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Temporal integration by multi-level regularities fosters the emergence of dynamic conscious experience

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Abstract

The relationship between integration and awareness is central to contemporary theories and research on consciousness. Here, we investigated whether and how information integration over time, by incorporating the underlying regularities, contributes to our awareness of the dynamic world. Using binocular rivalry, we demonstrated that structured visual streams, constituted by shape, motion, or idiom sequences containing perceptual- or semantic-level regularities, predominated over their nonstructured but otherwise matched counterparts in the competition for visual awareness. Despite the apparent resemblance, a substantial dissociation of the observed rivalry advantages emerged between perceptual- and semantic-level regularities. These effects stem from nonconscious and conscious temporal integration processes, respectively, with the former but not the latter being vulnerable to perturbations in the spatiotemporal integration window. These findings corroborate the essential role of structure-guided information integration in visual awareness and highlight a multilevel mechanism where temporal integration by perceptually and semantically defined regularities fosters the emergence of continuous conscious experience.

KEYWORDS

binocular rivalry, information integration, regularity, temporal structure, visual consciousness

INTRODUCTION

With a simple glance at Van Gogh's Starry Night, you would be impressed by a deep blue sky roiling with shining stars above a tranquil village, all as a meaningful whole rather than a collection of unrelated attributes. As you walk through the gallery, this particular conscious experience could be extended across space and over time, engendering a coherent and continuous awareness of the external world. In this regard, the emergence of visual consciousness entails the ability to bind different features into impartible objects^{1,2} and integrate disparate elements into a unitary conceptual structure across multiple spatial and temporal scales.^{3,4} Arguably, intelligent creatures who can generate highly composite conceptual structures that reflect the structural regularities of the external world may gain an adaptive advantage.⁵

Humans are endowed with a remarkable capability to capture regularities in spatial and temporal structures of the visual environment.⁶⁻⁸ While early research focused on the effects of spatial structures, there is an emerging interest in how observers utilize regularities from the temporal structure of dynamic information to enhance visual perception. Even without configurational cues, temporal structures defined by synchronous changes in a visual feature lead to the immediate perception of dynamic objects from a mixture of elements.^{9,10} Temporal structures based on statistical regularities in the sequence of meaningless symbols attract attention to specific visual features or spatial locations.¹¹ Temporal structures of sign languages, which show quasirhythmic characteristics, can entrain neural oscillations to maximize sensitivity to informational signals in language.¹²

While temporal structures defined by various types of regularities influence different aspects of visual information processing, whether regular temporal structure confers a benefit to the generation of

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conscious content remains undetermined. The answer to this question is of considerable importance because the content of consciousness is limited, in contrast to the seemingly unlimited information available in the visual environment.^{13,14} To resolve this paradox, the visual system has to prioritize certain types of content among the information competing for conscious awareness.^{15,16} Despite its significance, our knowledge about the rules and mechanisms governing such visual competition is far from complete.¹⁷

Here, we proposed that regularities in the temporal dimension could be a fundamental factor underlying the construction of continuous conscious content and modulating visual competition through visual integration. The Information Integration Theory (IIT) assumes spatiotemporal integration of the incoming visual information as a prerequisite for the construction of conscious experiences.^{3,5} If this holds true, a highly regular temporal structure that establishes predictable connections among individual items may facilitate the integration process, thereby empowering a structured stream to stand out from others during visual competition. On the contrary, if temporal integration is not essential for the generation of conscious content, then information streams with similar low-level physical attributes but differing only in the regularity conveyed in their temporal structures would not exhibit any differences in competition.

To test these hypotheses, we adopted binocular rivalry (BR), a phenomenon in which observers' conscious perception alternates spontaneously between two stimuli presented dichoptically to their left and right eyes.¹⁸ Relative longer dominance durations for a given rival stimulus indicate its advantage in the competition for consciousness.^{15,16} In Experiment 1, we pitted structured streams with their random counterparts to assess whether temporally structured information enjoys a privilege in BR. Moreover, we employed four types of structured streams (based on shape, motion, contrast, and idiom stimuli) to examine whether the rivalry advantage could extend across perceptualand semantic-level regularities. To elucidate the mechanisms underlying the observed effects, we further examined the advantages of different levels of regularities from the perspective of temporal information integration. In Experiments 2 and 3, we investigated whether the rivalry advantage is resistant to spatiotemporal variations in the integration window, considering the significance of a stable integration window to the extraction and utilization of temporal structures in visual information.¹⁹ In Experiments 4 and 5, we sought to disentangle the contributions of conscious and nonconscious integration processes to the observed effects, given that the continuous generation of conscious content in BR may be shaped by information integration both above and below conscious levels.²⁰

METHODS

Participants

A total of 156 native Chinese speakers (mean age \pm SD = 22.4 \pm 2.7 years, 81 females) took part in this study. Seventy-two participated in Experiment 1 (18 in each stimulus condition), 18 in Experiments 2

and 3 each, and 24 in Experiments 4 and 5 each. The sample size was determined based on previous studies that investigated high-level BR effects and nonconscious visual processing using similar paradigms as in the current study.^{21,22} A two-tailed power analysis using G*Power²³ (Version 3.1.9.7) suggests that 15 participants could afford 80% power and 0.05 significance to detect the rivalry effect with a high effect size (Cohen's $d \ge 0.8$). We increased the sample size to 18 to achieve adequate power in Experiments 1-3. For Experiments 4 and 5, we enlarged the sample size to 24 to ensure a reliable effect when disentangling the conscious and nonconscious processes. All participants reported normal color vision and normal or corrected-to-normal visual acuity with no reported history of strabismus, and exhibited a rivalry pattern without extreme eye/color dominance (less than 90%) or a large proportion of mixture state (less than 30% of the tracking period). All participants were naïve to the purpose of the experiment. They gave informed consent to participate in procedures approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences.

Apparatus and stimuli

Visual stimuli were generated using MATLAB (The MathWorks) with the Psychtoolbox extension,^{24,25} and displayed on a 21-inch CRT (cathode ray tube) monitor with a resolution of 1280×1024 at 60 Hz. For six participants in Experiment 5, the stimuli were displayed on a 27-inch LCD (liquid crystal display) monitor with a resolution of 1920×1080 at 60 Hz, and the stimuli size remained consistent on different monitors. Observers viewed the stimuli through a mirror stereoscope at a distance of 60 cm, with their heads stabilized by a chin rest.

