Prior reports demonstrate that simultaneity is judged less precisely in the right visual field (RVF) than in the left visual field (LVF). The present psychophysical study was conducted to provide new information about why and when (i.e., the visual information stage at which) RVF deficits arise in simultaneity judgments. In Experiment 1, participants judged either the simultaneity or the relative spatial frequency of Gabor targets in the right or left hemifield while distractors were randomly absent or present. When attention was not needed to exclude distractors, signal detection theory analyses revealed an RVF simultaneity deficit with an error pattern that implicates low RVF temporal acuity, not excessive RVF neural noise. Adding attentionally demanding distractors introduced a separate, significant RVF simultaneity deficit with error patterns that implicate the inappropriate integration of temporal asynchronies from distractor locations. Neither the distractor-independent RVF acuity deficit nor the distractor-induced RVF excessive spatial integration occurred for spatial frequency discrimination at the same retinal locations. In Experiment 2, a perceptual learning procedure significantly improved RVF simultaneity judgments. The learning was task-specific but generalized to the untrained (left) visual field and to novel retinal locations. This observation implicates the simultaneity decision as the visual information stage that sets the limit on performance.

Keywords: simultaneity, attention, temporal vision, spatial integration, visual field anisotropy, hemifield effects

that reveal what sets the limit on performance. Figure 2 schematizes Petrov, Dosher, and Lu’s (2005) original framework for interpreting such patterns in perceptual learning data. The bottom ovals represent ensembles of neurons (circles) whose response is driven entirely by the stimulus. These stimulus-driven ensembles connect (arrows) with other neural ensembles (top ovals) that comprise neurons (circles) responsible for a task-relevant decision. Configuration “A” is useful for interpreting the transfer of perceptual learning to a novel task. Significant transfer to a novel task—for example, from a simultaneity task (configuration “A”, left) to a spatial frequency discrimination task (configuration “A”, right)—would confirm the possibility that training improved the signal-to-noise ratio (SNR) at the stimulus-driven stage (bottom). An absence of transfer to a novel task would suggest that the SNR improvement was restricted to the task-relevant decision stage (top) and/or its connection (arrow) with the stimulus-driven stage. Configuration “B” is useful for interpreting the transfer of perceptual learning to a novel stimulus or retinal location. Significant transfer to a novel stimulus or retinal location would confirm the possibility that training improved the SNR at the task-relevant decision stage (top). An absence of transfer to a novel stimulus or retinal location would suggest that the SNR improvement was restricted to the stimulus-driven stage (bottom) and/or its connection (arrow) with the task-relevant decision stage.

Figure 3 schematizes our novel variation on Petrov et al.’s (2005) interpretive framework. Our variation is similar to their configuration “A” (Figure 2), except for the notable addition of a new retinal location and its connection to the decision, both shown in dotted line. These new (dotted line) components become critical if the practice-based improvements are task specific, i.e., do not generalize from the trained (simultaneity) task to the

Figure 1. Space–time integration windows as potential explanations for RVF deficits when judging simultaneity. (Left panel: Neural noise hypothesis) Random variability in the latency of neural responses (leftward or rightward time shifts) to either discriminandum could make simultaneous stimuli appear asynchronous or vice versa. RVF deficits arising from such neural noise would exhibit increased RVF false alarm rates and miss rates. (Center panel: Low temporal acuity hypothesis) RVF deficits arising from low temporal acuity (wider temporal, but not spatial, integration) would exhibit increased RVF miss rates, without an increase in RVF false alarm rates. (Right panel: Excessive spatial integration hypothesis) RVF deficits arising from a failure to exclude transients from distractor locations (wider spatial, but not temporal, integration) would exhibit increased RVF false alarm rates, without an increase in RVF miss rates. Inspired by Figure 4 in Vul, Hanus, and Kanwisher (2009).

Figure 2. Schematics for interpreting the transfer of perceptual learning (A) to novel tasks and (B) to novel stimuli or retinal locations. Adapted from Petrov et al. (2005).
untrained (spatial frequency) task. (Recall that if the practice-based improvements do generalize to the untrained task, then the stimulus-driven stage is implicated as the limiting neural source.) If task-specific learning occurs, the results from a post-training location transfer test can unambiguously determine whether initial performance had been limited by the decision stage or instead by the connection. Specifically, significant transfer to the new retinal location would point to the decision stage as the limiting neural source. Alternatively, a lack of transfer to the new retinal location would mean that the limiting factor had been the neural events that connect the trained stimulus-driven and decision stages. In short, by evaluating the task and location specificity of practice-based improvements, our variation on Petrov et al.’s (2005) framework can isolate the neural stage that sets the limit on RVF simultaneity judgments.

