

Attention modulates generalization of visuomotor adaptation

Patrick Bédard

Department of Neuroscience and Brown Institute for
Brain Sciences, Brown University, Providence, RI, USA



Joo-Hyun Song

Department of Cognitive, Linguistic, and Psychological
Sciences and Brown Institute for Brain Sciences,
Brown University, Providence, RI, USA



Generalization represents the ability to transfer what has been learned in one context to another context beyond limited experience. Because acquired motor representations often have to be reinstated in a different or novel environment, generalization is a crucial part of visuomotor learning. In daily life, training for new motor skills often occurs in a complex environment, in which dividing attentional resources for multiple stimuli is required. However, it is unknown how dividing attention during learning affects the generalization of visuomotor learning. We examined how divided attention during training modulates the generalization of visuomotor rotational adaptation. Participants were trained to adapt to one direction with or without dividing attention to a simultaneously presented visual detection task. Then, they had to generalize rotational adaptation to other untrained directions. We show that visuomotor training with divided attention multiplicatively reduces the gain and sharpens the tuning of the generalization function. We suggest that limiting attention narrowly restricts an internal model, reducing the range and magnitude of transfer. This result suggests that attention modulates a selective subpopulation of neurons in motor areas, those with directional tuning values in or near the training direction.

Introduction

In daily life, new visuomotor skills are often acquired in a complex environment in which attentional resources are divided between multiple stimuli. For instance, while acquiring the requisite motor skills to drive a car, attentional resources must be divided between learning to maneuver the car and processing various other stimuli such as road signs, traffic, people, and billboards. Although the effect of attention on perception and perceptual learning has been extensively studied (Gutnisky, Hansen, Iliescu, & Dragoi, 2009;

McAdams & Maunsell, 1999; Reynolds & Heeger, 2009; Schoups, Vogels, Qian, & Orban, 2001; Somers, Dale, Seiffert, & Tootell, 1999), the effect of divided attention on motor learning has received less consideration.

Recently, however, many studies have demonstrated an entangled relationship between motor skill learning (e.g., motor sequences) and various cognitive processes including declarative learning, attention, and awareness (Brown & Robertson, 2007; Hwang, Smith, & Shadmehr, 2006; Keisler & Shadmehr, 2010; Taylor & Thoroughman, 2007). For example, learning a word list after a motor sequence affects the consolidation of the motor skill (Brown & Robertson, 2007), and divided attention can affect motor sequence learning (Nissen & Bullemer, 1987). To further this knowledge, here we examine how divided attention during visuomotor learning affects its generalization. Generalization of motor learning refers to the ability to apply what has been learned in one context to other contexts beyond limited experience (Poggio & Bizzi, 2004).

Sensory-motor adaptation is a form of motor skill that entails developing new sensory-motor relationships to react to environmental changes and then storing that new information in an internal model (Shadmehr & Wise, 2005). Also, the internal model needs to be updated to reflect the state between the body and the new environment. Sensory-motor adaptation is a learning process usually considered implicit (Mazzoni & Krakauer, 2006), requiring little attention (Taylor & Thoroughman, 2007), although awareness of the perturbation may enhance adaptation (Keisler & Shadmehr, 2010; see also Benson, Anguera, & Seidler, 2011). Further, in both humans and nonhuman primates, generalization of visuomotor rotational adaptation is largely limited to the trained directions and only transfers partially to other untrained directions, gradually decreasing as a function of the angular difference between the trained and

Citation: Bédard, P., & Song, J.-H. (2013). Attention modulates generalization of visuomotor adaptation. *Journal of Vision*, 13(12):12, 1–10, <http://www.journalofvision.org/content/13/12/12>, doi:10.1167/13.12.12.