Each pair of the rival streams consisted of the same 120 items, which were presented in different orders to form the structured and random sequences. Four types of stimulus streams, including idiom, shape, motion, and contrast (for Experiment 1 only), were employed.

For the idiom condition, we randomly selected 30 different fourcharacter Chinese idioms from a pool of 60 idioms (familiarity > 6.4 on a 7-point scale) and concatenated them to form a structured stream for each trial. Each character subtended 2.12° of visual angle. A Chinese idiom, like an English idiom, is a brief, meaningful phrase that always consists of four Chinese characters, each of which is a semantic element like an English word. Therefore, a set of successively presented Chinese idioms can form a regularly structured stream based on its semantic meanings, with every four characters forming a semantically organized temporal structure. Figure 1A shows an example of a pair of structured and random streams composed of two idioms: "鸟语花香" and "乐不思蜀." "鸟" (bird) "语" (twittering) "花" (flower) "香" (fragrant) means the whispering of birds and the fragrance of flowers, which is used to describe a beautiful and vibrant scene of spring. "乐" (happy) "不" (not) "思" (miss) "蜀" (name of an ancient country, here referring to the homeland of a person) means a person is too happy to be homesick. To obtain a random counterpart of the idiom stream, we shuffled the structured stream at the whole-stream level to eliminate the semantic structure. For this particular structured stream, a possible random counterpart could be "思(miss)香(fragrant)语(twittering)蜀(name of an

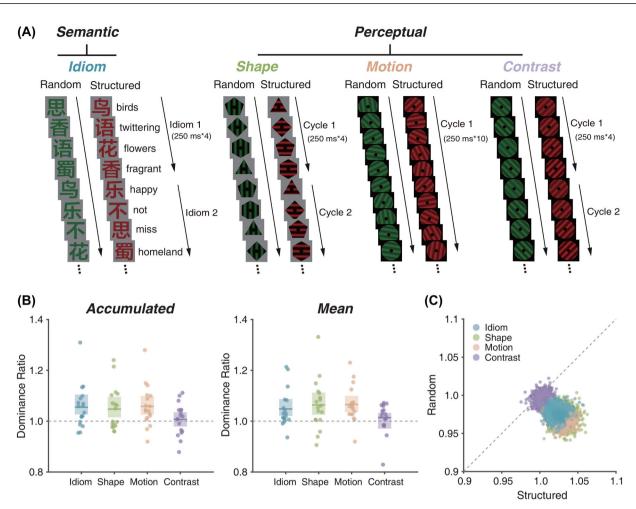


FIGURE 1 Example stimuli and results of Experiment 1. (A) For each stimulus type, structured and random streams composed of identical elements but with different stimulus sequences were presented dichoptically to participants. (B) Dominance ratios obtained by dividing the accumulated (trial-based) and mean (percept-based) dominance durations of the structured streams with that of the random streams for each stimulus condition. A dominance ratio larger than 1 reveals the predominance of the structured stream. Colored lines and bars represent the group means with bootstrapped 95% CIs, and each colored dot represents data from an individual participant. (C) Bootstrap distributions of mean normalized dominance durations show a dissociation between the contrast and the other stimulus conditions.

ancient country)鸟(bird)乐(happy)不(not)花(flower)" (Figure 1A). Note that in the formal experiments, each structured stream and its random counterpart consisted of 30 distinct idioms (120 Chinese characters).

For the shape condition, the structured streams were composed of Gabor patches embedded in polygonal contours. The edge number of the shape increased monotonically every four items (i.e., triangle \rightarrow diamond \rightarrow pentagon \rightarrow hexagon), yielding a rhythmic pattern throughout the trial. The random streams were generated by randomizing the sequence order within each rhythmic cycle of the structured streams, with the constraint that no two successive items were the same within the stream. The orientations of the Gabor patches for each rivalry pair were set to horizontal and vertical. Each polygonal shape subtended 1.51° of visual angle in terms of circumradius, with a spatial frequency of 2.4 cycles per degree (cpd) for Experiments 1–3, and 2.4 or 3.3 cpd for Experiment 4. The shape streams were superposed on a gray square (5.09° × 5.09°) to facilitate the perception of the edges.

For the motion condition, the structured streams consisted of a grating (radius: 1.51°; spatial frequency: 2.4 cpd or 3.3 cpd [for Experiment 4 only]; initial orientation set at -45° or 45° from vertical) rotating clockwise in 36° steps. Every 10 steps of movements formed one cycle of the rhythmic structure (i.e., a full circle of 360°). The random streams were generated following the same rule as in the shape condition.

For the contrast condition, the structured stream consisted of a grating whose Michelson contrast increased from 0.4 to 0.7 (step = 0.1) in each rhythmic cycle. The random streams were generated following the same rule as in the shape condition. In each trial, the paired gratings were tilted -45° and 45° from vertical with the other parameters identical to that for the motion condition.

Procedure

Prior to each experiment, participants were instructed to adjust the mirror stereoscope in order to achieve successful binocular fusion. In Experiment 1, participants were randomly assigned to one of the four stimulus conditions (i.e., idiom, shape, motion, or contrast). They

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completed 16 rivalry trials divided into two blocks, with the color assignment, the eye, and the stimulus orientation (for the shape and contrast conditions only) counterbalanced across trials within each block. Each trial began with a central fixation dot $(0.30^{\circ} \times 0.30^{\circ})$ presented to both eyes. Participants were instructed to maintain fixation on this point throughout the whole trial. After 2 s, the structured and random streams were presented dichoptically in synchronization, 250 ms for each item with no intervals, during the 30 s rivalry period. The rivalry streams were tinted in red and green with matched luminance values (4.87 cd/m²), and displayed on a black (or gray for the idiom condition) background. Participants were required to press and hold one of two keys to indicate which color (red or green) of the tinted streams was dominating perception, and to release keys when perceiving a fused plaid or a piecemeal rivalry. To avoid potential fatigue effects due to the interocular competition, each trial was followed by a compulsory break (inter-trial interval, ITI) of 8 seconds.