To summarize our study, we conducted two experiments to provide new information about why and when RVF deficits arise in simultaneity judgments. Experiment 1 required judging simultaneity and spatial frequency in the absence and presence of distractors. When distractors were absent, signal detection theory error analyses revealed significantly more RVF than LVF temporal asynchrony misses but no hemifield differences in false alarms. This error pattern suggests that when attention is not required for excluding distractors, the RVF simultaneity deficit reflects low RVF temporal acuity rather than excessive RVF neural noise. Adding attentionally demanding distractors to the displays did not significantly alter temporal asynchrony misses in either hemifield but significantly increased temporal asynchrony false alarms in the RVF only. This distractor-induced error pattern implicates an RVF attentional failure, an inability to exclude temporal asynchronies from the LVF. Neither the distractor-independent RVF acuity deficit nor the distractor-induced RVF excessive spatial integration occurred for spatial frequency discrimination at the same retinal locations. In Experiment 2, our perceptual learning procedure significantly improved RVF simultaneity judgments. The learning was task specific but generalized to the untrained (left) visual field and to novel retinal locations. This pattern implicates the simultaneity decision (Figure 3, top left oval) as the visual information

![Neural noise diagram](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932802/)

Figure 3. Novel variation on Petrov et al.’s (2005) perceptual learning framework. The dotted lines (left side) pertain to a post-training retinal location transfer test in our Experiment 2.

<table>
<thead>
<tr>
<th>Neural noise</th>
<th>Low temporal acuity</th>
<th>Excessive spatial integration</th>
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<tbody>
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<td>Stimulus-driven stage</td>
<td>RVF pre-attentive deficit</td>
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<td>Decision stage</td>
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Table 1. Why (columns) and when (rows) RVF deficits arise in simultaneity judgments. (Experiment 1) When distractors were absent, simultaneity judgments exhibited significantly more RVF than LVF misses but no hemifield differences in false alarms, implicating low RVF pre-attentive temporal acuity (center column). Adding distractors significantly increased RVF false alarms exclusively, implicating excessive spatial integration, i.e., a failure in the attentional selection of RVF targets (right column). Both of these RVF deficits were eliminated in Experiment 1 when the same participants viewed the same displays but judged spatial frequency rather than simultaneity. (Experiment 2) Perceptual learning on RVF simultaneity judgments was task specific but generalized to novel retinal locations and the untrained (left) hemifield, implicating the simultaneity decision as the limiting neural stage (bottom row).
stage that limits performance and disconfirms training-based SNR improvement in the stimulus-driven stage and its connection to the decision. Table 1 recaps our findings.

**Experiment 1: Distractor effects**

**Methods**

**Apparatus**

All experiments reported here were conducted on a 24-in. (60.96-cm) flat screen Apple LED Cinema Display that was controlled by a Macintosh Pro 4 Tower computer. The computer ran on a Mac OS X version 10.5.6 operating system. Matlab software called functions from the psychophysics toolbox (Brainard, 1997; Pelli, 1997). The vertical refresh rate of the monitor was 60 Hz, and the spatial resolution was 1024 × 768 pixels. A chin rest helped stabilize head position at 57 cm from the monitor.

**Targets and distractors**

The targets and distractors were achromatic Gabor patches, created by multiplying a sinusoidal luminance profile by a two-dimensional Gaussian envelope. The Gabor patches had maximum (108.00 cd/m²) and minimum (5.83 cd/m²) luminances that rendered high contrast (Michelson contrast = 89.76%) within the apparently gray surround (16.1 cd/m²). The orientation of each Gabor patch was chosen randomly from the full 180-degree range. The standard spatial frequency was 1.25 cycles per degree (cpd); these Gabor patches comprised four randomly phase-shifted light–dark cycles that collectively spanned a 3.2 × 3.2 degree (84 × 84 pixel) square region. Some displays also included randomly oriented and phase-shifted Gabor patches, having one of six other spatial frequencies lower than the standard 1.25 cpd by either 20%, 22%, 24%, 26%, 28%, or 30%. The method for determining the lower spatial frequency is described below in the Procedure section.

**Stimulus sequence**

**Distractor condition**

The stimulus sequence for a sample trial in our distractor condition is schematized in Figure 4. Each trial began with a central fixation marker shown simultaneously with a pair of peripheral cues (Figure 4A). The fixation marker was a small gray square (16.1 cd/m²; 0.44 deg or 12 pixels per side) that was inscribed in a larger square (1.33 deg or 36 pixels per side) of noise that rendered the central letter difficult to identify unless fixated directly. The peripheral cues were equiluminant solid red squares (16.1 cd/m²; CIE 0.615, 0.345; 3.2-deg (84-pixel) diameter) positioned where the two Gabor targets were to appear. A computerized voice immediately preceding the peripheral visual cues also indicated whether the two Gabor targets would be in the left or right visual field.

