation learned by one arm to the other. Recently, Taylor and Ivry (2013a) argued that the width of the generalization function is also influenced by the training environment. They examined whether an external contextual cue, created by a circular or rectangular target arrangement, affected the transfer of adaptation to untrained directions. Participants were trained either with a translational shift perturbation in the rectangular workspace or with a visuomotor rotation in the circular workspace. They found that switching the target arrangement in the visuomotor rotation condition from circular to rectangular broadened the generalization function. Conversely, switching the target arrangement from

rectangular to circular in the translational shift condition narrowed the generalization function. Therefore, the external environment modulated the width of the generalization function.

Beyond these external factors, Bédard and Song (2013) recently examined how concurrent cognitive processes affect the generalization of visuomotor adaptation. They observed that performing visuomotor training with a concurrent, attention-demanding discrimination task, such as a rapid serial visual presentation (RSVP) task, reduced the gain and narrowed the tuning of the generalization function. They suggested that divided attention narrowly restricts an internal model, reducing the range and magnitude of transfer by modulating a selective subpopulation of neurons in motor areas. This suggestion is consistent with a traditional notion that attention is a necessary resource that facilitates learning and therefore dividing attentional resources across tasks can impair learning (Pashler, 1998; Curran & Keele, 1993; Nissen & Bullemer, 1987; Taylor & Thoroughman, 2007, 2008).

Yet, we noticed that this effect of divided attention on generalization (Bédard and Song, 2013) was only studied under inconsistent task context between the training (dual-task) and the generalization phase (single-task). Based on a series of subsequent studies, we formulated an alternative hypothesis that the reduced generalization led by divided attention could be caused by inconsistency between task-contexts. Using a similar dual-task paradigm as in Bédard and Song (2013), Song and colleagues (Song and Bédard, 2015; Im, Bédard, & Song, 2015, 2016) examined how various attentional demands of a secondary task modulate immediate motor performance and how consistency in task-context between learning and recall affects memory formation and retrieval. Surprisingly,

123 they found that performing the distraction task did not impair the rate of initial
124 visuomotor learning. However, recall of visuomotor adaptation, learned with the
125 distractor present, required that the distractor also be present during the recall phase. In
126 the absence of a distractor task in the recall phase, there was no benefit of prior learning
127 for motor performance in recall (i.e. savings of learning). Importantly, this saving of
128 learning effect was not task specific. Song and Bédard (2015) showed that the type of
129 stimuli in the secondary task does not provide the context to facilitate recall; rather it is
130 the consistent state of attentional distraction generated by completing the secondary task.
131 Participants demonstrated superior recall of visuomotor adaptation even if they
132 completed two different secondary tasks in training (RSVP task) and recall (sound
133 discrimination task). This paradoxical result suggests that performing the dual-task
134 induces an attentional state (divided vs. undivided) that acts as a 'vital context' for
135 encoding and retrieval of motor memories (Song & Bédard, 2015; Im et al., 2015, 2016).
136 Extending beyond this result, Im et al. (2016) showed that this newfound paradoxical
137 benefit of consistent dual-task context lasts for more than one day as visuomotor memory
138 retrieval is enhanced under conditions in which it is more difficult to engage in
139 attentional selection of the motor task.

140 The current study compared two alternative hypotheses; 1) whether divided
141 attention impairs generalization or 2) whether consistent divided attention can operate as
142 an internal contextual cue for visuomotor generalization. In short, we applied the dual-
143 task paradigm (e.g., Bédard and Song; 2013) to visuomotor generalization. Participants
144 first completed the visuomotor adaptation task with and without a secondary task to one
145 direction. Then, participants generalized visuomotor adaptation with and without the

secondary task to untrained directions. If attention operates as a resource for processing, visuomotor generalization would be impeded whenever the secondary task is performed regardless of context consistency between the training and generalization phases. Conversely, if the consistent attentional context necessitates visuomotor adaptation generalization beyond the trained direction, those who consistently divide their attention to a secondary task across training and generalization phases would fully generalize their performance equivalent to those who consistently perform a single task.

Following Song and Bédard (2015) and Im et al. (2016), we introduced an additional group to determine whether the key to successful visuomotor generalization depends on the repetition of specific secondary task across training and generalization. In this group, participants completed two different secondary tasks within different sensory modalities in training and generalization (i.e. RSVP and sound discrimination). We hypothesize that attentional context is generated by the general nature of consistent attentional distraction and not the specific task. The transfer of adaptation in this group is expected to be analogous to generalization in the other consistent groups. Such a result would imply that context modulation of generalization and recall of visuomotor adaptation (i.e., Song & Bédard, 2015) share a common learning system.

Materials and Method

Participants

Fifty-two right-handed participants with normal color vision and normal or corrected-to-normal vision participated in the experiment in exchange for course credit. All participants were naïve to the goal of the experiment. The number of participants per

group (n = 13) was determined based on prior studies that utilized a similar dual-task paradigm and experimental design (Bédard & Song, 2013; Im et al., 2015, 2016; Song & Bédard, 2015). Reliable effect sizes were observed in these studies ($\eta^2 > 0.26$)[1]. The sample size is also within the range of sample sizes from previous visuomotor adaptation studies (e.g., Krakauer et al., 2000; Thoroughman & Taylor, 2007). The experimental protocol was approved by the Institutional Review Board at Brown University.

Apparatus and Materials

In a dimly illuminated room, participants sat in a chair approximately 57 cm from an Apple iMac computer with a 21-inch screen with refresh rate 60 Hz and native resolution of 1920 x 1080 pixels. Participants used a stylus pen to perform a goal-directed reaching task with their right hand. Movement of the stylus controlled a corresponding cursor on the screen (diameter 0.5 cm). The tips of the stylus rested on a touch screen (Magic Touch; Keytec, Garland TX) that lay flat on a table and aligned with each participant's midline and the center of the computer screen. Stimulus presentation and recording of cursor displacement was controlled by custom software written in MATLAB (Version 2008b; MathWorks Inc., Natick, MA) and functions from Psychtoolbox (Version 3; Brainard, 1997; Pelli, 1997).

