



Clarifying frequency-dependent brightness enhancement: delta- and theta-band flicker, not alpha-band flicker, consistently seen as brightest

Jennifer K. Bertrand^{1,2} · Alexandra A. Ouellette Zuk² · Craig S. Chapman^{1,2}

Received: 11 October 2018 / Accepted: 27 May 2019 / Published online: 6 June 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Frequency-dependent brightness enhancement, a perceptual illusion in which a flickering light can appear twice as bright as a constant light, has historically been reported to produce maximum effects at a flicker rate within the alpha (8–12 Hz) band (Bartley in *J Exp Psychol* 23(3):313–319, 1938). Our recent examinations of this phenomenon using brightness discrimination between two flickering stimuli, however, have instead revealed the brightest percepts from theta-band (4–7 Hz) flicker (Bertrand et al. in *Sci Rep* 8(1):6152, 2018). Two primary questions arise from these seemingly contradictory findings: first, could task differences between these studies have caused recruitment of discrete oscillatory processes? Second, could the reported theta-band flicker enhancement be the result of an aliased alpha rhythm, sequentially sampling two stimulus locations, resulting in an ~5 Hz half-alpha rhythm? Here, we investigated these questions with two experiments: one replicating Bartley's (1938) adjustment paradigm, and one containing both Bartley's adjustment task and Bertrand's (2018) discrimination task, but presenting stimuli only sequentially (rather than concurrently). Examination of a range of frequencies (2–12 Hz) revealed the greatest brightness enhancement arising from flicker in the delta- and theta-band across all conditions, regardless of the spatial or temporal configuration of the stimuli. We speculate that these slower rhythms play an integral role in complex visual operations (e.g., a discrimination decision) where the entrainment of the endogenous neural rhythm to matched exogenous rhythmic stimulation promotes more efficient processing of visual information and thus produces perceptual biases as seen in frequency-dependent brightness enhancement.

Keywords Visual perception · Flicker · Brightness enhancement · Neural oscillations · Discrimination

Introduction

Neuronal oscillations reflect spatially and temporally structured rhythmic fluctuations in neural excitability that manifest in a broad spectrum of endogenous frequencies (Hutcheon and Yarom 2000; Lakatos et al. 2008). These

oscillations have been shown to impact a variety of cognitive phenomena (Buzsáki and Draguhn 2004; Busch et al. 2009; Cravo et al. 2013). Most relevant to the current study, neuronal oscillatory activity has been demonstrated to cyclically modulate a range of visual perceptions, from visual detection (Mathewson et al. 2009; Busch et al. 2009), to attentional re-weighting between viewed targets (Fiebelkorn et al. 2013; Macdonald et al. 2014; Crouzet and VanRullen 2017), and visual recognition (Klimesch 1999; Burgess and Gruzelier 1997; Buzsaki 2006). It has been proposed that oscillations in visual cortex effectively establish a sampling frequency for incoming sensory information with an intrinsic alpha rhythm (ranging from 7 to 12 Hz) as a critical component (Klimesch 1999). Also labeled an inhibitory sampling rhythm (Klimesch et al. 2007; Jensen and Mazaheri 2010; Palva and Palva 2011), alpha oscillations appear to constrain visual processing to a cyclical periodicity. This means that visual perception is somewhat dependent on

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00221-019-05568-1>) contains supplementary material, which is available to authorized users.

✉ Jennifer K. Bertrand
jbertran@ualberta.ca

¹ Faculty of Kinesiology, Sport, and Recreation, University of Alberta, Edmonton, AB, Canada

² Neuroscience and Mental Health Institute, Faculty of Medicine and Dentistry, University of Alberta, Edmonton, AB, Canada

when the sensory information arrives with respect to the alpha band sampling cycle (VanRullen and Koch 2003; Busch and VanRullen 2010; VanRullen 2016). The periodicity of visual sampling can also be induced by an external stimulus. That is, oscillations in visual cortex will entrain to the frequency of a rhythmic visual stimulus, giving more experimental control over the specific timing of high and low excitability states (Lakatos et al. 2008; Calderone et al. 2014). As a result, neural entrainment can both enhance and suppress sensory processing and perceptions (Mathewson et al. 2012; VanRullen 2016; Spaak et al. 2014; Cravo et al. 2013; Bertrand et al. 2018).

One striking visual illusion thought to be rooted in the entrainment of neuronal oscillations is the Brücke effect. First reported by Bartley (1938), participants judged a stimulus flickering in the alpha range to be twice as bright as a steady one, despite them having the same luminance. In this study, participants judged brightness via a method of adjustment, changing the luminance of the flickering stimulus until its perceived brightness matched a steady, static light whose luminance never changed. While a range of slower flicker frequencies (1–17 Hz) elicited brightness enhancement, 10 Hz flicker demonstrated the greatest effect (Bartley 1938). In a recent attempt to replicate these findings we used a brightness discrimination task between pairs of flickering stimuli. Unlike Bartley, we found brightness enhancement was most pronounced for flicker within the theta frequency band (4.44 Hz), even when the counter stimulus flickered at an alpha-rate (9.23 Hz; Bertrand et al. 2018). In a second experiment we replicated this finding and also found evidence that neuronal entrainment in theta-band oscillations over visual cortex were predictive of brightness enhancement (Bertrand et al. 2018).

Exploring the discrepant results between Bartley (1938) and Bertrand et al.'s (2018) provides the main motivation for the current study. Is the brightness enhancement of a flickering stimulus most pronounced in the alpha band (e.g. ~ 10 Hz) or the theta-band (e.g. ~ 4 Hz)? And, how does this phenomenon relate to the purported roles of alpha and theta rhythms in the brain? Indeed, despite alpha oscillations having long been considered a crucial component in more sensory driven visual phenomena (Bartley 1938; Nelson et al. 1963; Buzsáki and Draguhn 2004; VanRullen 2016), theta oscillations have been implicated in higher-order visual processing (Klimesch et al. 1996) including working memory (Lopes da Silva 1992; Klimesch et al. 1996, 1997), recognition (Burgess and Gruzelier 1997), contrast sensitivity (Cravo et al. 2013), visual search (Buszák 2006) and brightness perception of 3D shapes (Han and VanRullen 2017). This suggests that theta is implicated in tasks requiring not just the detection of sensory information, but the maintenance and interrogation of the details of that information. These task demands are often present when participants

are required to “divide their attention” and sample from, or monitor, multiple stimuli (Fiebelkorn et al. 2013; Klimesch et al. 1998; Holcombe and Chen 2013; Macdonald et al. 2014). In fact, a related theory argues that there is a single, discrete sampling rhythm in the alpha band, and tasks that appear to be impacted by theta are actually the result of the alpha rhythm required to sequentially sample multiple locations (Macdonald et al. 2014; Crouzet and VanRullen 2017). In this model, a ~ 5 Hz half-alpha rhythm would result when alpha's ~ 10 Hz frequency alternates between two locations (Macdonald et al. 2014; Crouzet and VanRullen 2017).

To summarize, research suggests that the alpha rhythm establishes a lower-level, faster, sensory sampling rate. By comparison, the theta-rhythm either sets a slower, higher-order rate at which sensory information can be maintained and shared or is simply the result of an alpha rhythm sampling from multiple locations. Under this framework, we posit that our previous result (Bertrand et al. 2018) could have shown maximal brightness enhancement for theta-band flicker because our discrimination task critically involved the maintenance and manipulation of internal representations of two target stimuli from two sites (thus requiring theta either because of the need to interrogate the representations and/or the need to distribute monitoring across two sites). In comparison, Bartley's adjustment task (1938), which involved only a single flickering stimulus, and thus only one object that needed consistent monitoring, was most impacted by stimuli flickering in the alpha band.

