Left visual field attentional advantage in judging simultaneity and temporal order

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Dynamic environments often contain features that vary simultaneously as well as features that vary sequentially. In principle, the correspondingly distinct sensations of simultaneity and temporal order could arise from a single shared neural computation that involves differencing two arrival times. On the other hand, simultaneity judgments (SJs) and temporal order judgments (TOJs) have distinct informational requirements that could be optimized by distinct neural events. To explore overlap in the neural events mediating SJs and TOJs, the present experiments built on recent reports that SJ precision in the left visual field (LVF) exceeds that in the right visual field (RVF). Participants completed divided attention tasks requiring either SJs or TOJs to LVF or RVF targets. SJs exhibited a significant LVF advantage, as expected. TOJs also exhibited a significant LVF advantage. Specifically, simply repositioning targets from the LVF to the RVF generated mean TOJ threshold increases (temporal precision reductions) between 39% and 57%, an effect size equivalent to approximately two LVF detectors for each RVF detector. Control experiments indicated that this LVF advantage reflected the temporal resolution of visual attention, rather than lower-level flicker discrimination or masking. These findings constitute additional evidence for an LVF advantage in time-sensitive attentional tasks and further contradict our subjective experience of homogenous temporal precision across the visual field.

Introduction

Dynamic environments contain stimuli that vary simultaneously and stimuli that vary sequentially. Simultaneously varying stimuli often originate from "the same thing out there in the world" (Thomas & Shiffrar, 2010), and the temporal order of stimuli often

provides information about the direction of motion. As a result, evolution would likely favor animals that—at a sustainable metabolic cost—correctly judge simultaneity and temporal order. Here we explored the precision with which participants attentionally track simultaneity and temporal order in the left and right visual fields.

Several studies indicate that attention to the left visual field (LVF) requires neural resources distinct from those mediating attention to the right visual field (RVF; Alvarez & Cavanagh, 2005; Alvarez, Gill, & Cavanagh, 2012; Chakravarthi & Cavanagh, 2009; Delvenne, Castronovo, Demeyere, & Humphreys, 2011; Reardon, Kelly, & Matthews 2009; Shipp, 2011). This independence becomes even more evident with experiments revealing significantly greater LVF than RVF performance on time-sensitive attentional tasks. For example, salient LVF advantages occur on rapid serial visual presentation (RSVP) tasks that require participants to select from distractor streams targeted letters, shapes, or faces (Asanowicz, Śmigasiewicz, & Verleger, 2013; Holländer, Corballis, & Hamm, 2005; Scalf, Banich, Kramer, Narechania, & Simon, 2007; Śmigasiewicz et al., 2010; Verleger, Dittmer, & Śmigasiewicz, 2013; Verleger et al., 2009; Verleger et al., 2010; Verleger, Śmigasiewicz, & Möller, 2011). Along these lines, the motivation for the present study comes most directly from recent divided-attention experiments demonstrating significantly more precise LVF than RVF simultaneity judgments (SJs; J. G. Kelly & Matthews, 2011; Matthews, Vawter, & Kelly, 2012). SJs share computational similarities with temporal order judgments (TOJs), which share computational similarities with motion perception. We describe these similarities and their relationship to LVF attentional advantages in turn.

In principle, SJs could be based on a computation that also renders TOJs. A straightforward example
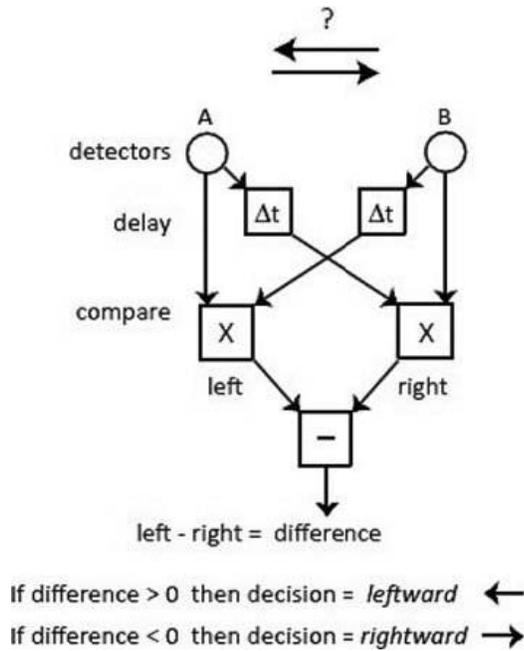
Figure 1. Cartoon motion-direction model inspired by Reichardt (1961). A and B are two spatially separated detectors. Their outputs go directly (vertical arrows) and indirectly (oblique arrows) with a temporal delay (Δt) to two comparators. If an object moved from left to right and was detected by A first and B second, the delayed A output and the direct B output would reach the right side comparator at the same time, causing that comparator to have a large output. The right side comparator's output is labeled "right." The A and B detectors are connected in a complementary manner with the left side comparator, whose output is labeled "left." A direction decision is based on the difference = left – right. If the difference is >0, then the decision is leftward; if the difference is <0, then the decision is rightward. The decisions could simply be renamed "B first" and "A first" to be appropriate for a temporal order judgment (TOJ), and the mechanism could be termed a temporal correlator.

entails finding the difference between the arrival time (AT) of two events, "a" and "b": $AT_a - AT_b$ (Allan, 1975; Sternberg & Knoll, 1973; Ulrich, 1987). Differences with magnitudes sufficiently similar to zero would be judged simultaneous; the sign of nonzero differences would specify temporal order. In addition, this

temporal order computation resembles various motion perception models (Adelson & Bergen, 1985; Pantle & Hicks, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Figure 1 shows a cartoon motion model inspired by Reichardt's (1961) model for insect motion discrimination. Like other motion perception models, the cartoon model serves as a temporal correlator. Temporal correlators register the timing of inputs to determine temporal order or, equivalently, the direction of visual motion.