Design and Procedure

Visuomotor task. Figure 1A outlines the visuomotor adaptation task. Participants were tasked to move a cursor from a starting position (annulus with a diameter of 1°, corresponding to 1 cm) in the center of the screen toward a reach target (solid white dot, 1 cm in diameter) located 5.5 cm from the starting position. Participants were specifically

[1] According to Cohen (1988) effect sizes of 0.02, 0.13, and 0.26 are considered small, medium, and large effect sizes respectively.

instructed to make fast and linear movements toward the target and then to return to the starting position immediately after reaching the target. Seven possible target directions were assigned to each participant: one training target (randomly selected from 3, 6, 9, or 12 o'clock directions from the starting position) and six other target directions located at ±22.5°, ±45°, and ±90° relative to the training target. The target remained visible for the entire duration of the trial (1500 ms). A trial started when cursor was positioned in the starting position and this triggered the appearance of the reach target in the visuomotor task as well as the visual or auditory stream in the secondary task. There were two types of experimental trials. In the no-rotation trials, the cursor followed the stylus movement. In the rotation trials, the cursor direction was rotated 45° counterclockwise (CCW) or 45° clockwise (CW). The direction of rotation was counterbalanced between participants. The rotation was applied for the entire duration of the trial (i.e. 1500 ms from trial onset), including both the outward and inward movements. Outside the trial, the unrotated cursor was visible to guide participants back to the starting position.

Secondary RSVP task. Figure 1B illustrates schematic outline of the RSVP tasks. A sequence of five Ts shapes (0.5° x 1°) was generated from pseudorandom permutations of letter orientation (inverted or upright) and color (red, white, green, blue, or yellow). The sequence was presented above the starting position and each T in the sequence appeared every 300 ms, remaining visible for only 150 ms (for a total of 1500 ms). Participants were required to detect conjunction targets (red upright Ts and green inverted Ts) and report the total number of targets detected at the end of teach trial by pressing a keyboard key with their left hand. The number of target Ts for each trial varied with a uniform distribution between one and three and thus 33% represents chance performance.

In order to control for the effect of divided attention on reaching, a control task was devised in which participants received instructions to ignore the Ts and simply press the key corresponding to the visual written cue such as "Press button 1" at the end of each trial with their left hand. The RSVP stream appeared on every trial of all experimental phases except during the sound discrimination task. This ensured that visual stimuli remained consistent for all groups.

In our previous studies (i.e., Song & Bédard, 2013, 2015) that have used a similar dual-task paradigm, we have repeatedly demonstrated that eye movements do not affect performance in the dual-task paradigm. Specifically, allowing participants to either make free eye movements or maintain central gaze fixation do not affect accuracy in the RSVP task or reach error in visuomotor adaptation. As a consequence, we did not constrain each participant's eye movements throughout the experiment.

Secondary sound discrimination task. Figure 1C illustrates the schematic outline of the sound discrimination task. Five tones of three different frequencies (200 Hz, 300 Hz, 450 Hz) appeared with the same timing as the RSVP task and participants were asked to count the number of low and high frequency tones within each sequence. The total number of relevant low and high frequency tones varied randomly between one and three with equal probability.

Experimental design. Figure 1D outlines the four phases within each experimental session: 1) familiarization (70 no-rotation trials with seven target directions), 2) baseline (70 no-rotation trials with seven target directions), 3) training (70 rotation trials with one target direction), and 4) generalization (70 rotation trials with seven target directions). The familiarization phase provided participants with the opportunity to practice reaching

to each target direction with continuous cursor feedback to all seven directions. The baseline phase was designed to measure for inherent bias in the reach movement to each direction. The cursor remained visible for only the training target (i.e. 0°) but disappeared once the cursor left the starting position for the six remaining directions. The position of the training target was counterbalanced between participants and it appeared at the 3, 6, 9, or 12 o'clock position. In the training phase, visuomotor adaptation was trained with the single training target. Participants received continuous feedback to the training target and their reach trajectory was rotated by either 45° clockwise (CW) or counterclockwise (CCW). The degree to which visuomotor adaptation transferred to untrained directions (±22.5°, ±45°, and ±90° relative to the training target) was measured in the generalization phase. Cursor feedback was rotated to the same direction as the training phase (i.e., either 45° CW or CCW) and continuous feedback was presented for the trained target but not for the untrained targets (Krakauer et al., 2000).

Experimental groups. Four experimental groups were created based on whether participants completed a concurrent secondary task during the training and/or generalization phases. For naming convention (see Song & Bédard, 2015), *RSVP* refers to participants completing the RSVP task with reaching (i.e. high distraction of attention), *sound* refers to participants completing the sound discrimination task, and *none* refers to participants completing the button press (control) task with reaching (i.e. no distraction of attention). In the *RSVP-RSVP* group, for example, participants completed the RSVP task during both the training and generalization phases of the experiment. Participants in the *none-none* group completed the button press task during both the training and generalization phases. In the *RSVP-sound* group, participants completed the RSVP task in

training and completed the sound discrimination task in generalization. Finally, in the *RSVP-none* group, participants completed the RSVP task in training and completed the button press task in generalization.

Data Analysis

Data analysis procedures generally followed those used in our previous studies (Bédard & Song, 2013; Im et al., 2015, 2016; Song & Bédard, 2015). For the visuomotor task, we filtered the *x* and *y* coordinated of the cursor displacements with a low-pass Butterworth filter using an 10 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 reaches 5% of peak velocity. We measured reaction time (RT) as the time elapsed from target appearance to movement onset and the movement time (MT) as the time elapsed between movement onset and movement end. We measured reach error by calculating the angle between the line that joined the starting position 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. In order to conduct the statistical analysis, individual participant's training and generalization data for each dependent variable (i.e. reach error, RT, and MT) were averaged across seven successive trials in order to create 10 blocks of seven trials.

Following previous studies (Bédard & Song, 2013; Krakauer et al. 2000), we calculated an adaptation index (Eq. 1) for each target direction in order to quantify the generalization function.

$$(1) \qquad Adaptation\ Index = 1 - \frac{E_{Gen} - E_{Base}}{45^{\circ}}$$

where E_{Gen} and E_{Base} represented the reach error during the generalization and baseline phases, respectively. An adaptation index of 0 or 1 represents no or full adaptation, respectively. In order to determine whether divided attention would alter the gain, shift, or width of the generalization function, we fitted a Gaussian function to the rotation adaptation index of each individual participant as a function of angular distance from the trained direction:

$$f(x) = ae^{\frac{-x^2}{2s^2}} + c \quad (2)$$

where parameters a is the gain, c is the constant shift, and s is the width of the Gaussian function, and x is the angular distance from the training target. We used MATLAB (2014b, Mathworks) and SPSS (version 22, IBM) for data and statistical analyses.