Thus, the two experiments reported here test whether our recent finding (Bertrand et al. 2018) of maximal brightness enhancement for stimuli flickering in the theta-band persists when (1) brightness is reported via adjustment (like Bartley 1938) rather than discrimination, and (2) when all stimuli appear in isolation at a single spatial location, and judgments (discrimination on half the trials and adjustment on half the trials) are made between sequentially presented stimuli. If brightness enhancement is related to the nature of the task, then, for Experiment 1, where we replicate Bartley's adjustment procedure, we would predict that we should replicate his result of maximal perceived brightness for stimuli flickering in the alpha band. However, if brightness enhancement is instead due to the presentation of more than one stimulus at a time, then for Experiment 2, where stimuli only ever appear one at a time, we would predict alpha enhancement regardless of whether the task is adjustment or discrimination. But we also consider that others have reported results that don't align with Bartley's findings: (1) Glad and Magnussen (1972) and Magnussen and Glad (1975) also used square wave flicker with brightness (and darkness) matching at a 1:1 light-to-dark ratio (LDR), and found that the “optimal frequency [for brightness enhancement] does not exceed 6.5 Hz”, and (2) Kohn and Salisbury's results (1967), elicited by square-wave 1:2 LDR flicker with a subjective

brightness matching task, suggest significant brightness enhancement from flicker as slow as 5 Hz. It is possible that the greatest brightness enhancement will always occur for stimuli flickering more slowly than alpha. If this is the case, it would suggest that an account of theta playing a role in higher-order cognition is true regardless of whether or not attention is divided across space.

Experiment 1

The primary objective of Experiment 1 was to test whether the previously reported discrepancy in the flicker frequency producing maximum brightness enhancement was due to task differences. Specifically, the original report (Bartley 1938, max enhancement around 10 Hz) used an adjustment task and our more recent study (Bertrand et al. 2018, max enhancement around 4 Hz) used a discrimination task. To rule out this explanation for our previously reported effects, here we replicate the adjustment task used by Bartley (1938) but update it to match other methodological details (e.g., use of computer monitor) employed in Bertrand et al. (2018).

Materials and methods

Participants

29 naive right-handed participants (18 females; mean age 19 ± 1.1 years) with corrected-to-normal vision and no sensitivity to flashing lights participated in the experiment. All experimental procedures were approved by the University of Alberta's Research Ethics Office (Pro00059044). Informed consent was obtained from all individual participants included in the study, and each was rewarded with credit toward their introductory psychology course after study completion.

Apparatus

A ViewPixx 120-Hz refresh rate monitor and a keyboard were placed 50 cm (cm) in front of a participant in a dimly lit room. This study was designed and executed with the Psychophysics toolbox (Brainard 1997) in MATLAB on a computer running Windows 7. The stimuli consisted of two circles 2.3° in diameter, one right and one left of a 0.4° fixation cross, with 4.6° between the center of the fixation and the center of each circle (consistent with Bertrand et al. 2018). Constant stimuli were grey, with a luminance pixel value of 128 to appear as a medium between 0 (black) and 256 (white) in RGB space. The to-be-adjusted flickering stimuli appeared at one of three RGB start values: 168, 128, or 88 for high, equivalent, and low luminance conditions, respectively. We converted RGB values to luminance

(cd/m^2) using an X-Rite i1Display Pro photometer by presenting each RGB grey value 10 times over two sessions and taking the average luminance readout produced by the photometer. Since the transformation from RGB space to luminance space is non-linear our high, equivalent, and low start values were not equidistant (high = $32.88 \text{ cd}/\text{m}^2$; equivalent = $15.75 \text{ cd}/\text{m}^2$; Low = $5.73 \text{ cd}/\text{m}^2$). Five flicker frequencies were employed: 2.03 Hz, 4.44 Hz, 7.05 Hz, 9.23 Hz, or 12 Hz. This frequency range was designed to specifically test frequencies spanning the theta and alpha bands, within the constraints of a 120 frames per second refresh rate monitor. Each individual flicker lasted for an identical period of six frames, independent of frequency, and was generated by the stimulus changing between its luminance value (dependent on the trial) and the black background colour. For example, a 4.44 Hz stimulus would flicker with 6 frames of grey followed by 21 frames of black (with ~ 4 flickers per second), while a 9.23 Hz stimulus would flicker with 6 frames of grey followed by 7 frames of black (with ~ 9 flickers per second). This flicker was square-wave luminance modulation (as opposed to sine-wave flicker), chosen to replicate the luminance stimulation used by Bartley (1938) and Bertrand et al. (2018). We do note that square-wave flicker has been reported to result in stronger M/EEG responses at two times the frequency of entrainment (Kim et al. 2011; Rager and Singer 1998). However, in our previous electrophysiological findings using the same stimuli, the maximum entrainment occurred at the rhythm of the stimulus (4.4 Hz), not its double (8.8 Hz). Moreover, Kim et al. (2011) suggest that this doubling effect may exist for only a narrow band of frequencies, which begins higher (6.25 Hz) than our stimuli of interest.

Procedure

Each trial began with a white fixation cross centered on a black background, flanked by a flickering stimulus and a constant stimulus on either side (left/right), as shown in Fig. 1a. Participants were instructed to fixate on the fixation cross and use the up and down arrow keys of the keyboard to adjust the luminance of the flickering stimulus until its brightness matched that of the constant. They indicated the adjustment was complete by pressing the spacebar. Luminance adjustment steps followed an adaptive staircase procedure. The steps adjusted by beginning with a step size of 10 RGB. Every change of direction (e.g., up arrow to down arrow) would reduce the step size by 4 RGB, to a minimum step size of 2 RGB. A run of 4 presses in the same direction would increase the step size by 4 RGB to a maximum step size of 10 RGB. Due to the non-linear relationship between RGB and luminance, step sizes were not equivalent for every button press (i.e., a step size of 4 RGB from 88 to 92 RGB is $0.73 \text{ cd}/\text{m}^2$, but from 168 to 172 RGB it is $2.14 \text{ cd}/\text{m}^2$). A

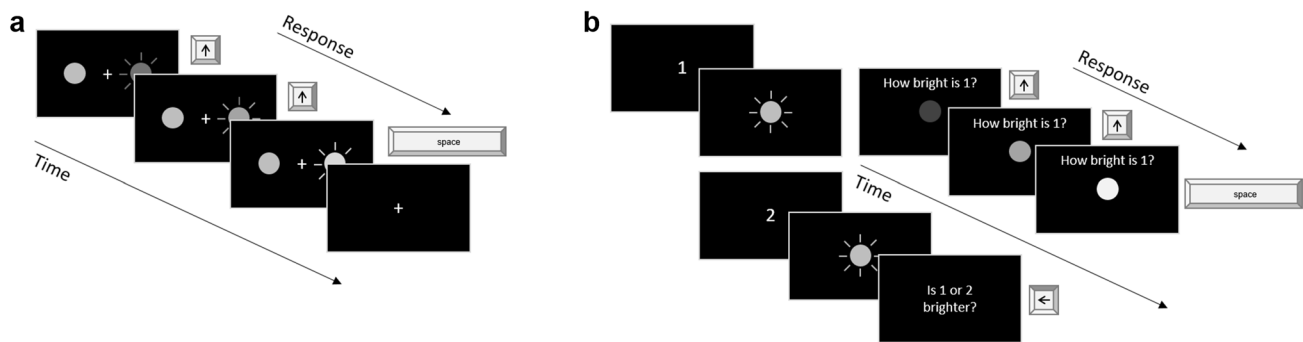


Fig. 1 The order of stimulus presentation for a single trial for each of Experiment 1 (a) and Experiment 2 (b), with an example sequence of key press responses. **a** Experiment 1. Two circle stimuli are presented for a maximum of 15 s, where the brightness of the flickering stimulus is matched to the brightness of the constant stimulus using up and down arrow keys. The final response is marked by a spacebar key press, and advances to the next trial, with a 500 ms ITI. **b** Experiment 2. An initial “1” is presented centrally for 750 ± 250 ms followed by a 2000 ms flickering circle stimulus. A trial was either an adjustment or discrimination task type. On adjustment task trials,

500 ms (ms) inter-trial interval (ITI) of a black screen and fixation cross separated trials. Participants had 15 s to adjust (arrow keys) and confirm (spacebar) their perceived equivalent brightness judgment. The ITI would initiate immediately after a spacebar key press. If an equivalence judgment was not made within 15 s, the ITI would begin, and the trial would be recorded as a non-response.