In Experiments 2 and 3, the procedure was the same as that for Experiment 1, but with the following exceptions. In Experiment 2, the duration of each individual item was no longer constant (250 ms) but changed irregularly with an up to 50% variance (ranging from 125 to 375 ms in 16.7 ms steps), thereby disrupting the regularities of stimulation in time. In Experiment 3, the location of each stimulus was no longer fixed but randomly jittered in the x and y directions between $\pm 0.30^{\circ}$ from the center, thus destroying the regularities of stimulation in space. In both Experiments 2 and 3, each participant completed two rivalry blocks (a total of 16 trials) for each of the three stimulus conditions (i.e., idiom, shape, and motion). The order of stimulus conditions was counterbalanced across participants.

In Experiment 4, we replicated Experiment 1 except for the contrast condition. For each stimulus type, we added a baseline condition (structured-control vs. random-control) to the experimental condition (structured vs. random) in order to dissociate the conscious and nonconscious effects in the rivalry advantage of structured sequences. Both the structured-control and random-control streams were deprived of semantic- or perceptual-level regularity as in the random streams. However, they differed from each other in regularityirrelevant aspects and could be compared with the structured and random streams, respectively, allowing us to separate the rivalry advantage of the structured stream during its conscious stage (dominance duration: structured vs. structured-control) and nonconscious stage (dominance duration: random vs. random-control). For the idiom condition, the random-control streams were constructed in the same way as the random streams. The structured-control streams were obtained by reversing the sequence order of the structured idiom streams to destroy the semantic-level regularity. For shape and motion conditions, simply reversing the structured streams would not disrupt the regularity. Therefore, we generated the structured-control and random-control streams in the same way as the random streams, while introducing different spatial frequencies to them to help discriminate between the rival stimuli. We also matched the spatial frequency between the experimental stimuli and their corresponding control streams (3.30 cpd for structured and structured-control streams and 2.40 cpd for random and random-control streams or vice versa) to facilitate the comparison between the experimental and control conditions. The spatial frequency of the rival streams and the order of stimulus conditions were counterbalanced with a Latin square design across participants. Each participant completed three BR blocks, each for one stimulus condition. Each block consisted of 16 trials, with the baseline and experimental trials presented in a pseudo-randomized sequence ("ABBABAAB" or vice versa for every eight trials).

In Experiment 5, we assessed the nonconscious processing of structured and random streams using the breaking continuous flash suppression (b-CFS) paradigm technique.²² In each trial, participants were asked to maintain fixation on a central cross that was continuously presented to both eyes. A dynamic Mondrian pattern was presented to the dominant eye of the observers at full contrast to suppress the awareness of a structured or random stream presented to the other eye. The suppressed streams (size: $2.12^{\circ} \times 2.12^{\circ}$ for idiom and motion, $2.42^{\circ} \times 2.42^{\circ}$ for shape) were rendered in gray against a black background but otherwise the same as the stimuli used in Experiment 1. The stimulus center was located 2.27° to the left or right of the fixation. The contrast of the stimulus stream was ramped up gradually from 0 to a value between 0.2 and 1 within a limited duration (1 or 2 s) and then remained constant until response or 10 s elapsed. The values were determined individually, based on the criteria that the stimulus streams could be suppressed from awareness for at least two cycles (>2 s) in 10 practice trials before the formal experiment. During each trial, participants were instructed to press the corresponding button to indicate on which side the target appeared as soon as possible once they saw any part of the test image. The experiment consisted of 270 trials, separated into three blocks, each for one stimulus type, with a Latin square design. Each block included 40 structured trials, 40 random trials, and 10 catch trials in which no stimuli appeared in the suppressed eve.

Data analysis

In Experiments 1-4, to obtain reliable estimates of the temporal dynamics of BR, we first identified and removed the unstable percepts based on the following criteria. Button press durations less than 200 ms were not counted as periods of exclusive dominance. Besides, during transitions from pressing one button to the other, participants sometimes accidentally pressed both buttons for short periods (<200 ms). Such responses were also excluded from further analysis. Based on the remaining responses, we computed the trial-based accumulated dominance duration (i.e., the overall dominance duration of a given percept within each 30 s trial averaged across all trials) and the percept-based mean dominance duration (i.e., the dominance duration of a given percept in all trials averaged across all percepts) for the structured and the random streams, respectively, for each stimulus type and each participant.^{21,26} To facilitate comparison among different stimulus types, we calculated the dominance ratios of the structured to the random stream based on the accumulated and mean dominance durations. In Experiment 1, we observed similar effects with the two dominance ratio indices for all stimulus types, so in Experiments 2-4, we only reported results based on the mean dominance ratios. Additional

analysis based on the accumulated dominance ratios yielded very similar patterns, which are reported in the Supporting Information.

To obtain a more robust estimate of the confidence intervals than the standard methods, we used a standard bootstrap procedure (n= 1000) to compute the bias-corrected and accelerated 95% confidence intervals (CI) for the average of these dominance ratios.^{27,28} The bootstrap procedure was also applied to the normalized dominance durations of the structured and random streams in Experiments 1 and 4 to illustrate the data distributions for different stimulus conditions. In Experiment 1, the normalization was carried out through dividing the mean dominance durations of the structured and the random streams, respectively, by the average of dominance durations of all percepts (across both streams) for each participant. In Experiment 4, the dominance durations of structured and random streams were divided, respectively, by the individual mean of overall dominance durations across the experimental and baseline conditions for each stimulus.

In Experiment 5, we measured the suppression time as the reaction times (RTs) needed for the participants to correctly indicate at which side of the fixation they saw the target stimulus. For each individual, only trials with RTs within three times of the standard deviation of the individual mean based on all trials were included in further analysis.

RESULTS

Visual awareness is biased toward temporally structured information

In Experiment 1, we pitted structured streams composed of periodically changing stimuli regarding their shape, motion, or contrast (perceptual-level regularity) and those of concatenated Chinese idioms (semantic-level regularity) against their physically matched but temporally randomized counterparts (Figure 1A). If dynamic information with regular temporal structure enjoys a privilege in the visual competition, we would observe prolonged dominance durations (or a dominance ratio larger than 1, see Methods for details) for the structured stream relative to the random one.

