Perceptual load modulates conscious flicker perception

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Subjective visual experience depends not only on the spatial arrangement of the environment, but also on the temporal pattern of stimulation. For example, flickering and steady light presented in the same location evoke a very different perceptual experience due to their different temporal patterns. Here, we examined whether the availability of processing resources affected the temporal resolution of conscious flicker perception—the ability to distinguish rapid changes in light intensity, detecting visual temporal patterns. Participants detected flicker in a fixated LED that flickered at or around the individually adjusted critical flicker fusion (CFF) threshold while searching for a target letter presented in the periphery either on its own (low perceptual load) or among other letters (high load). Physically identical flickering stimuli were more likely to be perceived as "fused" under high (compared to low) load in the peripheral letter search. Furthermore, psychophysical measures showed a reduction in flicker detection sensitivity under high perceptual load. These results could not be due to criterion or stimulus prioritization differences or to differential likelihood of forgetting the correct response under different load conditions. These findings demonstrate that perceptual load influences conscious perception of temporal patterns.

Keywords: attention, perceptual load, temporal resolution, flicker perception, critical flicker fusion threshold, conscious perception

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Introduction

The parsing of temporal patterns—the ability to individuate events closely separated in time—is a fundamental aspect of visual perception (VanRullen & Koch, 2003). The extent to which the detection of such temporal patterns is successful can determine phenomenal aspects of visual awareness. For example, flickering and steady light presented in the same location evoke a very different conscious experience due to their different temporal patterns. The fundamental significance of temporal pattern detection raises the question of whether it requires the allocation of limited-capacity attention or can occur in a capacity-free manner.

In recent years, there have been several demonstrations that another fundamental aspect of visual perception, the processing of *spatial* patterns (shapes), depends on the

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allocation of limited-capacity attention. For example, functional imaging studies show that engaging attention in demanding tasks is associated with reduced activity related to stimuli appearing outside the focus of attention. Examples include the modulation of activity related to unattended images of places in the parahippocampal place area (Yi, Woodman, Widders, Marois, & Chun, 2004) and colored patterns in V4 (Pinsk, Doniger, & Kastner, 2003). Furthermore, even the responses of early retinotopic visual cortex (areas V1–V3; Schwartz et al., 2005) and the lateral geniculate nucleus (O'Connor, Fukui, Pinsk, & Kastner, 2002) to large peripherally presented phase-reversing checkerboards are reduced when attentional capacity is exhausted by task requirements associated with other foveally presented stimuli.

These findings concur with the results of behavioral studies showing reduced interference and intrusions into awareness by irrelevant distractors under high perceptual load (e.g., Beck & Lavie, 2005; Cartwright-Finch & Lavie, 2006; Lavie, 1995; Lavie & Cox, 1997) and lend support to a load theory of attention (Lavie, 1995, 2005), which proposes that visual perception has capacity limits and that perception critically depends on attentional resources being available. However, no previous study has tested whether this is also the case for the perception of temporal patterns.

Here, we investigated this issue using the phenomenon of flicker fusion: When sufficiently fast, the luminance changes of a flickering stimulus are no longer perceived as flickering but as steady, or fused, illumination (Andrews, White, Binder, & Purves, 1996; Curran & Wattis, 1998; Kristofferson, 1967). At the critical flicker fusion (CFF) threshold (~25–50 Hz, depending on specific conditions), a flickering light has an equal probability of being perceived as flickering or fused.

In this study, we sought to establish whether conscious perception of flicker near the CFF threshold depended on the allocation of limited-capacity attention. This was achieved by varying the level of perceptual load in a visual search task comprising letters arranged in a circle around fixation and by assessing the effects this had on the perception of flicker at or around the CFF threshold. The involvement of spatial patterns was minimized by using a small point source of light at fixation.

If the detection of temporal patterns depends on the availability of attention, then load theory predicts that high attentional load should reduce the ability to distinguish separate events from each other, leading to a lowering of the CFF threshold. Interestingly, a different possibility is raised by recent studies (Yeshurun, 2004; Yeshurun & Levy, 2003) showing that using spatial cuing to vary the allocation of attention transiently impairs the ability to detect a temporal gap (rapid disappearance and reappearance) in a peripherally located stimulus. Though these results were obtained using a different experimental paradigm to that typically used in perceptual load studies (spatial cueing rather than visual search), they raise the possibility that the allocation of attention might play opposite roles in the processing of spatial and temporal patterns. Thus, the temporal resolution of perception might actually improve when deprived of attention in tasks involving high (compared to low) perceptual load. On the other hand, however, the effect of spatial cueing may be limited to situations where attention is recruited transiently and involuntarily by the cue. Finally, it has been suggested that the spatial and the temporal dimensions of visual stimuli are processed independently (Lehky, 1985; Wilson, 1980), which would imply that a manipulation of perceptual load using shapes in particular locations (i.e., spatial patterns) may have no effect on the perception of temporal patterns.

Experiment 1: Does perceptual load affect flicker perception?

Participants fixated a red LED mounted on the centre of a computer screen. On each trial, participants were briefly presented with a target letter in the periphery and were asked to report whether this letter was an X or an N. The target letter could appear in one of six locations, arranged in a hexagon around fixation. Under low perceptual load, the other five locations were occupied by small circles; under high load, they were occupied by nontarget letters. The fixated LED flickered simultaneously with the peripheral letter presentation, at or around participants' individually assessed CFF threshold (see Methods). After reporting the identity of the target letter, participants reported whether or not they had perceived the LED to be flickering. If perceptual load in a spatial search impairs flicker perception at fixation, then for the same frequencies participants should report flicker percepts on fewer trials under high than under low perceptual load.

