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Title: `50 Hz flicker triggers attentional selection without awareness`

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Abstract

Gamma-band modulations in neural activity have been proposed to mediate attentional processes. To support a causal link between gamma activity and attentional selection, we attempt to evoke gamma oscillations via 50 Hz subliminal flicker. We find that a subliminal 50 Hz flicker at a target location, prior to target presentation, speeds up and enhances target detection and discrimination. This effect is specific to the middle of the gamma range, as it is not evident below 35 Hz flicker. It requires 300 ms to build up, dissipates within 250 ms of flicker offset, and shows a tendency to invert after 500 ms. These findings are discussed in relation to a role for Gamma-band neural synchrony in the allocation of visual attention.

Introduction

The nature of the neural mechanisms underlying visual attention – i.e., the ability of humans and animals to select a limited number of stimuli, from the multitude simultaneously present in the visual field, for prioritized processing – remains a fundamental problem in visual neuroscience (1). A complete theory of visual attention must explain how the relative salience of selected stimuli is enhanced in neural terms, even though they are often not singled out by increased firing rates (2,3). One recently proposed solution is the 'Attention-Gamma' hypothesis, according to which synchronized gamma-band (40–70 Hz) modulations in neural activity mediate attentional processes (4–10). This is supported by a correlation, across trials, between the speed of behavioral responses in a visual detection task and the power in the gamma frequency range of V4 neurons (10–12). In these studies, Fries, Womelsdorf, and colleagues demonstrated that top-down visual attention is associated with internal gamma-band synchrony in task-specific neural populations, which could be generated by top-down attentional modulations (13,14). Thus it is possible that selected neural representations are given a gamma-band oscillatory tag by a top-down attention mechanism (15). If this is the case, it may be possible to trigger the effects of selective attention (enhanced selection and perception) by externally evoking gamma-band oscillations of the relevant neural representation, thus mimicking the attentional tag.

To test this hypothesis, we examined whether external stimulus flicker at a specific location, which is expected to evoke phase-locked neural activity at the same frequency, results in attentional orientation to that location – in the absence of conscious detection of the flicker; if the flicker were detectable, it could lead to an orienting of attention towards its location as a result of exogenous or endogenous processes that are not specific to the temporal modulation. To test whether subliminally evoked neural synchronization has an attentional effect, we built upon recent studies demonstrating that visual flicker in the mid gamma-band range (40–70 Hz) entrains periodic neural responses at the same frequency in the visual cortex (16,17; see also Supporting Information). As flicker within this frequency range is expected to be subliminal (the critical flicker fusion frequency is lower than 50 Hz with luminance levels obtained on CRT monitors (18–20)) it is possible to test the Attention-Gamma hypothesis psychophysically by examining whether subliminal flicker (that should evoke neural synchronization within this frequency band) triggers attentional orientation.

We carried out a set of experiments in which three Gabor patches (arranged equidistantly on an invisible circle; Fig. 1a) were shown on a CRT monitor, and we measured the response times (RTs) to the detection of a target: a subtle change in the spatial frequency of one of three patches (change-target), using a 3-alternative forced-choice (3AFC) task. During a preview interval that preceded the target, one patch, whose location could be congruent or incongruent with the target location, was temporally modulated by either a 50 Hz or a 30 Hz flicker (the latter just below the gamma range); the 'non-flickering' Gabors were presented at frequencies of 100 Hz or 120 Hz, respectively, which are too high to trigger evoked oscillatory responses (16,17), and their contrast was set at the average of the flickering Gabor's contrast (see Supporting Information). Observers were also tested in a closely matched 3AFC paradigm that assessed their ability to detect the location of the flicker, with the same flicker duration and frequencies (50 and 30 Hz), but without the subsequent change-target. In a series of follow-up experiments, we extended these results with additional flicker frequencies, aperiodic temporal modulations, additional detection tasks, and we examined the time course and nature of the effect providing evidence of a dissociation between an attentional effect and the awareness of the flicker that caused it.