doi: 10.1167/13.12.12

Received June 27, 2013; published October 16, 2013

ISSN 1534-7362 © 2013 ARVO

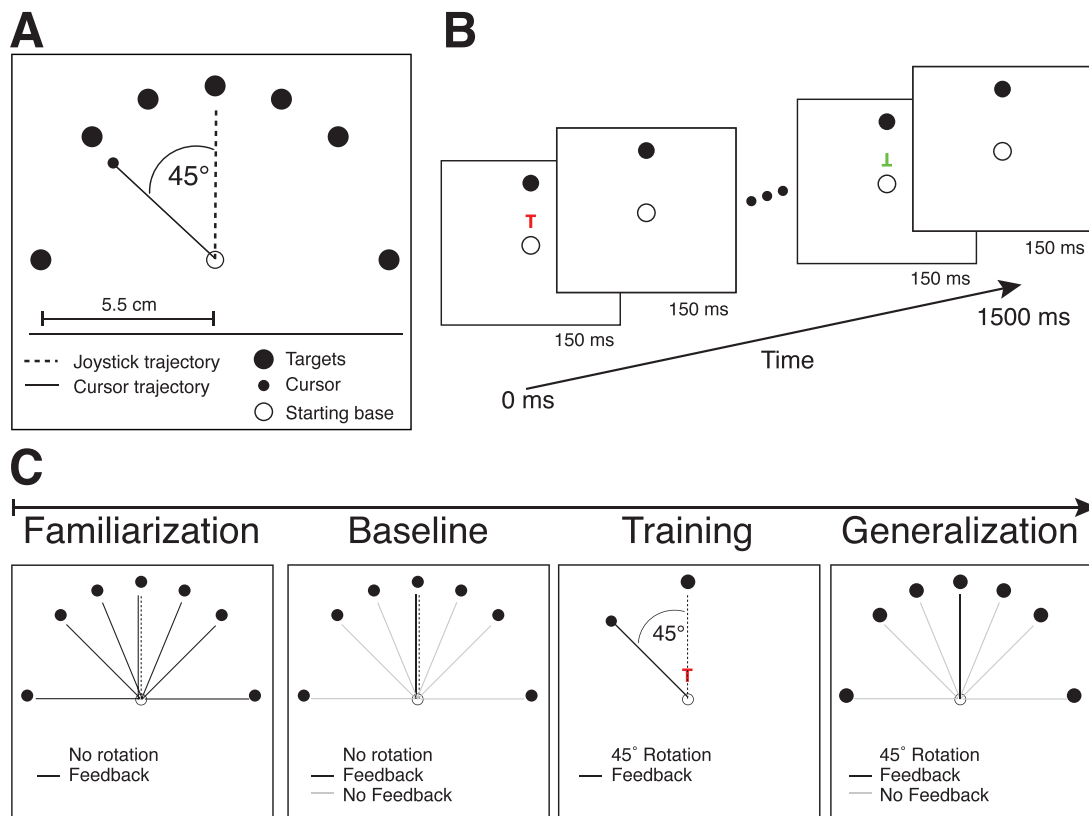


Figure 1. Task schematic. (A) Reaching task. Targets appeared one at a time and remained visible for the whole trial (1500 ms). In the Null condition, the cursor followed the mouse normally, whereas in a Rotation condition the cursor direction was rotated by 45° CCW from the joystick trajectory. (B) Rapid serial visual presentation task (RSVP). A sequence of five Ts were presented for 150 ms, each either upright or inverted in five different colors. Participants had to report how many Ts they detected (one, two, or three) by pressing a keyboard key at the end of each trial with their left hand. (C) Experimental design. Participants performed four sequential phases. Black and gray lines originating from the starting base to the targets indicate that the cursor was or was not visible, respectively. Dashed and straight lines represent the joystick and cursor trajectory, respectively. See Methods for details on each phase.

test stimuli (Bock & Schmitz, 2011; Donchin, Francis, & Shadmehr, 2003; Ghahramani & Wolpert, 1997; Imamizu, Uno, & Kawato, 1995; Krakauer, Pine, Ghilardi, & Ghez, 2000; Roby-Brami & Burnod, 1995).

Prior studies have demonstrated that attention enhances the signal-to-noise ratio of perceptual processing of attended stimuli (Martinez-Trujillo, Medendorp, Wang, & Crawford, 2004; McAdams & Maunsell, 1999; Spitzer, Desimone, & Moran, 1988; Treue & Maunsell, 1999). Yet, a recent study showed that when a trained stimulus is unattended during the training in perceptual discrimination rather than attended, discrimination performance is enhanced for stimulus orientations away from the trained orientation (Gutnisky et al., 2009). To examine how dividing attentional resources during training affects visuomotor adaptation and its generalization to a broader range of untrained directions, we used a dual-task paradigm combining a visuomotor adaptation task (Figure 1A) with an attention-demanding rapid serial

visual presentation (RSVP) task (Figure 1B; Song & Bédard, 2013). The RSVP task demands significant attentional resources for visual detection, which consequently limits the amount of residual attentional resources available for the visuomotor adaptation task (Joseph, Chun, & Nakayama, 1997; Raymond, Shapiro, & Arnell, 1992). In the visuomotor rotational adaptation task, participants learned to reach to a visual target while the cursor direction was rotated 45° counterclockwise (CCW) to force movement adaptation. This allows us to determine whether attention modulates visuomotor generalization, and if so, whether it alters the gain, the width of tuning (sharpening), or both in visuomotor generalization. If divided attention during training reduces generalizability, we would expect that the tuning of a generalization function would be sharpened and/or the gain would reduce when participants are required to perform the simultaneous RSVP task.

Methods

Participants

Eighteen right-handed participants (mean 21.9 years old; 10 females) with normal color vision and normal or corrected-to-normal vision participated in the experiment. All the participants were naive to the goal of the experiment. The experimental protocol was approved by Institution Review Board at Brown University. Participants received monetary compensation (\$8/hr) or a course credit.

Procedures

Overall, experimental procedures were similar to a previous study (Song & Bédard, 2013). In a dimly illuminated room, participants sat in front of a 21-in. Macintosh iMac computer (refresh rate of 60 Hz) viewed from a distance of 57 cm and used their right arm to perform a goal-directed reaching task using a joystick. We presented visual stimuli over a black background on the monitor and recorded data using Matlab (R2010; MathWorks Inc., Natick, MA) and functions from PsychToolbox (Brainard, 1997; Pelli, 1997). The joystick rested on the table, aligned with each participant's midline and the center of the monitor, and mouse movements displaced a cursor (round white dot; diameter 0.5 cm) on the monitor.

Participants were randomly assigned to a No-load or an Attention-load group ($n = 9$ in each group). All participants performed a modified version of the visuomotor adaptation task (Krakauer et al., 2000), while performing (Attention-load group) or not performing (No-load group) the RSVP task (see below). Importantly, the RSVP stream always appeared on every trial of all experimental phases. Thus, visual stimuli remained the same for both groups (Song & Bédard, 2013). A trial started when the participant positioned the cursor in the starting base that triggered reach target appearance in the visuomotor task and the visual stream in the RSVP task (Figure 1).