Methods

Participants

Six volunteers recruited through advertisements placed in UCL's Psychology Department participated in the experiment. Their mean age was 30.3 (range 22–44), three were female and five were right-handed. All participants in all the experiments reported here had normal or corrected-to-normal vision and had participated in psychological experiments before but were not highly experienced psychophysical observers.

Critical flicker fusion threshold measurement

The CFF threshold (the frequency at which a flickering light has an equal probability of being perceived as flickering or fused) was measured for each participant individually at the beginning of the experimental session, using the method of constant stimuli. On each trial, a flickering red LED (subtending 0.5° visual angle; CIE chromaticity coordinates x = 0.655, y = 0.344) was presented alone for 200 ms, at one of six different frequencies (26–36 Hz, in steps of 2 Hz; 20 trials per frequency). Trial order was random. Participants were given 2500 ms from stimulus onset to indicate whether they perceived the light to be flickering or fused (by pressing the left arrow key for "flicker" and the down arrow for "fused").

Stimuli and procedure

Participants sat in a room with ambient lighting, viewing a 14-in. CRT screen (Dell D825TM; 60 Hz refresh rate). A 57-cm viewing distance was maintained with a chin rest. Stimuli were created and presented using Matlab (Mathworks Inc.).

On each trial, participants were instructed to fixate a single red LED, which was mounted at the centre of the screen. A target letter (X or N) appeared in one of six equally likely locations, which were arranged in a circle with a radius of 2.9° centered on the LED. The other five locations were occupied by either five nontarget uppercase letters (U, F, S, P, and J, in the high load condition) or five small place holder circles (0.2° in diameter, in the low load condition). Letter dimensions were 0.7° vertically by 0.5° horizontally. Letters and place holders were presented in white on a black (0.03 cd/m^2) background. As the target letter was equally likely to appear in any of the six possible positions, anticipatory eye movements to the periphery would be disadvantageous, and the participants were informed about this in the instructions.

The LED flickered simultaneously with the letter presentation. LED flicker was controlled by a PIC (Programmable Interface Controller with a 20 Megahertz clock; PicMicro16C67 by Microchip Technology inc.), which was connected to the computer running the experiment through the serial port (used to specify flicker duration for each trial during the preceding intertrial interval) and a parallel port (used to send the start signal). Simultaneous timing of flicker and letter stimuli onset and offset was tested and verified, ensuring negligible discrepancies (<5 ms) using an optodiode and oscilloscope to measure timing of the letter display and LED flicker, respectively.

Pilot tests revealed that when combined with letter detection, the CFF threshold was lower compared to the threshold assessment. To accommodate this, the threshold frequency in the experiment was adjusted to 3 Hz lower than that found in the threshold measurement procedure. A preliminary study revealed that participants tended to adopt a constant response if only a single frequency was used in all trials. To prevent this, three frequencies were used in the experimental conditions: the adjusted threshold and frequencies 1 Hz lower and 1 Hz higher (square-wave flicker, 1:1 duty cycle; luminance 29 cd/m^2 at 30 Hz).

Each letter plus flicker display was presented for 200 ms. Eye position was not monitored, but the brief presentation prevented eye movements to the letter target (Carrasco, Ling, & Read, 2004; Mayfrank, Kimmig, & Fischer, 1987). The foveal presentation and brief duration of the flicker minimized temporal adaptation effects (Curran & Wattis, 1998). Stimulus presentation was followed by a 1300-ms blank. Participants were told to indicate during the blank period whether the target letter was X or N by pressing the left arrow for "X" and the down arrow for "N." Following the blank period (which elapsed regardless of whether a letter response was made or not), the question "Flicker or fused?" appeared above the LED and remained until a response was given. Participants again pressed either left or down arrow, this time to indicate whether the light was flickering or fused, respectively. The dependent variables were reaction time (RT) and accuracy in the letter search, and the percentage of "flicker" responses for each frequency under each load condition. An intertrial interval of 500 ms followed response to the flicker (Figure 1). No cue was given to indicate the onset of the next trial, but as the intertrial interval had a fixed duration, participants had a good idea of when a new trial would begin.

The experiment was conducted in a single session lasting about 1.5 hours (including the CFF threshold measurement and a short practice of the letter plus flicker task). Perceptual load conditions were blocked. Participants performed two practice blocks (one under each load condition), followed by eight experimental blocks. Blocks were arranged in an ABBABAAB order

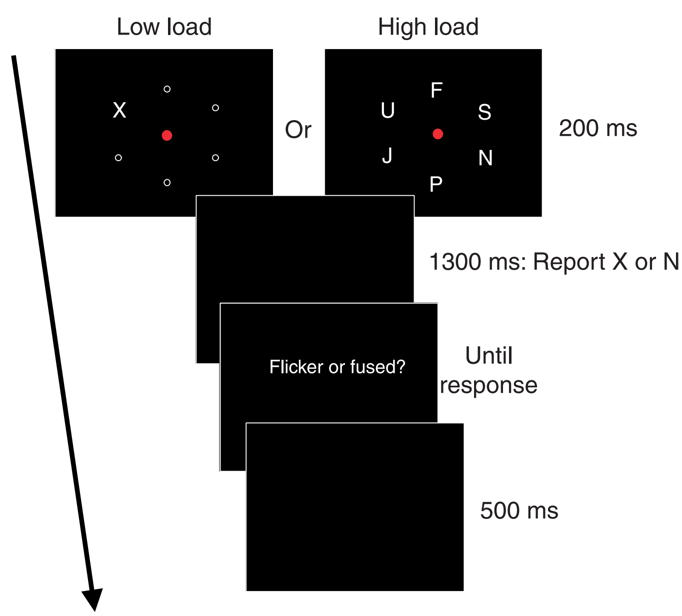

Figure 1. Experiment 1: Trial sequence. During each trial, participants observed a 200-ms simultaneous presentation of LED flicker (represented here by a red circle) at fixation and letter stimuli in the periphery. See main text for details. Figure not to scale.