Each participant completed 480 trials, broken into 16 blocks of 30 trials. A block consisted of the pseudo-random ordering of 2×15 conditions, with the 15 conditions created by all possible combinations of frequency (2, 4, 7, 9, or 12 Hz) and start luminance (high, equivalent, or low) for the flickering stimuli. To most closely replicate Bartley’s (1938) task, the flickering stimulus remained on the left or right side of the screen consistently for half the total trials (8 blocks, or 240 trials), switching to the opposite side of the screen for the second half of the experiment. This resulted in a between-subject factor of initial adjustment side, either Left-Adjust-First (LAF) or Right-Adjust-First (RAF), that coded where the stimulus was presented (side of space) for the first half of the total trials, and was counterbalanced across participants (LAF: $n = 15$; RAF: $n = 14$). Finally, we accounted for the possibility of experiment order effects by coding an adjustment order factor which indicated in which half of trials the adjusted stimulus was presented: adjusted first or adjusted second.

Dependent measures and statistical procedure

Brightness enhancement The difference (in luminance space) between the grey, constant, comparison stimulus (15.75 cd/m^2) and the final adjusted luminance value of

following the flickering circle, a constant circle stimulus appears with the text “How bright is 1?”, and arrow keys are used to adjust the brightness for up to 10 s until a response is confirmed with a spacebar key press. On discrimination task trials, following the first flickering circle, a “2” was presented centrally for 750 ± 250 ms, followed by a second flickering circle for 2000 ms. A response screen of “Is 1 or 2 brighter?” followed and allowed 5 s for a response with a left or right arrow key press for 1 or 2, respectively. Both trial types end with a 700 ms ITI

the flickering stimulus, where a positive difference indicates brightness enhancement (e.g., the final adjusted value was lower than 15.75 cd/m^2 , indicating less luminance was needed for the flickering stimulus to appear equivalently bright to the constant stimulus).

Time to first key press (sec) Time from stimulus onset to the first key press (up, down, or spacebar key).

Prior to any statistical analyses, all trials recorded as non-responses (i.e., no response within the 15 s limit; 0.85% of total trials) and all reaction times faster than 100 ms (i.e., a response beyond the abilities of the visual system; 0.22% of total trials) were removed, resulting in 98.93% usable data.

Statistical procedures were the same for each dependent measure, and started with a four-factor mixed model ANOVA which was used to test for main effects and interactions between the between-subjects factor initial adjustment side (LAF and RAF) and the within-subject factors frequency (2, 4, 7, 9, and 12 Hz), start luminance (high, equivalent, and low), and adjustment order (adjusted first and adjusted second). For all reported ANOVA results, we follow the same procedure. All interactions revealed by the omnibus ANOVA were followed-up with an appropriate repeated measures (RM) ANOVA that collapsed over any factors that did not interact. Interactions at the subsequent levels of analyses continued to be explored (with first separation into the between subjects groups where significant) until the simple main effects of each factor were examined at all levels of the other factors. Significant main effects were then explored with all pairwise comparisons. All RMANOVA p values reported include a Greenhouse–Geisser (GG) correction for violations of sphericity, and each RMANOVA

result includes a GG epsilon value. Following the valuable suggestion of an anonymous reviewer we hold the family wise error rate of any multi-way ANOVA to an alpha of 0.05 using remedy two reported in Cramer et al. (2016). This requires ordering the *p* values of all main effects and interactions by significance and applying a sliding adjusted alpha (starting with [alpha/number of tests] to alpha=0.05), taking as significant all of those results with *p* values less than the adjusted alpha until one result has a *p* value larger than the adjusted alpha. For follow-ups to single factor RMANOVAs, pairwise comparison tests were considered significant if the Tukey-HSD corrected *p* value was less than 0.05.

Results

Brightness enhancement

In general, brightness enhancement effects were driven by frequency, where 2 and 4 Hz stimuli were perceived as being the brightest while 7, 9, and 12 Hz were incrementally perceived as being less bright (see Fig. 2a, b and Online Resource 1). This was confirmed with a four-factor mixed model ANOVA which found no significant four-way interaction ($F_{(8,216)}=0.94$; $p=0.45$; $\epsilon=0.13$), but did reveal a significant main effect of frequency ($F_{(4,108)}=87.47$; $p=2.82e-16$; $\epsilon=0.13$) and a significant interaction between initial adjustment side and adjustment order ($F_{(127)}=13.56$; $p=0.001$; $\epsilon=0.13$). Pairwise comparisons between all levels of frequency demonstrated that 2 and 4 Hz stimuli were not judged to be significantly different ($p=0.12$), but all other stimuli were seen as different (all p 's < $1.0e-8$). To investigate the initial adjustment side by adjustment order interaction we ran a one-factor RMANOVA comparing adjustment order for each of the RAF and LAF groups. For the RAF group there was a significant difference in adjustment order ($F_{(1,13)}=31.11$; $p=8.95e-05$; $\epsilon=1$) while for the LAF group there was no such difference ($F_{(1,14)}=0.67$; $p=0.43$; $\epsilon=1$). This suggests the two-way interaction was mainly driven by differences between adjustment order for only one of our two groups (RAF), where stimuli adjusted in the first half of the experiment were perceived brighter, possibly indicating some effects of fatigue and/or it's interaction with side of space effects. Overall, the predominant effect on brightness perception is from frequency, which again shows that slower flickering stimuli are perceived as brighter.

Time to first key press

For a more complete understanding of the relative luminance results, we used the time to first key press as an indirect index of decision difficulty (Fig. 2c). In general, participants were slower to begin their response when stimuli were slower in frequency, and also when stimuli were at

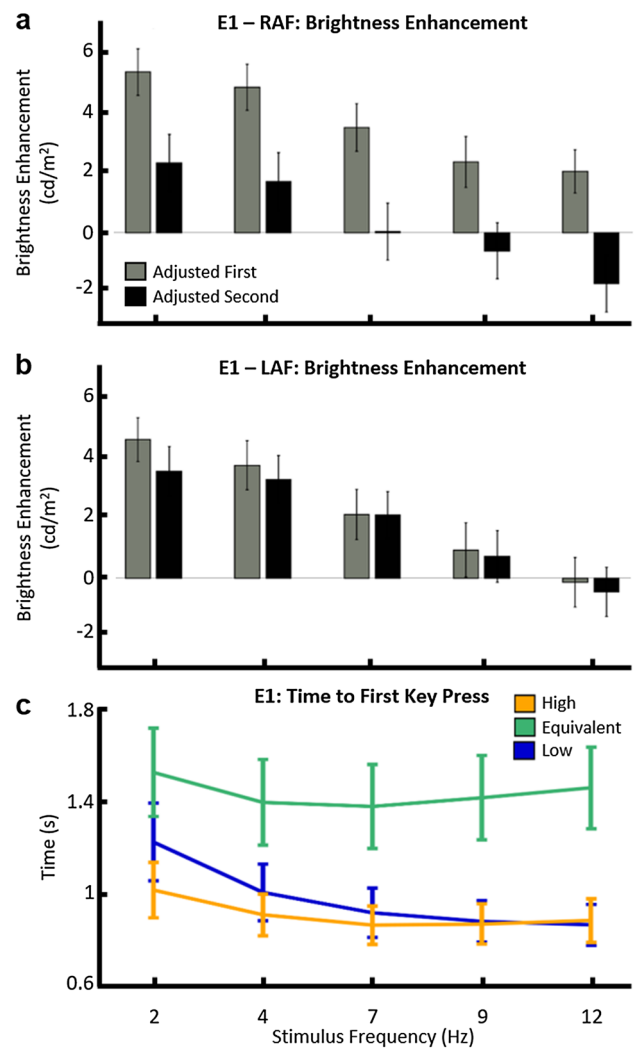


Fig. 2 Experiment 1 brightness enhancement and timing results. **a**, **b** Brightness enhancement (in cd/m^2 , measuring the amount below our mid-grey level) for each adjusted test frequency, separated by our between subjects groups, RAF (**a**) and LAF (**b**). Within each panel, results are separated by adjustment order into stimuli adjusted in the first half of trials (grey) or second half of trials (black). **c** Time to first key press results, measured from stimulus onset to the first key press of an adjustment (arrow) or confirmation (space bar) for flickering stimuli presented at each level of start luminance (high = yellow, equivalent = green, low = blue). Error bars in all panels represent averaged individual standard errors