In the visuomotor adaptation task (Figure 1A), participants had to reach from a central starting base (annulus 1° diameter, corresponding to 1 cm) towards a reach target (white dots 1-cm diameter) located 5.5 cm from the starting base. We assigned seven possible target directions to each participant: one predetermined training target, which was randomly selected from the 3, 6, 9, or 12 o'clock direction, and six other target directions located at $\pm 22.5^\circ$, $\pm 45^\circ$, $\pm 90^\circ$ relative to the training target. The distribution of the trained target locations did not differ between the No-load and Attention-load groups (*Kolmogorov–Smirnov*

test, $K(13) = 0.33$, $p = 0.60$). Reaching occurred in one of two conditions. In the Null condition, the cursor followed the joystick normally, whereas in the Rotation condition, the cursor direction was rotated 45° counterclockwise (CCW) to force movement adaptation. Participants performed four sequential phases (Figure 1C): (a) Familiarization (Null trials, seven target directions, 70 trials), (b) Baseline (Null trials, seven target directions, 70 trials), (c) Training (Rotation trials, one target direction, 70 trials), and (d) Generalization (Rotation trials, seven target directions, 210 trials). In the Familiarization phase, participants reached with continuous cursor feedback. In the Baseline phase, the cursor remained visible for the training target (white line) but disappeared as soon as it left the home starting base for the other six target directions (gray lines). In the Training phase, participants reached to the training target with the cursor's direction rotated by 45° CCW. The Generalization phase was identical to the Baseline phase except that the cursor's direction was rotated by 45° CCW and the cursor remained visible for the training target but not for the other six target directions.

In the RSVP task (Figure 1B), five upright or inverted Ts ($0.5^\circ \times 1^\circ$) of various colors (red, white, green, purple, or orange) were presented 0.5° above the starting base. Ts were sequentially presented every 300 ms, remaining visible for only 150 ms (for a total of 1.5 s). During the Training phase, participants in the Attention-load group were required to detect conjunction targets (red upright Ts and green inverted Ts) and report the number of targets detected at the end of each trial by pressing a keyboard key with their left hand. The number of relevant Ts varied randomly for each trial between one and three with equal probability, yielding chance level of 33%. Participants in the No-load group received the instruction to always ignore the Ts, and had to make a button response in response to a visual written cue: "Press button 1, 2, or 3" at the end of each trial by pressing a keyboard key with their left hand.

Data analysis

We filtered the x - and y -coordinates of the joystick displacements with a low-pass Butterworth filter using an 8 Hz cut-off 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 (Song & Bédard, 2013). We measured reaction time (RT) as the time elapsed from target appearance to movement onset and 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 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. We took the absolute values of the error. We used the R project (R Development Core Team) and Matlab for data and statistical analyses.

For the generalization analysis, we first calculated a rotation adaptation index for each target direction (Krakauer et al., 2000):

$$1 - (E_{\text{Learn}} - E_{\text{Baseline}})/45^\circ \quad (1)$$

E_{Learn} and E_{Baseline} represented the reach error during the Learning and Baseline phases, respectively. Then, to determine whether divided attention would alter the gain and/or the tuning width of adaptation generalization, we fitted a Gaussian function to the rotation adaptation index as a function of angular distance from the trained direction:

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

Parameters a and s control the gain and the width of the function, respectively, and e is exponential. Statistical effects were estimated using the maximum likelihood ratio test. The peak response was expected to be at the training direction with decay to other directions in accord with previous perceptual and visuomotor generalization studies (Orban de Xivry et al., 2011; Thoroughman & Taylor, 2005).

Results

RSVP accuracy

We found that the RSVP detection accuracy in the Attention-load group was $61.3\% \pm 4.9$ (mean \pm SE; chance level = 33%) while the button-press accuracy in the No-load group was $97\% \pm 0.9$. Thus, as we expected, participants allocated attention to perform the RSVP task, limiting available resources for the visuomotor adaptation in the Attention-load group.

Divided attention effect on visuomotor adaptation

Figure 2A shows trajectories for two representative participants for each of the No-load (left column) and Attention-load groups (right column) during the Training phase. Note all trials are realigned with the 12 o'clock target. As can be seen the first trial (red)