(with A representing low and B high perceptual load, or vice versa). The load of the first block was counterbalanced across participants. Each block comprised 96 trials, containing two repetitions of the 36 possible combinations of letter identity (X or N), letter location (6 possible locations), and three flicker frequencies. In addition, there were 24 catch trials. On half of these, the flicker frequency was 12 Hz below the threshold and on half it was 12 Hz above threshold. The catch trials were used to control for possible response biases and to make sure participants were attending to the task. For both load conditions, these frequencies were expected to be far enough from threshold to ensure that if participants were indeed attending to the flicker, they would almost never report flicker for the threshold plus 12 Hz frequency and nearly always do so for the threshold minus 12 Hz frequency. For each kind of catch trial, the trials included one presentation of each target letter (X or N) in each of the six possible locations. Trial order was randomized within each block. A participant-terminated break was given at the end of each block.

Results

Mean letter search RTs were significantly longer under high (866 ms) than under low (807 ms) perceptual load, $t(5) = 2.699$, $p = 0.043$, two-tailed, replicating the load effect found in previous research using this task (e.g., Lavie & Cox, 1997). Mean accuracy rates were identical under both load conditions (94%), ruling out a speed/accuracy trade-off. The load manipulation in the letter search was therefore effective.

For flicker detection, the average threshold frequency used in the experiment was 27 Hz (range 25–28 Hz). Only trials in which a correct response in the letter search was made were used in the analysis of flicker detection in all the experiments reported here. The percentages of flicker responses were entered into a 2 (Perceptual load: low or high) by 3 (Flicker frequency: threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated measures ANOVA. There was a significant main effect of perceptual load, $F(1, 5) = 15.918$, $p = 0.01$, indicating a reduction in flicker perception under high, compared to low load (35% versus 47% under high and low load, respectively, when collapsed across all three frequencies; see also Figure 2). There was also a significant main effect of frequency, $F(2, 10) = 20.317$, $p < 0.001$, demonstrating an increase in flicker responses as frequency was reduced. There was no interaction between perceptual load and flicker frequency ($F < 1$).

The main effect of perceptual load on the rate of flicker perception supports the central hypothesis of this study. Higher perceptual load in the letter search reduced the temporal resolution of conscious flicker perception at fixation.

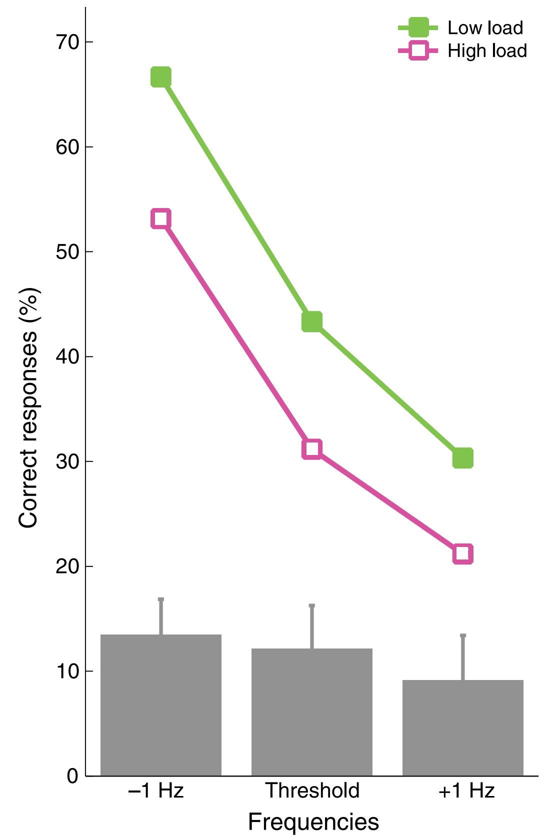

Figure 2. Experiment 1: Flicker detection results. Mean flicker categorization rates under the high (open magenta squares) and low (filled green squares) perceptual load conditions. Note that the threshold rate of 50% flicker categorization under low load falls, on average, within the range of frequencies used. The gray bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

The main effect of frequency shows that participants were indeed attending to the flicker rather than, for example, reverting to responding randomly under high perceptual load. This is further supported by the results of the catch trials: There was no significant difference between responses to catch trials under low and high perceptual load for the threshold minus 12 Hz frequency (97.1% versus 97.3% for low and high load, respectively), $t(5) = 0.115$, *ns*. The percentages of trials categorized as flicker for this frequency indicate that participants were indeed able to detect flicker while performing the letter search. There was also no difference between load conditions in responses to catch trials for the threshold plus 12 Hz frequency (10% versus 7% for low and high load, respectively), $t(5) = 0.656$, *ns*, indicating that participants were unlikely to report flicker if they did not perceive it. Taken together, the present results clearly demonstrate that increasing perceptual load in the peripheral letter search impaired flicker perception at fixation.

However, although the catch trial performance rules out a gross response bias, it remains possible that more subtle biases were induced by perceptual load at the threshold frequencies. This issue was addressed in Critical flicker fusion threshold measurement.

Experiment 2: Addressing response order and overall stimulus luminance

In Experiment 1, the letter search response was made before the flicker detection response. This was necessary in order to establish that the perceptual load manipulation was indeed effective, leading to longer letter search RTs under high (compared to low) load. However, it is possible that the effect of perceptual load on flicker perception was due to the delayed response to flicker. For example, the longer time it took participants to report the target letter under high load may have led to a weaker memory trace for the intended flicker report. In addition, high perceptual load may have led to reduced prioritization of the second response on each trial. In either of these cases, if participants were biased toward reporting a fused percept when they were uncertain, this could account for the observed results.

Another alternative account for the results of Experiment 1 is that because the place holders used in the low load condition were smaller than the letters, total luminance in the display was lower under low than under high perceptual load. It is therefore possible that the effect of load found in Experiment 1 is in fact due to this luminance difference between load conditions, as flicker may be harder to detect under conditions of greater overall illumination.