Visual motion perception can arise from various types of visual signals. Some of these visual signals stimulate the "luminance-based motion system," whereas others stimulate the "attention-based motion system" (Cavanagh, 1992; Lu & Sperling, 1995). The luminance-based motion system responds to positional changes in dark/light borders (Smith, 1994). The attention-based motion system responds when participants selectively track positional changes in features not defined by dark/light borders. For example, participants might perceive downward motion in two vertically aligned Gabor stimuli by selectively tracking an orientation change in the top stimulus followed by an orientation change in the bottom stimulus (see Figure 2). Temporal correlators offer considerable computational generalizability, describing both the luminance-based and the attention-based motion systems. Notably, though, the luminance-based and attention-based motion systems rely on distinct *neural* mechanisms, as demonstrated by various psychophysical experiments (Lu & Sperling, 1995).

One recent psychophysical experiment demonstrated that the luminance-based system exhibits an LVF advantage. Specifically, Bosworth, Petrich, and Dobkins (2012) found significantly lower LVF than RVF thresholds when participants discriminated directional differences among moving luminance dots in the periphery. This LVF advantage in luminance-based direction discrimination—combined with the fact that temporal correlators (Figure 1) bring luminance-based motion, direction discrimination, attention-based motion, and TOJs into a unified framework—raises an interesting question. Do attention-based motion judg-
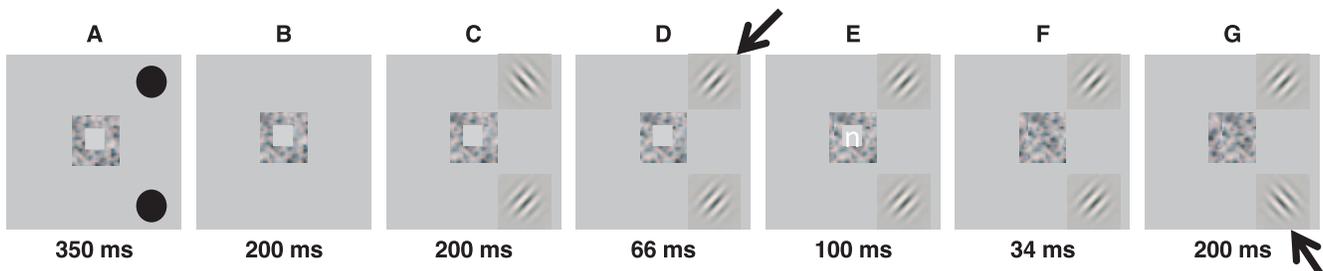

Figure 2. Stimuli for SJs and TOJs on a right hemifield trial. Arrows in panels D and G emphasize where orientation changes occur but did not appear in the actual displays.

ments—or equivalently, attention-based TOJs—exhibit an LVF advantage?

A reason to believe they would comes from the above-mentioned experiments showing that stimuli (such as those schematized in Figure 2) registered by the attention-based motion system generate an LVF advantage in SJs (J. G. Kelly & Matthews, 2011; Matthews et al., 2012). One might expect the LVF advantage in SJs to extend to TOJs, given that, in principle, these two tasks could share a temporal correlator's ATa – ATb computation. On the other hand, SJs and TOJs have distinct information requirements. SJs require *magnitude* information (the *absolute value* of ATa – ATb), whereas TOJs require *vector* information (the *sign* of ATa – ATb). These distinct information requirements might be met optimally by distinct neural implementations. For example, optimal magnitude estimates for SJs might arise from pooling across neurons with receptive fields spanning various spatial scales: the target size, a lateral hemifield, the full visual field. By contrast, optimal vector estimates for TOJs would require target-specific resolution, unachievable by neurons with receptive fields spanning an entire lateral hemifield or the full visual field. To the extent that distinct neural ensembles mediate SJs and TOJs, one would not necessarily expect the LVF advantage in SJs to extend to TOJs. Another reason why the LVF advantage in SJs would not necessarily extend to TOJs comes from tactile psychophysical experiments demonstrating a dissociation between these two tasks. Notably, crossing the arms impairs TOJs but not SJs when judging the relative timing of stimulation to the left and right hands (Axelrod, Thompson, & Cohen, 1968; Fujisaki & Nishida, 2009; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001).