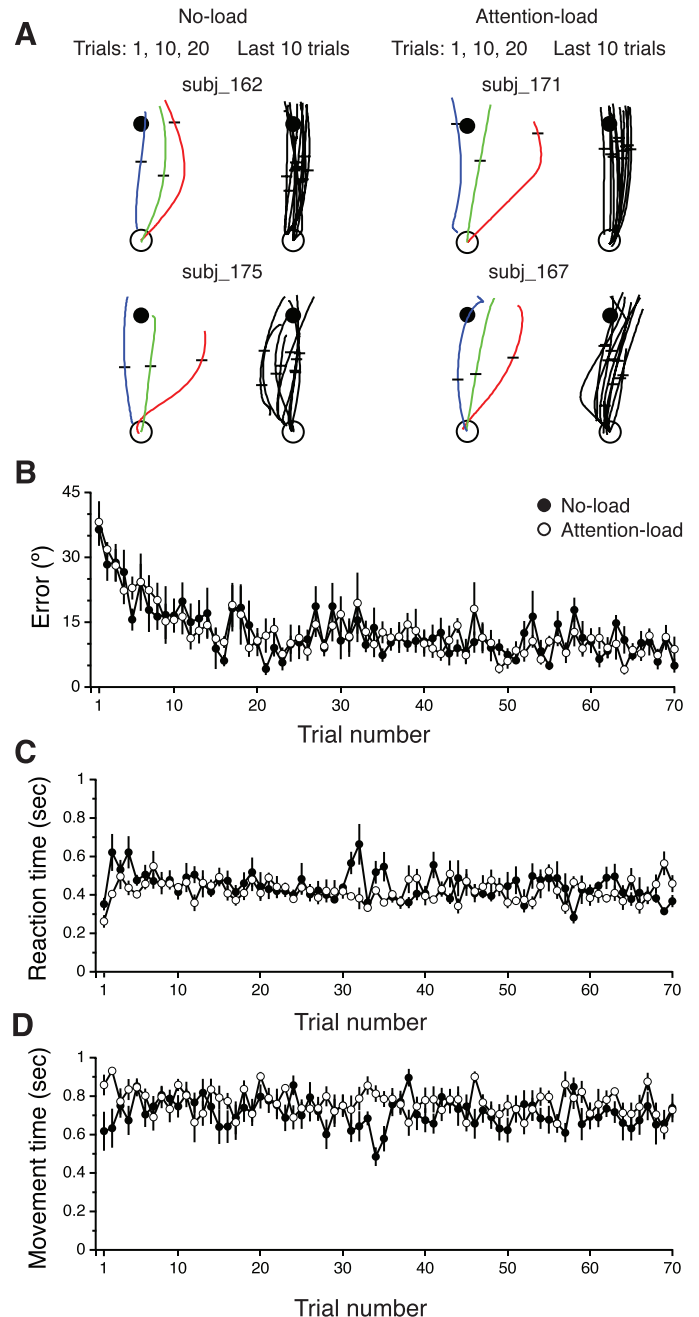


Figure 2. Performance on the visuomotor adaptation task for the No-load and Attention-load groups (mean \pm SE, $n = 9$ in each group). (A) Reaching trajectories for two representative participants of the No-load group (left) and Attention-load group (right). The horizontal lines in each trajectory indicate where error was measured. (B) Reach error. (C) Reaction time. (D) Movement time.

deviated from the intended target and resulted in high reaching error approaching 45° . For subsequent trials (green: 10th, blue: 20th) movements became more aligned to the target, and by the end of the Training phase (last 10 trials) movements were straight and accurate.

To examine whether there was difference in trajectories between the No- and Attention-load groups, we used the Linearity index (LI), which is the ratio of the maximal deviation perpendicular to a straight line between the start and end of movements and the length of that straight line (Atkeson & Hollerbach, 1985). $LI = 0$ indicates a perfect straight movement, while 0.5 indicates a semi-circle. We used a two-way ANOVA with Groups (No-load, Attention-load) and Trials as between group factor and repeated measures factor, respectively, and participants as a random factor. This analysis during the Baseline (last 40 trials) revealed no significant main effect of Groups, $F(1, 16) = 0.006$, $p = 0.94$; no significant main effect of Trials, $F(39, 624) = 0.90$, $p = 0.64$, and no significant interaction, $F(39, 624) = 0.57$, $p = 0.98$. During the Training phase (all 70 trials), there was no significant main effect of Groups, $F(1, 16) = 0.96$, $p = 0.34$; a significant main effect of Trials, $F(69, 1104) = 1.64$, $p = 0.001$; and no significant interaction, $F(69, 1104) = 0.88$, $p = 0.74$. The Trials main effect was caused by a reduction of LI across the first ~ 20 trials. Finally, during the Generalization phase the analysis did not reveal a significant main effect of Groups, $F(1, 16) = 0.001$, $p = 0.97$; no significant main effect of Trials, $F(48, 768) = 0.88$, $p = 0.70$; and no significant interaction, $F(48, 768) = 0.82$, $p = 0.81$.

Next, we examined whether divided-attention during Training affected visuomotor adaptation for the trained target (Figure 2B). In the Training phase, both groups reduced reach error similarly across the Training phase and attained comparable level of performance by the end of the phase. This is confirmed statistically by a two-way ANOVA with Groups (No-load, Attention-load) and Trials (all trials) and participants as a random factor, which revealed no significant main effect of Groups, $F(1, 16) = 0.02$, $p = 0.89$; an expected significant main effect of Trials, $F(69, 1104) = 7.65$, $p < 0.0001$, reflecting error decreasing over trials; and no significant interaction, $F(69, 1104) = 0.95$, $p = 0.59$. Thus, dividing attention via the RSVP task did not influence the rate of adaptation during the Training phase.

Furthermore, there was no difference in RT and MT between the No-load and Attention-load groups. Concerning RT (Figure 2C), there was no apparent group difference but a slight decrease of RT across trials. This is confirmed statistically by a two-way ANOVA that revealed no significant main effect of Groups, $F(1, 16) = 0.003$, $p = 0.95$; a significant main effect of Trials, $F(69, 1104) = 1.58$, $p = 0.002$; and a significant interaction, $F(69, 1104) = 1.33$, $p = 0.04$. The interaction was caused by two trials (31 and 32) with higher RT for the No-load than the Attention-load groups. Concerning MT (Figure 2D). There was no apparent group difference but again a slight decrease of

MT across the trials. This is confirmed statistically by a two-way ANOVA that revealed no significant main effect of Groups, $F(1, 16) = 1.06$, $p = 0.32$; a significant main effect of Trials, $F(69, 1104) = 1.36$, $p = 0.03$; and no significant interaction, $F(69, 1104) = 0.96$, $p = 0.57$. Thus, attention allocation did not alter reaching strategies in the visuomotor task, either.