After 350 ms, the peripheral cues were replaced by the gray surround (16.1 cd/m²) for 200 ms (Figure 4B). Gabor targets then appeared at the cued positions for 200 ms, concurrently with two other Gabor patches (distractors) in the non-cued quadrants (Figure 4C). The distances between the stimuli are detailed in Figure 5 and were well beyond the critical region for spatial crowding (Toet & Levi, 1992). For the next 66 ms, each quadrant’s Gabor patch either remained the same or changed orientation by 90 degrees, independent of the other Gabor patches. In the sample trial schematized in Figure 2, only the upper right Gabor patch (indicated by the green arrow) has changed orientation at this point in the sequence (Figure 4D). For the next 100 ms, one of ten randomly selected lowercase letters (31.20 cd/m²; 31.92% contrast; 12 point Helvetica font) appeared at fixation (Figure 4E; an “n” in our schematic). For the next 34 ms, the central letter was replaced by a noise mask having parameters identical to those in its surround (Figure 4F). During the final 200 ms,

![Figure 4](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932802/) Figure 4. Stimulus sequence for a sample distractor trial on which the participant was to judge the simultaneity of right hemifield targets, indicated by the red cues in (A). The orientation changes in this illustration are indicated by green arrows (D and G), which did not appear in the actual displays. The correct responses to the letter prompt and target-timing prompt (H and I, respectively) are “n” and “d” on this trial, as the right hemifield Gabor targets changed orientation at different times. Note that the correct simultaneity response would have been “s” if the left hemifield positions were cued. In this way, the correct simultaneity response depended on the cued hemifield, while retinal stimulation remained identical across the hemifield conditions.
the Gabor patches that had not previously changed orientation by 90 degrees now did so, as schematized by the green arrows in Figure 4G.

No-distractor condition

The no-distractor condition was identical to the distractor condition in all ways except for the absence of the “distractor” Gabor patches in the two non-cued corners. The no-distractor condition probed how performance would change, relative to the distractor condition, when Gabor targets did not have to be selected to the exclusion of Gabor distractors—an attentional requirement. This is an important distinction, as prior reports have demonstrated separate rules governing the temporal grain of stimulus-driven vision versus visual attention (Aghdaee & Cavanagh, 2007; Farzin, Rivera, & Whitney, 2011; Kelly & Matthews, 2011; Rogers-Ramachandran & Ramachandran, 1998). Indeed, Kelly and Matthews (2011) observed that simultaneity judgments exhibit an oblique effect in the presence, but not the absence, of attentionally demanding distractors.

Task

The task on each trial was twofold. First, to ensure control of fixation, the participant was required to correctly identify the central letter (Figure 2H). An incorrect letter response immediately aborted the trial and automatically restarted the trial sequence. Second, after making a correct letter response, the participant made a “same”/“different” peripheral judgment. On temporal task blocks, participants judged simultaneity, i.e., indicated whether the two cued peripheral Gabor targets changed orientation at the same time or at different times (Figure 2I). On spatial task blocks, participants judged the cued peripheral Gabor targets to be the same or different in spatial frequency. To maintain motivation, immediate auditory feedback identified each letter response and each peripheral response as either correct or incorrect. The computer also announced the percentage of correct letter responses and the percentage of correct peripheral responses after every 64 trials.

Participants

Denison University’s Human Subject Committee approved all experiments in this study, which were conducted with the understanding and written consent of each participant. All participants in the study had normal or corrected-to-normal acuity. Twenty-two naïve Denison University undergraduates completed Experiment 1.

Procedure

Each participant first completed a series of practice blocks to establish that the task could be performed at greater-than-chance levels before the actual trials began. Each participant then completed 512 actual trials divided into sixteen separate 32-trial blocks. Each 32-trial block comprised a single combination of a task (spatial or temporal) and an attended hemifield (left or right), with 16 distractor trials and 16 no-distractor trials randomly interleaved. Four such 32-trial blocks were completed for each of the four hemifield-by-task (2 x 2) combinations, using a block-randomized sequence. Within each 32-trial block, half the trials contained task-relevant physical differences, randomly ordered. Physical variability in the unattended feature was also simultaneously interleaved. Spatial and temporal physical differences were uncorrelated.

To avoid floor and ceiling effects, the computer assessed each participant’s performance every 64 trials—after a left and right block pair on the same task—and adjusted task-relevant stimulus parameters accordingly. The initial spatial frequency difference was 28% lower than the standard 1.25-cpd value. At each reevaluation point, if the participant’s spatial frequency judgments exceeded 75% correct, the spatial frequency difference was decreased by 2% of the standard 1.25-cpd value—down to the 20% minimum difference level. If the participant’s spatial frequency judgments fell below 65% correct, the spatial frequency difference was increased by 2% of the standard 1.25-cpd value—up to the 30% maximum difference level. For the temporal task, stimulus
durations were 600 (the default duration, Figures 4C–4G), 300, or 900 ms. At each reevaluation point, simultaneity performance below 65% or above 75% correct, respectively, triggered 300-ms increases or decreases (achieved by a 50% rescaling of the durations shown in Figures 4C–4G) until reaching our maximum (900 ms) or minimum (300 ms) durations. This procedure generated peripheral onset-to-onset asynchronies (Figures 4D–4G) of 100, 200, or 300 ms, depending on the participant’s performance. Critically, this performance-driven adjustment to the stimulus duration produced fixation letter durations (Figure 4E) of 50, 100, or 150 ms, intervals briefer than the 200 ms required for reliable eye movements (Salthouse & Ellis, 1980; Vaughan & Graefe, 1977).