Results

Training phase: No disruption of motor performance by attentional distraction

Performance accuracy in the RSVP task was first analyzed to confirm that participants effectively allocated their attention to the secondary task in training. Mean accuracy in the RSVP-none, 51% ±0.02, $t(12) = 10.47$, $p < 0.01$, $d = 2.94$, RSVP-RSVP, 55% ±0.03, $t(12) = 6.31$, $p < 0.01$, $d = 1.78$, and RSVP-sound 50% ±0.02, $t(12) = 7.49$, $p < 0.01$, $d = 2.08$, groups were all above chance performance (~33%). Mean accuracy was also not different between groups, $F(2, 36) = 1.35$, $p = 0.27$.

Figure 2A shows that attentional load did not affect reach error performance. In all four groups (none-none, RSVP-none, RSVP-RSVP, RSVP-sound), reach error was reduced across trial blocks and each group achieved a similar level of performance in the final block. We conducted a two-way group (none-none, RSVP-none, RSVP-RSVP,

RSVP-sound) x trial block (1st-4th, and 10th blocks) ANOVA of reach error using data from the first four training blocks as well as the final training block. The first four blocks were chosen because this range was most representative of learning. Reduction in reach error was greatest over this period and reach error approached asymptotic performance in the fourth block. The final block was included to indicate asymptotic performance. A Mauchly's test of sphericity showed that the assumption of sphericity was violated for the factor of trial block. Greenhouse-Geisser corrections were applied to subsequent ANOVAs involving this factor in order to reduce the chance of Type I error. This analysis revealed there was a significant main effect of trial block, $F(2.29, 109.80) = 117.52$, $p < 0.001$, $\eta^2 = 0.70$, $MSE = 44.66$, indicating visuomotor adaptation. Importantly, adaptation was not affected by attentional distraction as the main effect of group was not significant, $F(3, 48) = 1.13$, $p = 0.35$. The trial block x group interaction was not significant ($F < 1$). Therefore, performing the RSVP task does not impair visuomotor learning. This is consistent with previous studies that have used a similar procedure (Bédard & Song, 2013; Song & Bédard, 2015; Im et al., 2015, 2016).

RT and MT were analyzed in order to determine whether participants utilized a compensatory strategy in the dual-task procedure. For instance, participants may allocate extra cognitive resources to the RSVP task, allowing for longer initiations of movement (RT) or slower movements (MT). In such cases, RT and/or MT would be longer in the dual-task conditions. Figure 2B (left) shows the mean RT for the four groups. As per the analysis of reach error, we analyzed RT and MT data from the first four and final trial blocks. Analysis of RT revealed a main effect of trial block, $F(3.39, 162) = 22.83$, $p < 0.001$, $\eta^2 = 0.29$, $MSE = 0.006$, and group, $F(3, 48) = 6.41$, $p < 0.001$, $\eta^2 = 0.29$, $MSE =$

0.03. The two-way interaction was also significant, $F(10.13, 162) = 2.3$, $p = 0.01$, $\eta^2 = 0.1$, $MSE = 0.006$, and this implies that group difference was largest in the early blocks but reduced in the final block. We conducted a post-hoc contrast analysis to compare RT of the single-task group against the three dual-task groups. This analysis showed that RT in the three dual-task groups was not different to RT in the single task group, $F(1, 48) = 2.77$, $p = 0.1$. Instead, the main effect of group appears to be driven by some individual differences between the three dual-task groups. Such differences are unlikely to be interesting since each dual-task group followed an identical experiment procedure.

Figure 2C (left) shows that participants took less time to complete each movement with repeated trials as mean MT decreases across trial blocks. The group x trial block ANOVA confirms the main effects of trial blocks, $F(3.14, 150.77) = 7.74$, $p < 0.001$, $\eta^2 = 0.13$, $MSE = 0.006$, as well as group, $F(3, 48) = 4.1$, $p = 0.01$, $\eta^2 = 0.20$, $MSE = 0.05$. The two-way interaction was not significant, $F(9.42, 123.91) = 1.21$, $p = 0.39$. We again conducted a post-hoc contrast analysis of MT from the single task group and compared it to MT from the three dual-task groups. This analysis showed that MT was not affected by the presence of attentional distraction, $F(1, 48) = 1.02$, $p = 0.32$. The analysis of both RT and MT suggest that completing the RSVP task did not interfere with visuomotor learning. Participants did not appear to devise a cognitive or movement strategy in order to compensate for completing the RSVP task. This finding is consistent with studies that have utilized a similar dual-task paradigm (Bédard & Song, 2013; Song & Bédard, 2015; Im et al., 2015, 2016).

Generalization phase: Inconsistent attentional context impairs visuomotor generalization

The critical question is how consistency of attentional context affects visuomotor generalization. We compared generalization performance of the three consistent context groups, RSVP-RSVP (consistent divided attention), none-none (consistent undivided attention), and RSVP-sound (consistent divided attention across two secondary tasks), to generalization performance in the inconsistent group, RSVP-none (inconsistent divided-undivided attention). The RSVP-sound group is designed to show that attentional context is generated by the nature of consistent attentional distraction and not the specific task. Consequently, we expect the transfer of adaptation to be similar between the RSVP-RSVP and RSVP-sound groups.

Performance accuracy was analyzed to show that participants maintained their attention to the secondary task in the generalization phase. In the RSVP-RSVP group, participants performed above chance accuracy, 56% ±0.04, $t(12) = 6.10$, $p < 0.01$, $d = 1.72$, and their performance was not different from training, $t(12) = -1.24$, $p = 0.24$, $d = 0.34$. Similarly, sound discrimination performance in the RSVP-sound group was above chance accuracy, 61% ±0.03, $t(12) = 8.14$, $p < 0.01$, $d = 2.26$, but these participants showed better sound discrimination accuracy than their RSVP accuracy in training, $t(12) = -2.99$, $p = 0.01$, $d = 0.83$. Comparison of accuracy on the secondary tasks between the RSVP-RSVP and RSVP-sound groups yielded no difference ($t < 1$).

Dividing attentional resources during the training phase did not impair the degree of visuomotor adaptation for the trained target. Mean reach error to the trained target were not different between the none-none, RSVP-none, RSVP-RSVP, and RSVP-sound groups, 19.38° ± 12.23°, 19.03° ± 9.21°, 18.61° ± 7.04°, and 18.84° ± 7.66° respectively ($F < 1$).