Divided attention effect on visuomotor generalization

In the Generalization phase, mean reach error at the trained target was $4.79^\circ \pm 2.18$ and $7.38^\circ \pm 0.56$ (means $\pm SE$) for the No-load and Attention-load groups, respectively, $t(16) = 0.99$, $p = 0.34$. Thus, dividing attentional resources during the Training phase did not impair the degree of visuomotor adaptation for the trained target, suggesting that reach error reduction may be a relatively attention-independent process.

There was also no difference in RT and MT (Figure 3A, B) between the No-load and Attention-load groups, which was confirmed by a two-way ANOVA: (RT: Groups, $F[1, 16] = 0.18$, $p = 0.68$, Trials, $F[48, 768] = 1.15$, $p = 0.23$, and interaction, $F[48, 768] = 1.24$, $p = 0.13$; MT: Groups, $F[1, 16] = 0.18$, $p = 0.68$, Trials, $F[48, 768] = 1.15$, $p = 0.23$, and interaction, $F[48, 768] = 1.24$, $p = 0.13$). Thus, attention allocation did not alter reaching strategies in the Generalization phase, either.

RT and MT were shorter during the Generalization phase (Figure 3A, B) than the Training phase (Figure 2C, D) for the No-load group (paired t test, $t[8] = 4.5$, $p = 0.002$ and $t[8] = 4.6$, $p = 0.002$, for RT and MT, respectively) as well as for the Attention-load group ($t[8] = 6.99$, $p = 0.0001$ and $t[8] = 4.54$, $p = 0.002$, for RT and MT, respectively). However, the magnitude of the difference between the Training and Generalization phases was equivalent across the No-load and Attention-load group (RT: $t[16] = 1.39$, $p = 0.18$; MT: $t[16] = 0.26$, $p = 0.80$). Thus, both groups decreased their RT and MT between the Training and Generalization phases, but with no apparent difference between the two groups.

Our primary interest was whether limiting attentional resources during Training, via the RSVP task, affected visuomotor learning in other directions. Figure 4 shows the adaptation index (markers) as a function of angular distance between the training target and the other targets. To examine the changes in the width and the gain of the generalization by divided attention, we fitted Gaussian functions (lines). The abscissa represents the target direction relative to the trained target and the ordinate represents the adaptation index: 0 indicates no adaptation and 1 indicates full adaptation.

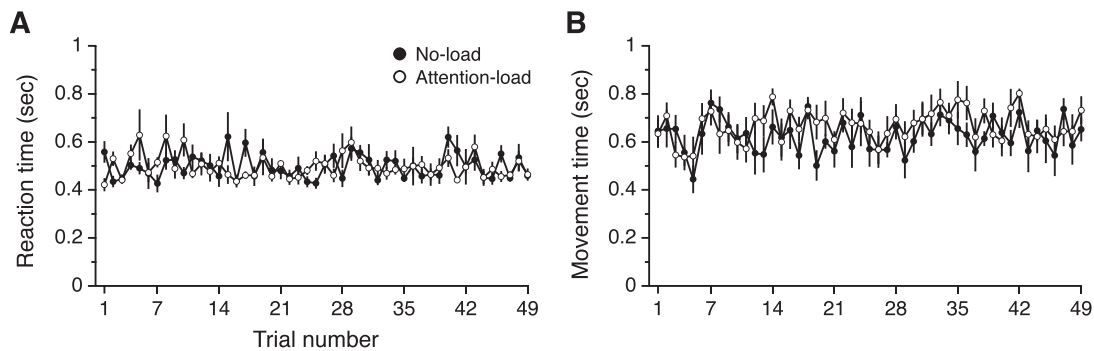


Figure 3. Generalization performance for the No-load and Attention-load. (A) Reaction time. (B) Movement time.

Figure 4A shows the change of the width of the Gaussian function (lines) when the gain was fixed for both groups, which was calculated based on the combined data of both groups. First, note that the Gaussian function fitted the data very well for the No-load and the Attention-load groups ($R^2 = 0.94$ and 0.86 , respectively). As can be seen, the Gaussian function was much wider for the No-load than the Attention-load group (means and SD of 68.5 ± 6.7 vs. 34.7 ± 4.07 , $p = 0.0006$; the gain was set at 0.41 ± 0.07 for both groups). Thus, these results show that when attentional resources are allocated to a secondary task during visuomotor adaptation, the pattern of generalization becomes strongly localized.

Then, we examined whether divided attention multiplicatively increases or decreases adaptation. Figure 4B shows the change of the gain of the Gaussian

function (lines) when the width was fixed across both groups. Again the Gaussian function fitted the data very well for both groups ($R^2 = 0.94$ and 0.82 , respectively). Also, the gain of the Gaussian function was much higher for the No-load than the Attention-load group (means and SD of 1.58 ± 0.08 vs. 1.04 ± 0.08 , $p = 0.0003$; the width was set at 56.9 ± 4.25 for both groups, which was driven based on combined group data). Thus, this result indicates that divided attention during training modulated adaptation by multiplicatively reducing the response gain as a function of angular distance.