Procedure: Data analysis

All statistics reported in Experiment 1 were based on a completely within-subject research design. The independent variables in Experiment 1 were distractor (absent versus present), task (spatial versus temporal), and attended visual field (left versus right). The dependent variables were $d’$ and its two constituent error types, misses and false alarms, computed according to standard signal detection procedures (Green & Swets, 1966). Misses (false negatives) and false alarms (false positives) were defined as incorrect “same” and “different” responses, respectively. A $d’$ value equaling 1.0 corresponded to 84% correct without response bias.

For each of the three dependent variables, we used a Bonferroni correction to avoid cumulative type 1 error across seven planned (a priori) statistical comparisons: the 3-way task-by-distractor-by-hemifield interaction; the 2-way distractor-by-hemifield interaction on the spatial task; the 2-way distractor-by-hemifield interaction on the temporal task; and four left-versus-right hemifield $t$ tests, one for each combination of task and distractor. All $p$ values reported here reflect the Bonferroni correction and were evaluated at the 0.05 alpha level. Partial eta-squared ($\eta^2 = SS_{effect} / [SS_{effect} + SS_{error}]$) indicates the effect size.

Results and discussion

The results from Experiment 1 are shown in Figure 6. The left (A, D), center (B, E), and right (C, F) panels, respectively, reflect our three dependent variables: $d’$ and its constituent misses and false alarms. Two of our independent variables—task (spatial versus temporal) and attended visual field (LVF versus RVF)—are shown within each panel. The levels of our third independent variable—distractors (absent versus present)—are separated across the top and bottom panels. The top panels (A–C) reflect performance on the less attentionally demanding displays, which contained targets only without distractors. The bottom panels (D–F) reflect performance on the more attentionally demanding displays, which contained targets and distractors.

Consider performance on the less attentionally demanding displays, which contained targets only (Figure 6, top row). Visually inspecting Figure 6A reveals a significant RVF deficit in $d’$ on the temporal task ($t(21) = 3.409, p = 0.019, \eta^2 = 0.356$). By contrast, $d’$ on the spatial task did not exhibit significant hemifield differences despite identical retinal locations across the two tasks. The RVF temporal deficit in $d’$ arose from significantly more RVF
than LVF misses (incorrect “same” responses) on the temporal task \((t(21) = 3.722, p = 0.009, \eta^2_T = 0.397)\)—a hemifield difference not paralleled on the spatial task (Figure 6B). The null differences seen across Figure 6C indicate that false alarms (incorrect “different” responses) did not contribute significantly to the RVF temporal deficit in \(d'\). Overall, Figure 6 (top row) reveals an RVF deficit that (1) was specific to the temporal task, (2) was driven by misses, not false alarms, and (3) did not require attention for excluding distractors.

Now consider how this error pattern changed when we made the displays more attentionally demanding by adding distractors (Figure 6, bottom row). The data on \(d'\) in Figure 6D exhibit significant spatial \((t(21) = 3.702, p = 0.010, \eta^2_T = 0.395)\) and temporal \((t(21) = 6.808, p < 0.001, \eta^2_T = 0.688)\) RVF deficits. These significant RVF deficits arose from very different sources, however. On the spatial task, distractors generated a significant RVF deficit in misses (Figure 6E; \(t(21) = 3.097, p = 0.039, \eta^2_T = 0.314\)) but not in false alarms (Figure 6F). Contrarily, on the temporal task, distractors did not significantly alter the magnitude of the RVF deficit in misses (compare Figures 5B and 5E) but generated a new and significant RVF deficit in false alarms (Figure 6F; \(t(21) = 4.039, p = 0.005, \eta^2_T = 0.437\)). Indeed, these task-specific distractor effects were evident statistically in the distractor-by-hemifield interactions. On the spatial task, the distractor-by-hemifield interaction was significant for misses \((F(1,21) = 16.350, p = 0.005, \eta^2_T = 0.438)\) but nearly zero for false alarms \((F(1,21) = 0.318, p = 1.000, \text{n.s., } \eta^2_T = 0.015, \text{ power} = 0.084)\). Contrarily, on the temporal task, the distractor-by-hemifield interaction was nearly zero for misses \((F(1,21) = 0.039, p = 1.000, \text{n.s., } \eta^2_T = 0.002, \text{ power} = 0.054)\) but significant for false alarms \((F(1,21) = 13.447, p = 0.011, \eta^2_T = 0.390)\).

Overall, Figure 6 demonstrates that, despite the co-presentation of spatial and temporal differences at identical retinal locations, our spatial and temporal tasks obeyed different rules. First, when attention was not required for excluding distractors, the spatial task exhibited no hemifield effects, while the temporal task exhibited an RVF deficit in \(d'\) driven by misses, not false alarms. Second, our attentionally demanding distractors generated task-specific error patterns, significantly more RVF misses on the spatial task and significantly more RVF false alarms on the temporal task.

