

# Visual speed sensitivity in the drum corps color guard

**Nestor Matthews**

Denison University, Department of Psychology & Neuroscience Program, Granville, OH, USA



**Leslie Welch**

Brown University, Cognitive, Linguistic, & Psychological Sciences, Providence, Rhode Island, USA



**F. Daniel Coplin**

The College of Wooster, Department of Psychology & Neuroscience Program, Wooster, OH, USA



**Allison J. Murphy**

Denison University, Department of Psychology & Neuroscience Program, Granville, OH, USA



**Megan R. Puritz**

Denison University, Department of Psychology & Neuroscience Program, Granville, OH, USA



Drum corps color guard experts spend years developing skills in spinning rifles, sabers, and flags. Their expertise provides a unique window into factors that govern sensitivity to the speed of rotational and radial motion. Prior neurophysiological research demonstrates that rotational and radial motion register in the Medial Superior Temporal (MST) region of the primate visual system. To the extent that shared neural events govern rotational and radial speed sensitivity, one would expect expertise on either task to transfer to the other. One similarly would expect shared neural events to generate correlations between rotational and radial speed sensitivity. We evaluated these predictions via visual speed sensitivity tests on drum corps color guard experts, drum corps low brass experts, and other age-matched control participants. Displays comprised bilaterally presented plaid patterns that rotated, radiated, or both. Participants reported which side contained faster motion. The data revealed a modest but reliably reproducible and specific group-by-task interaction; color guard speed sensitivity exhibited a rotational motion advantage and radial motion disadvantage. Additionally, rotational and radial speed sensitivity failed to predict each other significantly. Overall, the findings match predictions that follow from a dissociation between the neural events governing rotational and radial speed sensitivity.

## Introduction

Drum corps performances feature spectacular visual displays. These include rifles, sabers, and flags spiraling through the air—synchronously—at impressive heights and high speeds. Then the towering, twirling, trajectories tersely terminate—synchronously—snagged by smiling color guard.

Color guard experts possess specialized motor skills. The motor-nature of the color guard's expertise appears vividly in a coach's personal reflection. Across years of training, the coach had developed “muscle memory” for upwardly tossing a rifle through seven rotations before catching it, all with eyes closed. The coach's reflection emphasizes the color guards' expertise in motor skills which blossom for an audience into spectacular visual motion. The color guard's ability to generate visual motion spectacularity motivated our primary research question. Do color guard experts possess enhanced visual motion skills?

One plausibly might expect color guard experts to possess enhanced visual motion skills, especially rotational motion sensitivity. To appreciate this point, consider the rotational motion sensitivity required for maturing from color guard novice to color guard expert. Color guard novices might initially train by visually tracking the rotations that arise from their own motor activity. After achieving elementary rotational control, trainees might practice manipulating rotational speed—synchronizing to a conductor's hand signals or visual rotations from other trainees or

Citation: Matthews, N., Welch, L., Coplin, F. D., Murphy, A. J., & Puritz, M. R. (2017). Visual speed sensitivity in the drum corps color guard. *Journal of Vision*, 17(8):7, 1–14, doi:10.1167/17.8.7.

doi: 10.1167/17.8.7

Received September 26, 2016; published July 10, 2017

ISSN 1534-7362 Copyright 2017 The Authors



coaches. Next, trainees might proceed to tossing their object skyward while visually tracking the number of rotations before a catch. Here too, rotational speed sensitivity provides information about whether one's tossed and spinning object revolves too slowly or quickly relative to the ensemble. Importantly, tossed objects introduce a radial motion component. Specifically, the retinal size of the tossed object decreases (radially contracting) then increases (radially expanding) respectively as it rises and falls. These radial speeds—like the rotational speeds—often must synchronize or occur at precisely timed asynchronies to achieve a desired artistic visual-motion effect. Succinctly put, years of color guard training plausibly could enhance rotational speed sensitivity—and perhaps radial speed sensitivity as well.

A different line of reasoning predicts color guard experts would not possess enhanced rotational and radial speed sensitivity. This null prediction follows from the observation that rotational and radial motion occur regularly in optic flow—the dynamic patterns of retinal information. Indeed, for *any* given eye fixation, retinal information changes whenever objects or viewers move through an environment. These changes can trace simple linear (one-dimensional) trajectories, more complicated (two-dimensional) rotational or radial trajectories, and spiral trajectories containing rotational and radial components. Moreover, when adjacent trajectories that differ in speed or direction slide past each other, the resulting “shear” provides information about relative distance (Gibson, 1986; Tsujimura & Zaidi, 2002). The shear within optic flow guides reaching and locomotion across the lifespan, essentially rendering most people—indeed most animals with vision—“optic flow experts.” From this perspective, then, color guard training might involve visual information vastly similar to the already rotationally-and-radially rich optic flow that typifies everyday life. Consequently, one plausibly might expect color guard training to yield little or no enhancement to rotational and radial speed sensitivity.

The present investigation of color guard expertise in rotational and radial speed sensitivity also addressed psychophysically a question about underlying neural events. To what extent do shared versus distinct neural events govern rotational and radial speed sensitivities? If largely shared neural events govern both tasks, one would expect rotational and radial speed sensitivities to correlate strongly with each other. On the other hand, distinct neural events for the two tasks would predict little or no correlation between rotational and radial speed sensitivities.

Neurophysiological research shows that the rotational and radial components of optic flow register in the Medial Superior Temporal (MST) region of the primate visual system (Duffy & Wurtz, 1991a, 1991b; Lagae,

Maes, Raiguel, Xiao, & Orban, 1994; Morrone et al., 2000; Raffi & Siegel, 2007; Saito et al., 1986; Smith, Wall, Williams, & Singh, 2006; Tanaka & Saito, 1989). Portions of this neurophysiological research warrant predicting little or no correlation between rotational and radial speed sensitivities. This follows from seminal single-cell electrophysiological experiments demonstrating that some macaque MST neurons respond to rotational motion but not radial motion, or vice versa (Duffy & Wurtz, 1991a, 1991b; Lagae et al., 1994; Saito et al., 1986; Tanaka & Saito, 1989). More recent human fMRI (Wall, Lingnau, Ashida, & Smith, 2008) and steady-state-visual-evoked-potential (Gilmore, Hou, Pettet, & Norcia, 2007) experiments similarly demonstrate distinct neural responses to rotational and radial motion. These physiological dissociations plausibly could generate psychophysical dissociations between rotational and radial speed sensitivities.

Contrarily, one might instead predict significant psychophysical correlations between rotational and radial speed sensitivities using other neurophysiological evidence. For example, single-unit primate physiological experiments reveal that some MST neurons don't fit well in discrete “rotation-only” or “radial-only” cell groups. Rather, these MST cells respond along a continuum to rotational and radial optic flow components (Graziano, Andersen, & Snowden, 1994; Wurtz & Duffy, 1992). One extreme on this continuum comprises so-called “triple-component” MST neurons that respond to rotational, radial, and linear optic flow components (Duffy & Wurtz, 1991a, 1991b; Lagae et al., 1994; Wurtz & Duffy, 1992), and tend to cluster anatomically (Lagae et al., 1994). Activity from triple-component cells plausibly could drive significant correlations between rotational and radial speed sensitivities. Alternatively, or in addition, significant correlations could arise from neurons that register the local linear components of rotational and radial motion (Yu, Page, Gaboriski, & Duffy, 2010). To appreciate this point, consider Figure 1. The figure's panels show the local linear components (arrows) for radial expansion (top), clockwise rotation (right), radial contraction (bottom), and anticlockwise rotation (left). Note that the global motion can change from rotational to radial—and vice versa—simply by rotating the local linear motion components through 90°. Consequently, one could expect both rotational and radial speed sensitivity to depend on how precisely visual neurons register these shared local linear motion signals.