To sum up, we observed that changes resulting from divided attention could be explained by either decreased amplitude or width of the adaptation function. For instance, Figure 4C shows the Gaussian function (lines) when both the width and the gain were free to

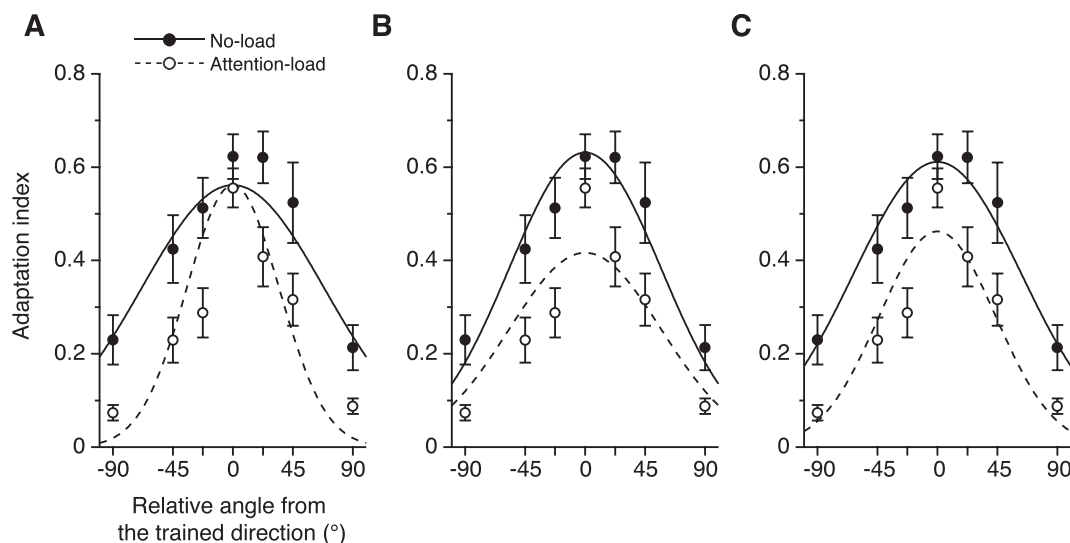


Figure 4. Adaptation index of the generalization and Gaussian fits for the No-load and Attention-load groups. (A) Different width with constant gain. The No-load group had significantly greater width than the Attention-load group. (B) Different gain with constant width. The No-load group had significantly higher gain than the Attention-load group. (C) Both the gain and width were free to vary. The No-load group had a significantly different function than the Attention-load group with greater width and higher gain. Dark circle and open circles represent the adaptation ratio for each direction averaged across participants in the No-load and Attention-load group, respectively. Solid and dashed lines represent corresponding Gaussian fits for the No-load and Attention-load group.

vary. The Gaussian function fitted the data very well for both groups ($R^2 = 0.94$ and 0.85 , respectively). Also, the Gaussian functions were significantly different between the groups ($p = 0.001$) with the width (means and SD 63.04 ± 5.7 vs. 43.7 ± 6.2) and the gain (1.53 ± 0.08 vs. 1.16 ± 0.1) being higher for the No-load than the Attention-load group. Thus, we found that divided attention significantly reduced the gain and the width of the generalization function. This result suggests that motor learning is less generalizable when learned in the context of a divided attentional state.

Discussion

In a constantly changing and complex world, we need to modify and develop new motor skills, often while having to divide our limited attentional resources between multiple tasks and stimuli (Cisek & Kalaska, 2010; Song & Nakayama, 2006, 2007). Furthermore, applying acquired skills in a new environment or context is critical for our ability to adapt to changing environments. To the best of our knowledge, the present study is the first to examine the effects of attentional modulation on visuomotor generalization.

We demonstrated that divided attention during Training did not change the immediate improvement of visuomotor adaptation at the trained direction as both the No-load and Attention-load groups performed similarly (Song & Bédard, 2013). Prior work showed that developing awareness during sensory-motor adaptation enhanced adaptation (Hwang et al., 2006; Benson, Anguera, & Seidler, 2011). Yet, contrary to prior work (Hwang et al., 2006; Benson et al., 2011), we found no difference between the groups during the Training phase. Thus, it is unlikely that awareness of adaptation primarily led to a difference between the two groups.

However, divided attention significantly narrowed the angular range of adaptation transfer to test directions, i.e., width, and also reduced its gain. Overall, the degree of adaptation transfer decreased as a function of the angular difference between the trained and test stimuli, indicating that such motor learning is local (Bock & Schmitz, 2011; Ghahramani & Wolpert, 1997; Imamizu et al., 1995; Krakauer et al., 2000; Roby-Brami & Burnod, 1995). The altered patterns of generalization in the present experiment provide insight that divided attention further limits the representation of the internal model for new visuomotor environments (Ghahramani & Wolpert, 1997; Imamizu et al., 1995).

Knowledge as to how the brain generalizes acquired visuomotor skills might represent a proxy to understand how the brain forms and stores motor knowledge. New data is emerging mainly from

neurophysiological studies during visuomotor rotational adaptation. The brain representations of generalization of visuomotor learning seem to include the motor cortex (M1), supplementary motor area, and premotor area (Gandolfo, Li, Benda, Schioppa, & Bizzi, 2000; Orban de Xivry et al., 2011; Paz, Boraud, Natan, Bergman, & Vaadia, 2003; Wise, Moody, Blomstrom, & Mitz, 1998). These studies have demonstrated that only a selective subpopulation of neurons in these areas, those with directional tuning values in or near the trained direction, participated in visuomotor adaptation. For instance, Paz et al. (2003) recorded single-unit activity in M1 in nonhuman primates before, during, and after visuomotor adaptation. In accord with the localized patterns of behavioral generalization (Bock & Schmitz, 2011; Imamizu et al., 1995; Krakauer et al., 2000; Roby-Brami & Burnod, 1995), changes in neuronal activity were mainly in neurons whose preferred direction was aligned with to the trained direction. Neurons tuned to directions far away from the trained direction did not change. This modulation often took the form of an increase in spiking rates (Paz et al., 2003; Wise et al., 1998). Based on these results and on those of the current work, we postulate that divided attention further reduced the neuronal directional representation of targets away from the trained direction. Thus, the patterns of generalization provide insight about the representation of internal models in the nervous system (Ghahramani & Wolpert, 1997; Imamizu et al., 1995).