The present study employed similar logic to investigate a possible dissociation between SJs and TOJs in visual attention. Specifically, we maintained identical retinal stimulation across the SJ and TOJ tasks while requiring participants to attentionally track subtle orientation-defined timing differences in either the LVF or RVF. To summarize briefly, the data revealed significant LVF attentional advantages for SJs and TOJs alike. The significant LVF advantage on each task occurred even in a control experiment that reduced the distinctiveness of luminance-transients exploitable by the luminance-based motion system. Additional control experiments disconfirmed the hypotheses that the LVF advantage arose from low-level temporal frequency discrimination or masking. Overall, these findings provide further evidence for a robust LVF advantage in time-sensitive attentional tasks and further contradict our subjective experience of homogenous temporal precision across the visual field.

Method

Apparatus

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

Discriminanda

The discriminanda 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/m^2) and minimum (5.83 cd/m^2) luminances that rendered high contrast (Michelson contrast = 89.76%) within the apparently gray surround (16.1 cd/m^2). The orientation of each Gabor patch came randomly from the full 180° range. With a spatial frequency of 1.25 cycles per degree, each Gabor patch comprised randomly phase-shifted light-dark cycles that collectively spanned a 3.2° × 3.2° (84 × 84 pixel) square region.

Stimulus sequence: Main experiment

Figure 2 schematizes the stimulus sequence for a sample RVF trial. Each trial began with a central fixation marker shown simultaneously with a pair of peripheral cues (Figure 2A). The fixation marker was a small gray square (16.1 cd/m^2; 0.44° or 12 pixels per side) inscribed in a larger square (1.33° 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 circles (16.1 cd/m^2; CIE 0.615, 0.345; 3.2° [84-pixel] diameter; shown here in black) 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 LVF or RVF.

After 350 ms, the peripheral cues were replaced by the gray surround (16.1 cd/m^2) for 200 ms (Figure 2B). Gabor targets then appeared at the cued positions for 200 ms (Figure 2C). The distances between the stimuli are detailed in Figure 3 and were well beyond the critical region for spatial crowding (Toet & Levi, 1992). For the next 66 ms, one Gabor patch changed
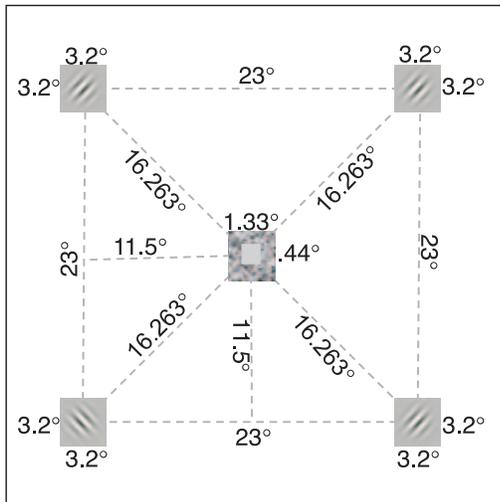
Figure 3. Stimulus spacing and size. Each trial contained a central letter at fixation and either two LVF Gabor targets or two RVF Gabor targets.

orientation by 90°. In the sample trial schematized in Figure 2, only the upper right Gabor patch (indicated here by the black arrow) has changed orientation at this point in the sequence (Figure 2D). For the next 100 ms, 1 of 10 randomly selected lowercase letters (31.20 cd/m²; 31.92% contrast; 12-point Helvetica font) appeared at fixation (Figure 2E; 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 2F). During the final 200 ms, the Gabor patch that had not previously changed orientation by 90° now did so, as schematized by the black arrow in Figure 2G.

SJ and TOJ tasks

The task on each trial comprised two responses. First, to ensure control of fixation, the participant had to correctly identify the central letter (shown in Figure 2E). 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 peripheral judgment. In SJ trial blocks, participants indicated whether the two peripheral Gabor targets changed orientation at the same time or at different times. In TOJ trial blocks, participants indicated whether the changes in peripheral Gabor-target orientation generated a positive (upward: bottom first, top second) or negative (downward: top first, bottom second) motion direction. To maintain motivation, immediate auditory feedback identified each letter response and each peripheral response as either correct or incorrect. The computer also announced the per-

centage of correct letter responses and the percentage of correct peripheral responses after every 128 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 were Denison University undergraduates who reported normal or corrected-to-normal vision. Separate groups participated in the main experiment ($n = 21$), luminance transient control experiment ($n = 18$), temporal frequency discrimination control experiment ($n = 18$), and masking control experiment ($n = 23$).

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. Subsequently, each participant completed 512 actual trials divided into four separate 128-trial blocks. The 128-trial blocks comprised four block-randomly ordered 32-trial sets: one in each of the four (2×2, visual field by task) experimental conditions. Randomly within each 32-trial set, we presented four trials at each of six temporal asynchronies (± 100, ± 200, ± 300 ms) and eight trials on which the orientation changes were synchronized. We randomly predesignated these synchronized trials as either "positive" or "negative" with equal probability on the TOJ task. This prevented biasing responses on TOJ trials when there was not a physically correct answer. To reduce floor and ceiling effects on the peripheral tasks, we adjusted the central-letter task difficulty when necessary. Specifically, after every 128 trials—and uniformly across all four (2×2) experimental conditions—we reduced the central-letter duration from 100 ms to 50 ms if peripheral performance exceeded 75% correct. If the participant's 128-trial peripheral performance fell below 65% correct, we increased the letter duration by 50 ms until reaching the 150-ms maximum. All trials contained letter durations briefer than the 200 ms required for reliable eye movements (Salthouse & Ellis, 1980; Vaughan & Graefe, 1977).