In addition to registering rotational, radial, and linear motion signals, MST neurons also exhibit attentional modulation. Specifically, MST neurons fire reliably more when a given stimulus serves as a task-relevant target than when the same stimulus serves as a task-irrelevant distractor (Treue & Maunsell, 1996, 1999). That finding highlights the importance of investigating attentional selection as a type of visual

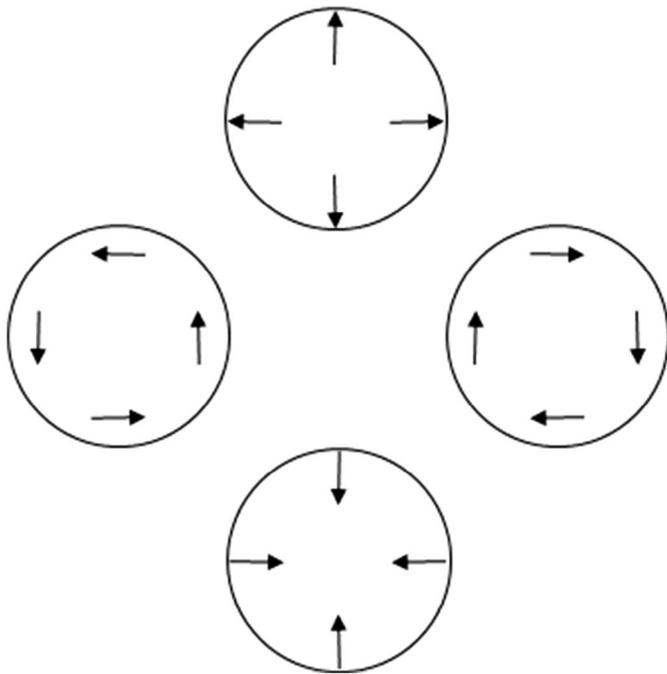


Figure 1. Relationships among radial, rotational, and linear motion. Rotating the local linear motion signals (arrows)  $90^\circ$  changes global radial motion to global rotational motion, and vice versa. Neurons in cortical area MST respond to one, two, or all three of these motion types. The diverse MST responses generate diverging predictions about psychophysical correlations between rotational and radial speed sensitivity.

motion expertise. For example, experts might outperform novices in attentionally selecting task-relevant rotational speeds while excluding task-irrelevant radial speeds, or vice versa. In principle, this sort of attentional selection advantage could occur regardless of whether experts differ from novices on rotational motion alone or radial motion alone.

Here, we observed modest, but reliably reproducible and task-specific speed sensitivity differences between color guard experts and controls. These group differences occurred whether participants judged isolated rotational and radial stimuli, or the more attentionally demanding combination of those two motion types. Additionally, rotational and radial speed sensitivities correlated poorly with each other. Together the task-specific group differences and poor intertask correlations disconfirm what one would expect if largely shared neural events governed rotational and radial speed sensitivity.

## Method

Denison University's Human Subject Committee approved the study, which we conducted with the

| Spinning experience | Lifetime total in years | January–May 2016, hours/week |
|---------------------|-------------------------|------------------------------|
| Flags               | 7.08 (0.46)             | 11.02 (1.87)                 |
| Rifles              | 5.00 (0.45)             | 9.42 (1.94)                  |
| Sabers              | 4.92 (0.44)             | 6.40 (1.67)                  |
| Other               | 1.62 (0.63)             | 0.27 (0.20)                  |

Table 1. Summary of color guard spinning experience. *Notes:* Values reflect means, and parentheses contain the standard error.

understanding and written consent of each participant. The research adheres to the October 2008 Declaration of Helsinki. To promote reproducibility, the Open Science Framework (<https://osf.io/nt52b/>) contains the complete data set and all software necessary for replicating the study.

## Participants

Eighty-five college age (18–22 year-old) adults participated. These included 25 Denison University students, and 60 members of Drum Corps International's 2016 World Champion "Bluecoats," a highly competitive music and dance ensemble. The 60 Bluecoat members comprised 30 low brass musicians, and 30 color guard members with extensive rotational motion experience (Table 1).

## Materials and apparatus

The experiment ran on HP EliteOne 800 desktop computers, each with a Microsoft Windows 7 Enterprise operating system. SuperLab 5.0 presentation software (Cedrus) controlled 23 inch flat screen HP LCD displays with a 60 Hz refresh rate and  $1920 \times 1080$  spatial resolution. Although we did not stabilize head position, participants typically viewed the monitor at a distance of  $\sim 57$  cm.

## Plaid stimuli

On each trial participants viewed two simultaneously presented dynamic plaid stimuli, shown in a 1-s (60-frame) movie. A sample frame from one such movie appears in Figure 2. We centered each plaid  $9.7^\circ$  left or right of a white fixation point ( $152 \text{ cd/m}^2$ ) in a gray surround ( $32.5 \text{ cd/m}^2$ ). Each plaid had 95.47% Michelson contrast, a two dimensional Gaussian window, and a  $9.7^\circ$  diameter. Within each plaid the two component gratings had identical spatial frequencies and identical spatial phases. The component spatial frequencies ranged randomly across four octaves



Figure 2. Sample movie frame. On each trial, a pair of bilaterally presented plaids either rotated, radiated, or both. The faster plaid's component gratings moved at two revolutions per second or two octaves per second, respectively, in rotational and radial trial blocks. The other plaid's component gratings moved slower by various amounts. Across trials the faster and slower speeds occurred randomly on the left and right, and participants reported which side had faster rotational or radial motion.

(0.125–2.0 cycles/°), and the spatial phases ranged randomly across 360°. Across trials, the angle between each plaid's component gratings ranged randomly between 45° and 135°.

### Rotational speed task and stimuli

On the rotational speed task, participants pressed different keys to indicate whether the left or right plaid rotated faster. One plaid always rotated at two revolutions per second—a common speed for spinning color guard rifles, given music played at 120 beats per minute. (Coincidentally, prior psychophysical experiments also suggest two revolutions per second as an upper limit for attentionally tracking two rotating stimuli [Verstraten, Cavanagh & Labianca, 2000; Thornton & Gilden, 2001; Holcombe & Chen, 2013]). The other plaid rotated more slowly by 10%, 15%, 20%, 30%, or 40%, a range that minimized floor and ceiling effects in a pilot study. Despite their speed differences, the two plaids on each trial always rotated in the same direction, i.e., both clockwise or both anticlockwise, counter-balanced across trials. Counterbalancing the directions helped to reduce directional adaptation and the corresponding rotational motion aftereffects. We chose same-direction rotations rather than opposite-direction rotations to mimic the same-direction rotations that typify adjacent spinning rifles in color guard performances.

In addition to the plaid's rotational motion, we superimposed task-irrelevant *radial* motion on half the trials randomly. For these trials either both plaids expanded (spatial frequencies decreased) when rotating anticlockwise, or both plaids contracted (spatial frequencies increased) when rotating clockwise. These task-irrelevant expansions and contractions arose by modulating each plaid's component gratings at two spatial-frequency octaves per second (2 OPS). Notably, because this two OPS radial speed remained constant

across both plaids' component gratings, it provided no information about which plaid *rotated* faster. And, because cortical area MST registers both radial and rotational motion, the task-irrelevant radial motion served as an MST-mediated distractor. In short, by superimposing task-irrelevant radial motion on task-relevant rotational motion, these “combined-motion” trials required attention to select one MST-mediated motion type while excluding another.

### Radial speed task and stimuli

On the radial speed task, participants pressed different keys to indicate whether the left or right plaid-components radiated faster. One plaid comprised component gratings that radiated at two spatial-frequency octaves per second (2 OPS). The other plaid's component gratings radiated more slowly by 17.5%, 26.25%, 35%, 52.5%, or 70%, a range that minimized floor and ceiling effects in a pilot study. Despite these speed differences, the two plaids on each trial always radiated in the same direction, i.e., both expanded or both contracted, counterbalanced across trials. Counterbalancing the directions helped to reduce directional adaptation and the corresponding radial motion aftereffects.