These experimentally generated task-specific error patterns provide information about why temporal precision was worse in the RVF. The RVF temporal deficit that occurred when attention was not required to exclude distractors arose from misses, not false alarms. This error pattern is consistent with the possibility that when distractors are absent the neural events responsible for the RVF have lower temporal acuity, not greater noise. The noise hypothesis predicts that the RVF would also exhibit significantly elevated false alarms, contrary to our data (Figure 6C). Moreover, our data suggest that the neural events responsible for RVF temporal precision are vulnerable to excessive spatial integration when attention is needed to exclude distractors. This excessive spatial integration was evidenced by the finding that distractors increased RVF false alarms, but not misses, when participants judged temporal differences (Figure 6F). Critically, at the same retinal locations, the same distractors did not induce excessive spatial integration on the spatial task, where false alarm rates remained unaffected by the addition of distractors. Instead, distractors on the spatial task reduced RVF spatial acuity, as evidenced by the increased RVF misses (Figure 6E).

Indeed, on the spatial task, this elevation in RVF misses coupled with the absence of an RVF false alarm effect disconfirms the noise hypothesis, which predicts distractor-induced elevations in both error types.

To summarize, Experiment 1 revealed an RVF simultaneity deficit that had distinct distractor-independent and distractor-induced components. The error patterns suggest that the distractor-independent component arose from low RVF temporal acuity. Adding distractors introduced a separate, significant RVF deficit that appears to reflect inappropriately integrated temporal asynchronies from LVF distractors. Neither the distractor-independent RVF deficit nor the distractor-induced RVF excessive spatial integration occurred on the spatial task at the same retinal locations.

## Experiment 2: Perceptual learning

In Experiment 1, we analyzed error patterns to determine why temporal precision is worse in the right than in the left visual field. In Experiment 2, we analyzed the pattern of practice-based transfer effects to determine when (i.e., the information stage at which) the RVF simultaneity deficit arises in the visual pathway.

### Methods: Procedure

All twenty-two Denison University undergraduates who completed Experiment 1 returned to complete Experiment 2’s seven additional daily sessions.

#### Session 1: Pre-training—The tasks and stimuli (Figure 4) in the pre-training session were identical to those in Experiment 1’s distractor conditions. Specifically, for each participant, the temporal and spatial differences to be discriminated were set to the final level achieved in Experiment 1. Each participant completed 512 actual trials. As in Experiment 1, these trials were divided into 32-trial blocks comprising each combination of the task (spatial or temporal) and attended hemifield (right or left).
variables. The sequence was block randomized. Overall, during the pre-training session, each participant completed 128 trials in each of four conditions (two tasks by two hemifields).

**Sessions 2 through 5: Training**—During each of the four training sessions, all participants trained exclusively on the temporal (simultaneity) task in the RVF. Each training session comprised 512 actual trials. Stimulation was identical to that during pre-training.

**Session 6: Post-training**—The post-training session was identical to the pre-training session in all ways.

**Session 7: Retinal Location Transfer Test**—This session comprised only temporal task trials and was conducted in the event that our training had generated task-specific learning. Recall from Figure 3 that task-specific learning would indicate that our training regimen improved either the decision stage or its connection to the stimulus-driven stage. To distinguish these possibilities in the retinal location transfer test, half of the trial blocks comprised stimuli at the novel retinal locations schematized in Figure 7. The remaining trial blocks comprised stimuli at the prior locations, schematized in Figure 5. Testing at the novel and prior locations was block-randomly sequenced. As always, peripheral cues and blocking provided complete certainty about the locations to be attended before each trial. Each participant completed 512 trials: 128 trials in each combination of a retinal location (prior or novel) and an attended hemifield (right or left).

Methods: Data analysis

All statistics reported in Experiment 2 were based on a completely within-subject research design. For assessing perceptual learning, the independent variables were training (pre-training versus post-training), task (spatial versus temporal), and attended visual field (left versus right). The dependent variables were d’ and its two constituent error types, misses and false alarms, as defined in Experiment 1. For each of the three dependent variables, we used a Bonferroni correction to avoid cumulative type 1 error across seven planned (a priori) statistical comparisons: the 3-way training-by-task-by-hemifield interaction; the 2-way training-by-task interaction in the trained (right) hemifield; the 2-way training-by-task interaction in the untrained (left) hemifield; and four pre-training-versus-post-training t tests, one for each combination of task and hemifield.

For assessing generalization to novel retinal locations, the independent variables were retinal location (prior versus novel) and attended visual field (left versus right). The dependent variables were d’ and its two constituent error types, misses and false alarms, as defined in Experiment 1. For each of the three dependent variables, we used a Bonferroni correction to avoid cumulative type 1 error across five planned (a priori) statistical comparisons: the 2-way location-by-hemifield interaction; the main effect of retinal location; the main effect of hemifield; and two prior-location-versus-novel-location t tests, one in each hemifield.

All p values reported here reflect the Bonferroni correction and were evaluated at the 0.05 alpha level. Partial eta-squared ($\eta^2_{p}$) indicates the effect size.

Results and discussion

The perceptual learning data from Experiment 2 are shown in Figure 8. The left (A, D), center (B, E), and right (C, F) panels, respectively, reflect our three dependent variables: d’ and its constituent misses and false alarms. Two of our independent variables—task (spatial versus temporal) and training (pre versus post)—are shown within each panel. The levels of our third independent variable—attended visual field (left versus right)—are separated across the top and bottom panels. The top panels (A–C) reflect performance in the trained (right) visual field. The bottom panels (D–F) reflect performance in the untrained (left) visual field.