In accordance with our assumption, one sample *t*-test revealed an accumulated dominance ratio significantly greater than 1 for the idiom streams (Figure 1B; *t* (17) = 2.79, *p* = 0.01, Cohen's *d* = 0.66, BF₁₀ = 4.36, two-tailed, the same below), suggesting that semanticlevel regularities can promote awareness dominance during the visual competition. Similar patterns were observed for perceptual-level regularities in the shape and motion conditions (Shape: *t* (17) = 2.40, *p* = 0.03, Cohen's *d* = 0.57, BF₁₀ = 2.29; Motion: *t* (17) = 3.07, *p* < 0.01, Cohen's *d* = 0.72, BF₁₀ = 7.15), while not in the contrast condition (*t* (17) = 0.48, *p* = 0.63, Cohen's *d* = 0.11, BF₁₀ = 0.27). Consistent with these findings, analyses on the mean dominance ratios yielded similar results: the temporal structure advantage was found in the idiom (*t* (17) = 2.80, *p* = 0.01, Cohen's *d* = 0.66, BF₁₀ = 4.48), shape (*t* (17) = 2.77, *p* = 0.01, Cohen's *d* = 0.65, BF₁₀ = 4.24), and motion (*t* (17) = 3.97, *p* < 0.001, Cohen's *d* = 0.94, BF₁₀ = 37.70) conditions, but not in the contrast condition (t (17) = 1.01, p = 0.33, Cohen's d = 0.24, BF₁₀ = 0.38). The same pattern was observed when we discarded the last percept if a button was still being pressed at the end of the trial (see Supporting Information). Additional data analysis reveals no initial dominance bias toward structured streams in any stimulus condition (see Supporting Information).

To verify the differences among stimulus conditions, 1000 bootstrapped samples of the normalized dominance durations for each stimulus condition are shown in Figure 1C, with the horizontal axis representing the structured streams and the vertical axis representing the random streams. While the distribution of the contrast stimulus is clustered around and nearly bisected by the diagonal line (y = x), clusters of the other stimuli all fall below this line, confirming that only in the later conditions, the dominance durations are reliably prolonged by structured visual information.

Dissociation between semantic- and perceptual-level regularities: The resistance to spatiotemporal perturbations

We have shown that temporal structure based on regularities at the semantic (as in the idiom condition) and the perceptual (as in the shape and motion conditions) levels both had prolonged dominance durations during visual competition. Is such cross-level advantage driven by a common mechanism related to the perception of meaningful events (e.g., successive idioms or rotating motions) regardless of the properties of the stimuli? Or does it result from the temporal integration process that may have different constraints for the perceptual- and semantic-level information? To address this issue, we examined whether the privilege enjoyed by different levels of regularities would be constrained, to a different extent, by the uniformity of the spatiotemporal integration window.

A recent study suggests that a uniform temporal integration window (e.g., constant stimulus intervals) is critical to the extraction and utilization of rhythmic temporal structures built on perceptual-level regularities.¹⁹ On the contrary, the utilization of temporal structure based on semantic-level regularities may be less susceptible to spatiotemporal variations in the integration window, given that the "meaning" in the idiom stream is defined by the particular order of the semantic elements over time, not by their durations or positions.^{21,29} Therefore, if temporal integration with different levels of regularities is key to the rivalry advantage of structured streams, we would expect the advantage based on perceptual- but not semantic-level regularities to be disrupted by a varying spatiotemporal integration window. Alternatively, if the advantage of shape and motion streams comes from the effect of meaningful events like that for idiom streams, spatiotemporal perturbations on the stimulus integration window should have little influence on the observed advantages in all stimulus conditions, as such manipulation would not prevent observers from perceiving the meaning of the events.

To assess these possibilities, we disrupted the uniform spatiotemporal arrangement of individual items in the rivalry streams by adding

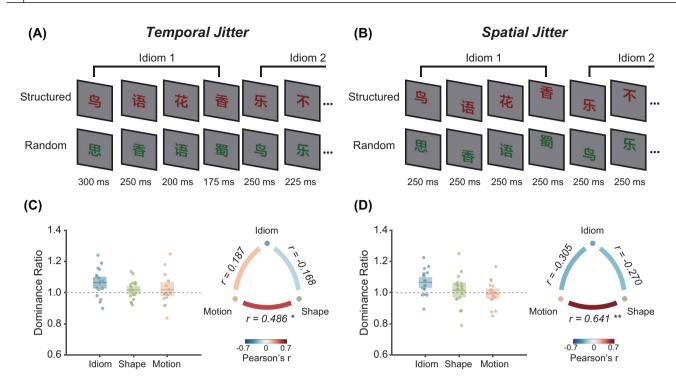


FIGURE 2 Illustrations of experimental manipulations and results of Experiments 2 and 3. Stimulus streams used in Experiments 2 and 3 (illustrated on idiom stimuli as examples) were the same as those in Experiment 1, except that (A) the temporal duration of each stimulus in Experiment 2 was not constant, but ranged randomly from 125 to 375 ms; and (B) the spatial location of each stimulus in Experiment 3 was not fixed, but varied randomly from 0° to 0.30° to the retinal center. (C) and (D) Dominance ratios of the three stimulus conditions and the pairwise Pearson correlation results for Experiments 2 and 3. The colored lines and bars represent the averaged dominance ratios with bootstrapped 95% Cls, and each colored dot represents one participant. * p < 0.05; ** p < 0.01.

temporal (Experiment 2) or spatial (Experiment 3) jitters. In this way, we varied the temporal or spatial properties of the integration window without changing the information of the rivalry streams (Figure 2A,B). In the temporal jitter experiment, the dominance ratio of structured idiom streams over the random counterparts remained significantly greater than 1 (Figure 2C; t(17) = 3.18, p < 0.01, Cohen's d = 0.75, $BF_{10} = 8.74$), with the effect comparable to that observed with the isochronous sequences, whereas for the shape and motion conditions, the advantage of structured streams over the random ones no longer existed (Figure 2C; Shape: t (17) = 1.18, p = 0.25, Cohen's d = 0.28, $BF_{10} = 0.44$; Motion: t (17) = 0.81, p = 0.43, Cohen's d = 0.19, BF_{10} = 0.33). Similar results were observed in the spatial jitter experiment. While the structured idiom streams had a dominance ratio significantly larger than 1 (Figure 2D; t (17) = 3.49, p < 0.01, Cohen's d = 0.82, $BF_{10} = 15.35$), other stimulus conditions revealed no such tendency (Figure 2D; Shape: t(17) = 0.59, p = 0.56, Cohen's d = 0.14, BF₁₀ = 0.28; Motion: t(17) = -0.42, p = 0.68, Cohen's d = -0.10, BF₁₀ = 0.26).