We again analyzed RT and MT data to ensure that participants did not utilize a strategy to compensate for the secondary task in the generalization phase. Recall that only the RSVP-RSVP and RSVP-sound groups completed a secondary task in generalization. Figure 2B (right) shows longer mean RT in the none-none group than the other three groups. The trial block x group ANOVA confirmed that both the main effects of group, $F(3, 48) = 3.76$, $p = 0.02$, $\eta^2 = 0.19$, $MSE = 0.05$, and trial block, $F(6.99, 335.45) = 2.89$, $p = 0.01$, $\eta^2 = 0.06$, $MSE = 0.004$, were significant. The two-way interaction was not significant, $F(20.33, 325.22) = 1.1$, $p = 0.35$. Participants did not appear to compensate for the RSVP task by devising a strategy, since RT was not higher in either the RSVP-RSVP or RSVP-sound groups. This was confirmed by a post-hoc contrast analysis of the single-task and dual-task groups ($F < 1$). Figure 2C (right) shows the mean MT for each group in the generalization phase. From the figure, it is clear that there is no difference in mean MT between groups, $F(3, 48) = 1.15$, $p = 0.34$, but MT appears to decrease with increased trial blocks, $F(6.23, 300) = 2.25$, $p = 0.04$, $\eta^2 = 0.05$, $MSE = 0.003$. The two-way interaction was not significant, $F(18.69, 300) = 1.45$, $p = 0.08$.

Our primary interest is whether consistency of the attentional state (i.e. divided vs. undivided) between training and generalization affects visuomotor adaptation to untrained directions. To recap, we hypothesized that performing the RSVP task concurrently with the visuomotor adaptation task did not impair immediate motor performance during training, but it may lead to impaired consolidation of learning. This leads to weaker transfer of visuomotor adaptation to the untrained directions in all three RSVP groups (RSVP-none, RSVP-RSVP, RSVP-sound). In contrast, the consistency of attentional contexts (undivided vs. divided attention) between the training and

generalization phases could modulate the transfer of adaptation. In this case, generalization should be weakest for the RSVP-none group.

Figure 3 shows the adaptation index (Eq.1; markers) as a function of angular distance between the trained target directions and other untrained target directions. An adaptation index of 0 indicates no adaptation and 1 indicates full adaptation. Consistent with previous visuomotor generalization studies, the peak responses for all the groups are at the trained direction with decay to untrained directions, suggesting that adaptation is localized to the trained direction (e.g., Krakauer et al., 2000; Taylor et al., 2013). To further examine how diverting attention to the secondary task affects the width, the gain, or constant shift of the generalization, we fit Gaussian functions (Eq.2; lines) to individual data. An increase in gain represents increase of adaptation transfer to the trained direction. The width represents the angular range of visuomotor adaptation transfer to untrained directions, and thus increased width results in greater adaptation indices to untrained directions. The constant shift parameter represents a global generalization component that may be applied to each target direction by the participant (Brayanov, Petreska & Smith, 2011). For each participant, we fit their data by minimizing the negative log-likelihood of the Gaussian function, using the Hookes-Jeeves (1961) optimization method.

Figure 3 shows the mean model predictions generated from the best fitting parameters of each individual data. A summary of the best fitting parameters for each group is presented in Table 1. The model predictions accurately capture the overall pattern of the generalization function for each group. In particular, the predicted generalization functions of the three context consistent groups, none-none (blue line),

RSVP-RSVP (green line), and RSVP-sound (purple line), are similar to each other. Conversely, the generalization function of the RSVP-none group (orange line) appears to be narrower and shorter than the three other groups. We conducted a one-way ANOVA on the best fitting parameters in order to verify these observations. The statistical analysis reveals that there is a main effect of group for width, $F(3, 48) = 5.52$, $p < 0.01$, $\eta^2 = 0.26$, $MSE = 168.6$, but there is no effect of group for either gain, $F(3, 48) = 1.61$, $p = 0.2$, or constant shift ($F < 1$). To further investigate the main effect of width, we conducted three pairwise t-tests between the inconsistent group and the three consistent groups (Bonferroni corrected, $k = 3$, $\alpha_{Bonferroni} = 0.017$). This analysis revealed that width was narrower in the RSVP-none group compared to the none-none, $t(24) = 3.43$, $p < 0.01$, $d = 0.70$, RSVP-RSVP, $t(24) = 3.58$, $p < 0.01$, $d = 0.74$, and RSVP-sound groups, $t(24) = 2.61$, $p = 0.015$, $d = 0.53$. In sum, a broader generalization function was observed in the three context consistent groups than in the RSVP-none group.

The none-none and RSVP-none groups are replications of the no-load and attention-load groups reported by Bédard and Song (2013). Like us, they reported that inconsistent attentional context between training and generalization reduced the width of the generalization function. According to their Gaussian fit, Bédard and Song reported that gain was also reduced in their attention-load group, whereas we reported no such difference in our RSVP-none group. However, comparison of the two models in which either the gain or width parameter was allowed to vary between groups showed that the width model provided a better fit of the generalization function than the gain model in the attention-load group ($R^2 = 0.86$ vs. 0.84). Therefore, the width-only model provides the

simplest and best explanation for the Bédard and Song data, and this is consistent with the current observation.

Discussion

In the current study, we demonstrated that a change in the attentional state from training to generalization phases (e.g., from divided to undivided) restricted the range of transfer of visuomotor adaptation to untrained targets. Importantly, the presence of a secondary task during training itself did not impair visuomotor adaptation as long as a secondary task was consistently performed during generalization. Importantly, the ability for attentional context to modulate visuomotor generalization is not task specific. The width of the generalization function was similar for the groups that completed either the same (RSVP-RSVP) or different (RSVP-sound) secondary tasks in the training and generalization phases. The critical requirement is that a similar level of attentional discrimination is maintained across training and generalization.

The findings are inconsistent with Bédard and Song's (2013) suggestion that divided attention during visuomotor adaptation restricts learning by the internal model. Previous studies have shown that consistent attentional distraction can enhance motor memory recall in trained directions (Song & Bédard, 2015; Im et al., 2015; 2016). The current findings show this is extended to the transfer of adaptation to untrained directions. The consistency of the attentional state, generated by external distraction, appears to modulate adaptation to both trained and untrained directions. In the following sections, we discuss how the current findings fit within existing computational, neurophysiological, and cognitive frameworks of visuomotor adaptation.