These possibilities were addressed in Critical flicker fusion threshold measurement by switching the order in which the letter search and flicker detection responses were given and by replacing the small place holders in the low load condition with the letter "O." In all other respects, this experiment was identical to Experiment 1. If the results of Experiment 1 were indeed due to the effect of perceptual load (rather than being a memory-related artifact or the by-product of luminance differences between conditions), they should be replicated here.

Methods

Participants

Six new volunteers (five females) took part in the experiment. The average age was 23.7 (range 19–28). All were right-handed and had normal or corrected-to-normal vision.

Stimuli and procedure

These were identical to those of Experiment 1 except for the following differences. First, the order of responses was reversed so that participants responded to the flicker first, during the first 1500-ms response window. Then the question "X or N?" appeared on the screen and remained until a response to the letter search was given. Second, in the low perceptual load condition, the small, circular place holders used in Experiment 1 were replaced by the letter "O," so that the total luminance of each stimulus display was similar under the low and high load conditions.

Results

Letter search RTs could not be measured in this experiment, as on each trial responses to the flicker were made first. Mean accuracy rates, however, were significantly better under low (92.3%) than under high (87.3%) perceptual load, $t(5) = 2.459$, $p = 0.028$, confirming the effectiveness of the load manipulation.

For flicker, the average threshold frequency used in the experiment was 26 Hz (range 25–28 Hz). The percentages of flicker reports were again entered into a 2 (Perceptual load: low or high) by 3 (Flicker frequency: threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated measures ANOVA. There was a significant main effect of perceptual load, $F(1, 5) = 9.567$, $p = 0.027$. This replicates the result of Experiment 1, showing that for the same frequencies, there was a reduced rate of flicker perception under high compared to low perceptual load (37.5% versus 31.8% under low and high load, respectively, when collapsed across all three frequencies; see Figure 3). Though the magnitude of the effect of load (an average difference of 5.7% between low and high load) was reduced compared to Experiment 1 (average difference of 12%), the results in the present experiment clearly rule out alternative accounts for the effect of load on flicker perception in terms of a memory degradation or deprioritization of the second response. The fact that the letter stimuli in this experiment had similar luminance under both load conditions also rules out alternative accounts for the effects of load in terms of luminance differences in the display.

As in Experiment 1, there was also a significant main effect of frequency, $F(2, 10) = 19.104$, $p < 0.001$, indicating a decline in flicker perception rates as frequency increased (Figure 3), and no interaction between perceptual load and flicker frequency ($F < 1$).

Catch trial results for the threshold minus 12 Hz frequency again showed that there was no significant difference in participants' ability to perceive and to report flicker under both perceptual load conditions (95.2% and 92.7% for low and high load, respectively), $t(5) = 1.185$, *ns*. For the threshold plus 12 Hz catch trials,

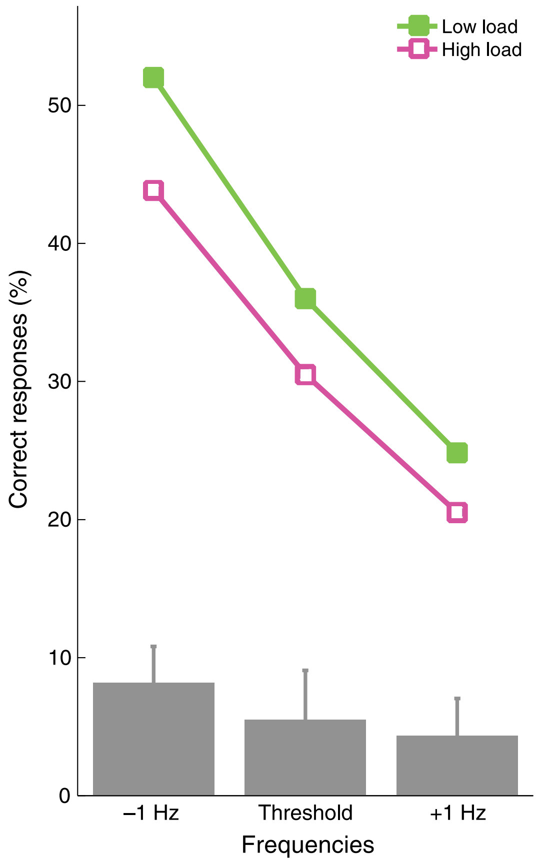

Figure 3. Experiment 2: Flicker detection results. Mean flicker categorization rates under high (open magenta squares) and low (filled green squares) perceptual load. As in Experiment 1, the threshold rate of 50% flicker categorization under low load again falls, on average, within the range of frequencies used. The gray bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

results again showed that participants were equally unlikely, under both load conditions, to report flicker if they did not perceive it (3.8% and 3.3% for low and high load, respectively), $t(5) = 0.217$, *ns*. Taken together with the main effect of frequency, the results for the catch trials demonstrate that participants were indeed attending to the task rather than responding randomly under high perceptual load.

Experiment 3: Assessing the effect of perceptual load on flicker detection sensitivity

In Experiment 1 and Critical flicker fusion threshold measurement, flicker reports were reduced under high perceptual load. This may reflect either a reduction in perceptual sensitivity to flicker under high load or a criterion shift such that under high (compared with low) load participants were simply more reluctant to classify a near-threshold event as flicker.