Consider performance in the trained (right) visual field (Figure 8, top row). Visually inspecting Figure 8A reveals that training significantly improved d’ on the temporal task ($t(21) = 4.979, p < 0.001, \eta^2_{p} = 0.541$) but not on the spatial task. Indeed, an ANOVA on the training-by-task interaction in the RVF confirmed significantly more learning on the temporal task than on the spatial task.
This task-specific learning occurred even though the retinal stimulation and the attended locations were identical across the two tasks. Our error analyses indicate that the RVF task specificity was driven less by misses (Figure 8B) than by false alarms (Figure 8C). Training significantly reduced misses on the spatial ($t(21) = 3.415, p = 0.019, \eta^2 = 0.357$) and temporal ($t(21) = 4.295, p = 0.003, \eta^2 = 0.468$) tasks, and the training-by-task interaction for misses was non-significant. By contrast, training significantly reduced false alarms on the temporal task ($t(21) = 4.409, p = 0.002, \eta^2 = 0.481$) but not the spatial task, and the training-by-task interaction for false alarms was significant ($F(1,21) = 26.500, p = 0.001, \eta^2 = 0.558$).

Overall, the top row of Figure 8 reveals that our training significantly improved temporal precision in a task-specific manner. While the improvement in RVF temporal precision arose from significant reductions in misses and false alarms alike, the observed task specificity arose mostly from reductions in false alarms.

The data pattern in the untrained LVF (Figure 7, bottom panels) was similar, albeit not identical, to that observed in the trained RVF. As was true for $d'$ in the RVF (Figure 8A), Figure 8D reveals that our RVF training regimen significantly improved LVF $d'$ on the temporal task ($t(21) = 4.845, p = 0.001, \eta^2 = 0.528$) but not on the spatial task. The training-by-task interaction here likewise confirmed significantly greater learning on the temporal task ($F(1,21) = 8.99, p = 0.048, \eta^2 = 0.300$). The LVF improvement in temporal precision ($d'$) arose from significant reductions in misses ($t(21) = 3.965, p = 0.005, \eta^2 = 0.428$) and marginally significant reductions in false alarms ($t(21) = 2.930, p = 0.056, \eta^2 = 0.290$), as can be seen, respectively, in Figures 7E and 7F. Figure 8F also reveals that, like the RVF case, RVF training did not significantly reduce LVF false alarms on the spatial task. Indeed, the LVF and RVF training effects (i.e., pre- to post-training changes) differed notably from each other only on spatial task misses, which training significantly reduced solely in the RVF (compare Figures 8B to 8E). Overall, the similarities between top and bottom panels of Figure 8 indicate that the learning on the temporal task generalized from the trained (right) to the untrained (left) hemifield. This hemifield generalization was confirmed formally via post-hoc training-by-hemifield interactions on $d'$, which were non-significant on the temporal and spatial tasks even without correcting for multiple post-hoc comparisons.

We also evaluated whether our training effects generalized to novel retinal locations (Figure 7), which were neither cued nor stimulated during our pre-training, training, and post-training sessions. The results from the retinal location transfer test are shown in Figure 9. Visual inspection reveals that performance in each hemifield was comparable at the prior and novel locations for $d'$, misses, and false alarms (panels A, B, and C, respectively). Indeed, the six corresponding $t$ tests were non-significant. Similarly, the main effect of location and the location-by-hemifield interaction were non-significant on each of the three dependent variables. Overall, these results indicate that our training effects generalized to novel retinal locations.

The results in Figures 8 and 9 can be interpreted within the framework introduced in Figure 3 to provide information about the neural events that our training modified. To begin, the task-specific learning evident in Figure 8 suggests that our training generated neural modifications at some point after the stimulus-driven stage (Figure 3,
solid bottom oval). If significant neural modifications had occurred at the stimulus-driven stage, significant post-training improvements would be expected on the untrained (spatial) task—contrary to our findings. The observed task-specific learning therefore implicates either the temporal decision stage or the connection to it as the modified source. That our learning effects generalized to the untrained hemifield (Figure 8) and to novel retinal locations (Figure 9) suggests that training modified the temporal task's decision stage. Had training modified its connection instead, one would expect learning to be specific to the trained hemifield and retinal locations—contrary to our findings. Only the temporal decision stage shared input from both stimulus-driven stages. Thus, the combination of task specificity and location generalization suggests that the perceptual learning observed here reflects neural modification at the temporal decision stage.

Interestingly, the location generalization in Figure 9 implicates neural modification at the temporal decision stage for misses (Figure 9B) and false alarms (Figure 9C) alike. In principle, these two error types—which, respectively, indexed low temporal acuity and excessive spatial integration (see Experiment 1)—could have been implicated at distinct stages schematized in Figure 3. Specifically, either misses or false alarms could have exhibited location specificity rather location generalization, and such an outcome would have implicated neural modification at a stage preceding the decision. Instead, the data suggest that pre-attentive (Figure 9B) and attentional (Figure 9C) contributions to the RVF deficit arose at the temporal decision stage, as noted in Table 1.