Contextual modulation of visuomotor adaptation

Existing computational models of visuomotor adaptation provide clear explanatory frameworks for both the time course of visuomotor adaptation as well as generalization of adaptation to untrained directions. For instance, a prediction error model in which the error between motor output and visuomotor feedback is minimized through training adequately accounts for the time course of visuomotor adaptation (i.e., Smith et al., 2006). To explain generalization, training may be assumed to update learning to both the trained direction as well as surrounding directions. The angular distance between the trained and untrained directions determines the amount of adaptation updated to surrounding directions. Specifically, a Gaussian tuning function has been used to model this process (see Tanaka et al., 2009; 2012). A wider tuning function implies that more untrained directions are updated during adaptation and this leads to greater transfer of adaptation (Bock & Schmitz, 2011; Ghahramani & Wolpert, 1997).

The aforementioned framework, however, is unable to explain adaptation with different external context cues. For instance, participants can adapt to several different visuomotor rotations associated with separate cues, such as color cues or separate target locations (Imamizu et al., 2007; Lee & Schweighofer, 2009). Lee and Schweighofer (see also Smith et al., 2006) suggest that visuomotor learning is mediated by two learning systems, a fast process that learns rapidly but retains information poorly, and a slow process that learns more gradually but has excellent retention. To explain the role of contextual cues, Lee and Schweighofer proposed that a number of parallel states within the slow process that corresponds to the number of contextual cues in training. This account adequately explains a host of adaptation phenomena including savings,

anterograde interference, and dual adaptation (Franklin & Wolpert, 2011; Wolpert, Diedrichsen, Flangan, 2011). The outstanding question is how attentional contexts interact with the fast and/or slow process to modulate visuomotor generalization.

We propose that attention plays a critical role during visuomotor adaptation in selecting and associating multisensory signals with motor memory, which operates as an internal contextual cue for motor learning (Song & Bédard, 2015; Im et al., 2015). Extending Lee and Schweighofer's (2009) model, we conjectured that the state of divided and undivided attention to the secondary task could be represented as separate contexts in the slow process. As a consequence, switching the attentional context from divided to full attention rendered weaker generalization to the untrained direction in the RSVP-none group since the slow process associated with the divided attentional context during training discontinues when the slow process is associated with the undivided attentional context during generalization. Greater generalization in the RSVP-sound group than in the RSVP-none also implies that the contextual cue is generated from the state of the attentional distraction and not from the specific task. The current findings however, do not allow us to specify the exact architecture of this model. For instance, an alternative model with parallel fast processes and a single slow process can account for our findings. This problem can only be solved by developing a formal computational model and further empirical investigation.

Neurophysiological basis for visuomotor adaptation

A strength of the aforementioned computational models is that they provide biologically plausible explanations for generalization of motor adaptation (Poggio & Bizzi, 2004; Pouget & Snyder, 2000). For instance, Paz et al. (2003) recorded single-unit

activity in M1 in nonhuman primates before, during, and after visuomotor adaption. Increases in the spiking rates of the neuron were observed in neurons whose preferred direction closely matched the trained direction. The spiking rates do not change for neurons whose preferred directions that were away from the trained direction. This shows that a selective subpopulation of neurons in M1, whose preferred tuning direction are similar to the trained direction, are active during visuomotor adaptation.

Recent data from neurophysiological studies during visuomotor adaptation show that multiple brain regions, such as the motor cortex (M1), posterior parietal cortex (PPC), ventral premotor cortex, and cerebellum, are involved in adaptation (Orban de Xivry et al., 2011; Paz et al., 2003; Wise et al., 1998, Gandolfo et al., 2000; Della-Maggiore and McIntosh 2005; Krakauer et al. 2004; Tseng et al. 2007; Diedrichsen et al., 2005). Activation of multiple regions may suggest that multiple learning systems are engaged during visuomotor learning and that each region may serve a different function during learning. For instance, Graydon et al. (2005) showed that PPC learning-related activation decreases during the later stages of visuomotor adaptation, but cerebellum learning-related activation increase during this period. Importantly, both these regions have been shown to process motor error during visuomotor adaptation (Della-Maggiore et al., 2004; Diedrichsen et al., 2005; Bédard & Sanes, 2014) but studies have also identified functional differences between these regions. This dissociation corresponds to the notion that multiple learning systems, with separate time scales, concurrently operate during visuomotor learning (e.g., Lee & Schweighofer's, 2009). Neuroimaging studies have also demonstrated that the cerebellum is involved in the organization of multiple

internal models, where each model corresponds to a different motor action (Imamizu et al., 2003; 2004; Imamizu & Kawato, 2008).

Cognitive factors involved visuomotor learning

Multiple motor learning models have been studied extensively. For instance, an error-based model can make predictions about the sensory consequences of a selected action to improve motor control (Smith et al. 2006; Krakauer et al., 2005; Herzfeld et al., 2014). Further, a reinforcement learning model can account for processes such as movement aiming direction when the goal is to maximize the rate of reward (Shmuelof et al., 2012; Pekny et al., 2015). These models have focused on sensorimotor aspects of immediate performance but have often overlooked how higher-order cognitive functions, such as attention and memory, operate to facilitate motor learning process and cope with interferences arising from a complex daily environment.

Recently, Taylor et al. (2014; see also Taylor & Ivry, 2012; 2013b) demonstrated that during abrupt visuomotor adaptation, participants developed an aiming strategy towards a reach target to counteract for the rotational perturbation. For example, participants aimed at 45^{o} CCW location when 45^{o} CW rotation was introduced. By asking participants in advance to report which location they aimed at before reach movement, Taylor et al. (2014) could partition the contribution of improved aiming strategy from visuomotor adaptation performance. They suggested that visuomotor adaptation is the summation of explicit strategy and implicit learning driven by a sensory-prediction error signal, which also closely mapped onto the fast and slow learning processes, respectively (McDougle, Bond, and Taylor, 2015; McDougle, Ivry, & Taylor, 2016).