To quantify the association of the observed effects across stimulus types, we calculated the pairwise Pearson correlation coefficients of dominance ratios based on the mean dominance durations among the three stimulus conditions (Figure 2C,D). For both Experiments 2 and 3, we observed a significant correlation, particularly within perceptual-level regularities, that is, between the shape and motion conditions (Experiment 2: r = 0.49, p < 0.05; Experiment 3: r = 0.64, p < 0.01). By contrast, no significant correlations were observed across the

perceptual and semantic levels, that is, between the idiom and shape (Experiment 2: r = -0.17, p = 0.51; Experiment 3: r = -0.27, p = 0.28) or between the idiom and motion conditions (Experiment 2: r = 0.19, p = 0.46; Experiment 3: r = -0.30, p = 0.22).

Taken together, these results reveal a clear dissociation between the semantic- and perceptual-level regularities regarding the boundary conditions for them to modulate awareness. Only the privilege of idiom streams was tolerant of spatiotemporal perturbations on the integration window, pointing to the existence of a specialized and robust mechanism for prioritizing structured semantic information during visual competitions. For motion and shape streams, the absence of the temporal structure advantage may reflect a limitation of visual feature integration with respect to variations in the width and length of the integration window.

Dissociation between semantic- and perceptual-level regularities: Conscious and nonconscious benefits

Although some theories of consciousness hold that the ability of information integration depends on or requires conscious processing, recent studies suggest a more complex relationship between information integration and consciousness and reveal that the spatiotemporal integration of dynamic visual information may occur, at least to some extent, beyond awareness.²⁰ It poses another fundamental question:

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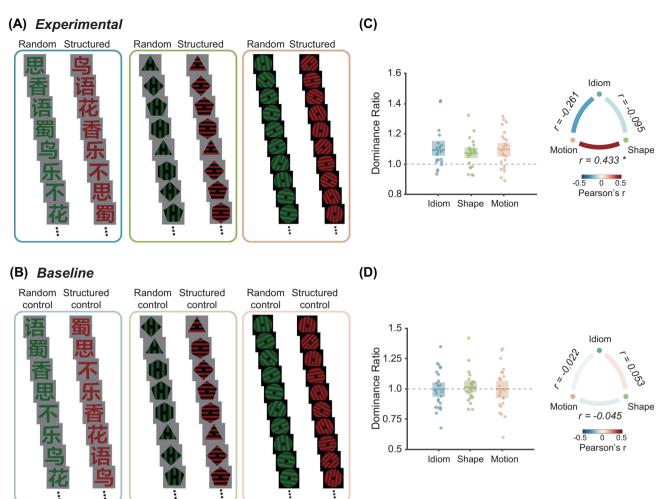


FIGURE 3 Stimuli and results of Experiment 4. (A) In the experimental conditions, the stimuli were the same as that in Experiment 1, except that for shape and motion, different spatial frequencies were assigned to the structured and random streams. (B) In the baseline conditions, the random-control streams were generated in the same way as that for the random streams. The structured-control streams were obtained by temporally reversing the corresponding structured streams (for idioms), or by randomizing the stimulus order (for motion and shape). The structured-control and random-control streams for shape and motion had the same spatial frequencies as their corresponding counterparts in the experimental conditions. (C) and (D) Dominance ratios and the pairwise Pearson correlation results for the experimental and baseline conditions. The colored lines and bars represent the averaged dominance ratios with 95% CIs, and colored dots represent individual data. * p < 0.05; ** p < 0.01.

whether the observed privileges of different types of regularities originate from the conscious or the nonconscious visual integration process. Regularities in dynamic visual information may lengthen the dominance durations of the structured streams when they are consciously perceived (i.e., during the dominance phase of BR³⁰) or reduce the suppression durations of the structured streams when they are inhibited from awareness (i.e., during the dominance phase of the random streams^{31,32}), both of which can lead to a greater percentage of perceptual dominance. To distinguish between these possibilities, in Experiment 4, we added a baseline condition (structured-control vs. random-control) for each experimental condition (structured vs. random) (Figure 3A,B). Both of the control streams lacked regular temporal structures but shared other aspects of the corresponding streams in experimental conditions (see Methods for details), which allowed us to disentangle the conscious and nonconscious components of temporal structure advantage by comparing the experimental and the baseline conditions. On the one hand, lengthened perceptual durations for structured streams relative to the structured-control streams may indicate the advantage of structured streams when they enter consciousness (conscious benefits). On the other hand, shortened perceptual durations of random streams versus the random-control streams may reflect the effect of structural streams when suppressed from consciousness (nonconscious benefits).