Procedure: Data analysis

For SJs, we assessed temporal precision using standard signal detection procedures to determine d' (Green & Swets, 1966). Computationally, d' corresponds to (zHits) – (zFalse Alarms) with $d' = 0.6745$

reflecting the nonbiased 75% discrimination threshold. Operationally, hits and false alarms occurred when participants made "different" responses to asynchronized and synchronized targets, respectively. For each participant, we determined 12 d' prime values: one at each asynchrony (−300, −200, −100, +100, +200, +300 ms), separately for the LVF and RVF conditions.

For TOJs, we assessed temporal precision by constructing psychometric functions separately for each hemifield (LVF vs. RVF). The psychometric function's abscissa comprised target asynchronies ranging between −300 ms (top stimulus changed orientation first) and +300 ms (bottom stimulus changed orientation first) in 100-ms steps. The psychometric function's ordinate reflected the proportion of "positive" (upward motion) responses. We used a least-squares procedure to fit the data with a sigmoid of the form

$$\frac{1}{1 + \exp\left(-K(X - Xo)\right)}$$

where K and Xo determine the slope and midpoint of the sigmoid, respectively. From the best-fitting sigmoid, we interpolated—separately for each lateral hemifield condition—the nonbiased 75% just noticeable difference, which indexed time discrimination. These discrimination thresholds corresponded to half the stimulus (target asynchrony) change required to alter the response rate from 0.25 to 0.75. In the main experiment and the temporal frequency discrimination control experiment (detailed below), we determined the LVF and RVF discrimination thresholds separately for each participant. For those experiments, the best-fitting sigmoid correlated well with each participant's responses (mean correlation coefficient (r) = 0.92, median = 0.96, range = 0.72–0.99). However, noisier data in the luminance transient control experiment (detailed below) necessitated computing discrimination thresholds by first averaging performance across participants within each lateral hemifield condition. To fairly compare TOJs across experiments, for each participant we recorded the proportion correct at each asynchrony (±100, ±200, ±300 ms), separately for the LVF and RVF conditions.

All inferential statistics reported here reflect our completely within-subject research designs, with p values evaluated at the two-tailed 0.05 alpha level. Partial eta-squared ($_p\eta^2$ = SSeffect/[SSeffect + SSerror]) indicates the effect size. The Supplementary Information contains the raw data from all present experiments and additional graphs comparing LVF and RVF performance.

Control experiments

Except when otherwise noted, the stimuli in the control experiments exactly matched those of the main

experiment. Also, as in the main experiment, we ensured fixation in each control experiment by requiring participants to correctly identify the central letter before judging peripheral Gabor targets.

Luminance transient control experiment

Each trial in the luminance transient control experiment comprised two 0.625 cycles per degree Gabor targets that flickered continuously at 30 Hz. The 30-Hz flicker arose from toggling each Gabor target in counterphase according to a square-wave temporal profile on alternate 60-Hz frames. In this way, many task-irrelevant luminance transients preceded and followed the luminance transient that arose from the orientation change.[1] The orientation change remained the discriminative stimulus for SJs and TOJs in the luminance transient control experiment, thereby maintaining parody with the main experiment.

Temporal frequency discrimination control experiment

Each trial in the temporal frequency discrimination control experiment comprised two Gabor targets that flickered at rates differing from each other randomly by one of the following four temporal periods: 33 ms (133 vs. 166 ms), 100 ms (100 vs. 200 ms), 167 ms (66 vs. 233 ms), and 234 ms (33 vs. 267 ms). The flicker arose from toggling each Gabor target in counterphase according to a square-wave temporal profile. Participants reported the location (top or bottom) of the faster flickering peripheral Gabor target. The faster flickering target appeared with equal probability in the top and bottom locations. Participants completed 256 trials (excluding practice trials), divided into four 64-trial blocks. Each 64-trial block comprised two separate randomly ordered LVF and RVF sets of 32 trials.