In addition to the plaid's radial motion, we superimposed task-irrelevant *rotational* motion on half the trials randomly. For these trials either both plaids rotated anticlockwise when radially expanding, or both plaids rotated clockwise when radially contracting. These task-irrelevant rotations occurred at two revolutions per second (2 RPS). Notably, because this 2 RPS rotational speed remained constant across the plaids, it provided no information about which plaid *radiated* faster. And, because cortical area MST registers both rotational and radial motion, the task-irrelevant rotational motion served as an MST-mediated distractor. In short, by superimposing task-irrelevant rotational motion on task-relevant radial motion, these “combined-motion” trials required attention to select one MST-mediated motion type while excluding another.

### Procedure

Each participant completed rotational speed judgments in one trial block and radial speed judgments in another, with the task-sequence counterbalanced across participants. On each task, each participant first completed 20 practice trials containing only the task-relevant motion type, and the largest speed difference in the above-shown list. Each participant next completed 20 additional practice trials that combined task-

relevant and task-irrelevant motion types—again at the largest speed difference. Subsequently, each participant completed 200 trials for analysis, block-randomized across five 40-trial blocks. Each 40-trial block comprised two randomly interleaved sets of 20 trials displaying either task-relevant motion alone, or task-relevant and task-irrelevant motion combined. Each of those 20-trial sets comprised four randomly sequenced instances of the five above-shown speed differences. Within each speed difference, the faster plaid-components occurred on the left and right sides equally often. Error feedback immediately followed each response. Each participant repeated these steps for the other task as well, generating 400 (200 rotational and 200 radial) trials for analysis per participant. Members of the Bluecoats' color guard and low brass groups completed these steps twice, in separate sessions three weeks apart. The second session for these Bluecoat groups allowed us to evaluate reproducibility.

## Design and analysis

The independent variables of primary interest included Group (color guard, low brass, and college students) and Task (judging rotational speed vs. radial speed). To assess whether attention moderated those primary variables, our secondary independent variable distinguished plaids containing only one motion type from those combining rotational *and* radial motion. Our control variables included manipulating which plaid (left or right) contained faster motion, and the magnitude of the speed difference (five signal strengths per motion type).

For each participant, we used standard procedures from Signal Detection Theory (Green & Swets, 1966) to compute our dependent variable, speed sensitivity ( $d'$ ). Operationally, hits and false alarms occurred when participants made “right side” responses and the plaid-gratings on the right contained, respectively, faster or slower motion. Computationally, we determined each participant's  $d'$  value in each task-and-speed combination using the formula  $d' = Z_{\text{Hits}} - Z_{\text{FalseAlarms}}$ , with the  $Z$ -distribution's  $SD = 0.5$ . Accordingly,  $d' = 0.67$  corresponded to nonbiased 75% correct performance. For participants achieving 20 of 20 possible hits in a single task-and-speed combination, we assumed 19.5 of 20 hits to generate  $Z_{\text{Hits}}$ . Conversely, for participants achieving zero of 20 possible false alarms in a single task-and-speed combination, we assumed 0.5 of 20 false alarms to generate  $Z_{\text{FalseAlarms}}$ . We then estimated speed sensitivity for each participant and task by averaging each task's five constituent (speed specific)  $d'$  values. This parallels the process of using multiple speed signal strengths in a psychometric function to estimate a

single speed threshold. We chose not to measure speed thresholds, however, because distinct physical dimensions index rotational speed thresholds (RPS) and radial speed thresholds (OPS). Physically distinct dimensions preclude ANOVA-based comparisons, which require a shared dependent variable across conditions. Contrarily, the dimensionless nature of  $d'$  permitted ANOVA-based comparisons between rotational and radial speed sensitivity.

We evaluated speed sensitivity ( $d'$ ) with mixed-participants ANOVAs and Pearson correlations. The ANOVA's  $2 \times 2$  (Group by Task) interactions indexed the extent to which the groups exhibited task-specific advantages in motion sensitivity. The Pearson correlations indexed within-task and between-task correlations for each group. The Open Science Framework (<https://osf.io/nt52b/>) contains all of our statistical analyses.

We also performed Monte Carlo simulations. These provided statistical contexts for comparing various  $2 \times 2$  (Group by Task) interactions *to each other*. The  $2 \times 2$ -interaction simulations entailed randomly shuffling Group (e.g., color guard vs. low brass) and Task (rotational vs. radial) designations across empirically observed *pairs* of scores. Keeping the empirically observed pairs of scores intact allowed each simulation to retain exactly the empirically observed consistent individual differences. The computer generated 10,000 such simulations, and determined the  $F$  value associated with each simulated  $2 \times 2$  (Group by Task) interaction. Repeating those steps using data from a different Group (e.g., color guard vs. students) and Task (radial vs. rotational)  $2 \times 2$  interaction produced 10,000 additional  $F$  values. Having two lists of 10,000 simulated  $F$  values, the computer next performed pairwise subtractions to obtain 10,000  $F$ -difference scores. Lastly, we sorted these 10,000 computer-simulated  $F$ -difference scores from low to high, and evaluated where various empirically observed  $F$ -difference scores ranked within this simulated distribution.

Lastly, rather than controlling type 1 error with posthoc statistical adjustments, we directly retested our effects empirically in a second session. Stated differently, we reduced the probability of false positives by conducting a direct empirical replication, rather than by manipulating alpha levels on a singular experiment.

## Inclusion/exclusion criteria

We excluded data from six participants who either failed to perform above chance levels or failed to return for the second testing day (Table 2). Three of these six participants failed on the rotational task, one failed on

| Group            | Enrolled | Met criteria | Radial failure | Rotational failure | Day two absence |
|------------------|----------|--------------|----------------|--------------------|-----------------|
| Color guard      | 30       | 26           | 1              | 1                  | 2               |
| Low brass        | 30       | 29           | 0              | 1                  | 0               |
| College students | 25       | 24           | 0              | 1                  | n/a             |
| Total            | 85       | 79 (92.9%)   | 1 (1.2%)       | 3 (3.5%)           | 2 (2.4%)        |

Table 2. Summary of included and excluded participants. *Note:* Failures on either the radial or rotational task occurred when performance fell below 56% correct (binomial  $p$  value  $> 0.05$  across 200 trials).

the radial task, and two failed to return for Day 2. The remaining 79 (92.9% of 85) participants performed well enough to avoid those exclusion criteria. Their data appear in the Results. Table 2 summarizes the group membership. As noted above, the Open Science Framework (<https://osf.io/nt52b/>) contains the raw data from *all* 85 participants.

## Results

### Group by task interactions

Figure 3 shows our primary findings. Panel A displays speed sensitivity ( $d'$ ) for the Bluecoats' color