556 It remains unclear as to how explicit and implicit processes are distinctively
557 affected by internal attentional contexts and generalized to untrained directions. Perhaps
558 attentional distraction has a greater and immediate effect on explicit strategy since the
559 latter is highly susceptible to an external cue and instruction (Taylor & Ivry, 2014). In
560 contrast, the implicit learning process might globally carry long-term memory of internal
561 attentional contexts. Our previous work (Im et al., 2016) has shown that attentional
562 context can modulate motor memory retrieval one day after initial training, indicating its
563 long-term association.
564 The question remains as to how the cognitive and implicit learning systems are
565 organized. For example, the dichotomy proposed by Taylor and colleagues (McDougle,
566 Bond, & Taylor, 2015; McDougle, Ivry, & Taylor, 2016) maps closely onto the notion of
567 model-based and model-free reinforcement learning (Dayan & Niv, 2008). Model-based
568 learning emphasizes the construction of an internal model that is used to support goal-
569 directed action. Conversely, model-free learning uses reward prediction errors (i.e.,
570 Rescorla and Wagner, 1972; Sutton and Barto, 1998) to augment behavior without the
571 construction of an internal model.
572 In addition to explicit strategy, other cognitive influences on motor learning have
573 been reported. For example, visual-spatial working memory has been show to positively
574 correlate with the learning rates in both motor sequence learning and visuomotor
575 adaptation tasks (Bo et al., 2011; Seidler et al., 2012). Moreover, the brain areas
576 associated with visual-spatial working memory, such as the dorsolateral prefrontal cortex
577 and bilateral inferior parietal lobules, are active during the early, but not late, stages of
578 learning in these tasks (Seidler et al., 2012). Overall, it suggests that any motor learning

model solely based on error-based learning needs to be updated to account for cognitive effects such as robust attention-context modulation on motor learning. This integration will provide a deeper, more principled understanding of training, retention and generalization of motor skills.

Attentional distraction as an internal context for visuomotor memory

The success of episodic memory retrieval has been shown to depend on whether the environmental context is matched at the times of encoding and recall (e.g., Godden & Baddeley, 1975; Smith & Vela, 2001). This effect has also been observed in studies of motor learning (e.g., Krakauer et al., 2006; Ruitenberg et al., 2012; Taylor & Ivry, 2013a), such as the recall of a motor sequence is faster when the context of recall is matched with that of learning. The current experiment extended this notion by showing that consistency in the attentional or internal context, as generated by the secondary task, affects retrieval of visuomotor adaptation.

Prior studies on episodic memory (e.g., Eich, 1980) showed that consistent external contextual cues took priority over consistent internal states for memory retrieval. By contrast, we showed that consistent task demands generate an internal cue that overrides the same external environment (i.e., the RSVP stream was displayed throughout the experiment). In addition, the attentional state generated by the secondary task is not task specific. Song and Bédard (2015) showed that using two different attention-demanding tasks in adaptation training (i.e. RSVP task) and in recall (i.e. sound discrimination task) facilitates recall equally well as having the same attention-demanding task in both phases. This effect persisted for when recall was tested one day after initial training (Im et al., 2016). The current experiment extends this finding by

showing that attentional distraction, generated by two different secondary tasks, modulates the transfer of adaptation. Evidence for context modulation of both visuomotor generalization and recall indicate that they share a common learning process. Completing a secondary task generates an internal cue related to the cognitive state and this serves as a contextual cue for encoding and retrieval.

This notion is consistent with studies that demonstrate internal physiological states induced by various drugs, such as alcohol, morphine, and cigarettes, affect memory recall in both human and nonhuman animals (e.g., Blasi et al., 2002; DeCarli et al., 1992; Goodwin et al., 1969; Nishimura et al, 1990; Peters & Mcgee, 1982). As a consequence, the current findings support previous studies (Im et al., 2015; 2016; Song & Bédard, 2015) that show attentional state modulates the retrieval of visuomotor memory in a manner analogous to the modulation of external contexts on memory retrieval.

Conclusion

The current study shows that inconsistency in attentional context between training and generalization phases narrows the width of the generalization function. As a consequence, we propose that attentional contexts serve as an internal cue that allows for the encoding and retrieval of different motor representations. Recent behavioral and neurophysiological data suggest that multiple learning systems are responsible for visuomotor adaptation. Further investigation is required to identify which system is responsible for context modulation of adaptation. In sum, the current study provides insight into how cognitive processes affect internal representation of the visuomotor memory.

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Tables

Table 1. Mean best fitting parameters

	Parameter Values		
	Gain (SEM)	Width (SEM)	Shift (SEM)
None-None	0.41 (0.04)	45.08 (3.59)	0.15 (0.04)
RSVP-None	0.39 (0.02)	28.59 (3.25)	0.14 (0.02)
RSVP-RSVP	0.43 (0.03)	43.67 (3.53)	0.15 (0.04)
RSVP-Sound	0.46 (0.02)	40.82 (3.74)	0.10 (0.03)