In contrast to the motor system, in the visual system the impact of how attention modulates neural population has been extensively characterized (Cisek & Kalaska, 2010; Reynolds & Chelazzi, 2004). For instance, single-unit recordings and fMRI studies showed that attention allocation increases neuronal responses multiplicatively by applying a fixed response gain factor (McAdams & Maunsell, 1999; Treue & Maunsell, 1999), while others showed a change in additive gain (Buracas & Boynton, 2007; Williford & Maunsell, 2006). In addition, attention-dependent sharpening of neuronal tuning has been also reported both at the level of the individual neuron (Spitzer et al., 1988) and the neural population (Martinez-Trujillo et al., 2004; Serences, Saproo, Scolari, Ho, & Muftuler, 2009).

Although prior work on the effects of attention has mainly focused on sensory processing in visual systems (Huang & Dobkins, 2005; McAdams & Maunsell, 1999; Reynolds & Heeger, 2009; Somers et al., 1999), a strong relationship between attention and visuomotor processing has also been established. For instance, attention is also allocated to the target before a reaching movement (Baldauf & Deubel, 2009; Khan, Song, & McPeck, 2011; Schiegg, Deubel, & Schneider, 2003; Song & Nakayama, 2006, 2007). Furthermore,

prior single-unit recording and fMRI studies have shown that attention can modulate reach movement-related signals in frontal and parietal cortices as well as subcortical structures (Boussaoud, 2001; Boussaoud & Wise, 1993; Indovina & Sanes, 2001; Lebedev & Wise, 2001). These brain areas are also involved in reach movement generation, target selection, and motor learning (Cisek & Kalaska, 2005; Pesaran & Movshon, 2008; Song & McPeck, 2010; Westendorff, Klaes, & Gail, 2010).

Based on these results, we conjectured that dividing attention between visual and motor tasks during learning might overall reduce the activity of motor areas involved in visuomotor adaptation such as primary motor cortex, the posterior parietal cortex, premotor area (PM), basal ganglia, cerebellum, and prefrontal cortex (Doyon et al., 2009; Kelly & Garavan, 2005). Furthermore, limited attention might restrict neural responses more tuned to the trained direction. Future brain imaging or neurophysiological studies would be required to examine these predictions.

Conclusion

In the present study, we showed that attention is crucially involved in generalization of visuomotor learning by showing that when a new skill is acquired with limited attentional resources, it is less transferrable to new situations at behavioral level. This underscores the importance of attentional resources in the ability to transfer newly learned motor skills to novel contexts. This process is critical in numerous real-world contexts, such as motor vehicle training, classroom learning, and visuomotor rehabilitation.

Keywords: attention, visuomotor adaptation, generalization

Acknowledgments

This study was supported by a Brown University faculty start-up fund and a Salomon research award to J. H. S. We thank Xiaoxing Cheng and Dr. Xi Luo for implementing the data analysis on the generalization functions, as well as Drs. Jeff Moher and Leslie Welch for helpful discussion.

Commercial relationships: none.

Corresponding author: Joo-Hyun Song.

Email: joo-hyun_song@brown.edu.

Address: Department of Cognitive, Linguistic, and Psychological Sciences, Brown University, Providence, RI, USA.

References

- Atkeson, C. G., & Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *Journal of Neuroscience*, *5*(9), 2318–2330.
- Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: An event-related potential study. *Journal of Cognitive Neuroscience*, *21*(1), 18–29.
- Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, *105*(6), 2843–2851.
- Bock, O., & Schmitz, G. (2011). Adaptation to rotated visual feedback depends on the number and spread of target directions. *Experimental Brain Research*, *209*(3), 409–413.
- Boussaoud, D. (2001). Attention versus intention in the primate premotor cortex. *Neuroimage*, *14*(1 Pt 2), S40–S45.
- Boussaoud, D., & Wise, S. P. (1993). Primate frontal cortex: Neuronal activity following attentional versus intentional cues. *Experimental Brain Research*, *95*(1), 15–27.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Brown, R. M., & Robertson, E. M. (2007). Inducing motor skill improvements with a declarative task. *Nature Neuroscience*, *10*, 148–149.
- Buracas, G. T., & Boynton, G. M. (2007). The effect of spatial attention on contrast response functions in human visual cortex. *Journal of Neuroscience*, *27*(1), 93–97.
- Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, *45*(5), 801–814.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, *33*, 269–298.
- Donchin, O., Francis, J. T., & Shadmehr, R. (2003). Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: Theory and experiments in human motor control. *Journal of Neuroscience*, *23*(27), 9032–9045.
- Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., et al. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research*, *199*(1), 61–75.