Results from the experimental condition replicated that from Experiment 1 as all three types of structured streams held a perceptual advantage over their random counterparts (Figure 3C; Idiom: t (23) = 3.80, p < 0.001, Cohen's d = 0.78, BF₁₀ = 38.00; Shape: t (23) = 3.75, p < 0.001, Cohen's d = 0.77, BF₁₀ = 33.85; Motion: t (23) = 3.93, p < 0.001, Cohen's d = 0.80, BF₁₀ = 50.10). Moreover, Pearson correlation analysis of dominance ratios yielded a significant correlation only between

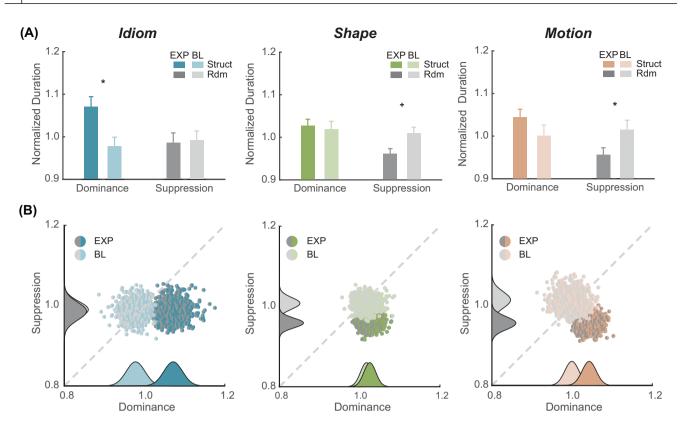


FIGURE 4 Conscious and nonconscious benefits for semantically and perceptually defined temporal structures during the BR. (A) Normalized mean percept durations of structured and structured-control streams during their dominance phase (color bars) and suppression phase (gray bars, when random/random-control streams were in dominance). Error bars: standard error of the mean. * p < 0.05, + p = 0.06. (B) For each stimulus, the bootstrapped data for the dominance and suppression phases of the structured stream were projected onto the x and y axes, respectively, with the projected data fitted using a Gaussian probabilistic density function (PDF). The evaluated values of the two PDFs were pooled together and then remapped into an appropriate range on the x or the y axis by applying a linear transformation for visualization purposes. These fitted curves showed a clear dissociation of the idiom and the other stimuli along the conscious and nonconscious dimensions. Abbreviations: BL, baseline; BR, binocular rivalry; EXP, experimental; Rdm, random; Struct, structured.

the shape and motion conditions (r = 0.43, p = 0.03), but not between idiom and shape (r = -0.10, p = 0.66) or between idiom and motion conditions (r = -0.26, p = 0.22). For the baseline conditions, by contrast, the benefit in BR was eliminated for the structured-control streams, in all three stimulus types (Figure 3D; ps > 0.5; Idiom: Cohen's d = 0.01, BF₁₀ = 0.22; Shape: Cohen's d = 0.11, BF₁₀ = 0.25; Motion: Cohen's d < 0.01, BF₁₀ = 0.22). In addition, there was no reliable correlation between any of the stimulus pairs (ps > = 0.8).

More importantly, for each stimulus type, we evaluated whether the structured streams gained perceptual advantages from the dominance (conscious) or the suppression (nonconscious) period of BR. During the dominance phase (Figure 4A), the mean normalized duration was significantly prolonged for the structured streams relative to the corresponding baseline for the idiom condition (t (23) = 2.30, p = 0.03, Cohen's d = 0.47, BF₁₀ = 1.92), but not for the shape (t (23) = 0.26, p = 0.80, Cohen's d = 0.05, BF₁₀ = 0.22) or the motion condition (t (23) = 1.23, p = 0.23, Cohen's d = 0.25, BF₁₀ = 0.42), indicating a privilege of regular structure at the conscious level restricted to semantic-level regularities. During the suppression phase of the structured information (Figure 4A), on the other hand, we found significantly reduced suppression durations for the structured streams as compared with the baseline for the motion conditions (t (23) = -2.16, p = 0.04, Cohen's d = -0.44, BF₁₀ = 1.50), and marginally significant reduced suppression durations for the shape condition (t (23) = -2.02, p = 0.06, Cohen's d = -0.41, BF₁₀ = 1.20), but not for the idiom condition (t (23) = -0.15, p = 0.88, Cohen's d = -0.03, BF₁₀ = 0.22), suggesting an advantage at the nonconscious level induced by perceptual-level regularities.

For better comparison within each stimulus condition, we visualized the bootstrap distributions of normalized durations in the experimental and the baseline conditions based on 1000 resampled data sets (Figure 4B). The horizontal and vertical axes represent the conscious (dominance) and the nonconscious (suppression) phases of the structured/structured-control stream, respectively. It is clearly shown that, for the idiom stimuli, the resampled data sets separate in the dominance rather than the suppression dimension, which means the observed privilege of structured idiom streams arises mainly from lengthened perception when they dominate conscious awareness. By contrast, for the shape and motion streams, the experimental and baseline conditions diverge primarily at the suppression phase, highlighting the contribution from nonconscious processing of the structured information.

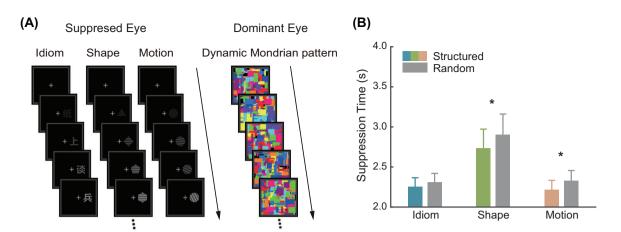


FIGURE 5 Schematics of the stimulus sequences used in the b-CFS Experiment and the suppression time results. (A) A dynamic Mondrian pattern was presented to the observer's dominant eye to suppress a structured or a random stream presented to the nondominant eye from the beginning of each trial. Participants were instructed to indicate on which side of the fixation the target appeared, and their reaction times (i.e., suppression times) for each stimulus condition were shown in (B). Error bars: standard error of the mean. Abbreviation: b-CFS, breaking continuous flash suppression. * p < 0.05.

Privilege of the perceptual-level temporal structures in conscious access

From the start to the end of a rivalry trial, the same stimulus stream can be consciously perceived at some moments but suppressed by the rival stream into nonconsciousness at other moments, resulting in a confounding effect that the conscious and nonconscious processing interferes with each other. Some may argue that the lack of nonconscious privilege of the structured idiom stream in Experiment 4 may result from the disturbance of the conscious processes. To solve this problem, in Experiment 5, we directly probed the role of regular temporal structures in nonconscious visual processing using the b-CFS paradigm.²² By presenting a salient dynamic noise to one eye and the target stimulus to the other, we created a situation where the target was continuously suppressed until it broke into awareness (Figure 5A). The time for the target to reach awareness can serve as an index to assess the potential effects associated with nonconscious visual perception.