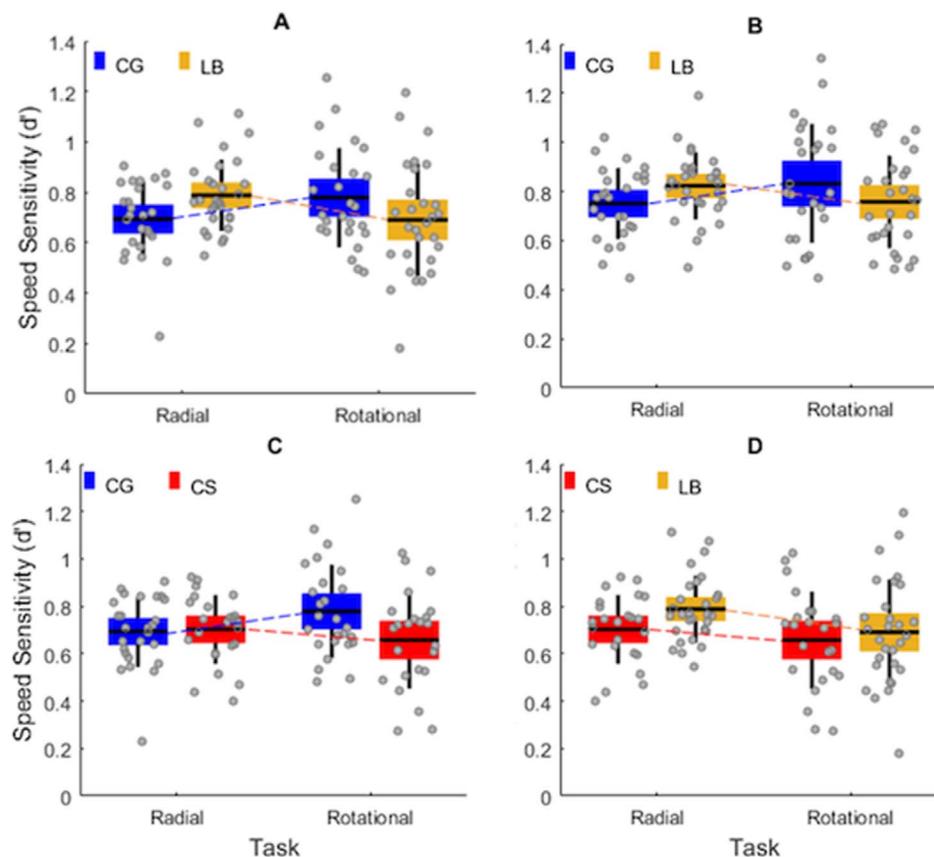


Figure 3. Group by Task interactions. Panels plot speed sensitivity ( $d'$ ) separately for the radial and rotational tasks. Box colors distinguish the color guard (CG: blue boxes), low brass (LB: gold boxes), and college students unaffiliated with drum corps (CS: red boxes). Relative to the low brass, the color guard exhibited better rotational and worse radial performance on Day 1 (panel A: crisscrossing blue and gold dashed lines). This modest but significant Group by Task interaction recurred on Day 2 (panel B: crisscrossing blue and gold dashed lines). It replicated also when comparing color guard on Day 1 to college students unaffiliated with drum corps (panel C: crisscrossing blue and red dashed lines). By contrast, replacing the color guard data with low brass data (both from Day 1) eliminated the significant Group by Task interaction (panel D: uncrossed red and gold dashed lines). Colored boxes reflect 95% confidence intervals. Horizontal and vertical black lines respectively mark the means and standard deviations. Gray dots denote the  $d'$  (speed sensitivity) values for each participant on each task. The data within each condition satisfied the ANOVA's Gaussian-distribution assumption according to Lilliefors' test. The between-group data in each panel satisfied the ANOVA's equal-variance assumption according to Levene's test.

guard (blue boxes) and low brass (gold boxes) on Day 1. The color guard outperformed the low brass on the rotational speed task, and this pattern reversed on the radial speed task. The intersecting blue and gold dotted lines elucidate this modest but statistically significant Group by Task interaction,  $F(1, 53) = 7.960$ ,  $p = 0.007$ ,  $\eta^2 = 0.062$ . Given the relatively small effect size, the Group by Task interaction on Day 1 could reflect mere chance. If so, one would expect the effect to not replicate on Day 2. Contrary to this expectation, Day 2 generated the same small but statistically significant Group by Task interaction (panel B):  $F(1, 53) = 6.082$ ,  $p = 0.017$ ,  $\eta^2 = 0.040$ . Moreover, the modest interaction replicated again when comparing the color guard's Day 1 performance to students unaffiliated with drum corps (red boxes, panel C):  $F(1, 48) = 4.288$ ,  $p = 0.044$ ,  $\eta^2 = 0.033$ . Critically, the significant Group by Task interaction decreased to nonsignificance when we compared the unaffiliated students to the low brass on Day 1 (panel D):  $F(1, 51) = 0.638$ ,  $p = 0.427$ ,  $\eta^2 = 0.005$ . To summarize, Figure 3 evidences the color guard's visual expertise. Their performance advantage—though modest—exhibited specificity to rotational motion, and replicated across days and different control groups. This specific, reproducible effect occurred while visual stimulation remained identical across groups and daily sessions.

In addition to determining whether Figure 3's various Group by Task interactions reached statistical significance or not, we also compared them directly *to each other*. These comparisons occurred via the Monte Carlo procedure described in the Method (and available in the Open Science Framework <https://osf.io/nt52b/>). Our Monte Carlo procedure randomly shuffled the original data sets to generate a distribution of 10,000 simulated Group by Task interaction effects, and their  $F$  values. This simulated distribution provided a statistical context for interpreting the empirically observed differences among Figure 3's various Group by Task interactions. Specifically, we compared the Day 1 Group by Task interactions involving the color guard (panels A and C) to those that did not (panel D). The Group by Task interactions in Figure 3's panels A and D have empirically observed  $F$  values respectively corresponding to 7.960 and 0.638. The difference between those empirically observed  $F$  values ( $7.960 - 0.638 = 7.322$ ) ranked at the 99.6th percentile among 10,000 Monte Carlo simulated differences. Likewise, the Group by Task interactions in Figure 3's panels C and D have empirically observed  $F$  values respectively corresponding to 4.288 and 0.638. The difference between those empirically observed values ( $4.288 - 0.638 = 3.650$ ) ranked at the 91st percentile among 10,000 Monte Carlo simulated differences. In short, the magnitudes of Group by

Task interaction effects that involved the color guard tended to exceed those that did not. More broadly, the Monte Carlo simulations corroborate a modest but reliable color guard advantage in rotational speed sensitivity.

Figure 4 further describes speed sensitivity ( $d'$ ) differences between the color guard and low brass. The top and bottom panels respectively pertain to radial and rotational motion, while the left and right panels respectively pertain to Days 1 and 2. Each panel separates trials that contained only one motion type (“alone”) from those that contained rotational *and* radial motion (“combined”). Across the alone and combined conditions, and across both days, the color guard exhibited slightly lower radial speed sensitivity than did the low brass. The upward tilting red arrows in panels A and B elucidate this small but consistent group difference in radial speed sensitivity. This group difference reversed, however, when the task changed to judging rotational speeds (C and D). Here, the downward tilting red arrows in panels C and D elucidate the color guards' small but consistent advantage in rotational speed sensitivity. The change from upward to downward tilting arrows provides further descriptive evidence for a persistent –albeit modest– Group by Task interaction. This interaction effect persisted whether the task demanded attention to select one motion type while excluding the other (“combined” condition) or not (“alone” condition).

One feature of our speed sensitivity ( $d'$ ) data emerged unexpectedly. Specifically, Figure 4 shows that combining radial and rotational motion generated significantly greater impairments to radial speed sensitivity than to rotational speed sensitivity. Table 3 summarizes this significant Task by Alone/Combined interaction effect, separately for each Group and Day. Because this effect does not pertain directly to our primary research question, we postpone considering it until the Discussion. Now, we turn to regression analyses that provide additional information about whether shared versus distinct neural events govern rotational and radial speed sensitivity.