Results

Attentional effects of subliminal flicker and frequency specificity

The localization of 50 Hz flicker was at chance level in the detection task: 34% (SE 1%), demonstrating that the flicker was subliminal. For 30 Hz flicker, the contrast modulation was manipulated to reduce detectability of the flicker (which could otherwise provide a conscious cue for voluntary orienting): the contrast was set to a level that resulted in low but above-chance localization accuracy, 42% (SE 1%). The slightly higher detection rate was intended to impose a conservative criterion: the evoked response at 30 Hz should be at least as strong as that at 50 Hz, to obtain a stringent test of the Attention-Gamma hypothesis.

FIGURE 1

The RTs in the change-detection task and the congruency effects [RT(incongruent) – RT(congruent)] are given in Figure 1. Consistent with the Gamma-Attention hypothesis, we found a robust congruency effect in the 50 Hz condition: RTs were 23 ms (SE = 4 ms) faster when the target appeared at the location preceded by the flicker cue, relative to incongruent locations ($t19 = 9.34$, $P < 0.001$); a congruency effect was evident for 19 out of 20 observers, and this effect was not due to trials on which observers perceived the flicker (see Supporting Information, Fig. S2). In contrast, there was no evidence of a reliable congruency effect in the 30 Hz condition (3 ms, SE = 7 ms; $t19 = 0.44$, $P = 0.67$), and the effect was larger with the 50 Hz than with the 30 Hz flicker ($t38 = 2.83$, $P < 0.01$; see Fig. 1b).

In order to further validate this result and also to test whether the effect is due to the periodic 50 Hz modulation, rather than to any fluctuations in firing rate of neural detectors responding to the Gabors, we carried a second experiment in which we contrasted the gamma-band (50 Hz) flicker cue with two new conditions: 1) a 25 Hz flickering cue, and 2) a non-oscillatory (aperiodic) temporal modulation (see Fig. 1d), where ‘temporal events' (consisting of a 10 ms contrast increment followed by a 10 ms decrement) were presented at random times. In all conditions, the ‘non-flickering’ Gabors were presented at 100 Hz. The contrast changes for the 25 Hz and aperiodic cues were modulated to prevent detection, and the allocation of trials to conditions was randomized within blocks of trials. 8 observers were tested, first on change-detection and then, separately, on flicker detection without any change-target. Once again, although the modulation was such that the flicker detection was lowest for 50 Hz (see Fig. 1f), this frequency modulation produced a reliable congruency effect (22 ms, SE = 4 ms; $t7 = 3.31$, $P = 0.01$), evident in 7 out of the 8 observers, which was significantly larger than those obtained with the 25 Hz cue ($t7 = 3.83$, $P < 0.01$) and the aperiodic modulation ($t7 = 2.70$, $P = 0.03$); the congruency effects in the latter two conditions was not significantly different from zero (see Fig.1e). As shown in the Supporting Information, we have obtained similar congruency effects with 40 Hz, but not with 35 Hz modulations. Thus, subliminal mid-range gamma-band, but not supraliminal, aperiodic or below-gamma periodic, flicker results in faster detection of targets presented at the flicker location, consistent with an attentionally enhanced processing at this location.

Setting the flicker congruency and validity in opposition

To further demonstrate the dissociation between the 50 Hz congruency effect and visual awareness of the cue (22), *within the same task*, and to demonstrate that the attentional congruency effects reported in the previous experiments are not contaminated by the detection of the flicker in a subset of trials, we carried out a second experiment that set the flicker – either a 50 Hz subliminal or a 25 Hz *supraliminal* flicker – and its cue validity in opposition (a display consisting of only two stimulus locations was used in this experiment). In this way, any perception of the 50 Hz flicker cue should result (as for the supraliminal 25 Hz cue) in a reorientation of attention to the valid location (opposite to the flicker).

Observers were informed that a flicker-cue, which was either easy (25 Hz) or very difficult (50Hz) to dtect, would be presented before the change-target. The observers were told that, in 80% of the trials, the target would appear at the location opposite to the cue (valid condition), rather than at the location of the cue (invalid condition), and were instructed that, if they did not see a flicker, they should still do their best to respond to the change-target, as soon as they spot it. These instructions encouraged the observers to pay close attention to the presence of flicker in the preview. If observers were able to detect the flicker cue (in a fraction of trials), a positive validity effect should result (equivalent to a negative congruency effect). In contrast, if they did not detect the cue, a negative validity effect should result (positive congruency effect) – if the subliminal flicker oriented attention towards the cue, but observers were not aware of it and so could not redirect attention to the opposite site.