Masking control experiment

Unlike the main experiment, in the masking control experiment, one of the two targets remained unchanged on half the trials, randomly. Participants reported whether one or two ("single" or "double") orientation changes occurred. Single and double orientation changes occurred with equal probability. Participants completed 256 trials (excluding practice trials), divided into four 64-trial blocks. Each 64-trial block comprised two separate randomly ordered LVF and RVF sets of 32 trials. On trials containing two orientation changes, the interstimulus interval (ISI) was constant for an entire 64-trial block at just one of three values: 100, 200, or 300 ms. To reduce floor and ceiling effects, we adjusted the ISI brevity as needed after every 64 trials and uniformly across both hemifield conditions when peripheral performance fell below 65% correct or
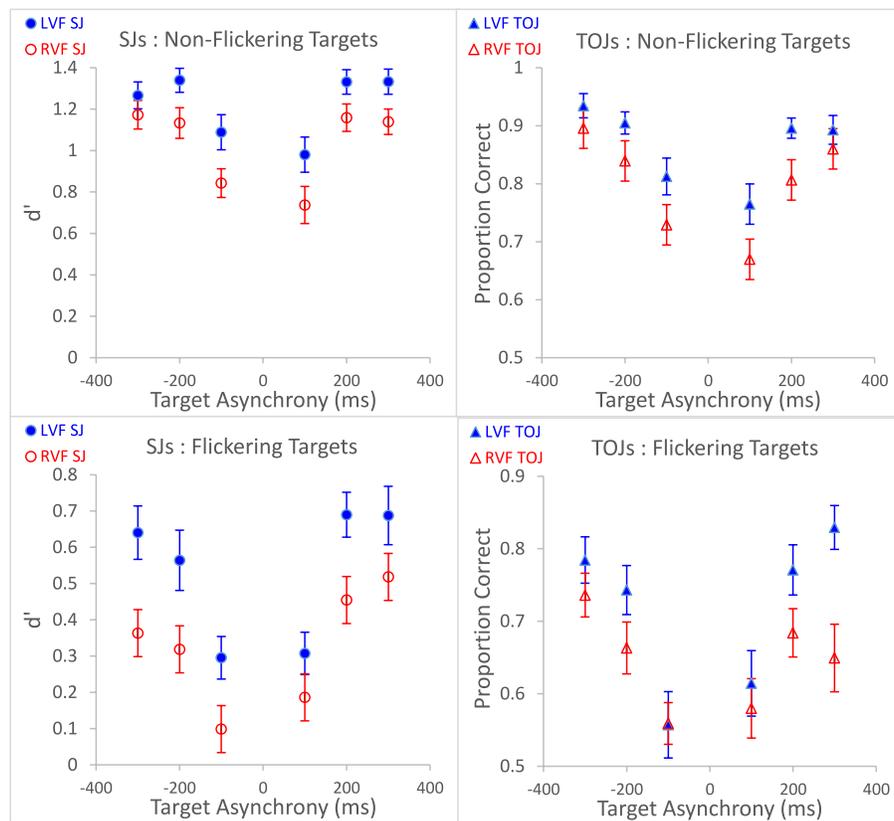
Figure 4. Descriptive statistics. Top panels depict performance on nonflickering targets in the main experiment ($n = 21$). The bottom panels depict performance on flickering targets in the luminance transient control experiment ($n = 18$). Note that the *y*-axes span a smaller range for flickering targets. The left and right panels, respectively, depict SJs (d'; circles) and TOJs (proportion correct; triangles). Within each panel, the LVF performance (closed blue symbols) exceeds the RVF performance (open red symbols) at all or most asynchronies. Error bars reflect ± 1 *SEM*.

exceeded 75% correct. This procedure resulted in 5, 15, and 3 participants, respectively, requiring 100-, 200-, and 300-ms ISIs by the end of the experiment.

Results

Our primary findings appear in Figure 4, where an LVF advantage can be seen in each panel. The figure's upper left panel displays SJ precision (d') for the main experiment's nonflickering targets. Here, the precision of LVF-SJs (closed blue circles) significantly exceeded, $t(20) > 2.582$, $p < 0.0183$, $_p\eta^2 > 0.259$, that of RVF-SJs (open red circles) at each target asynchrony except -300 ms, where the LFV advantage fell shy of significance, $t(20) = 1.758$, $p = 0.0948$, n.s., $_p\eta^2 = 0.139$. SJ precision also exhibited a significant LVF advantage at each asynchrony when targets flickered in the luminance transient control experiment (Figure 4's lower left panel; $t(17) > 2.107$, $p < 0.048$, $_p\eta^2 > 0.189$). Visually inspecting Figure 4's right panels similarly reveals an LVF advantage in the proportion of correct

TOJs, although this advantage diminishes when performance nears the floor or ceiling. As noted in the Method section, we compared LVF and RVF TOJ precision via discrimination thresholds. Simply repositioning our main experiment's nonflickering targets from the LVF to the RVF significantly increased TOJ discrimination thresholds from 92 to 141 ms, a 57% temporal precision decrease, $t(20) = 3.969$, $p = 0.001$, $_p\eta^2 = 0.441$. Thresholds also increased (temporal precision decreased) 39% (from 223 to 310 ms) when we moved the luminance transient control experiment's flickering targets from the LVF to the RVF.

To appreciate the magnitude of these LVF-TOJ threshold advantages, recall that thresholds improve as neural signal-to-noise ratios (SNRs) improve. Recall also that neural SNRs improve (thresholds decline) when the number of independent detectors (n) increases, because noise can be expressed in standard errors, which decrease by the square root of n ($SE = SD \div \sqrt{n}$). Consequently, the LVF-TOJ threshold advantages in our main experiment (57%) and luminance transient control experiment (39%), respectively, reflect effect sizes equivalent to 2.5 and 1.9 LVF detectors for

Hemifield	Mean PSE (ms)	*SEM* (ms)	*p* value	95% Confidence Interval (ms)
LVF	−34.36 (top faster)	10.130	0.0035	−55.735 to −12.991
RVF	−65.946 (top faster)	9.957	0.0001	−86.953 to −44.939

Table 1. Points of subjective equality (PSE) from the flicker discrimination control experiment. *Notes*: Participants exhibited a "top faster" bias in the LVF (~34 ms) and RVF (~66 ms). One-sample *t* tests with a zero PSE as the test value generated the *p* values shown here.

each RVF detector.[2] The larger LVF-TOJ advantage in the main experiment might reflect a luminance-based motion contribution and/or an artifactual difference between the main experiment's noiseless signals and the luminance transient control experiment's noisy signals. Indeed, noisy signals at the luminance transient control experiment's ±100-ms asynchronies generated floor effects that eliminated the LVF-TOJ advantage clearly seen at the same asynchronies in the main experiment (compare Figure 4's right panels).