Paired sample t-tests revealed that for the shape and motion conditions, the perceptual-level structured streams emerged from suppression significantly faster than the random ones (Figure 5B, Shape: t (23) = -2.51, p = 0.02, Cohen's d = -0.51, BF₁₀ = 2.79; Motion: t (23) = -3.07, p = 0.01, Cohen's d = -0.63, BF₁₀ = 8.08); whereas for the idiom condition, the difference of suppression time between the structured and random streams was not significant (t (23) = -1.18, p = 0.25, Cohen's d = -0.24, BF₁₀ = 0.40). These findings suggest that perceptual-level regularities in temporal structures of visual information could be extracted without awareness, while semantic-level structures could not, which is in good accordance with the dissociation of conscious and nonconscious privileges of temporal structures observed in the BR experiment.

DISCUSSION

A multi-level privilege of regular temporal structure in visual competition

By adopting dynamic visual streams in BR, our study provides novel evidence that visual awareness is biased toward information with regular temporal structures. Specifically, temporally structured streams formed by several types of visual stimuli, including Chinese idiom, shape, and motion, enjoyed longer dominance durations relative to their random counterparts in BR. Such an advantage is not attributable to low-level factors, as the rivalry streams always consisted of the same elements though being arranged in different sequences. Nor can it be accounted for solely by the repetitions of physical stimuli, given that the effect persisted even for structured streams constructed by nonrepeated Chinese idioms. Alternatively, the current findings suggest that regular information structure in the temporal dimension can robustly facilitate visual competition across different stimulus levels.

These findings, however, do not warrant that the prioritization of regularity in dynamic visual competition is a universal rule that applies to all types of visual stimuli. Indeed, the perceptual advantage induced by perceptual-level regularities did not extend to rhythmic structures defined by contrast change. The difference between contrast and the other stimulus conditions probably lies in that contrast is among the most basic visual features that can be well resolved by neuronal responses within the primary visual cortex,³³ making contrast perception more vulnerable to changes in stimulus strength. For perceptual-level stimuli, including the contrast, the overall stimulus intensity change was more evident for the random streams than for the structured streams. In particular, the random streams convey more abrupt transitions in low-level visual features, which can yield higher salience and attract more attention. Such imbalance in rival stimuli would predict stronger BR dominance for random visual streams, given that perceptual predominance in BR is sensitive to low-level stimulus differences related to stimulus strength or salience.³⁴ This might cancel out the integration benefits of structured information and lead to the lack of perceptual advantage for the structured contrast streams. However, this low-level influence seems to be overwhelmed by the facilitation effect of regular temporal structure in shape and motion conditions, suggesting that the observed advantage may rely on a higher-level mechanism that is sensitive to the temporal structure of the stimuli and probably operates beyond the early (monocular) stage of visual processing.

Despite the lack of effect in the contrast condition, what gives rise to the observed advantage of the structured shape, motion, and idiom streams? Does a common mechanism underlie the advantage shared across these stimulus types? The inter-stimulus correlation analysis provided an initial hint on these issues: significant correlations of the dominance ratio were found only between the motion and shape, but not between the idiom and the other two stimulus conditions, indicating that perceptual- and semantic-level regularities might not modulate perceptual awareness via a unified mechanism. A more powerful way to test this proposition is to identify the boundary conditions for the observed effect with different stimuli. To this end, we disrupted the uniformity of the spatiotemporal integration window of the rivalry streams (Experiments 2 and 3), and found the perceptual advantage of structured streams persisted in the idiom condition but disappeared in the motion and shape conditions, suggesting a dissociation between the effects caused by semantic- and perceptual-level regularities. Intriguingly, such dissociation was also manifested in the results that structured streams defined by two types of regularities modulated visual competition at different conscious stages (Experiments 4 and 5). Collectively, these results suggest that the privileges of perceptual- and semantic-level regularities are unlikely to be driven by a simple common mechanism, albeit there is a general tendency for the human brain to prioritize multi-level structured information during visual competition.

Information integration and consciousness

The current findings provide valuable insights into the relationship between integration and awareness, an issue central to the contemporary research of consciousness.^{5,20,35,36} The IIT proposes that the content of consciousness can be qualitatively identified and quantitatively measured by the process of information integration. In particular, a conscious experience is identical to a conceptual structure encompassing a maximum of integrated information, with the extent of integration specified by the variable Φ^{max} .⁵ Thus, the alternation of conscious experience in BR can be explained by the competition between the conceptual structures separately corresponding to the information presented to the two eyes, while the experiential contrast between seeing one percept and the other depends on the extent of integration of the corresponding conceptual structures.³⁷ Specifically, when two conceptual structures specified by corresponding neural complexes coexist in the brain, the one with a greater amount of integration or intrinsic irreducibility (with a larger Φ^{max}) has an advantage in accessing consciousness. Based on the computational rule of IIT,³⁸ the Φ^{max} of a system can be calculated based on the underlying cause–effect repertoire defined by the transition probability of past and future states relative to the current state. Accordingly, the conceptual structure specifying the structured streams should have a higher estimated Φ^{max} value than that for the random streams. It is because in the former case, the probability distribution of past and future states is more constrained by the current state and far from the unconstrained distribution (higher irreducibility), whereas in the latter case, the system is less constrained and close to the unconstrained condition (lower irreducibility).

In this view, the observed perceptual advantage of structured information streams may arise from enhanced temporal information integration in the corresponding conceptual structure. In other words, the integration of visual elements over time may benefit from their intrinsic connections defined by certain types of regularities, allowing the incorporation of discrete events into a conceptual structure with a higher amount of integration such that facilitates the emergence of subjective conscious experience.^{5,38} Note that IIT would predict an overall advantage of structured streams during the visual competition, but cannot explain the lack of effect for contrast sequences and the different boundary conditions for the observed effects between semantic- and perceptual-level stimuli. Therefore, although our findings are in line with the assumption of IIT, they also emphasize the necessity to complement the theoretical framework by specifying the associations between the generation of conscious content and information integration over different stimulus levels.