an equivalent start luminance (i.e., the same luminance as the constant reference circle simultaneously presented with the stimulus). A four-factor mixed model ANOVA revealed a significant three-way interaction between frequency, start luminance and adjustment order ($F_{(8,216)}=4.2045$; $p=0.0021$; $\epsilon=0.1887$), and no significant four-way interaction ($F_{(8,216)}=1.28$; $p=0.28$; $\epsilon=0.19$). To follow-up, we compared frequency and start luminance at each level of adjustment order with a two-factor RMANOVA. For adjusted first, there was a significant two-way interaction

between frequency and start luminance ($F_{(8,224)} = 8.70$; $p = 1.06e-05$; $\epsilon = 0.24$), and one-factor follow-up RMANOVAs at each level of start luminance found significant main effects of frequency at low ($F_{(4,112)} = 67.50$; $p = 7.07e-23$; $\epsilon = 0.77$), equivalent ($F_{(4,112)} = 3.10$; $p = 0.043$; $\epsilon = 0.60$) and high levels ($F_{(4,112)} = 8.27$; $p = 3.73e-5$; $\epsilon = 0.82$). Pairwise comparisons of frequency at each level of start luminance found no significant differences in key press time for any frequency pairs for the equivalent start luminance (all p 's > 0.0649), significantly slower key press times for both 2 Hz relative to all other faster frequency stimuli (all p 's $< 5.54e-8$) and 4 Hz relative to all other faster frequency stimuli (all p 's $< 9.69e-4$) for the low start luminance, and, for the high start luminance, significantly slower key press times for 2 Hz relative to all other faster frequency stimuli (all p 's < 0.0070). When testing the adjusted second level, no significant two-way interaction was found ($F_{(8,224)} = 0.89$; $p = 0.49$; $\epsilon = 0.34$), but there were significant main effects of start luminance ($F_{(2,56)} = 75.00$; $p = 1.23e-12$; $\epsilon = 0.34$) and frequency ($F_{(4,112)} = 9.88$; $p = 6.05e-6$; $\epsilon = 0.34$). Follow-up pairwise comparisons for start luminance found that key press times on equivalent trials were significantly longer than both low and high trials (both p 's $< 7.07e-9$), and frequency pairwise comparisons showed results similar to adjusted first, where effects were driven by significantly slower key press times for 2 Hz relative to all other faster frequency stimuli (all p 's < 0.0047). Taken together, we see an effect of frequency, mostly driven by slower time to first key press responses to 2 Hz stimuli, and an effect of start luminance, mostly driven by slower time to first key press responses for equivalent stimuli. We suggest that, for a 2 Hz stimulus, participants are waiting for more samples of the stimulus before initiating their adjustment decision. For the slowing effect related to equivalent start luminance trials, we suggest this is due to decision difficulty. That is, it is well known that discrimination decisions between stimuli that are more similar generally lead to longer reaction times (for review see Wispinski et al. 2018) and here, the equivalent start luminance is creating a case of maximal similarity.

Experiment 2

The primary objective of Experiment 2 was to test whether the number of items simultaneously presented affects flicker-related brightness enhancement. Specifically, some recent theories (Macdonald et al. 2014; Crouzet and VanRullen 2017) have argued that we visually sample only a single spatial location at a rhythm of about 10 Hz. Thus, if brightness enhancement occurs because the onset of a target aligns with this rhythm, then when only a single target is present, it should produce maximum enhancement around 10 Hz. If a second stimulus is presented simultaneously (as in

Experiment 1), then each individual item is sampled at half of the overall rate, leading to enhancement when stimuli are presented at about 5 Hz. Therefore, to rule out this explanation of our previously reported enhancement for 4 Hz stimuli (Bertrand et al. 2018), in Experiment 2 we have participants judge the brightness of stimuli, but present only a single stimulus on the screen at a time.

Materials and methods

Except for the following noted changes, Experiment 2 replicated the methods of Experiment 1.

Participants

26 naïve individuals (12 females; mean age 19.7 ± 1.3 years) participated in the experiment, none of whom had participated in Experiment 1. One participant's behavioural data were excluded from analysis due to a failure to comply with task instructions, resulting in 25 data sets for analysis.

Apparatus

Stimuli in Experiment 2 were presented sequentially in the center of the screen such that only one spatial location needed to be monitored (see Fig. 1b). The frequencies of the flickering stimuli were limited to 0 Hz (no flicker), 4.44 Hz and 9.23 Hz to directly compare results in the baseline, theta, and alpha frequencies, respectively. 0 Hz (no flicker) was used as a baseline measure to both remain consistent with our previous studies (Bertrand et al. 2018) and to also provide an order effect measure unbiased by flicker effects. Experiment 2 was comprised of two different tasks. The adjustment task first presented a flickering stimulus that varied in frequency (0, 4, or 9 Hz) followed by a constant stimulus that varied in start luminance (high, equivalent, or low—same values as Experiment 1) which was to be adjusted to match the previously seen flickering stimulus. The discrimination task presented two consecutive flickering stimuli, each varying in frequency (0, 4, or 9 Hz), and participants were asked to judge which was perceived as brighter.

Procedure

Adjustment and discrimination trials were randomly interleaved. Both tasks began with a “1” in the middle of the screen for 750 ± 250 ms, followed by a centered flickering stimulus for 2000 ms (see Fig. 1b). On adjustment trials, a constant stimulus would follow the flickering stimulus, appearing with the text prompt “How bright is 1?” (or dark, see counterbalancing details below). Participants then had up to 10 s to adjust the luminance of the constant stimulus

to match its brightness to that of the previously displayed flickering stimulus, using the up and down arrow keys to change the luminance and finalizing their response by pressing the space bar. On discrimination trials, following the first flickering stimulus, a “2” would appear in the center of the screen for 750 ± 250 ms. This was then replaced by a second centered flickering stimulus which was on the screen for 2000 ms. A final screen then appeared with the text “Is 1 or 2 brighter?” (or darker, see counterbalancing details below). Participants then had up to 5 s to enter their response using the left or right arrow key to denote if the first or second stimulus was brighter, respectively. A 700 ms black screen ITI followed each trial, independent of task type. Trials would proceed to the ITI screen at the time of the final response or at the end of the response period (after 10 or 5 s for adjustment or discrimination, respectively), whichever occurred first.

Experiment 2 consisted of 252 trials, broken into 14 blocks of 18 trials. Each block contained 18 unique pseudo-randomized trial conditions, with 9 trial conditions per task type. Adjustment trials consisted of one repetition of all pairwise combinations of flicker frequency (0, 4, and 9 Hz) and constant stimulus start luminance (high, equivalent, and low). Discrimination trials consisted of one repetition of all pairwise combinations of flicker frequency for both the first stimulus and the second stimulus (0, 4, and 9 Hz for both). Participants were randomly assigned to one of two experimental groups which informed whether they would make judgments about the brightness ($n = 13$) or the darkness ($n = 12$) of the circles. We called this between-subject factor question-framing, and text of adjustment and discrimination tasks would instead read “How dark is 1?” and “Is 1 or 2 darker?” if the questions were framed for darkness judgments.