In Experiment 2, we therefore used a two-interval forced-choice (2IFC) paradigm to distinguish the effects of perceptual load on sensitivity from those on criterion. Rather than a single presentation containing flicker at fixation and a search array in the periphery, each trial in Experiment 2 consisted of two consecutive presentations. Each of the displays contained a target letter, and the letter search now required participants to report whether the two displays contained the same target letter or a different one. Attention to the search array was thus required on both presentations. For the fixated LED, one of the presentations was of a near-threshold flicker event (as in the previous experiments), while the other was at a high frequency (100 Hz) that produces a fused percept. Participants were asked to report which of the two intervals contained the flicker. If the effect of perceptual load on flicker perception was indeed due to a change in sensitivity, accuracy and d' scores for flicker detection should both be reduced under high (compared to low) perceptual load in the letter search.

Methods

Participants

Eight new volunteers took part in the experiment. Their mean age was 25 (range 17–32), six were female and all were right-handed. All participants had normal or corrected-to-normal vision.

Critical flicker fusion threshold measurement

This measurement again employed the method of constant stimuli, but like the main experiment it now involved a 2IFC. On each trial, two 200-ms flicker events were presented alone, separated by 300 ms. One was at a frequency chosen randomly from 6 different frequencies (26–36 Hz, in steps of 2 Hz; 20 trials per frequency). Each frequency was presented in the first and second presentation on an equal number of trials. The other flicker presentation in each trial was at a frequency of 100 Hz, far above the CFF threshold. A high frequency, rather than fused light, was used so that the total amount of illumination in each presentation would be the same. Six hundred milliseconds after the offset of the second display, the question "1st or 2nd?" appeared above the LED and remained until a response was given. Participants pressed the left arrow key to report flicker on the first presentation and the down arrow key for the second presentation. An intertrial interval of 1000 ms followed response. The CFF threshold was defined as the frequency at which participants would make correct responses on

75% of trials (halfway between chance and perfect performance).

Stimuli and procedure

The stimuli were similar to those of Experiment 1. The design and procedure were similar to those of the previous experiments, but each trial now consisted of two stimulus presentations. Each presentation lasted 200 ms and the two displays were separated by 300 ms. Each display contained a target letter (X or N). As in the previous experiments, a frequency 3 Hz lower than the threshold found in CFF threshold measurement was designated as the threshold for the experiment, and frequencies 1 Hz lower and higher were also used. On one of the two stimulus presentations, the LED flickered at one of these near-threshold frequencies. On the other display, the flicker frequency was 100 Hz. The question "Same or different letter?" appeared above the LED 500 ms after the second stimulus offset. Participants reported whether the target letters in the two displays were the same (both X or both N) by pressing the left arrow key or different (X and N in either order) by pressing the down arrow. Once a response was given, the question was replaced by the question "Flicker 1st or 2nd?" Participants pressed the left or down arrow to report flicker on the first or second display, respectively. Once a response was given, the question disappeared, and the next trial began after an intertrial interval of 1000 ms (Figure 4).

The experiment consisted of four blocks in an ABBA order (with A representing low and B high perceptual load, or vice versa). The load of the first block was counterbalanced across participants. Each block consisted of 144 trials, and participant-terminated breaks were given after every 72 trials. Each block contained all 144 combinations of letter-target identity (X or N) and location (six possible locations) on the first and second display. The threshold frequency, threshold minus 1 Hz, and threshold plus 1 Hz were each used on 25% of the trials in each block. Catch trials (half with a frequency of threshold minus 12 Hz and half with a frequency of threshold plus 12 Hz) were used in the remaining 25% of trials. The flicker occurred in the first presentation of the trial on half of each frequency's trials, and in the second on the other half. Trial order was randomized independently for the letter search and flicker frequencies within each block. Participants performed two 72-trial blocks (one under each load condition) as practice before the experiment began. The entire experimental session lasted about 2 hours.

d' scores were calculated using the formula $d' = (1/\sqrt{2})[Z(H) - Z(F)]$ (Macmillan & Creelman, 1991). $Z(H)$ stands for the Z score associated with the probability of a Hit, and $Z(F)$ for that associated with the probability of a false alarm. A hit was defined as a trial in which flicker was reported to have occurred in the first display, when it was indeed presented in the first display. A false alarm was defined as a trial in which flicker was again reported to have occurred on the first display but was actually presented in the second display. Accuracy rates and the criterion measure c were also examined. c was calculated using the formula $c = -0.5[Z(H) + Z(F)]$ (Macmillan & Creelman, 1991).

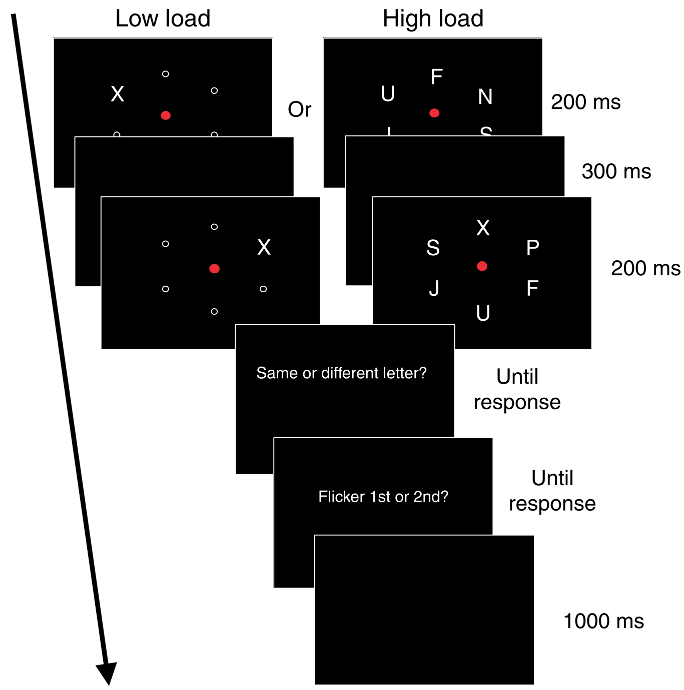

Figure 4. Experiment 2: Trial sequence. Two consecutive displays of simultaneous letter and flicker stimuli were followed by questions regarding the letter search and flicker (see main text for details). Here, the answer to the letter question would be "same" for the low-load example on the left and "different" for the high-load example on the right. Figure not to scale.