We refrain from quantitatively comparing SJ precision to TOJ precision. To appreciate why, note that that the stimulus asynchronies necessary for determining *nonbiased* SJ precision differ from those necessary for determining *nonbiased* TOJ precision. One controls for biased SJ hit rates by subtracting false alarms, objectively indexed by factually incorrect ("different") responses on synchronized *SJ* trials. Responses on synchronized *TOJ* trials, though, cannot be objectively classified as factually correct or incorrect. Consequently, these task-specific stimulus requirements undermine fair, quantitative comparisons of precision on the SJ and TOJ tasks. By contrast, within each task, LVF precision can be fairly compared quantitatively to RVF precision. The data from our main experiment and luminance transient control experiment clearly demonstrate greater LVF than RVF temporal precision for SJs and TOJs alike. Accordingly, we turn now to further experiments on this pervasive LVF advantage.

The LVF advantage in our SJs and TOJs seems surprising because, to our knowledge, individual neurons in the early visual pathway do not exhibit hemifield differences in temporal tuning. Nevertheless, in principle, it remains possible that neural *ensembles* in the early visual pathway have higher temporal precision for LVF than for RVF targets. This predicts better temporal performance in the LVF than in the RVF when discriminating the rates of flickering stimuli. We tested this prediction with flickering peripheral Gabor targets that differed from each other by temporal periods ranging between 33 and 234 ms, in 67-ms steps (see the Temporal Frequency Discrimination Control Experiment section). Participants reported the location (top or bottom) of the faster flickering peripheral Gabor target on each trial. We found similar temporal-period discrimination thresholds in the LVF ($M = 75.9$ ms, *SE* $= 6.6$ ms) and RVF ($M = 79.4$ ms, *SE* $= 7.2$ ms), $t(17) = 0.442$, $p = 0.664$, n.s., $_p\eta^2 = 0.011$, power $= 0.07$. This

argues against the hypothesis that the LVF advantage in our SJs and TOJs arose from hemifield-specific temporal precision in low-level neural ensembles.

An alternative explanation for the LVF advantage in our SJs and TOJs pertains to masking. Masking could have occurred in our SJs and TOJs if one orientation transient impaired detection of ("masked") the other (e.g., Sperling, 1965). With either of the two transients perceptually unavailable, participants would be reduced to guessing about the transients' relative timing. Greater LVF than RVF immunity to masking could generate the observed LVF advantage in SJs and TOJs alike. Critically, the masking hypothesis also predicts an LVF advantage in simply *counting* the transients (i.e., one versus two per trial). We tested this prediction with displays that contained one or two transients, and participants indicated how many they saw. In all ways, the displays matched those in Figure 2, except now one of the two transients was eliminated on half of the trials, randomly (see the Masking Control Experiment section). We found similar LVF ($M = 21.5\%$, $SE = 2.7\%$) and RVF ($M = 23.8\%$, $SE = 2.4\%$) miss rates (incorrect "single transient" responses; $t[22] = 0.716$, $p = 0.481$, n.s., $_p\eta^2 = 0.023$, power $= 0.105$) and similar LVF ($M = 24.8\%$, $SE = 2.5\%$) and RVF ($M = 29.1\%$, $SE = 2.3\%$) false alarm rates (incorrect "double transient" responses; $t[22] = 1.366$, $p = 0.186$, n.s., $_p\eta^2 = 0.078$, power $= 0.257$). This performance similarity disconfirms the hypothesis that the LVF advantage in SJs and TOJS reflects greater LVF immunity to masking (i.e., greater perceptual availability of LVF transients).

Our temporal frequency discrimination and masking control experiments each required participants to divide attention between the fovea and the periphery. Neither experiment generated an LVF advantage. This demonstrates that the significant LVF advantages observed in our main and luminance transient control experiments did not arise solely as an artifact of a divided attention task.

Lastly, we have postponed describing until now an intriguing post hoc observation. Although this observation does not relate directly to our investigation of lateral hemifield differences (LVF vs. RVF), it pertains to upper versus lower hemifield differences. Specifically, participants in our flicker discrimination control experiment reported seeing the faster flicker significantly more often at the top than at the bottom of the display.[3] Table 1 shows the data for this "top faster"

bias, derived from the midpoints (points of subjective equality [PSEs]) of the psychometric functions that we fit to estimate the above-mentioned temporal period discrimination thresholds. Accordingly, the negative PSEs in Table 1 correspond to top temporal periods appearing briefer (faster flickering) than bottom temporal periods by ~34 and ~66 ms in the LVF and RVF, respectively. This might simply reflect a motor response bias. Future experiments using motor response options that link only indirectly to the upper and lower hemifields could distinguish motor from perceptual biases. In any case, the significant upper/lower hemifield differences observed here for *low-level* flicker discrimination do not parallel results from a prior experiment that found no upper/lower hemifield differences in *visual attention* (Aghdaee & Cavanagh, 2007). Likewise, TOJ PSEs from our main and luminance transient control experiments—also designed to measure *visual attention*—did not exhibit significant "positive" (upward)/"negative" (downward) motion biases (see the Supplementary Information). It therefore remains possible that low-level flicker discrimination and visual attention have distinct vertical hemifield dependencies.