Dependent measures and statistical procedure

Adjustment task

Brightness enhancement The difference (in luminance space) between 15.75 cd/m^2 (the luminance value of the flickering stimulus) and the final adjusted luminance value of the constant stimulus, where a positive difference indicates brightness enhancement (e.g., the final adjusted value was higher than 15.75 cd/m^2 , indicating more luminance was needed for the constant stimulus to appear equivalently bright to the flickering stimulus).

Time to first key press (sec) Time from the constant stimulus onset to the first key press (up, down, or spacebar key).

The same statistical procedure used to analyze Experiment 1 was applied to Experiment 2 adjustment trials, only substituting a three-factor (frequency \times start

luminance \times question-framing) mixed-model ANOVA as the omnibus test for main effects and interactions.

Discrimination task

Choice proportion Proportion of trials where the first stimulus was selected as brighter (or, second stimulus selected as darker) by left (first) or right (second) arrow key press.

Reaction time (sec) Time from second flickering stimulus offset to left or right key press.

Data was cleaned in the same fashion as Experiment 1, with 0.009% of total trials removed for non-responses, and 0.03% of total trials removed for reaction times faster than 100 ms, yielding 99.96% usable data.

The same statistical procedure used to analyze Experiment 1 was applied to Experiment 2 discrimination trials, only substituting a three-factor (1st stimulus frequency \times 2nd stimulus frequency \times question-framing) mixed-model ANOVA as the omnibus test for main effects and interactions. Finally, to test for possible order effects (e.g., always see the first thing as brighter) we used a *t* test of choice proportion against 50% for the three frequencies on same-frequency trials (e.g., 4 Hz first vs 4 Hz second).

Results

Adjustment task

Brightness enhancement

Like Experiment 1, brightness enhancement results were primarily driven by frequency, where 4 Hz stimuli appear significantly brighter than both 0 and 9 Hz stimuli (see Fig. 3a). This was confirmed with a three-factor question-framing \times frequency \times start luminance mixed model ANOVA, which revealed a significant two-way interaction between frequency and start luminance ($F_{(4,92)} = 6.64$; $p = 4.17e-4$; $\epsilon = 0.32$) and no significant three-way interaction ($F_{(4,92)} = 0.78$; $p = 0.52$; $\epsilon = 0.32$). Examining the significant interaction with one-factor RMANOVAs comparing frequency at each level of start luminance, there were significant main effects of frequency for low ($F_{(2,48)} = 21.07$; $p = 3.70e-7$; $\epsilon = 0.97$), equivalent ($F_{(2,48)} = 31.22$; $p = 3.81e-8$; $\epsilon = 0.83$) and high ($F_{(2,48)} = 15.27$; $p = 1.72e-5$; $\epsilon = 0.91$) levels. Pairwise comparisons of frequency at each level of start luminance showed that 4 Hz stimuli were always perceived as significantly brighter than 0 and 9 Hz stimuli (all p 's $< 4.91e-4$), while 0 and 9 Hz were mostly perceived as being not significantly different (both p 's > 0.097), except for at the equivalent level ($p = 0.026$). Importantly, a 4 Hz stimulus still appears the brightest even

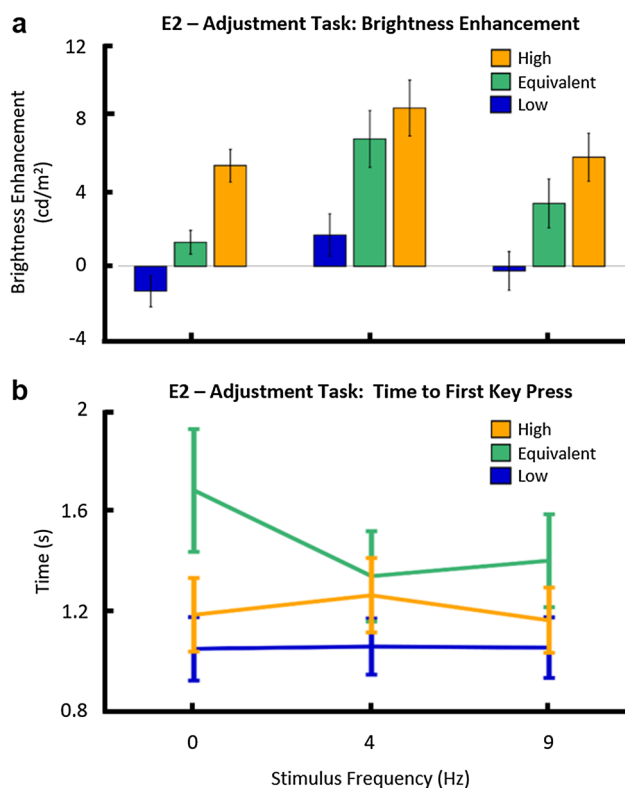


Fig. 3 Experiment 2 adjustment task brightness enhancement and timing results. **a** Brightness enhancement (in cd/m^2 , measuring the amount above our mid-grey level) results for each flicker frequency for an adjusted, constant stimulus that started at a high (yellow), equivalent (green) or low (blue) start luminance. **b** Time to first key press results, measured from stimulus onset to the first key press of an adjustment (arrow) or confirmation (space bar) for constant stimuli presented at each level of start luminance. Error bars in both panels represent averaged individual standard errors

when stimuli appear sequentially as opposed to simultaneously. This brightness enhancement from a 4 Hz stimulus persisted across subject group and start luminance, and was most pronounced at the equivalent start luminance level, which drove the initial 2-way interaction.

Time to first key press

Like Experiment 1, we find a pattern suggesting that perceptually similar stimuli lead to longer initial key press responses. This was confirmed via a three-factor mixed model ANOVA of question-framing \times frequency \times start luminance which found a significant two-way interaction between frequency and start luminance ($F_{(4,92)} = 10.27$; $p = 1.39\text{e-}5$; $\epsilon = 0.53$), and no significant three-way interaction ($F_{(4,92)} = 0.0075$; $p = 0.97$; $\epsilon = 0.54$). Subsequent 1-factor RMANOVAs comparing frequency at each level of start luminance found a main effect of frequency only for equivalent ($F_{(2,48)} = 14.11$; $p = 2.24\text{e-}5$; $\epsilon = 0.95$) and high

($F_{(2,48)} = 3.43$; $p = 0.045$; $\epsilon = 0.92$) levels. Follow-up pairwise comparisons found significant differences only for the equivalent level, where first adjustment responses to 0 Hz were significantly slower than first adjustment responses to both 4 Hz and 9 Hz (both p 's < 0.0022 ; see Fig. 3b). Taken together, when any stimulus starts at the low luminance level, the initial response is fast since it is clear of the need to adjust upward. When the stimulus starts at the equivalent luminance level, it causes a significant slowing of initial responses, especially for 0 Hz stimuli. We take this as evidence that the decision is difficult for the 0 Hz equivalent stimuli, but comparatively easy for the 4 and 9 Hz equivalent stimuli. This suggests that the perceived brightness of these flickering stimuli is brighter, so an upward adjustment is easier to initiate. Finally, when the stimulus starts at the high luminance level, while no pairwise comparisons are significant, it is interesting to note that the slowest response is to 4 Hz stimuli, suggesting it is perceptually closer to this start value than the 0 and 9 Hz stimuli.

Discrimination task

Choice proportion

We found 4 Hz stimuli were consistently perceived as being the brightest (see Fig. 4) based on the proportion of time participants selected them as being the brighter of two sequentially presented stimuli. The three-factor question-framing \times first stimulus frequency \times second stimulus frequency mixed model ANOVA for the discrimination task revealed a significant main effect of both first stimulus frequency ($F_{(2,46)} = 31.48$; $p = 2.81\text{e-}8$; $\epsilon = 0.52$) and second stimulus frequency ($F_{(2,46)} = 60.89$; $p = 1.69\text{e-}13$; $\epsilon = 0.52$). The three-way interaction was not significant ($F_{(4,92)} = 0.69$; $p = 0.57$; $\epsilon = 0.52$) nor were any of the two-way interactions. For both the first and second stimulus frequency effects, we conducted pairwise comparisons across the frequency levels and found for the first stimulus frequency all pairs were significantly different (all p 's < 0.0091) and for the second stimulus frequency all pairs were significantly different (all p 's $< 2.45\text{e-}4$). Thus, across all levels and factors, it appears that 4 Hz stimuli, whether presented first or second, generate the greatest brightness percepts, followed by 9 Hz, and then 0 Hz.