Results

Mean letter search accuracy rates were significantly higher under low (94.6%) than under high (86.5%) perceptual load, $t(7) = 2.767$, $p = 0.014$, confirming that the load manipulation was effective. As responses in the letter search were delayed (participants could not give a response until 700 ms after the onset of the second display), RT data were not examined.

For flicker detection, the average threshold frequency used in the experiment was 28.9 Hz (range 27–31 Hz). The percentages of correct responses were entered into a 2 (Perceptual load: low or high) by 3 (Flicker frequency: threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated measures ANOVA. There was a significant main effect of perceptual load, $F(1, 7) = 12.045$, $p = 0.01$. There was also a marginally significant main effect of frequency,

Perceptual load	Threshold minus 1 Hz	Threshold	Threshold plus 1 Hz	Collapsed across all frequencies
Low	80.2	76.4	69.4	75.4
High	69.1	67.5	65.4	67.1

Table 1. Percentages of correct flicker detection responses in Experiment 2.

$F(2, 14) = 3.603$, $p = 0.055$, and no interaction between load and frequency, $F(2, 14) = 1.472$, *ns*. As predicted, the main effect of load was due to a reduction in accuracy under high perceptual load (Table 1). Note that the threshold rate of 75% accuracy under low load fell, on average, within the range of frequencies used.

The same ANOVA conducted on the d' scores also revealed a main effect of perceptual load, $F(1, 7) = 11.801$, $p = 0.011$: d' was significantly reduced under high load (Figure 5). The main effect of frequency did not reach significance, $F(2, 14) = 2.172$, *ns*, and there was no interaction between load and frequency, $F(2, 14) = 2.232$, *ns*.

As in the previous experiments, the results of the catch trials show that participants were indeed at chance when the two presentations were rendered indistinguishable due to being above the CFF threshold (49.4% versus 52.1% for low and high load, respectively), $t(7) = 1.045$, *ns*, and that participants were capable of detecting flicker under both load conditions when the flicker was at a very low frequency, though here there was a trend toward flicker being less detectable under high load (95.7% versus 86.6% for low and high load, respectively), $t(7) = 2.052$, $p = 0.079$. This indicates that the effect of load might be powerful enough to affect flicker frequencies far below the threshold.

Finally, the criterion measure c, indicating the degree to which participants had a bias toward reporting the first or the second presentation as containing flicker, was entered into a similar ANOVA as the accuracy and sensitivity measures. There were no main effects for either perceptual load or frequency ($F < 1$, *ns* for both), and no interaction, $F(2, 14) = 1.4$, *ns*.

The results of Experiment 2 therefore demonstrate that increasing perceptual load in the periphery impairs sensitivity to flicker at fixation, and that the effect cannot be due to a difference in bias toward reporting one or the other display under different load conditions.

Experiment 4: Addressing response order

Experiment 2 showed that high (compared to low) perceptual load in the letter search impaired flicker perception at fixation. However, this effect may have been due to degradation of the memory trace under high load, as the response to flicker was given only after the response to the letter search. If more forgetting occurred under high (compared to low) load, this would lead to a higher percentage of random responses and hence lower detection sensitivity. In Stimuli and procedure, this possibility was addressed by reversing the order of the two responses so that the flicker detection response was now made before the letter search response.

Methods

Participants

Seven new volunteers participated in the experiment. One was excluded from the analysis, as his low performance on the letter search (68%) under high perceptual load meant an insufficient number of trials was collected. The remaining six participants (three females) had a mean age of 30.7 (range 21–66). All were right-handed and had normal or corrected-to-normal vision.

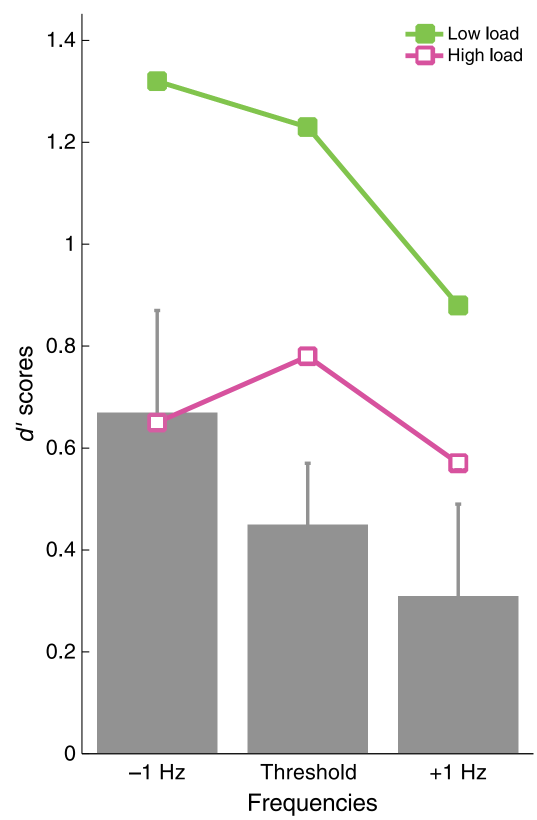

Figure 5. Experiment 3: Flicker detection results. Mean d' scores under high (open magenta squares) and low (filled green squares) perceptual load. The gray bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

Stimuli and procedure

These were identical to Experiment 2, except that the order of responses was reversed, so that participants first reported which display contained flicker, and then whether the target letters in the two displays were the same or different.

Results

As in Experiment 3, mean accuracy rates in the letter search were significantly higher under low (90.2%) than under high (83.2%) perceptual load, $t(7) = 3.24$, $p = 0.011$, indicating the load manipulation was again effective.