Finally, even though participants trained exclusively in the RVF, post-training temporal precision (d') still exhibited an RVF deficit. This can be seen in Figure 9, where all the data are post-training and the main effect of hemifield reveals that d' (Figure 9A) was significantly lower in the RVF than in the LVF (F(1,21) = 16.115, p = 0.004, $\eta^2_p = 0.434$). This RVF deficit in d' arose more from misses (Figure 9B; $F(1,21) = 22.213$, $p < 0.001$, $\eta^2_p = 0.514$) than from false alarms (Figure 9C; $F(1,21) = 6.704$, $p = 0.086$, n.s., $\eta^2_p = 0.242$, power = 0.695). The preponderance of RVF misses implies that temporal acuity remained worse in the right than left visual field, despite significant RVF practice-based improvements. In short, although RVF temporal training significantly improved RVF temporal precision (Figure 8), the training did not eliminate the RVF temporal deficit (Figure 9).

**General discussion**

Experiment 1 provided new information about why simultaneity judgments are less precise in the right visual field (RVF) than in the left visual field (LVF). The data revealed two causes, distinguishable from each other by attentional demands. First, when attention was not needed to exclude distractors (our no-distractor condition), participants exhibited an RVF simultaneity deficit driven by temporal asynchrony misses, not false alarms. This error pattern is consistent with low RVF temporal acuity, not excessive RVF neural noise; the neural noise hypothesis also predicts more RVF than LVF false alarms, contrary to the data. Second, when attentionally demanding distractors were added on the simultaneity task, RVF false alarms increased significantly, but RVF misses did not. This suggests an RVF attentional failure; participants were unable to exclude temporal asynchronies from LVF distractors when judging the simultaneity of RVF targets. Thus, (1) distractor-independent low RVF temporal acuity combined with (2) distractor-induced excessive spatial integration to generate the present RVF simultaneity deficits.

Experiment 1’s distractor effects were task specific. On the simultaneity task, distractors significantly increased RVF false alarms but not RVF misses; conversely, distractors significantly increased RVF misses but not RVF false alarms on the spatial frequency task. These task-specific effects confirm and extend prior reports that distinct rules govern attention’s temporal versus spatial grain (Aghdaee & Cavanah, 2007; Dye & Bavelier, 2010; Kelly & Matthews, 2011; Yeshurun & Levy, 2003).

Experiment 1’s distractor effects were also hemifield-specific. Indeed, in sharp contrast to the above-mentioned distractor effects that occurred when participants attended RVF targets, distractors did not significantly alter misses or false alarms on either task when participants attended
LVF targets. Critically, this hemifield difference arose despite symmetrical retinal stimulation in the left and right hemifields. This in turn implies that asymmetric neural events governed LVF versus RVF attention in the present study.

Several physiologically oriented studies have also revealed lateral hemifield attentional asymmetries. These studies suggest that the left cortical hemisphere mediates attention to the RVF while the right cortical hemisphere mediates attention to both the LVF and RVF (Badzakova-Trajkove et al., 2010; Heilman & Van Den Abell, 1980; Mesulam, 1981; Nobre et al., 1997; Szczepanski, Koenen, & Kastner, 2010; Vandenberghhe et al., 1997). It is intriguing, then, that all of the present distractor-induced impairments occurred only when participants attended targets in the RVF—which is presumably monitored by both hemispheres. To appreciate this counterintuitive point, consider current thinking about another attentional hemifield asymmetry, the lower (versus upper) hemifield attentional advantage (He, Cavanagh, & Intriligator, 1996; Lakha & Humphreys, 2005). He et al. (1996) have explained this lower field attentional advantage by noting that the parietal lobe—an attention related region (Buschman & Miller, 2007)—receives more projections from the lower than the upper hemifield (Van Essen, Newcombe, & Maunsell, 1984). Enhanced lower hemifield visual performance also correlates retinotopically with enhanced fMRI activity patterns in early visual cortical areas (Liu, Heeger, & Carrasco, 2006), which impose an important constraint on visual attention (Carlson, Alvarez, & Cavanagh, 2007). Extending this reasoning, the presumed RVF representation in both cortical hemispheres would seemingly predict greater (not less) distractor immunity in the RVF than in the LVF—opposite to the present findings. Perhaps there are important qualitative differences between the neural resources mediating attention to the left versus right hemifields. In fact, experimental manipulations involving EEG (Verleger et al., 2009) and transcranial magnetic stimulation (Müri et al., 2002; Woo, Kim, & Lee, 2009) coupled with clinical reports of split brain (Forster, Corballis, & Corballis, 2000) and right parietal lobe patients (Battelli et al., 2001; Battelli, Cavanagh, Martini, & Barton, 2003; Rorden, Mattingley, Karnath, & Driver, 1997) suggest that the right parietal lobe is specialized for temporal judgments. Such findings have led to recent speculation about a “when” pathway (Battelli, Pascual-Leone, & Cavanagh, 2007; Battelli, Walsh, Pascual-Leone, & Cavanagh, 2008; Davis, Christie, & Rorden, 2009) that is distinct from the “what” (ventral) and “where” (dorsal) pathways (Mishkin & Ungerleider, 1982). The task- and hemifield-specific error patterns in our Experiment 1 provide further evidence that distinct neural events set the limit on temporal versus spatial judgments.