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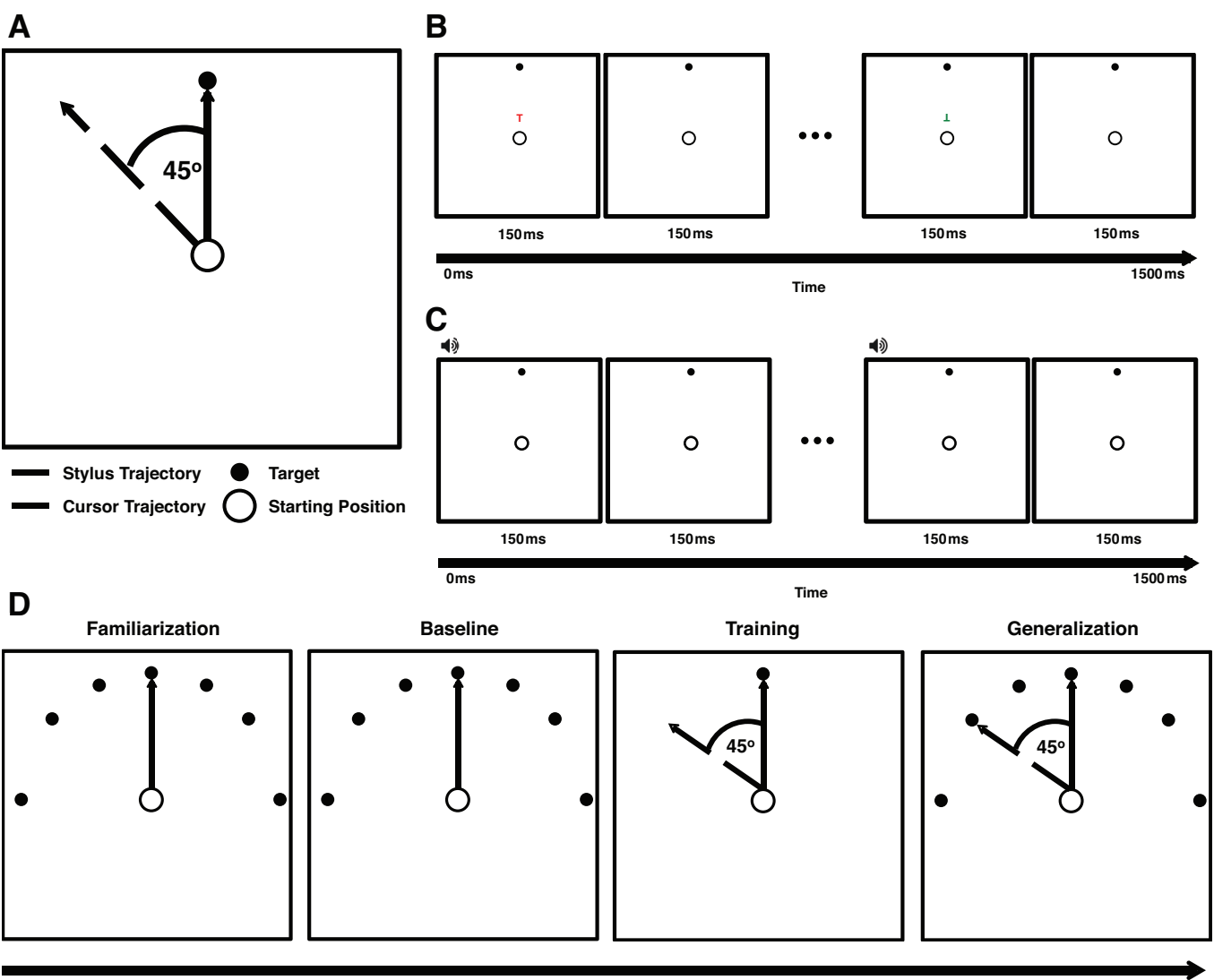
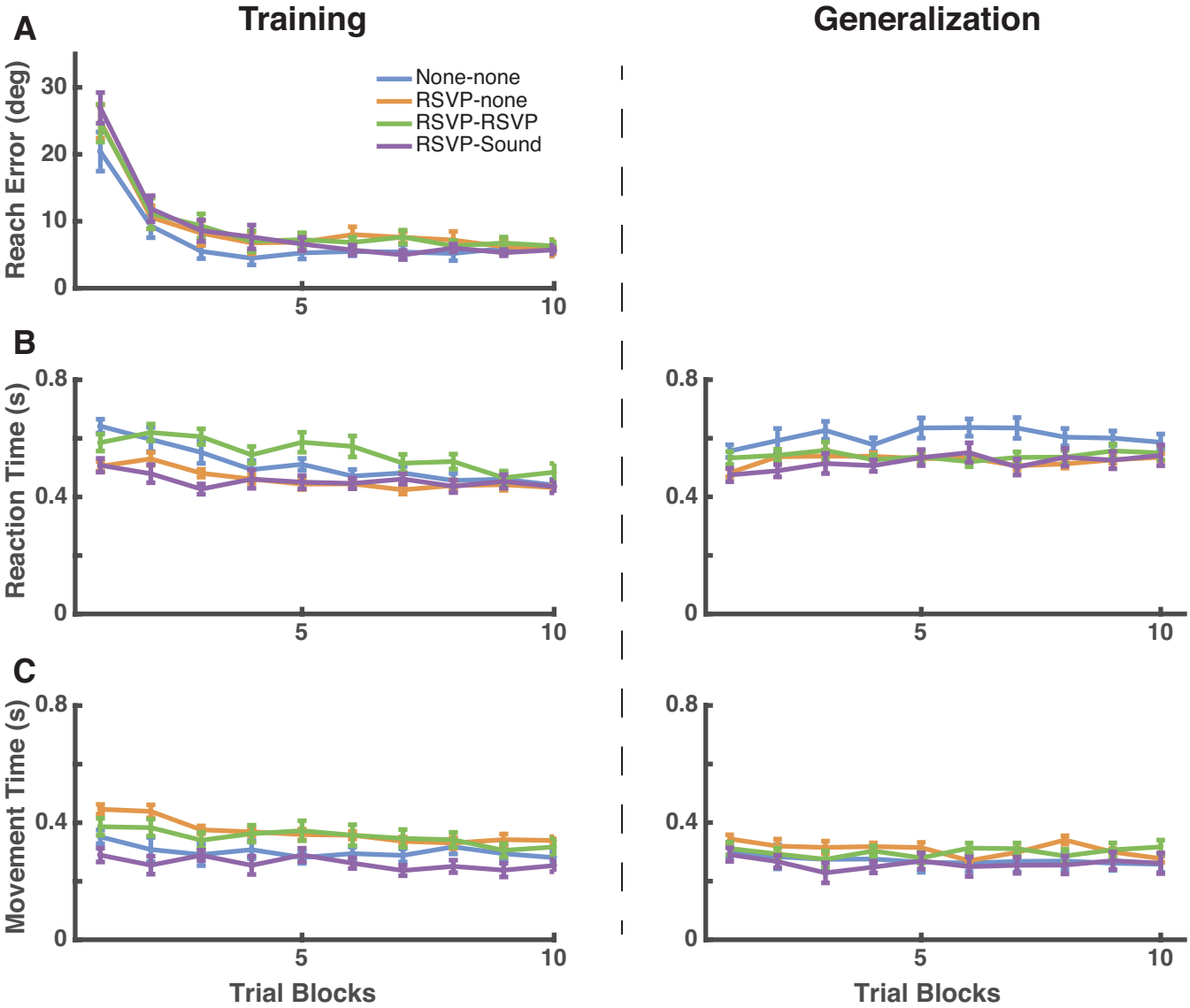
Figures