For flicker, the average threshold frequency used in the experiment was 29 Hz (range 26–32 Hz). As in Experiment 2, the percentages of correct responses were entered into a 2 (Perceptual load: low or high) by 3 (Flicker frequency: threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated measures ANOVA. There was a significant main effect of perceptual load, $F(1, 5) = 20.535$, $p = 0.006$. There was also a significant main effect of frequency, $F(2, 10) = 25.521$, $p < 0.001$, and no interaction between load and frequency, $F(2, 10) = 1.094$, *ns*. The main effect of load was again due to a reduction in accuracy under high perceptual load, with a monotonic decrease in mean accuracy as frequency increased (Table 2). As in Experiment 2, the threshold rate of 75% accuracy under low load fell, on average, within the range of frequencies used.

The same ANOVA conducted on the d' scores again revealed a significant main effect of perceptual load, $F(1, 5) = 7.618$, $p = 0.04$. There was also a significant main effect of frequency, $F(2, 10) = 12.417$, $p = 0.002$. There was no interaction between load and frequency ($F < 1$). The main effect of load was again due to a reduction in sensitivity under high perceptual load (Figure 6). As with accuracy rates, the data show that the main effect of frequency was due to a monotonic decrease in d' scores as frequency increased.

Catch trial results showed that the participants were capable of detecting and reporting flicker, under both load conditions, when it was at a very low frequency (97% versus 91.7% for low and high load, respectively; there was no significant difference between load conditions), $t(5) = 1.528$, *ns*, and that participants were indeed at chance when the two displays were rendered indistinguishable due to both being above the CFF threshold (48% versus 57.2% for low and high load, respectively), $t(7) = 1.799$, *ns*.

The criterion measure c was entered into a similar ANOVA as the accuracy and the sensitivity measures. There were no main effects for either perceptual load, $F(1, 5) = 3.363$, *ns*, or frequency ($F < 1$), and no interaction ($F < 1$).

The results of Stimuli and procedure clearly confirm that sensitivity to flicker at fixation is indeed reduced under high perceptual load in the periphery. This effect cannot be due to increased forgetting of the correct response under high load, as in this experiment participants responded to the flicker first. Furthermore, performance on the catch trials, taken together with the monotonic decrease in accuracy and d' scores as flicker frequency increased, confirms that participants were

Perceptual load	Threshold minus 1 Hz	Threshold	Threshold plus 1 Hz	Collapsed across all frequencies
Low	82.5	73.2	72.8	76.2
High	76.8	71	64.7	71

Table 2. Percentages of correct flicker detection responses in Stimuli and procedure.

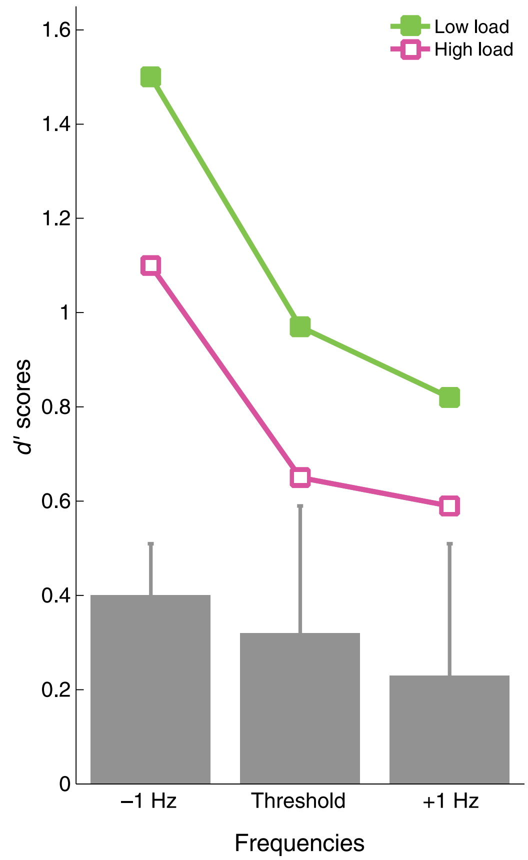

Figure 6. Experiment 4: Flicker detection results. Mean d' scores under high (open magenta squares) and low (filled green squares) perceptual load. The gray bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

indeed attending to the flicker. Finally, a difference in bias between load conditions cannot account for the pattern of results.

Discussion

The present results clearly demonstrate that a fundamental aspect of visual perception, the parsing of temporal patterns, has limited capacity and therefore critically depends on the availability of attention. The level of perceptual load in a spatial visual search determined the accuracy and the sensitivity of flicker perception at fixation.

These findings also generalize load theory (Lavie, 1995, 2005) to the temporal domain. Previous studies have only shown effects of perceptual load on the conscious perception of spatial patterns. Recent examples include demonstrations that the level of perceptual load in similar search tasks to that used here determines the rates of "change blindness" (Beck & Lavie, 2007; Lavie, 2006), "inattentional blindness" for an unexpected shape (Cartwright-Finch & Lavie, 2006), and detection sensitivity for expected shapes (Carmel, Rees, & Lavie, 2006; Macdonald & Lavie, 2007). Here we extend the evidence for load theory to show that the level of perceptual load in a visual search task determines the conscious detection of a temporal pattern.