A t test was also used to compare choice proportion on trials of same-frequency stimuli (i.e., 4 Hz vs 4 Hz) to a guess rate of 50% to determine if any order effects existed. Both 4 Hz and 0 Hz paired same-frequency conditions were found to be significantly different than 50% (4 Hz: $t_{(24)} = -3.27$; $p = 0.0032$; 0 Hz: $t_{(24)} = 2.63$; $p = 0.010$), with 4 Hz stimuli shown second and 0 Hz stimuli shown first being more likely to be selected as brighter. We interpret these order effects as indicative first, that the novelty of the

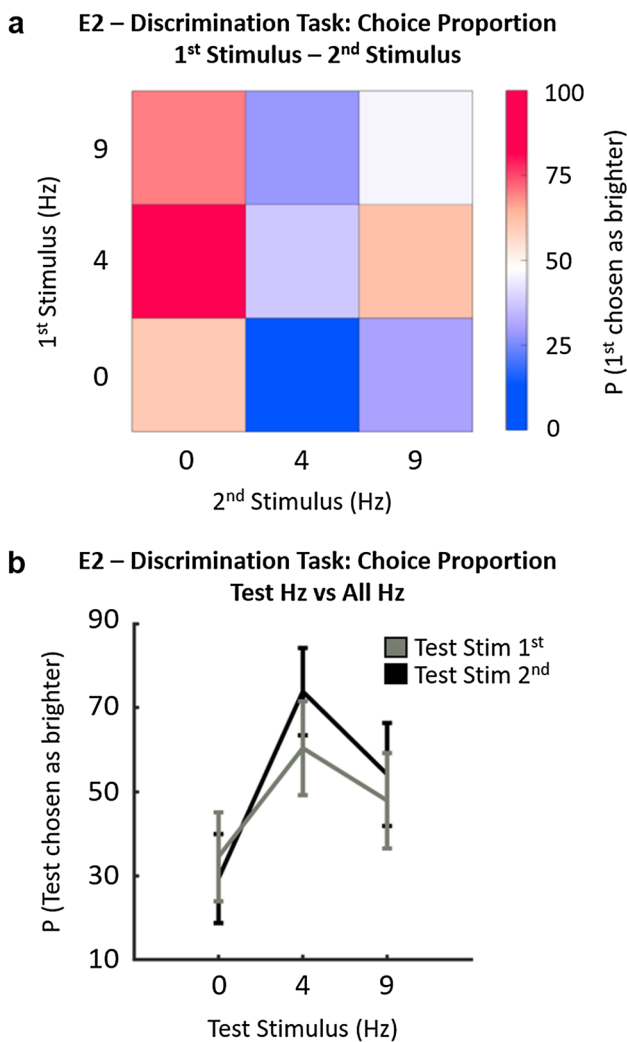


Fig. 4 Experiment 2 discrimination task choice proportion results. **a** Proportion choosing the first stimulus frequency as brighter over the second stimulus frequency. White denotes 50% choice proportion, red represents a greater choice proportion of the first stimulus frequency, and blue represents a greater choice proportion of the second stimulus frequency. **b** Choice proportion of choosing the test-frequency (on x-axis) over all frequencies, separated by the order of which the test-frequency appeared (first=grey, second=black). Error bars represent the average of individual standard errors

first of two non-flickering stimuli means its brightness is enhanced and second, that the inducement of brightness enhancement by a flickering stimulus is even stronger with consecutive presentations. This latter conclusion is consistent with our previous work (Bertrand et al. 2018) in that the brain’s entrainment to a flickering stimulus increases as the duration of the stimulus increases.

Reaction time

The 3-factor question-framing × first stimulus frequency × second stimulus frequency mixed model ANOVA

for the discrimination task reaction time revealed no significant three-way interaction ($F_{(4,92)} = 0.54; p = 0.67; \epsilon = 0.58$) nor any significant two-way interactions or main effects.

Discussion

In two experiments, we tested whether the brightness enhancement observed for flickering stimuli (the Brucke effect) was more prominent for flicker rates in the alpha (~9 Hz) or theta (~4 Hz) band, when the task was to adjust the flickering stimuli (Experiment 1, Fig. 1a, like Bartley 1938) or when only a single stimulus appeared on the screen at a time (Experiment 2, Fig. 1b). These two experiments in turn tested possible reasons why our previous report (Bertrand et al. 2018) of maximal brightness enhancement for stimuli flickering at a theta-band frequency differed from the classical report of maximal brightness enhancement for stimuli flickering at an alpha band frequency (Bartley 1938). This discrepancy could have arisen because of differing task demands between a discrimination (Bertrand) and adjustment (Bartley) task or (and not mutually exclusive) could have arisen due to an aliased alpha rhythm whose effective sampling rate is halved when monitoring two spatial locations. Thus, in Experiment 1 we replicated Bartley’s task as closely as possible (within the design constraints of modern digital displays), and had participants adjust the luminance of a flickering stimulus (2, 4, 7, 9, or 12 Hz) such that it matched in brightness to a simultaneously presented constant stimulus (Fig. 1a). Even though we tried to replicate Bartley’s methods we again failed to replicate his result. That is, rather than uncover a maximal brightness percept for alpha range flickering stimuli, we instead found that 2 and 4 Hz stimuli were perceived as brightest and generally not different from each other (Fig. 2a). This was accompanied by 7, 9 and 12 Hz stimuli being perceived as incrementally less bright, indicating a decrease in brightness enhancement effects as the frequency of flicker increases. While our results diverge from Bartley’s, they do align with others who also found maximal brightness enhancement at slower frequencies (Glad and Magnussen 1972; Magnussen and Glad 1975; Kohn and Salisbury 1967). As an indirect measure of decision difficulty, the time taken for the first key press response (either the first luminance adjustment up or down, or a confirmation press of matched brightness) was recorded (Fig. 2c). We found that slower initial responses were elicited by: (1) the slowest frequency (2 Hz) flicker, indicating perhaps the need to delay for more samples of information, and (2) stimuli equiluminant to the reference circle (equivalent start luminance), indicating a more difficult discrimination decision. These results complement our 2018 findings, but now also suggest that this brightness enhancement effect exists for theta and slower frequency flicker, including

our 2 Hz stimuli, which falls into the range of delta oscillations—a point we return to later in the discussion.

In Experiment 2, we presented stimuli one at a time (Fig. 1b) to test whether the requirement to monitor two spatial locations at once had produced the maximal theta-band flicker brightness enhancement in our previous study (Bertrand et al. 2018) and in Experiment 1. Even when only one flickering stimulus was on the screen at a time, we again found that 4 Hz stimuli were subject to the greatest brightness enhancement. This was true whether perceived brightness was reported via adjustment (half the trials; Fig. 3a) or discrimination (half the trials; Fig. 4a, b). The timing results for Experiment 2 help reveal which decisions participants found hardest to make (Fig. 3b). During the adjustment task, constant, 0 Hz stimuli took the longest to react to initially, suggesting that the perceptual similarity of a 0 Hz stimulus to an equiluminant second stimulus (i.e., identical stimulus) prompted a more difficult initial decision. Together, Experiment 1 and 2 results further corroborate Bertrand et al.'s notion that alpha-rate flicker is not responsible for enhanced brightness perception as Bartley suggested (1938). Instead, these two experiments definitively show that brightness enhancement occurs maximally for stimuli flickering slower than alpha, in the theta or delta band (Figs. 2, 3, 4), even when the brightness is reported via an adjustment task and even under conditions when only a single stimulus is being monitored at a time.