## Regression analyses

We disaggregated the data that appear in Figure 3 to create the scatter plots in Figure 5. Figure 5's scatter plots display speed sensitivity for individual color guard (blue) and low brass (gold) members on each Day and Task. Panel A reveals that Day 1 rotational speed sensitivity significantly predicted Day 2 rotational speed sensitivity for each group: color guard,  $r^2(24) = 0.653$ ,  $p < 0.001$ ; low brass,  $r^2(27) = 0.317$ ,  $p < 0.001$ . Likewise, panel B reveals that Day 1 radial speed sensitivity significantly predicted Day 2 radial speed

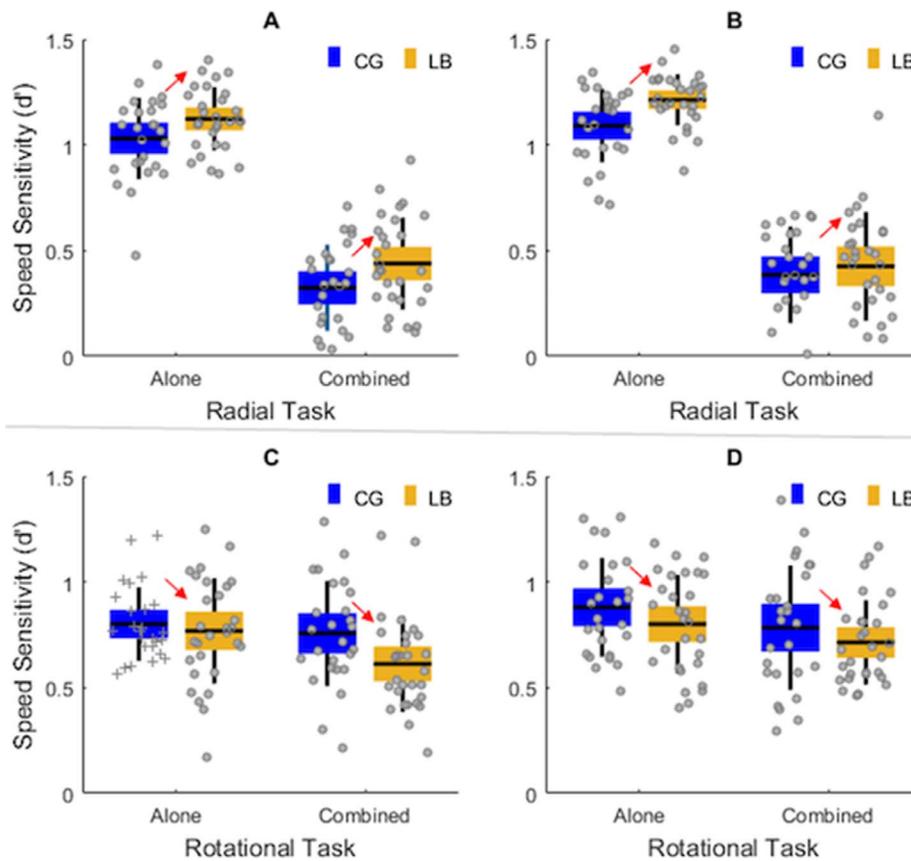


Figure 4. Descriptive statistics on group differences in speed sensitivity. Panels A and B respectively show radial motion speed sensitivity ( $d'$ ) on Days 1 and 2. Upward tilting red arrows highlight lower radial speed sensitivity among the color guard (CG: blue boxes) than among the low brass (LB: gold boxes). This group difference held regardless of whether the stimulus contained either radial or rotational motion alone, or both motion types combined. Downward tilting arrows in panels C and D indicate the opposite pattern—a modest but consistent rotational speed sensitivity advantage in the color guard. Colored boxes reflect 95% CI. Horizontal and vertical black lines respectively mark the means and standard deviations. Gray dots denote the  $d'$  (speed sensitivity) values for each participant on each task. Lilliefors' test indicated Gaussian-distribution data within each condition except when the color guard judged isolated rotational motion on Day 1 (panel C: gray crosses). The skew in that condition arose because no color guard member scored lower than  $d' = 0.5$ , i.e., not much lower than one standard deviation from the group mean.

sensitivity for each group: color guard,  $r^2(24) = 0.387$ ,  $p < 0.001$ ; low brass,  $r^2(27) = 0.470$ ,  $p < 0.001$ . These significant *within-task* associations demonstrate test-retest reliability in our speed sensitivity measures. The significant *within-task* associations also contrast with the non-significant *between-task* associations that each

| Group/day                  | $F$                  | $p$ value |
|----------------------------|----------------------|-----------|
| Color guard day 1          | $F(1, 25) = 121.255$ | $< 0.001$ |
| Color guard day 2          | $F(1, 25) = 131.556$ | $< 0.001$ |
| Low brass day 1            | $F(1, 28) = 91.465$  | $< 0.001$ |
| Low brass day 2            | $F(1, 28) = 107.225$ | $< 0.001$ |
| College students (day n/a) | $F(1, 23) = 74.696$  | $< 0.001$ |

Table 3. Task by alone/combined interactions. *Note:* Combining radial and rotational motion generated significantly greater reductions in radial speed sensitivity than in rotational speed sensitivity.

group demonstrated on Day 1 (panel C) and Day 2 (panel D). Indeed, the  $r^2$  values across Figure 5 show  $\sim 32$  to  $\sim 65$  percent of speed-sensitivity ( $d'$ ) variation explained *within-tasks* (panels A and B) versus  $\sim 0$  to  $\sim 14$  percent *between-tasks* (panels C and D).

In addition to determining whether Figure 5's various correlations reached statistical significance or not, we also compared them directly *to each other*. We replot these correlations ( $r$  values) in Figure 6. Recall that  $r$  values correspond to standardized regression coefficients, i.e., the slope of the regression line on scatter plots comprising  $z$ -transformed scores. The error bars in Figure 6 reflect one standard error of the estimate, i.e., the uncertainty surrounding each standardized slope estimate (Keppel, Saufley, & Tokunaga, 1992). Visually inspecting Figure 6 reveals stronger within-task (left) than between-task (right) correlations for color guard (blue bars) and low brass