Furthermore, identifying the limits of nonconscious visual processing is vital to revealing the function of consciousness. It has been widely recognized that the perceptual processing of some basic visual elements, such as orientation,³⁹ as well as certain higher-level information, such as recognizable words,²² can occur without awareness. But to achieve a coherent and continuous conscious experience, the visual system has to go beyond the perceptual processing of separate visual elements and integrate the sensory information across multiple spatial and temporal scales. To what extent such integrative processes can take place without awareness, or the scope of unconscious integrative processes, is a critical issue that remains to be resolved.²⁰ The current study casts light on this issue from the aspect of temporal integration. We found structured shape and motion streams but not idiom streams enjoyed a perceptual privilege even below consciousness. These observations coincide with previous findings of nonconscious adaption to invisible apparent motion and biological motion sequences,⁴⁰ suggesting that consciousness may not be required for the temporal integration of certain types of rhythmically changed visual patterns. By contrast, empirical results concerning the integrative processing of invisible semantic information seem more complicated. Although there has been evidence for nonconscious temporal integration of meaningful contents based on semantic or arithmetic relations,^{41,42} others failed to find such an effect for sequentially presented

characters within an idiomatic context.^{43–45} Our finding that the perceptual advantage of concatenated idiom streams in BR transpired primarily above the conscious level supports the notion that the temporal integration of symbolic information based on complex rules may, to some extent, require the awareness of the visual elements.

In addition, Mudrik and colleagues have raised the window of integration (WOI) hypothesis predicting wider-range integration and a bigger integration window for conscious processing versus nonconscious processing.^{20,46} Here, we observed dissociation of the conscious and nonconscious rivalry advantages for semantic- and perceptual-level regularities, with different susceptibility to spatiotemporal perturbations on the integration window. While these findings do not provide direct evidence for the WOI hypothesis, they support a general distinction between integration windows for conscious and nonconscious visual processing, and highlight the need to take into account the stability of the integration window besides its size when evaluating the difference between conscious and nonconscious processing.

Other possible mechanisms underlying the temporal structure privilege

One might argue that the temporal structure advantage observed in the current study can be adequately explained by the attentional processes. Based on the biased competition theory of attention, the modulation of attentional control occurs on different stages of BR, particularly when there is unresolved stimulus conflict (e.g., after the stimuli are initially presented) and when conflict is resolved at a higher level of processing (e.g., sustained stimulus rivalry).⁴⁷

On the one hand, there has been substantial evidence that objectbased attention and endogenous attention can bias initial dominance in BR after stimulus onset.^{48,49} To test whether initial attentional selection contributed to the current study, we conducted additional analysis on the initial dominance data (more details are available in the Supporting Information). The analysis revealed no evidence for an initial attentional bias, excluding the influence of initial attentional selection on the observed advantage of structured streams in BR dominance.

On the other hand, rivalry dominance at the sustained rivalry stage appears less susceptible to attentional modulation and hinges on task relevance of the stimuli. Meng and Tong instructed subjects to hold one of the two rival stimuli dominant for as long as possible.⁵⁰ The results showed only a weak and statistically unreliable attentional modulation effect over the dynamics of BR, in contrast to the strong attention modulation effects observed in studies of perceptual reversals for other bistable stimuli.⁵⁰⁻⁵² Moreover, Chong et al. found that enhancing task relevance of a rival stimulus (e.g., directing observers' attention to a changing feature of that stimulus) can lengthen perceptual dominance.⁵³ These attentional modulation effects are not applicable to the current research, as neither voluntary control nor task-driven attentional selection was involved in our behavioral task (i.e., color discrimination).

While the biased competition theory of attention deals with how stimulus- and task-driven attentional selection modulates BR, the

possible effect of history-driven selection, a process that can influence the allocation of attention parallel to top-down and bottom-up selection,⁵⁴ remains to be examined. The history of attentional deployment can elicit attention bias toward regularity through statistical learning.^{11,55} Future research could examine whether temporal structures defined by perceptual- and semantic-level regularities modulate visual attention and identify whether the findings contribute to the advantage of structured streams in BR. Addressing these issues may help advance our understanding of the intricate relationship between attention and awareness.⁵⁶

Besides, our research seems relevant to one high-level factor that modulates BR, that is, the predictive context. A previous study showed that viewing a regular sequence of rotating gratings (the context) prior to a BR trial will bias the onset percept toward a grating predicted by the context.⁵⁷ The stimuli used in that study were similar to our motion streams but those stimuli preceded the rivalry trial and were explicitly perceived by observers. Thus, observers may voluntarily direct their attention to the predictable pictures at the beginning of the rivalry trial, an effect referred to as "attentional expectations." In the motion (as well as the shape and contrast) conditions of our study, observers were unaware of the regularities embedded in the rival streams, as revealed by the debriefing assessment following the experiment. Therefore, the observed structure advantage throughout sustained rivalry is not likely to arise from the endogenous "attentional expectations." However, there remains a possibility that predictive processing of visual information, which may not require the awareness of the regularity, may foster the continuous generation of conscious content. The predictive processing theory assumes that BR results from the competition between two perceptual hypotheses (best guesses) and the one winning the competition will dominate consciousness.^{58,59} Thus, the advantage of structured streams that we observed may be attributed to the high predictability of the structured streams induced by temporal regularities. The neural mechanism behind the predictive processing may involve recurrent interactions among brain regions supporting conscious generation and visual temporal integration, given the significance of recurrent signals in conscious perception.³⁷

CONCLUSION

To recapitulate, we show that during dynamic visual competition, visual awareness is biased toward information with regular temporal structures. While such advantages can be generalized to semanticand perceptual-level regularities, the underlying benefits, respectively, stem from conscious and nonconscious temporal integration with different susceptibility to variations in the spatiotemporal integration with different susceptibility to variations in the spatiotemporal integration window, suggesting that they are mediated by partially overlapping but distinct mechanisms. These findings corroborate and extend the IIT by highlighting the crucial role of structure-guided information integration in the continuous emergence of conscious content. They also shed light on the relationship between integration and awareness across the hierarchy of visual information processing.

AUTHOR CONTRIBUTIONS

Y.W. conceived the study concept. R.H., Y.W., and Y.J. designed the experiments. R.H., S.L., and P.Y. collected the data. R.H. and S.L. performed the data analysis. All authors contributed to the writing of the manuscript.

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COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in PsyDB at https://doi.org/10.57760/sciencedb.12835.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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