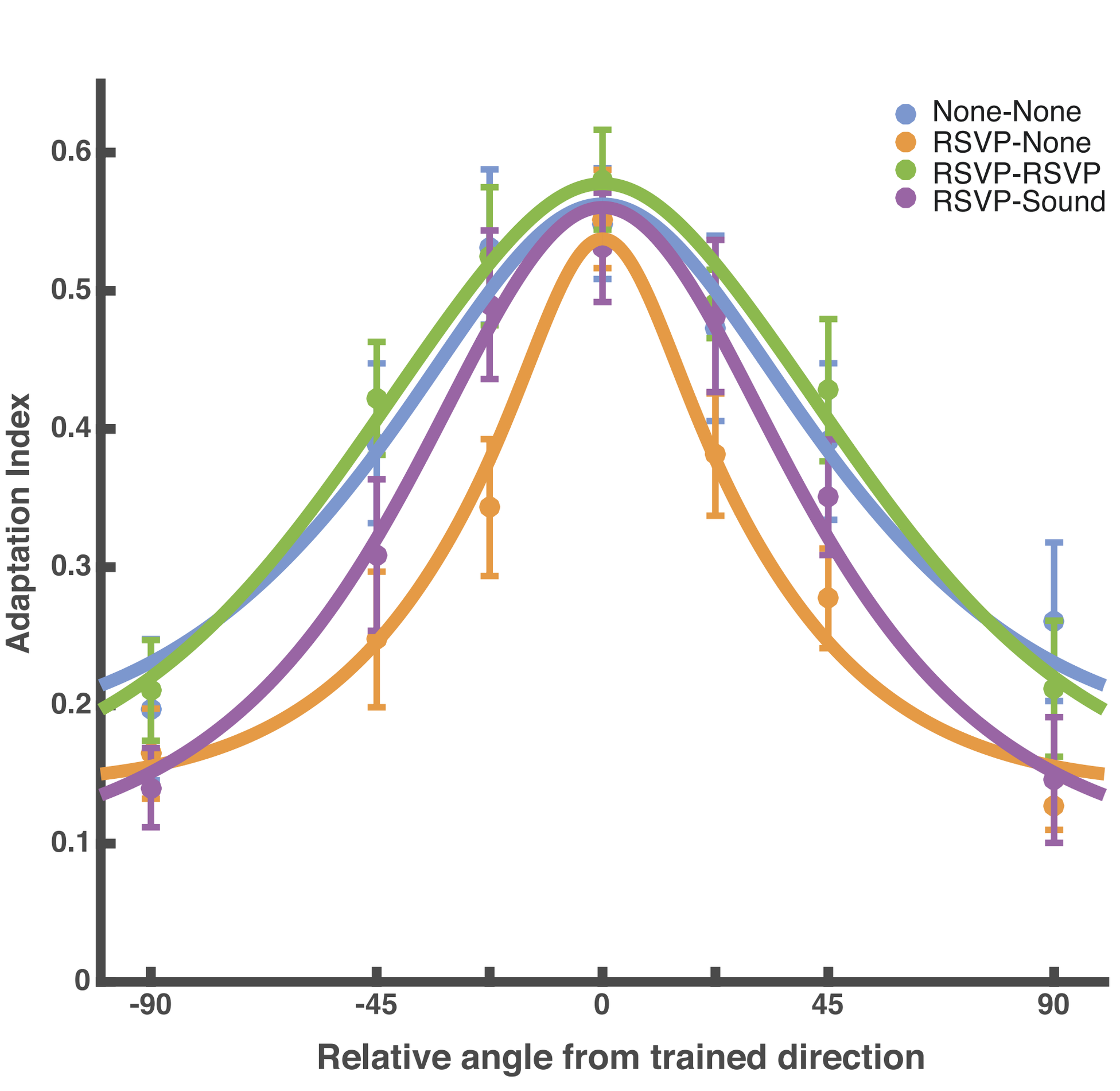
Figure 1. Task schematics. **A**. Reaching task: The filled circle indicates a reach target location and the open circle indicates the starting position. Reach targets appeared one at a time and remained visible for the entire trial (1500 ms). In no-rotation trials, the cursor (dotted line) followed stylus motion (solid line) normally, whereas in rotation trials, the cursor direction was rotated by 45º CCW or CW from the reach trajectory. **B**. Secondary rapid serial visual presentation (RSVP) task: Five upright or inverted Ts of various colors were each presented sequentially for 150 ms, with 150 ms gaps between stimuli (total of 1500 ms). Participants had to report at the end of each trial how many relevant targets (1, 2 or 3) were presented in that trial. Targets were defined as inverted green and upright red Ts. **C**. Secondary sound discrimination task: Five tones of three different frequencies (200 Hz, 300 Hz, 450 Hz) appeared again with the same timing as the RSVP task. Participants had to report the total number of high and low frequency tones. **D**. Experimental phases: The filled circles indicate locations of seven reach targets. Reach targets appeared one at a time. Participants performed four consecutive experimental phases. In the familiarization phase (no-rotation), participants made reaching movements to seven target directions with cursor feedback. The baseline phase (no-rotation) is the same as the familiarization phase except cursor feedback was only visible to the trained direction. In the training phase (rotation), participants reached to only the trained direction with rotated cursor feedback. In the generalization phase (rotation), participants reached to seven target directions. Cursor feedback was provided only for the trained direction.

Figure 2. Mean performance during the training and generalization phases for the none-none (blue), RSVP-none (orange), RSVP-RSVP (green), and RSVP-sound groups (purple). Each trial block represents the mean performance from every two trials in the training phase and seven trials in the generalization phase. **A.** Reach error during the training phase. We measured reach error 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. **B.** Reaction time (RT) during training (left) and generalization (right). RT was defined as the time elapsed from target appearance to movement onset. **C.** Movement time (MT) during training (left) and generalization (right). MT was defined as the time elapsed between movement onset and movement. Error bars represent SEM.

Figure 3. Adaptation index of the generalization and Gaussian fits for the none-none (blue), RSVP-none (orange), RSVP-RSVP (green), and RSVP-sound groups (purple). The markers represent the mean adaptation index at each target direction. The solid lines represent the mean predictions of the best fitting Gaussian function for each participant. The error bars represent SEM.


A
45º
Stylus Trajectory
Cursor Trajectory
Target
Starting Position
B
150ms
150ms
150ms
150ms
0ms
1500ms
Time
C
150ms
150ms
150ms
150ms
0ms
1500ms
Time
D
Familiarization
Baseline
Training
Generalization
45º
45º


A
Training
Generalization
None-none
RSVP-none
RSVP-RSVP
RSVP-Sound
Reach Error (deg)
30
20
10
0
5
10
B
Reaction Time (s)
0.8
0.4
0
5
10
C
Movement Time (s)
0.8
0.4
0
5
10
Trial Blocks
Trial Blocks


None-None
RSVP-None
RSVP-RSVP
RSVP-Sound
Adaptation Index
0.6
0.5
0.4
0.3
0.2
0.1
0
-90
-45
0
45
90
Relative angle from trained direction