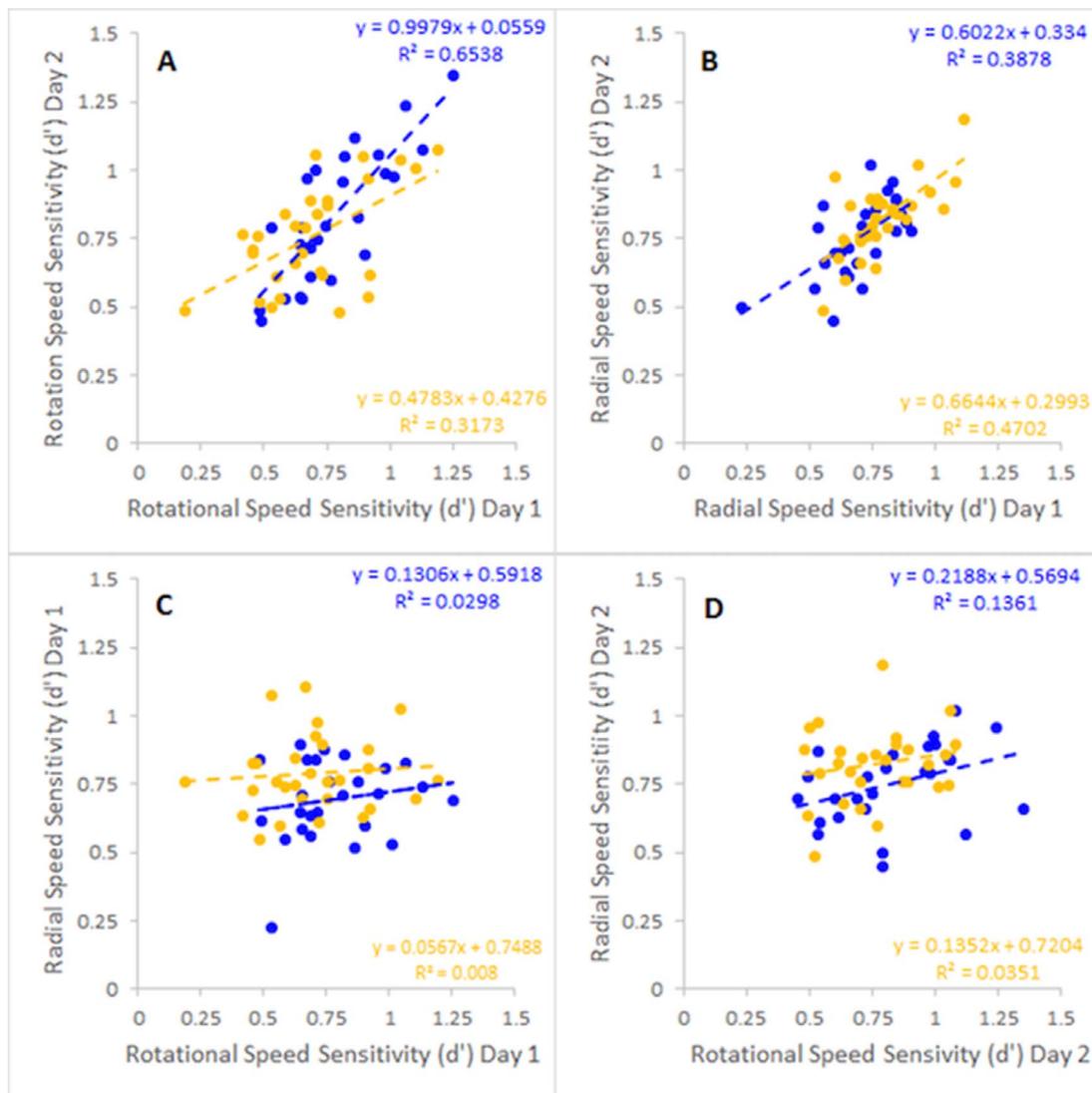


Figure 5. Speed sensitivity correlations across Days and Tasks. Panel A shows that rotational speed sensitivity on Day 1 significantly predicted rotational speed sensitivity on Day 2. This significant prediction occurred for color guard and low brass (shown respectively in blue and gold) alike, and accounted for large proportions of variance. Panel B shows a similar pattern for radial speed sensitivity across Days 1 and 2. Dissimilarly, rotational speed sensitivity failed to predict significantly radial speed sensitivity on Day 1 (panel C) and Day 2 (panel D). The large within-task  $r$ -squared values (top panels) and near-zero between-task  $r$ -squared values (bottom panels) disconfirm shared neural events governing performance on the two tasks.

(gold bars) alike. Figure 6 also displays largely (albeit not entirely) nonoverlapping error bars; slope estimates *within* tasks have relatively little overlap with slope estimates *between* tasks. We used Howell's (2002) method for testing the difference between two nonindependent  $r$  values to formally compare within-task correlations to between-task correlations. The comparisons between within-task correlation Rotation1:Rotation2 and between-task correlation Rotation1:Radial1 reached significance for both groups: CG,  $t(23) = 3.697$ ,  $p = 0.0012$ ; LB,  $t(26) = 2.241$ ,  $p = 0.034$ . The comparison between within-task correlation Radial1:Radial2 and between-task correlation Rotation2:Radial2 fell shy of significance for the color

guard,  $t(23) = 1.213$ ,  $p = 0.237$ , but reached significance for the low brass,  $t(26) = 2.628$ ,  $p = 0.0142$ . This tendency toward stronger within- than between-task associations also recurred after conducting regression analysis separately for the "alone" and "combined motion" conditions (see Open Science Framework <https://osf.io/nt52b/>). The additional control group—college students, who completed just one daily session—similarly exhibited nonsignificant relationships between radial and rotational speed sensitivity. Overall, our regression analyses reveal low between-task associations, disconfirming what one would expect if significantly shared neural events governed radial and rotational speed sensitivity.

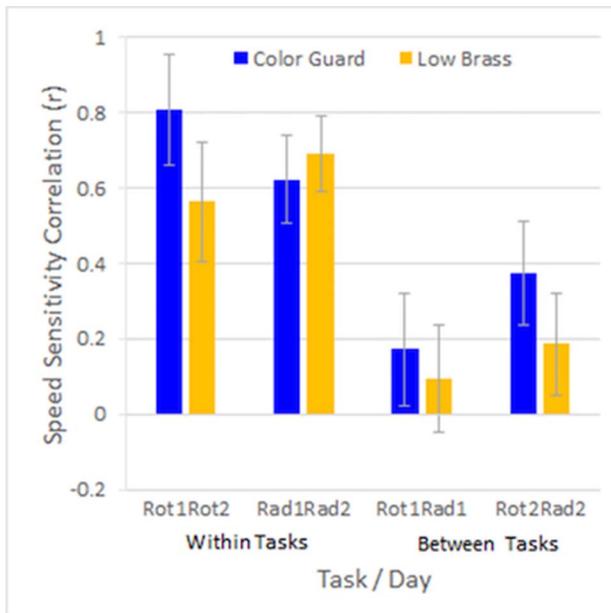


Figure 6. Comparing speed sensitivity correlations to *each other*. Color guard (blue) and low brass (gold) alike generated greater speed sensitivity ( $d'$ ) correlations ( $r$ ) within-tasks (left) than between-tasks (right). Error bars show one standard error of the estimated regression slope. Recall that the  $r$  statistic reflects the slope of the regression line for  $z$ -transformed scores. (Rot = Rotational Speed Task; Rad = Radial Speed Task; 1s and 2s in abscissa-labels correspond to Day 1 and Day 2).

## Discussion

The present experiments assessed rotational and radial speed sensitivity in color guard experts. Their expertise in rotating flags, rifles, and sabers afforded a novel test of diverging predictions. These diverging predictions spring from previous physiological investigations of cortical area MST that plausibly could support correlations or dissociations between rotational and radial speed sensitivity. We found that, relative to low-brass control participants, the color guard's speed sensitivity exhibited a modest but reliable rotational advantage *and* radial disadvantage. This statistically significant interaction replicated across sessions, and also when we compared color guard experts to controls who had no drum corps affiliation. Additionally, the effect occurred in each of our attentional conditions—judging one motion type alone versus selecting one motion type while ignoring a distractor motion. Taken together, the patterns observed in our group-by-motion-type comparisons more strongly support distinct—rather than shared—neural events governing rotational and radial speed sensitivity.

Further evidence that distinct neural events govern rotational and radial speed sensitivity comes from our regression analyses. Specifically, rotational and radial

speed sensitivities failed to significantly predict each other. This predictive failure seems surprising for two reasons. First, one might expect significant *between*-task correlations to arise even from nonsensory factors. These include consistent individual differences in motivation, attentional lapses, and/or motor errors. Second, the same data set exhibited significant *within*-task correlations across days and regardless of attentional conditions. Overall, our regression analyses and the above-mentioned interaction effects independently point toward dissociation between the neural events that govern rotational and radial speed sensitivity.

An alternative interpretation of the present findings entails reconceptualizing our rotational and radial motions into local linear motion components (Barraza & Grzywacz, 2002, 2005; Clifford, Beardsley, & Vaina, 1999; Freeman & Harris, 1992; Koenderink & van Doorn, 1976; Wurfel, Barraza, & Grzywacz, 2005). As noted in the Introduction, Figure 1 shows how rotational motion and radial motion differ in local linear *directions*. Importantly, local linear *speeds* also distinguish rotational from radial motion. In the present rotational stimuli, the maximum local linear speed reached  $60.95^\circ/\text{s}$  ( $9.7^\circ$  diameter  $\times \text{Pi} \times 2$  revolutions per second). Dissimilarly, the maximum local linear speed in our radial motion stimuli reached only  $11.31^\circ/\text{s}$ . (This speed estimate assumes a  $90^\circ$  plaid expanding or contracting between 0.125 and 0.5 cycles/ $^\circ$  per second obliquely, i.e., horizontally *and* vertically.) Stated differently, the maximum local linear speeds in our rotational stimuli exceeded those of our radial stimuli by approximately fivefold. Consequently, our results could reflect a color guard advantage in fast-linear-speed sensitivity ( $\sim 60$  degrees per second), and disadvantage in slow-linear-speed sensitivity ( $< 12^\circ/\text{s}$ ). Correspondingly, one might interpret our regression analyses as evidence that distinct neural events govern speed sensitivity at fast versus slow local linear speeds.