Although these findings are consistent with load theory, they appear to be at odds with a recent finding (Yeshurun, 2004; Yeshurun & Levy, 2003) that cueing attention to the stimulus location impairs, rather than facilitates, temporal resolution (assessed by sensitivity to the rapid disappearance and reappearance of a stimulus, a method known as double pulse resolution, DPR). Yeshurun and colleagues obtained their results using spatial cueing, whereas we used a visual search paradigm to vary load on attention. However, as both the spatial cuing paradigm and our manipulation of load in visual search serve to vary the allocation of attention, the contrast in results may at first sight appear surprising, whereas directing attention with a spatial cue seems to impair temporal resolution; our findings clearly demonstrate that such resolution benefits from the allocation of attention. Our results are also hard to reconcile with the theoretical account proposed by Yeshurun and Levy (2003). They suggested that spatial cueing facilitates the activity of parvocellular neurons in retinotopic regions corresponding to the attended location, which in turn leads to inhibition of magnocellular neurons at the same location. This impairs temporal resolution at attended locations due to the longer response durations of parvocellular neurons (Merigan & Maunsell, 1993; Schiller & Logothetis, 1990). Clearly, our findings cannot be accounted for by this mechanism. If the greater availability of attention under low perceptual load was mediated by an increase in parvocellular activity, this account would predict impaired (rather than improved) temporal resolution under low (compared to high) load. It is therefore likely that rather than the availability of attention per se being the element common to both our paradigm and that of Yeshurun and colleagues, the different results are instead due to the different way in which availability of attention was varied between the two paradigms. Specifically, the spatial cueing task employed by Yeshurun (2004) and Yeshurun and Levy (2003) invoked transient attention, known to be reflexively drawn to the cued location for a limited duration (less than 250 ms; Carrasco & McElree, 2001). Such reflexive shifts of attention toward a peripheral cue may interfere with DPR because of the involvement of transients in such cueing and in the detection of the pulse onset and offset. The level of perceptual load in the task used here affects the allocation of attention to the fixated flickering LED without involving such transient reflexive shifts. In this case, the lower demands on attentional resources under low load clearly benefit temporal resolution.

This possibility is further supported by another recent study (Poggel, Teutwein, Calmanti, & Strasburger, 2006), which used the DPR method to show that temporal resolution at fixation is improved when the spatial extent of the attentional focus is reduced. Poggel et al. (2006) asked participants to detect a double pulse in one of nine stimuli (one at fixation and eight arranged in a peripheral circle). The eccentricity (though not the size) of the peripheral stimuli was varied. Temporal resolution for the fixated stimulus was better when the peripheral stimuli were at a smaller eccentricity. Here the allocation of spatial attention varied without involving any transient reflexive shifts, and temporal resolution benefited from greater availability of attention.

The results of Poggel et al. (2006) are consistent with load theory (Lavie, 1995, 2005): When attending to both fixated and peripheral locations, increasing the eccentricity of peripheral stimuli leads to increased demands on divided spatial attention. This can be construed as an increase in perceptual load, since both visual acuity and DPR sensitivity decline as eccentricity increases. Importantly, however, the present study demonstrates the effect of perceptual load on temporal resolution independently of the extent of spatial attention, as the eccentricity of stimuli in the letter search was identical for both load conditions. Perceptual load was therefore dissociated from spatial attention by keeping the spatial extent of divided attention constant. Future research may attempt to further eliminate the involvement of spatial attention in the effects of perceptual load by varying load for stimuli that spatially overlap with the flickering stimulus.

The effect of perceptual load in a spatial latter search on flicker detection suggests that temporal pattern perception shares capacity limits with spatial information processing. Though the luminance contrast of the flickering light was kept constant throughout the study, the high contrast used was clearly supra-threshold. This makes it is unlikely that the effects of perceptual load on the perception of near-threshold temporal frequency was mediated by any effect of perceptual load on contrast perception for the LED.

What is the neural resource shared by temporal and spatial processes? Although our behavioral data cannot directly implicate any neural substrates, previous research facilitates speculation on the processes involved. Imaging studies have associated the level of neural activity in posterior parietal cortex with the effects of perceptual load (e.g., Schwartz et al., 2005; Wojciulik & Kanwisher, 1999) and neuropsychological work suggests that neglect patients with parietal lesions have reduced perceptual capacity overall (Lavie & Robertson, 2001), not only in spatial tasks (Cusack, Carlyon, & Robertson, 2000). Indeed, our recent neuroimaging work (Carmel, Lavie, & Rees, 2006) showed that flicker detection is associated with activity in similar parietal regions to those implicated in neglect and the effects of perceptual load. These regions included the intraparietal sulcus and inferior parietal lobule. Though anatomical overlap at the gross scale of fMRI does not necessarily imply shared neural circuitry or function, it raises the possibility that the same attentional resources, mediated by activity in the above areas, may be recruited for both spatial search tasks and flicker detection. The specific neural mechanism underlying such recruitment awaits characterization. However, it is likely to mediate the allocation of limited-capacity attention to sensory information received from early visual cortex, enabling conscious access to such information (for reviews of the involvement of overlapping regions of frontal and parietal cortex in both awareness and attention, see Naghavi & Nyberg, 2005; Rees, Kreiman, & Koch, 2002).

Finally, it is important to note that although we have shown effects of perceptual load on conscious perception of flicker (as expressed by the explicit reports of our participants), we by no means suggest that these effects are confined to conscious representations of flicker. It remains possible that perceptual load can affect earlier, preconscious processing of flicker. Indeed, the effects seen at the conscious level may be due to the effects of perceptual load on such earlier levels of flicker processing; recent research (Bahrami, Carmel, Walsh, Rees, & Lavie, 2007; Bahrami, Lavie, & Rees, 2007) shows that perceptual load affects both unconscious perception of task-irrelevant stimuli (e.g., orientations, or images of tools) and the activity they evoke in V1. Whether perceptual load in a spatial search can affect early unconscious processing of flicker remains an interesting topic for future research.

Conclusion

Increasing perceptual load in a task that involved attention to letters in specific spatial locations impaired conscious flicker perception at fixation. This effect was apparent for both the phenomenal percept evoked by near-CFF threshold flicker, which was more likely to be perceived as fused under high load, and for flicker detection sensitivity, which was reduced under high load. The current results therefore provide strong evidence that the temporal resolution of conscious perception is determined by the availability of attention.

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