This suggests that slow waves in the brain (4 Hz and less), which we have shown are entrained by external stimuli (Bertrand et al. 2018), serve a unique role in brightness enhancement. This conclusion differs from theories that speculate the nature of the task (Bartley 1938), or the need to divide attention across space (Macdonald et al. 2014; Crouzet and VanRullen 2017), are responsible for stimulus rhythms that induce illusory percepts. We therefore spend the remainder of the discussion situating our results in other theoretical and empirical frameworks which have speculated a special role for delta and theta oscillations in visual information processing.

The first domain in which we see the relevance of slower-than-alpha oscillations in visual processing is when a task demands knowledge not about the presence of a stimulus (like a detection task), but instead about a feature of the stimulus (like a discrimination task). For example, when Cravo et al. (2013) presented a target in a regular, rhythmic stream of noise (i.e., inducing entrainment), the accuracy of participants' discrimination of the orientation of the target (tilted 45° counterclockwise or clockwise) could be predicted by the phase of slow neural oscillations (~1–4 Hz) in visual cortex. Similarly, with a rhythmic stream of events (~3 Hz stimulus rate), Lakatos et al. (2008) found response gain modulations related to the phase of prestimulus delta oscillations. Dugué et al.

(2015) also show evidence for theta oscillations acting as a facilitator of visual processing in tasks more complicated than simple detection. In a visual search task, the success of the search, or the efficiency of target selection, could be predicted by the prestimulus phase of ~6 Hz neural oscillations (Dugué et al. 2015). Critically, the predictive power of ~6 Hz oscillations disappeared for easy, pop-out visual search tasks, suggesting again that these slower rhythms might be required for more complex tasks, where the qualities, and not the mere presence, of the stimuli need to be interrogated. Finally, Harris et al. (2017) also found evidence to support the theory of theta oscillations in “feature-based signal enhancement” as a feed-forward mechanism to bias subsequent processing. Together, these studies demonstrate results similar to those we report here and previously (Bertrand et al. 2018), where the visual processing of the quality of the information, like its identity, its specific brightness or its orientation, is closely linked with slower-frequency neural oscillations.

There is also evidence for delta and theta oscillations playing an important role in sharing, or broadcasting, visual information across the brain, thus playing an important role in tasks requiring high-level visual processing. For example, when a rapid stream of oriented Gabor patches was presented, with the task of determining the average tilt, Wyart et al. (2012) found that the accumulated evidence fluctuated with the phase of slow oscillations (1–3 Hz) in parietal regions. This evidence accumulation was subsequently integrated by higher-frequency oscillations in motor cortex in preparation for response (Wyart et al. 2012). Han and VanRullen (2016, 2017) also interpret their brightness discrimination results as a function of top-down integration of theta oscillations (~5 Hz), where visual stimuli with 3D line images were perceived as brighter than random-line versions. They suggest that the 3D line image extracted from higher-order brain areas promotes predictive feedback, with visual information cascading back to the visual cortex. They suggest that the phase of frontal theta and faster occipital oscillations are indicative of the effectiveness of this feedback (Han and VanRullen 2017). We have also predicted this information sharing to be a central role of theta oscillations (Bertrand et al. 2018) when trying to understand the brightness enhancement afforded by theta-rate flicker. This would further fit with an already-accepted role of theta for memory processes (Klimesch 1999; Wang 2010; Buzsaki 2006), including, in specific, theta phase synchronization between sensory areas predicting the formation of multi-sensory memories (Wang et al. 2018), and theta power predicting both the encoding (Klimesch et al. 1996) and remembering (Klimesch et al. 1997) of new information. Perhaps these slower rhythms are thus relevant in our task as they are needed to retrieve stored information from different areas (i.e., the last stimulus on the screen) to integrate and

compare to new information (i.e., the current stimulus on the screen) from a sensory area.

It is important to note that the suggestion of slow rhythms as critical for visual processing is not meant to discount the role of alpha oscillations to the visual system. Rather, we propose that alpha performs a complementary, but separate task. We characterize the alpha rhythm as a sensory sampling rhythm, critical for determining the presence of a visual stimulus. Therefore, presenting a visual target at the precise timing of the alpha rhythm (either endogenous or entrained) can facilitate or inhibit its detection (e.g., Mathewson et al. 2009; Busch et al. 2009). We also see this sensory sampling effect in work from Sokoliuk and VanRullen (2013) where illusory flicker (~9 Hz) of a wheel stimulus was induced by power fluctuations at the individual alpha frequency, exposing a pulsed inhibition sensory sampling effect. However, in more complex tasks, where specific information about the identity or quality of a visual stimulus is required, and where this information needs to be shared amongst areas of the brain beyond the visual cortex, slower rhythms, like delta and theta, play a primary role in visual processing. Thus, when we deliver visual information at the precise timing of the slower rhythm (either endogenous or entrained) involved in its higher-order processing and transfer, the quality of the information can be best interrogated and is preferentially processed, resulting in phenomena like brightness enhancement (e.g., the current study, Bertrand et al. 2018; Han and VanRullen 2017), increased orientation sensitivity (Cravo et al. 2013), or superior target search (Dugué et al. 2015). Further, it appears that while alpha and theta rhythms may serve distinct roles in the visual system, they are likely connected and show a level of reciprocation. For example, increasing the demands of a task to make it more complex elicits both a decrease (or desynchronization) in alpha power and an increase (or synchronization) of theta power (Klimesch et al. 1996, 1997). However, we acknowledge further work is required to properly disentangle these two rhythms, as it is possible that the square-wave flicker employed in this experiment could induce entrainment at double the frequency of stimulation (Kim et al. 2011). This would suggest that, at least for 4 Hz flicker (though, not for the behaviourally similar 2 Hz flicker result), there might be entrainment of the alpha rhythm and a need to consider an alternative explanation given its implications on visual perception (Spaak et al. 2014; Gulbinaite et al. 2017).

We therefore situate these findings in an emerging theoretical framework arguing first for the vital role oscillations play in establishing and regulating functional networks in the brain (Buschman and Kastner 2015), and second, for the specific roles rhythms in the classic delta-theta range (Fiebelkorn and Kastner 2018) play as compared to those in the alpha range (VanRullen 2016). In all of these accounts, slower rhythms, centered around 4 Hz but extending from

as slow as 1 Hz to as high as 7 Hz, have been implicated in so-called “attentional sampling” (VanRullen 2016) or, the vacillation between a state of engagement and a state of disengagement with a stimulus (Buschman and Kastner 2015; Fiebelkorn and Kastner 2018). These slow rhythms then cascade throughout the brain—carrying information from sensory areas to high-order areas, and back, likely transmitting the information by coupling (in phase and/or amplitude) with local, faster, rhythms in each specific brain area. Under this framework, there is room to explain how you can get both sensory sampling effects, as in the wagon wheel illusion that appears to flicker at an alpha rhythm which is also reflected in alpha EEG (Sokoliuk and VanRullen 2013), and “attention” sampling effects (Landau and Fries 2012; Harris et al. 2018) as in studies showing that exploratory eye movements are more probable at specific phases of slow neural oscillations (Hogendoorn 2016; Wutz et al. 2016). Given that our task requires participants to sample, retain and compare two stimuli (either across space, Experiment 1 or time, Experiment 2) we believe slower rhythms are playing a more dominant role in the observed brightness enhancement. That is, the slow-flickering stimuli are first entraining precisely the slow rhythms required for the successful broadcasting of information, and then aligning with these entrained rhythms, resulting in an enhanced percept of brightness.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

References

- Bartley SH (1938) Subjective brightness in relation to flash rate and the light–dark ratio. *J Exp Psychol* 23(3):313–319
- Bertrand JK, Wispinski NJ, Mathewson KE, Chapman CS (2018) Entrainment of theta, not alpha, oscillations is predictive of the brightness enhancement of a flickering stimulus. *Sci Rep* 8(1):6152
- Brainard DH (1997) The psychophysics toolbox. *Spat Vis* 10:433–436
- Burgess AP, Gruzeliér JH (1997) Short duration synchronization of human theta rhythm during recognition memory. *Neuroreport* 8(4):1039–1042
- Busch NA, VanRullen R (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc Natl Acad Sci USA* 107(37):16048–16053
- Busch NA, Dubois J, VanRullen R (2009) The phase of ongoing EEG oscillations predicts visual perception. *J Neurosci* 29(24):7869–7876