Discussion

We conducted the present study to provide new information about attention's temporal precision in the left and right visual fields. In particular, we asked whether the LVF advantage recently observed on SJs (J. G. Kelly & Matthews, 2011; Matthews et al., 2012) would extend to TOJs. The question intrigued us given plausible arguments for and against expecting TOJs to exhibit an LVF advantage. For example, the fact that temporal correlators could execute a shared computation (ATa – ATb) for the two tasks (Allan, 1975; Sternberg & Knoll, 1973; Ulrich, 1987) would make it plausible for TOJs to share the LVF advantage observed on SJs. On the other hand, distinct neural events might optimize the distinct information requirements for SJs (magnitude) and TOJs (direction). To the extent that these two tasks rely on distinct neural events, one would not necessarily expect TOJs to parallel the LVF advantage observed on SJs. Indeed, the arm-crossing manipulation demonstrates a dissociation between the neural events mediating SJs and TOJs in the tactile sense (Fujisaki & Nishida, 2009; Shore et al., 2002; Yamamoto & Kitazawa, 2001), even though the ATa – ATb computation could mediate both tasks within and across sensory modes.

We found significant LVF advantages in SJs and TOJs alike. These LVF advantages occurred both in the main experiment and our luminance transient control experiment, which contained Gabor targets that flickered

continuously at 30 Hz. The continuous 30-Hz flicker rendered the luminance transient from the task-relevant orientation change less distinct. Indeed, correct SJs and TOJs in the luminance transient control experiment required extracting an orientation transient from a stream of task-irrelevant luminance transients, an attentional requirement. Moreover, the LVF advantage did *not* occur in additional control experiments that assessed low-level factors, namely, temporal frequency discrimination and masking (i.e., the perceptual availability of the orientation transients). Collectively, the four present experiments reveal that the LVF advantage previously observed for SJs (J. G. Kelly & Matthews, 2011; Matthews et al., 2012) extends to TOJs and that this hemifield asymmetry reflects the temporal precision of visual attention, not low-level visual factors.

Our finding that the LVF advantage in SJs extends to TOJs could be explained in at least two ways. A simple yet plausible possibility would be that SJs and TOJs rely on identical or very similar neural events throughout the visual pathway. If so, the factors generating the LVF advantage in SJs obviously would induce the same hemifield asymmetry in TOJs. Alternatively, or in addition, SJs and TOJs might rely on distinct early or intermediate visual pathway events, which independently feed into a common later stage that exhibits an LVF advantage. Holcombe (2009) proposed this sort of late-stage possibility to parsimoniously explain the relatively low temporal precision observed across a group of so-called "slow" visual tasks. These slow visual tasks include binding form and color (Clifford, Holcombe, & Pearson, 2004), perceiving acceleration and direction change (Werkhoven, Snippe, & Toet, 1992), and—most relevant for our purposes—attention-mediated motion (Cavanagh, 1992; Lu & Sperling, 1995). Indeed, the TOJ thresholds from our main experiment (92–141 ms) and luminance transient control experiment (223–310 ms) quantitatively match well with the ~10-Hz and slower temporal precision in Holcombe's (2009) slow-task group. Intriguingly, our luminance transient control experiment's 30-Hz flicker may have been invisible to the comparatively sluggish (<~10 Hz) attention-based motion system (Cavanagh, 1992; Lu & Sperling, 1995; Verstraten, Cavanagh, & Labianca, 2000) while generating masking-like interference in the faster (≥30 Hz) luminance-based motion system (Andrews, White, Binder, & Purves, 1996; D. H. Kelly, 1961; Rovamo & Raninen, 1984). These quantitative considerations constitute another reason to believe that LVF advantages in our luminance transient control experiment reflect attention-based motion rather than luminance-based motion. We will return to discussing attention-based motion and luminance-based motion after first considering qualitative evidence that our LVF advantages in SJs and TOJs arose from a shared, late visual stage (Holcombe, 2009).