An explanation in which distinct neural events govern speed sensitivity at fast versus slow local linear speeds seems at odds with an important earlier finding. Specifically, prior psychophysical experiments demonstrate that speed sensitivity remains *constant* (Weber fractions  $\sim 7\%$ ) for local linear speeds ranging between  $4^\circ/\text{s}$  and  $64^\circ/\text{s}$  (De Bruyn & Orban, 1988). However, the stimuli in that study (De Bruyn & Orban, 1988) differ considerably from the stimuli tested here. The earlier study (De Bruyn & Orban, 1988) used linearly translating random dot patterns. These generate local linear speeds that remain *uniform* (ungraded) across space and time. This contrasts sharply with the present plaid patterns' rotational or radial motion, which generated local linear speed *gradients* in space and time. For example, our rotating plaid pattern's center-to-edge local linear speed gradient ranged between zero and  $\sim 61$  degrees per second. Note that using local

linear speeds to judge the difference between two rotational or radial speed gradients demands attentional selection. For example, rotational speed judgments would necessitate selecting local linear speeds near the edge while ignoring those near the center. This attentional demand did not arise in the earlier study (De Bruyn & Orban, 1988), wherein translating random-dot stimuli generated uniform local linear speeds, not speed gradients. In short, the ability to precisely *register* local linear speeds (De Bruyn & Orban, 1988) may differ from the ability to *attentionally select* local linear speeds.

An interpretive framework based on the ability to attentionally select local linear speeds also helps explain an unexpected asymmetry arising from our attentional manipulation. Namely, task-irrelevant rotational motion impaired radial speed sensitivity significantly more than task-irrelevant radial motion impaired rotational speed sensitivity (Table 3). Rather than interpreting this as an asymmetry between rotational and radial motion sensitivities, one could instead posit asymmetric attentional selection of local linear speeds. According to this account, faster linear speeds impaired slow-linear-speed selection significantly more than vice versa. This seems intuitive because one would expect greater perceptual salience to arise from (fivefold) faster than from slower motion signals. Indeed, temporal-vision masking experiments have demonstrated that high temporal frequencies suppress low temporal frequencies, but low temporal frequencies do not suppress high temporal frequencies (Cass & Alais, 2006). Similarly, prior attentional experiments on visual-search asymmetries in linear motion demonstrate that fast-moving distractors impair the detection of slow-moving targets but not vice versa (Ivry & Cohen, 1992). Ivry and Cohen (1992) modeled this asymmetry via speed detectors that operate as high pass filters. This simulates the high pass filtering characteristic of Middle Temporal (MT) neurons that register linear motion (Allman, Miezin, & McGuinness, 1985; Maunsell & Van Essen, 1983b).

MT neurons that register linear motion innervate MST neurons that register rotational and radial motion (Maunsell & Van Essen, 1983a; Ungerleider & Desimone, 1986). Consequently, the above-mentioned linear-motion and radial/rotational motion interpretations of the present data respectively could reflect neural events in MT and MST, or both. We refrain, though, from speculating further about precise neural loci given our study's purely psychophysical design. Future experiments might determine the extent to which linear (MT) and rotational/radial (MST) speed detectors underlie the task-dissociations and color-guard-specific speed sensitivity observed here.

How might the present controlled laboratory findings—and the linear versus rotational/radial motion

debate—relate to the color guard's real-world field conditions? Consider a line of color guard members, synchronously spinning their rifles. This synchrony arises from adhering to a shared *rotational* speed, *not* a shared local linear speed. Indeed, for any given member in the color guard line, the other members' rifles generate a complex retinal gradient of local linear speeds. Nearer rifles create relatively larger retinal images, and correspondingly faster local linear speeds per revolution. More distant rifles generate relatively smaller retinal images, and correspondingly slower local linear speeds per revolution. Moreover, these diverse retinal sizes and local linear speeds change whenever color guard members scurry to new field locations for artistic effect. All the while, though, the rifles' *rotational* speed remains constant. Simply put, rotational speed serves as a visual invariant (Gibson, 1986). Color guard can parsimoniously track this visual invariant to regulate motor actions that earn rewards: cheers from fans, points from referees, smiles galore. Our results match what one would predict if color guard expertise included enhanced sensitivity to the speed of visual rotations.

The speed of visual rotations, however, constitutes just one cue in the rich information available to color guard members. The following quotation from a color guard participant demonstrates the broad range of cues that color guard experts exploit.

“. . .there are certain parts of the equipment that we, as color guard members, are told to look at. For example, on a rifle we generally have an outstanding piece of tape by the bolt of the rifle (or the center of the rifles mass). The reason for this is because when the rifle is in the air, we are watching that outstanding piece of tape as a centralized location. If the tape is placed correctly, it should appear as if the tape is simply moving straight up and straight down while the rifle is in the air. If we were to look anywhere else on the rifle, our ability to visualize the equipment into our hands would be much harder. I wouldn't say that we are watching the rotations in the air as much as we are performing the rotations with our muscles. We are simply watching the equipment into our hands in the most effective way visually.

However, along with watching the equipment into our hands, we rely on muscle-memory. In other words, repetition of the same motion using the same piece of equipment helps our brain and bodies to perform a toss the exact same way each time. And within a toss, yes the rotations are important. However, the height of the toss is just as important. Color guard members have different release points in relation to their bodies with their

left hands in order to appropriately release the toss at the correct height. Additionally, another important element is the timing of the toss. The time between the release and the catch is just as important as the height and rotations of the toss. In fact, it is actually the result of both the height and rotation. Once the equipment is in the air, the color guard member is not only aware of the rotations and placements of the object, but also the speed at which it is descending.

Some additional food for thought: There are some instructors at advanced levels who use the phrase “You should be able to do this with your eyes closed.” Obviously, that is not recommended. However, they are correct. If the color guard member is able to release the toss at the appropriate height, using the appropriate speed and rotation, and understand the element of time in which that rotational amount is in the air for, then he/she should be able to successfully toss and catch their equipment without looking at it” (M. E. Dufala, personal communication, March 21, 2017).

The quotation above emphasizes the importance of cues beyond rotational speed. Indeed, the modest but reliable color guard advantage in rotational sensitivity observed here could reflect a rotational-motion exposure effect. Moreover, like the coach’s reflection described in our m, the color guard participant’s quote above highlights the role of “muscle memory”. A significant body of research similarly corroborates motor-related factors when visually tracking a falling object before interception (Brenner, Driesen & Smeets, 2014; Brenner & Smeets, 2015; Brenner et al., 2016). The quotation above also emphasizes nonmotor factors. Two of these include tracking time and the speed at which a spinning object descends/ascends. We did not measure time sensitivity in the present experiments, as stimulus durations remained constant at one second. By contrast, the present radial speed task’s spatial frequency modulations presumably indexed sensitivity to the speed at which a tossed object ascends/descends. Spatial frequencies increase and decrease, respectively, as the tossed object rises from and falls toward the color guard member. Yet the results revealed lower (not higher) radial speed sensitivity in the color guard than in the low brass controls. Why?

One possibility involves a mismatch between the spatial frequencies of our laboratory stimuli and real-world spinning rifles, sabers, and flags. Pairing a highly practiced rotational speed (~2 RPS) with very unfamiliar spatial frequency content may have impaired the color guard’s radial speed judgments. This parallels

professional baseball players who swing less accurately at unfamiliar large (low spatial frequency) softballs than at familiar but smaller (higher spatial frequency) baseballs.<sup>1</sup> In fact, sensory expertise in various domains depends highly on stimulus context. For example, luminance contrast reversals (Bruce, 1994) and orientation reversals (Valentine, 1988) each impair our expertise in identifying faces and facial expressions. More broadly, chess experts (Reynolds, 1982) and musical experts (Halpern & Bower, 1982) exhibit superior recall only under stimulus conditions that match their experiential base. Accordingly, visual stimuli that more closely match real-world drum corps conditions will provide further insights about visual speed sensitivity in the color guard.