- Gandolfo, F., Li, C. S. R., Benda, B. J., Schioppa, C. P., & Bizzi, E. (2000). Cortical correlates of learning in monkeys adapting to a new dynamical environment. *Proceedings of the National Academy of Sciences, USA*, 97(5), 2259–2263.
- Ghahramani, Z., & Wolpert, D. M. (1997). Modular decomposition in visuomotor learning. *Nature*, 386(6623), 392–395.
- Gutnisky, D. A., Hansen, B. J., Iliescu, B. F., & Dragoi, V. (2009). Attention alters visual plasticity during exposure-based learning. *Current Biology*, 19(7), 555–560.
- Huang, L., & Dobkins, K. R. (2005). Attentional effects on contrast discrimination in humans: Evidence for both contrast gain and response gain. *Vision Research*, 45(9), 1201–1212.
- Hwang, E. J., Smith, M. A., & Shadmehr, R. (2006). Dissociable effects of the implicit and explicit memory systems on learning control of reaching. *Experimental Brain Research*, 173, 425–437.
- Imamizu, H., Uno, Y., & Kawato, M. (1995). Internal representations of the motor apparatus: Implications from generalization in visuomotor learning. *Journal of Experimental Psychology: Human Perception & Performance*, 21(5), 1174–1198.
- Indovina, I., & Sanes, J. N. (2001). Combined visual attention and finger movement effects on human brain representations. *Experimental Brain Research*, 140(3), 265–279.
- Joseph, J. S., Chun, M. M., & Nakayama, K. (1997). Attentional requirements in a ‘preattentive’ feature search task. *Nature*, 387(6635), 805–807.
- Keisler, A., & Shadmehr, R. (2010). A shared resource between declarative memory and motor memory. *Journal of Neuroscience*, 30(44), 14817–14823.
- Kelly, A. M., & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex*, 15(8), 1089–1102.
- Khan, A. Z., Song, J. H., & McPeck, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, 11(1):9, 1–14, <http://www.journalofvision.org/content/11/1/9>, doi:10.1167/11.1.9. [PubMed] [Article]
- Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience*, 20(23), 8916–8924.
- Lebedev, M. A., & Wise, S. P. (2001). Tuning for the orientation of spatial attention in dorsal premotor cortex. *European Journal of Neuroscience*, 13(5), 1002–1008.
- Martinez-Trujillo, J. C., Medendorp, W. P., Wang, H., & Crawford, J. D. (2004). Frames of reference for eye-head gaze commands in primate supplementary eye fields. *Neuron*, 44(6), 1057–1066.
- Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *Journal of Neuroscience*, 26, 3642–3645.
- McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron*, 23(4), 765–773.
- Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, 19, 1–32.
- Orban de Xivry, J. J., Marko, M. K., Pekny, S. E., Pastor, D., Izawa, J., Celnik, P., et al. (2011). Stimulation of the human motor cortex alters generalization patterns of motor learning. *Journal of Neuroscience*, 31(19), 7102–7110.
- Paz, R., Boraud, T., Natan, C., Bergman, H., & Vaadia, E. (2003). Preparatory activity in motor cortex reflects learning of local visuomotor skills. *Nature Neuroscience*, 6(8), 882–890.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Pesaran, B., & Movshon, J. A. (2008). What to do, or how to do it? *Neuron*, 58(3), 301–303.
- Poggio, T., & Bizzi, E. (2004). Generalization in vision and motor control. *Nature*, 431(7010), 768–774.
- Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception & Performance*, 18(3), 849–860.
- Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, 27, 611–647.
- Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, 61(2), 168–185.
- Roby-Brami, A., & Burnod, Y. (1995). Learning a new visuomotor transformation: Error correction and generalization. *Brain Research: Cognitive Brain Research*, 2(4), 229–242.
- Schiegg, A., Deubel, H., & Schneider, W. X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*, 10(4), 409–431.
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves ori-

- entation coding in V1 neurons. *Nature*, 412(6846), 549–553.
- Serences, J. T., Saproo, S., Scolari, M., Ho, T., & Muftuler, L. T. (2009). Estimating the influence of attention on population codes in human visual cortex using voxel-based tuning functions. *Neuroimage*, 44(1), 223–231.
- Shadmehr, R., & Wise, S. P. (2005). *The computational neurobiology of reaching and pointing: A foundation for motor learning*. Cambridge, MA: MIT Press.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. H. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences, USA*, 96(4), 1663–1668.
- Song, J. H., & Bédard, P. (2013). Allocation of attention for dissociated visual and motor goals. *Experimental Brain Research*, 226(2), 209–219.
- Song, J. H., & McPeck, R. M. (2010). Roles of narrow- and broad-spiking dorsal premotor area neurons in reach target selection and movement production. *Journal of Neurophysiology*, 103(4), 2124–2138.
- Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision*, 6(9):11, 982–995, <http://www.journalofvision.org/content/6/9/11>, doi:10.1167/6.9.11. [PubMed] [Article]
- Song, J. H., & Nakayama, K. (2007). Fixation offset facilitates saccades and manual reaching for single but not multiple target displays. *Experimental Brain Research*, 177(2), 223–232.
- Spitzer, H., Desimone, R., & Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science*, 240(4850), 338–340.
- Taylor, J. A., & Thoroughman, K. A. (2007). Divided attention impairs human motor adaptation but not feedback control. *Journal of Neurophysiology*, 98(1), 317–326.
- Thoroughman, K. A., & Taylor, J. A. (2005). Rapid reshaping of human motor generalization. *Journal of Neuroscience*, 25(39), 8948–8953.
- Treue, S., & Maunsell, J. H. (1999). Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience*, 19(17), 7591–7602.
- Westendorff, S., Klaes, C., & Gail, A. (2010). The cortical timeline for deciding on reach motor goals. *Journal of Neuroscience*, 30(15), 5426–5436.
- Williford, T., & Maunsell, J. H. (2006). Effects of spatial attention on contrast response functions in macaque area V4. *Journal of Neurophysiology*, 96(1), 40–54.
- Wise, S. P., Moody, S. L., Blomstrom, K. J., & Mitz, A. R. (1998). Changes in motor cortical activity during visuomotor adaptation. *Experimental Brain Research*, 121(3), 285–299.