Experiment 2’s perceptual learning procedures provided new information about when (i.e., the visual information stage at which) RVF deficits arise in simultaneity judgments. Training on RVF simultaneity judgments generated significant improvements that were task specific but generalized to the untrained hemifield and to novel retinal locations. The observed task specificity implies that the neural modifications underlying the behavioral improvement occurred subsequent to the stimulus-driven stage (see Figures 2 and 3). This in turn suggests that the training modified either the neural events mediating the simultaneity decision or those connecting the stimulus-driven and simultaneity decision stages. That the improvement generalized to the untrained hemifield and to novel retinal locations implicates the simultaneity decision—the only visual information stage receiving input from both the trained and untrained retinal locations (see Figure 3). Additionally, our retinal location transfer test revealed that despite significant practice-based improvements in RVF simultaneity judgments, a significant RVF simultaneity deficit remained. This post-learning RVF simultaneity deficit predominantly reflected excessive RVF misses, suggesting low post-learning RVF temporal acuity. It would be parsimonious to speculate that this low post-learning RVF temporal acuity occurs at the simultaneity decision stage—the information stage that appears to have been modified by training.

The present results confirm and extend the implications of recent reports on feature-based attention. These include psychophysical (White & Carrasco, 2011) and fMRI (Jehee, Brady, & Tong, 2011) experiments demonstrating that feature-based attention to a cued location boosts sensitivity to that feature even at task-irrelevant locations. This global feature-based attentional selection fits well with the present perceptual learning, which was specific to the feature attended during training (simultaneity, not spatial frequency) but generalized to locations that were irrelevant during training. It is notable, too, that our feature-based learning occurred despite identical retinal stimulation on the trained (simultaneity) and untrained (spatial frequency) features. Indeed, our learning effects mirror those of several prior studies in which practice improved performance on only the attended feature when task-irrelevant features had been co-presented in space and time (Ahissar & Hochstein, 1993; Saffell & Matthews, 2003; Shiu & Pashler, 1992).

**Conclusion**

We aimed to provide new information about why and when RVF deficits arise in simultaneity judgments. Accordingly, we generated an informative pattern of errors based on signal detection theory (Green & Swets, 1966) and generated an informative perceptual learning pattern (Petrov et al., 2005). The error pattern suggests that RVF simultaneity deficits reflect low RVF temporal
acuity and excessive RVF spatial integration, respectively, in the absence and presence of attentionally demanding distractors. The perceptual learning pattern suggests that RVF simultaneity deficits reflect neural events at the simultaneity decision stage.

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Footnotes

1A recent article demonstrates that temporal order judgments (TOJs) and simultaneity judgments can parsimoniously arise from the same neural computational model (Roach, Heron, Whitaker, & McGraw, 2011). Nevertheless, psychophysical data reveal that these two seemingly similar tasks operate hierarchically; the precision of TOJs depends on one’s sensitivity to simultaneity and not vice versa (van Eijk et al., 2010).
2Toet and Levi (1992) found that spatial crowding occurs when the center-to-center distance between targets and distractors is less than 0.25 times the target eccentricity in the tangential direction and 0.5 times the target eccentricity in the radial direction. The center-to-center distance between our targets and distractors always exceeded 1.0 times the target eccentricity.
3In all experiments reported here, the accuracy of the initial letter response for each participant far exceeded the chance performance level of 10% correct. Within each experimental condition, the mean accuracy of the initial letter response always exceeded 91% correct and typically ranged from 93% to 97% correct.
4We did not ask our participants to indicate handedness. Although Efron (1963) reported that handedness was correlated with hemifield differences in simultaneity and temporal order judgments, subsequent and more complete psychophysical (Newman & Albino, 1977) and fMRI (Badzakova-Trajkov, Haverling, Roberts, & Corballis, 2010) findings have argued against this handedness effect.
5We also measured reaction times (RTs) for each letter response and each peripheral response. This allowed us to assess whether any RVF deficits in d’ might simply reflect a trade-off between the speed and precision of responding. Across all distractor and task conditions, however, mean letter RTs and mean peripheral RTs were longer for RVF than for LVF discriminda. Thus, the RVF deficits reported here are conservatively estimated, and we omit further discussion of RTs.
6Kastner, Pinsk, De Weerd, Desimone, and Ungerleider (1999) offer an exception to this hemispheric asymmetry, as their imaging results indicated largely symmetrical left and right hemisphere activations.
7Similar to our attentional lateral hemifield effects, the lower hemifield advantage in these studies (He et al., 1996; Lakha & Humphreys, 2005) arose from endogenous attention, i.e., excluding distractors. There is also evidence that exogenous (transient, stimulus driven) attentional enhancement is greater in the lower than the upper hemifield (Fuller, Rodriguez, & Carrasco, 2008), despite distinct neural events mediating endogenous versus exogenous attention (Buschman & Miller, 2007).

References


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