- Buschman TJ, Kastner S (2015) From behavior to neural dynamics: an integrated theory of attention. *Neuron* 88(1):127–144
- Buzsáki G (2006) Rhythms of the brain. Oxford University Press, Oxford
- Buzsáki G, Draguhn A (2004) Neuronal oscillations in cortical networks. *Science* 304(5679):1926–1929
- Calderone DJ, Lakatos P, Butler PD, Castellanos FX (2014) Entrainment of neural oscillations as a modifiable substrate of attention. *Trends Cogn Sci* 18(6):300–309
- Cramer AOJ, van Ravenzwaaij D, Matzke D, Steingroever H, Wetzels R, Grasman RPPP, Waldrop LJ, Wagenmakers EJ (2016) Hidden multiplicity in exploratory multiway ANOVA: prevalence and remedies. *Psychon Bull Rev* 23(2):640–647
- Cravo AM, Rohenkohl G, Wyart V, Nobre AC (2013) Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *J Neurosci* 33(9):4002–4010
- Crouzet SM, VanRullen R (2017) The rhythm of attentional stimulus selection during visual competition. *bioRxiv*. <https://doi.org/10.1101/105239>
- Dugué L, Marque P, VanRullen R (2015) Theta oscillations modulate attentional search performance periodically. *J Cogn Neurosci* 27(5):945–958
- Fiebelkorn IC, Kastner S (2018) A rhythmic theory of attention. *Trends Cogn Sci* 23(2):87–101
- Fiebelkorn IC, Saalman YB, Kastner S (2013) Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr Biol* 23(24):2553–2558
- Glad A, Magnussen S (1972) Darkness enhancement in intermittent light: an experimental demonstration. *Vis Res* 12(1):111–115
- Gulbinaite R, van Viegen T, Wieling M, Cohen MX, VanRullen R (2017) Individual alpha peak frequency predicts 10 Hz flicker effects on selective attention. *J Neurosci* 37(42):10173–10184
- Han B, VanRullen R (2016) Shape perception enhances perceived contrast: evidence for excitatory predictive feedback? *Sci Rep*. <https://doi.org/10.1038/srep22944>
- Han B, VanRullen R (2017) The rhythms of predictive coding? Pre-stimulus phase modulates the influence of shape perception on luminance judgments. *Sci Rep*. <https://doi.org/10.1038/srep43573>
- Harris AM, Dux PE, Jones CN, Mattingley JB (2017) Distinct roles of theta and alpha oscillations in the involuntary capture of goal-directed attention. *Neuroimage* 152:171–183
- Harris AM, Dux PE, Mattingley JB (2018) Detecting unattended stimuli depends on the phase of prestimulus neural oscillations. *J Neurosci* 38(12):3092–3101
- Hogendoorn H (2016) Voluntary saccadic eye movements ride the attentional rhythm. *J Cogn Neurosci* 28(10):1625–1635
- Holcombe AO, Chen WY (2013) Splitting attention reduces temporal resolution from 7 Hz for tracking one object to < 3 Hz when tracking three. *J Vis* 13:1–19
- Hutcheon B, Yarom Y (2000) Resonance, oscillation and the intrinsic frequency preferences of neurons. *Trends Neurosci* 23(5):216–222
- Jensen O, Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci*. <https://doi.org/10.3389/fnhum.2010.00186>
- Kim YJ, Grabowecy M, Paller K, Suzuki S (2011) Differential roles of frequency-following and frequency-doubling visual responses revealed by evoked neural harmonics. *J Cogn Neurosci* 23(8):1875–1886
- Klimesch W (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res Rev* 29(2–3):169–195
- Klimesch W, Doppelmayr M, Russegger H, Pachinger T (1996) Theta band power in the human scalp EEG and the encoding of new information. *Neuroreport* 7:1235–1240
- Klimesch W, Doppelmayr M, Schimke H, Ripper B (1997) Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology* 34(2):169–176
- Klimesch W, Doppelmayr M, Russegger H, Pachinger T, Schwaiger J (1998) Induced alpha band power changes in the human EEG and attention. *Neurosci Lett* 244(2):73–76
- Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition–timing hypothesis. *Brain Res Rev* 53(1):63–88
- Kohn H, Salisbury I (1967) Electroencephalographic indications of brightness enhancement. *Vis Res* 7(5–6):461–468
- Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320(5872):110–113
- Landau AN, Fries P (2012) Attention samples stimuli rhythmically. *Curr Biol* 22(11):1000–1004
- Lopes da Silva F (1992) The rhythmic slow activity (theta) of the limbic cortex: an oscillation in search of a function. In: Baar E et al (eds) *Induced rhythms in the brain*. Springer Science, New York, pp 83–102
- Macdonald JS, Cavanagh P, VanRullen R (2014) Attentional sampling of multiple wagon wheels. *Atten Percept Psychophys* 76(1):64–72
- Magnussen S, Glad A (1975) Brightness and darkness enhancement during flicker: perceptual correlates of neuronal B- and D-systems in human vision. *Exp Brain Res* 22(4):399–413
- Mathewson KE, Gratton G, Fabiani M, Beck DM, Ro T (2009) To see or not to see: prestimulus α phase predicts visual awareness. *J Neurosci* 29(9):2725–2732
- Mathewson KE, Prudhomme C, Fabiani M, Beck DM, Lleras A, Gratton G (2012) Making waves in the stream of consciousness: entraining oscillations in EEG alpha and fluctuations in visual awareness with rhythmic visual stimulation. *J Cogn Neurosci* 24(12):2321–2333
- Nelson TM, Bartley SH, Jewell RM (1963) Effects upon brightness produced by varying the length of the null interval separating successive “single” pulses: sensory implications of the alternation of response theory, I. *J Psychol* 56(1):99–106
- Palva S, Palva JM (2011) Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Front Psychol*. <https://doi.org/10.3389/fpsyg.2011.00204>
- Rager G, Singer W (1998) The response of cat visual cortex to flicker stimuli of variable frequency. *Eur J Neurosci* 10:1856–1877
- Sokoliuk R, VanRullen R (2013) The flickering wheel illusion: when α rhythms make a static wheel flicker. *J Neurosci* 33(33):13498–13504
- Spaak E, de Lange FP, Jensen O (2014) Local entrainment of alpha oscillations by visual stimuli causes cyclic modulation of perception. *J Neurosci* 34(10):3536–3544
- VanRullen R (2016) Perceptual cycles. *Trends Cogn Sci* 20(10):723–735
- VanRullen R, Koch C (2003) Is perception discrete or continuous? *Trends Cogn Sci* 7(5):207–213
- Wang XJ (2010) Neurophysiological and computational principles of cortical rhythms in cognition. *Physiol Rev* 90(3):1195–1268
- Wang D, Clouter A, Chen Q, Shapiro KL, Hanslmayr S (2018) Single-trial phase entrainment of theta oscillations in sensory regions predicts human associative memory performance. *J Neurosci*. <https://doi.org/10.1523/jneurosci.0349-18.2018>
- Wispirski NJ, Gallivan JP, Chapman CS (2018) Model, movements, and minds: bridging the gap between decision making and action. *Ann N Y Acad Sci*. <https://doi.org/10.1111/nyas.13973>
- Wutz A, Muschter E, van Koningsbruggen MG, Weisz N, Melcher D (2016) Temporal integration windows in neural processing

and perception aligned to saccadic eye movements. *Curr Biol* 26(13):1659–1668

Wyart V, De Gardelle V, Scholl J, Summerfield C (2012) Rhythmic fluctuations in evidence accumulation during decision making in the human brain. *Neuron* 76(4):847–858

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.