Perceptual learning experiments provide qualitative evidence that the present study's LVF advantages reflect an asymmetry in a late visual stage. This evidence comes from informative patterns of learning transfer versus learning specificity. Notably, SJ training on displays like those used here (see Figure 2) significantly improved SJs in the untrained lateral hemifield but did not affect spatial frequency discrimination on the same stimuli at the trained location (Matthews et al., 2012). Such hemifield-independent, feature-specific learning implicates neural events occurring *after* the early visual neurons that detect stimuli—a pattern consistent with the reverse hierarchy theory of perceptual learning (Hochstein & Ahissar, 2002). This theory posits that "reverse hierarchy routines focus attention to specific, active, low-level units, incorporating into conscious perception detailed information available there" (Hochstein & Ahissar, 2002, p. 791). Indeed, the pattern of learning transfer and specificity in various perceptual learning studies (Matthews et al., 2012; Saffell & Matthews, 2003; Shiu & Pashler, 1992) confirms late-stage, task-specific attentional reweighting (Petrov, Dosher, & Lu, 2005) rather than improvements in early visual neurons that detect stimuli. Critically, displays similar to those used here (see Figure 2) generate an LVF advantage in SJs but *not* spatial frequency discrimination, even when retinal stimulation remains identical across these two tasks (J. G. Kelly & Matthews, 2011; Matthews et al., 2012). This task specificity points to visual attention's *temporal* properties as the source of the LVF advantage. The hypothesis that attention's *temporal* properties generated the LVF advantages reported here makes two interesting, testable predictions. Specifically, the hypothesis predicts finer LVF than RVF temporal thresholds when attentionally pairing dynamic luminance/orientation combinations across spatially distinct retinal locations and when attentionally pairing color changes with motion direction changes. Bilateral versions of the dynamic stimuli described in Holcombe and Cavanagh (2001) and Nishida and Johnston (2002), respectively, could be used to test the predicted LVF attentional advantages.

The LVF advantage observed here for the attention-based motion system extends the previously mentioned work by Bosworth et al. (2012) that revealed an attentionally mediated LVF advantage in the luminance-based motion system. Importantly, they found that attention improved LVF but not RVF performance when participants discriminated the direction of moving peripheral luminance dots and that attention had no effect in either hemifield on peripheral orientation discrimination. To explain this task-specific hemifield effect, they noted that motion discrimination and orientation discrimination rely on distinct neural streams, respectively, the "where" (dorsal) and "what" (ventral) visual pathways (Mishkin & Ungerleider, 1982). Their LVF advantage—like that of the present study—could also reflect involvement of the so-called "when" pathway (Battelli, Pascual-Leone, & Cavanagh, 2007; Battelli, Walsh, Pascual-Leone, & Cavanagh, 2008), to which we now turn.

Evidence for a "when" pathway, which tracks the timing of visual events, comes from methodologically varied sources that implicate the right parietal lobe. For example, physiological manipulations involving transcranial magnetic stimulation (Müri et al., 2002; Woo, Kim, & Lee, 2009) and clinical reports of split brain (Forster, Corballis, & Corballis, 2000) and right parietal lobe patients (Battelli et al., 2001; Battelli, Cavanagh, Martini, & Barton, 2003) confirm the right parietal lobe's special role in temporal judgments. Indeed, Rorden, Mattingley, Karnath, and Driver (1997) found impaired TOJs in patients with left-sided visual extinction caused by right parietal lobe damage. Further support for a right parietal lobe "when" pathway comes from event-related potentials (ERPs). Specifically, Verleger et al. (2011) and Verleger et al. (2013) found that N2pc (parietal contralateral) ERPs—a marker of selective attention (Hopf et al., 2000)—peaked ~50 ms earlier for LVF than for RVF targets on a dual-stream RSVP identification task. This hastened neural response to LVF targets could explain why participants perceive LVF targets significantly sooner than RVF targets in dual-stream RSVP displays (Matthews, Welch, Festa, & Clement, 2013).

Finally, we find intriguing recent attentional experiments that show that multiple object tracking (MOT) can exhibit an *RVF* advantage (Holcombe, Chen, & Howe, 2014). To explain the RVF advantage in MOT, Holcombe et al. (2014) cite clinical evidence that the left hemisphere mediates RVF attention whereas the right hemisphere mediates attention to *both* hemifields (Mesulam, 1999). The RVF receives "double coverage." This explanation comports with psychophysical studies that suggest MOT depends on attentional resources that are not completely distinct for the two lateral hemifields (Chen, Howe, & Holcombe, 2013; Holcombe & Chen, 2012; Hudson, Howe, & Little, 2012). An exciting direction for future research entails developing a single, dynamic display that generates LVF advantages, RVF advantages, and no hemifield differences depending *entirely* on experimentally manipulated attentional demands. This would demonstrate considerable theoretical understanding of attention's temporal properties.

Conclusion

Overall, the present study's LVF SJ and TOJ advantages in attention-based motion provide further evidence for a right parietal lobe "when" pathway that

mediates diverse stimulus conditions across diverse time-dependent tasks. In addition, our control experiments suggest that LVF advantages in these time-dependent tasks reflect neural events beyond those mediating low-level functions such as visual sampling rates or the discriminanda's perceptual availability. This corroborates clinical results from Battelli, Cavanagh, Martini, and Barton (2003), who found that right parietal lobe damage impaired patients' ability to time transients without impairing low-level temporal precision. In addition, our results further contradict the subjective experience of comparable temporal precision in the LVF and RVF.

Keywords: temporal vision, motion perception, attention-based motion, simultaneity, temporal order

Acknowledgments

Footnotes

[1] We thank Dr. Alex Holcombe for suggesting this control experiment.
[2] We note the 2.5- and 1.9-fold increases in the number of independent detectors solely to describe the effect size of our hemifield manipulation. Evidence from primate anatomical research argues against LVF-RVF asymmetries even remotely approximating this magnitude (Van Essen, Newsome, & Maunsell, 1984).
[3] We thank Dr. Alex Holcombe for inquiring about upper-versus-lower hemifield biases.

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