*Keywords:* visual motion, rotational motion, radial motion, speed sensitivity, speed discrimination, perceptual learning, color guard, expert-novice-differences, drum corps

## Acknowledgments

A Denison University Research Foundation grant to NM supported this research. The authors thank Alex Holcombe and two anonymous reviewers for helpful comments, and Peter Bex for conversations describing rotationally selective MST neurons as isotropic shear detectors. The authors thank Megan Dufala, Allen Whitfield, Genevieve Geisler and David Glasgow for insights about drum corps skills and training.

Commercial relationships: none.

Corresponding Author: Nestor Matthews.

Email: matthewsn@denison.edu.

Address: Department of Psychology & Neuroscience Program, Denison University, Granville, OH, USA.

## Footnote

<sup>1</sup> <https://www.si.com/more-sports/2013/07/24/sports-gene-excerpt>

## References

- Allman, J., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception*, 14(2), 105–126.
- Barraza, J. F., & Grzywacz, N. M. (2002). Measure-

- ment of angular velocity in the perception of rotation. *Vision Research*, 42(21), 2457–2462.
- Barraza, J. F., & Grzywacz, N. M. (2005). Parametric decomposition of optic flow by humans. *Vision Research*, 45(19), 2481–2491, doi:10.1016/j.visres.2005.04.011.
- Brenner, E., Driesen, B., & Smeets, J. B. (2014). Precise timing when hitting falling balls. *Frontiers in Human Neuroscience*, 8, 342, doi:10.3389/fnhum.2014.0034.
- Brenner, E., & Smeets, J. B. (2015). How people achieve their amazing temporal precision in interception. *Journal of Vision*, 15(3):8, 1–21, doi:10.1167/15.3.8. [PubMed] [Article]
- Brenner, E., Rodriguez, I. A., Munoz, V. E., Schootemeijer, S., Mahieu, Y., Veerkamp, K., . . . Smeets, J. B. (2016). How can people be so good at intercepting accelerating objects if they are so poor at visually judging acceleration? *Iperception*, 7(1), 2041669515624317, doi:10.1177/2041669515624317.
- Bruce, V. (1994). Stability from variation: The case of face recognition. The M.D. Vernon Memorial Lecture. *Quarterly Journal of Experimental Psychology A*, 47(1), 5–28.
- Cass, J., & Alais, D. (2006). Evidence for two interacting temporal channels in human visual processing. *Vision Research*, 46(18), 2859–2868, doi:10.1016/j.visres.2006.02.015.
- Clifford, C. W., Beardsley, S. A., & Vaina, L. M. (1999). The perception and discrimination of speed in complex motion. *Vision Research*, 39(13), 2213–2227.
- De Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research*, 28(12), 1323–1335.
- Duffy, C. J., & Wurtz, R. H. (1991a). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology*, 65(6), 1329–1345.
- Duffy, C. J., & Wurtz, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*, 65(6), 1346–1359.
- Freeman, T. C., & Harris, M. G. (1992). Human sensitivity to expanding and rotating motion: Effects of complementary masking and directional structure. *Vision Research*, 32(1), 81–87.
- Gibson, J. J. (1986). *The ecological approach to visual perception*. London, UK: Lawrence Erlbaum Associates Publishers.
- Gilmore, R. O., Hou, C., Pettet, M. W., & Norcia, A. M. (2007). Development of cortical responses to optic flow. *Visual Neuroscience*, 24(6), 845–856, doi:10.1017/s0952523807070769.
- Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience*, 14(1), 54–67.
- Green, D. M., & Swets, J. W. (1966). *Signal detection theory and psychophysics*. New York, NY: John Wiley & Sons.
- Halpern, A.R., & Bower, G.H. (1982). Musical expertise and melodic structure in memory for musical notation. *American Journal of Psychology*, 95, 31–50.
- Holcombe, A. O., & Chen, W. Y. (2013). Splitting attention reduces temporal resolution from 7 Hz for tracking one object to <3 Hz when tracking three. *Journal of Vision*, 13(1):12, 1–19, doi:10.1167/13.1.12. [PubMed] [Article]
- Howell, D.C. (2002). *Statistical methods for psychology* (5th ed.). Stamford, CN: Thompson Learning, Inc.
- Ivry, R. B., & Cohen, A. (1992). Asymmetry in visual search for targets defined by differences in movement speed. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 1045–1057.
- Keppel, G., Saufley, W. H., & Tokunaga, H. (1992). *Introduction to design & analysis*, 2nd ed. New York, NY: W. H. Freeman & Company.
- Koenderink, J. J., & van Doorn, A. J. (1976). Local structure of movement parallax of the plane. *Journal of the Optical Society of America*, 66(7), 717–723.
- Lagae, L., Maes, H., Raiguel, S., Xiao, D. K., & Orban, G. A. (1994). Responses of macaque STS neurons to optic flow components: A comparison of areas MT and MST. *Journal of Neurophysiology*, 71(5), 1597–1626.
- Maunsell, J. H., & Van Essen, D. C. (1983a). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience*, 3(12), 2563–2586.
- Maunsell, J. H., & Van Essen, D. C. (1983b). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, 49(5), 1127–1147.
- Morrone, M. C., Tosetti, M., Montanaro, D., Fior-

- entini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, 3(12), 1322–1328, doi:10.1038/81860.
- Raffi, M., & Siegel, R. M. (2007). A functional architecture of optic flow in the inferior parietal lobule of the behaving monkey. *PLoS One*, 2(2), e200, doi:10.1371/journal.pone.0000200.
- Reynolds, R. I. (1982). Search heuristics of chess players of different calibers. *American Journal of Psychology*, 95(3), 383–392.
- Saito, H., Yukiie, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience*, 6(1), 145–157.
- Smith, A. T., Wall, M. B., Williams, A. L., & Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST. *European Journal of Neuroscience*, 23(2), 561–569, doi:10.1111/j.1460-9568.2005.04526.x.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, 62(3), 626–641.
- Thornton, T., & Gildea, D. L. (2001). Attentional limitations in the sensing of motion direction. *Cognitive Psychology*, 43(1), 23–52, doi:10.1006/cogp.2001.0751.
- Treue, S., & Maunsell, J. H. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature*, 382(6591), 539–541, doi:10.1038/382539a0.
- 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.
- Tsujimura, S., & Zaidi, Q. (2002). Similarities between visual processing of shear and uniform motion. *Vision Research*, 42(28), 3005–3017.
- Ungerleider, L. G., & Desimone, R. (1986). Projections to the superior temporal sulcus from the central and peripheral field representations of V1 and V2. *Journal of Comparative Neurology*, 248(2), 147–163, doi:10.1002/cne.902480202.
- Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, 79(4), 471–491.
- Verstraten, F. A., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, 40(26), 3651–3664.
- Wall, M. B., Lingnau, A., Ashida, H., & Smith, A. T. (2008). Selective visual responses to expansion and rotation in the human MT complex revealed by functional magnetic resonance imaging adaptation. *European Journal of Neuroscience*, 27(10), 2747–2757, doi:10.1111/j.1460-9568.2008.06249.x.
- Wurfel, J. D., Barraza, J. F., & Grzywacz, N. M. (2005). Measurement of rate of expansion in the perception of radial motion. *Vision Research*, 45(21), 2740–2751, doi:10.1016/j.visres.2005.03.022.
- Wurtz, R. H., & Duffy, C. J. (1992). Neuronal correlates of optic flow stimulation. *Annals of the New York Academy of Science*, 656, 205–219.
- Yu, C. P., Page, W. K., Gaborski, R., & Duffy, C. J. (2010). Receptive field dynamics underlying MST neuronal optic flow selectivity. *Journal of Neurophysiology*, 103(5), 2794–2807, doi:10.1152/jn.01085.2009.