The results revealed a highly significant Frequency x Validity interaction ($F(1,5) = 113.01$, $P < 0.001$): with 25 Hz cues, observers were able to take advantage of their perception of the flickering cue and reorient attention to the opposite location (faster RTs on valid than on invalid trials, 405 vs. 559 ms, t5 = 9.85, $P < 0.001$), whereas they were not with 50 Hz cues. For the latter, RTs were slower on valid compared to invalid trials (485 vs. 466 ms, t5 = -3.31, $P < 0.03$): attention was exogenously oriented towards the 50 Hz flicker and, as the cue was subliminal, observers were unable to reorient their attention towards the likely target location (congruency effects depicted in Fig. 2a). The negative validity effect shows that, despite being informed of the presence of a flicker cue, it was not possible for the participants to detect the 50 Hz flicker – even though it was predictive of the target location, providing observers with a strong motivation to use it (see the 25 Hz condition). Moreover, as their attention was oriented towards the subliminal 50 Hz flicker, they were faster to respond on invalid trials (where the change-targets are congruent with the flicker location). Thus, the 50 Hz priming effect was automatic and not subject to concious strategic (top-down) control.

Discrimination sensitivity

It is possible that the RT enhancement triggered by the 50 Hz flicker resulted from shifts in response criteria for the cued location, or from an enhanced perceptual sensitivity (23). To examine this, we assessed whether 50 Hz flicker influences perceptual sensitivity, separately from any shift in response criterion. To do so, we determined the thresholds of the magnitude of the spatial-frequency change (i.e., the threshold for which observers were 71% correct) for a non-speeded discrimination of increases versus decreases in the spatial frequency of the Gabor patches at congruent and incongruent locations. Observers' discrimination thresholds were significantly lower at congruent than at incongruent locations (t6 = -4.01, *P* = 0.006), as indicated by a congruent/incongruent ratio of .86 (SE = 0.03). Thus, the gamma-cueing produces an increase in perceptual sensitivity for the location of the flicker.

Facilitation/Inhibtion Components

To examine whether the 50Hz congruency effect was due to facilitation at the cued location, inhibition at the uncued locations, or a combination of both, we repeated the 50 Hz flicker experiment (N=10 observers) with the addition of a neutral condition in which none of patches flickered during the preview period. The results replicated the significant congruency effect for the 50 Hz cue (29ms, SE=3.1; t6 = 8.44, P<0.001). The RT for the neutral condition fell in between those of the congruent and the incongruent ones ( ), so that there was a significant speedup in RT to targets after a congruent flicker (21 ms; t, p). The cost due in incongruent flicker was smaller (9 ms) and did not reach significance.

Time course of the attentional effect

In two further experiments, we tested the dependency of the 50 Hz congruency effect on the duration of the flicker cue and on the length of the ('non-flicker') inter-stimulus interval (ISI) between the flicker cue and the change detection target. Figure 2b shows that the congruency effect is not evident at short (100–200 ms) flicker durations that follow the 800–900 ms static preview (t6 = -1.35, *P* = 0.22 and t6 = -0.19, *P* = 0.85, respectively); rather, it emerges only at longer flicker durations of 300 and 400 ms (t6 = -4.08, *P* = 0.006 and t6 = -4.67, *P* = 0.003, respectively). Figure 2c shows that the congruency effect persists after a very short cue-target interval (50 ms, t10 = -4.38, *P* < 0.01), but disappears 250 ms after offset of the flicker cue and eventually, after 500 ms, reverses such that observers exhibit a cost when the target is presented at the cued location (Congruency x ISI interaction, *F* (2,20) = 11.66, *P* < 0.001). That is, the effect of the flickering patch requires about 300 ms to build up, dissipates within 250 ms after flicker offset, and shows a tendency to invert after 500 ms.

Extending the task: contrast modulation and dot probe experiments

We carried out two further experiments in which two new types of targets were implemented: (i) contrast modulation and (ii) dot probe detection. Both of these targets resulted in identical patterns of effects to those in the previous experiments, ruling out the possibility that the effect is specific for targets defined by a spatial-frequency modulation. All participants (Tables S3 and S4, Supporting Information) were faster (by 29 ms, SE = 3.42 ms, t6 = 6.86, $P < 0.001$) in reporting the contrast modulation of the Gabor, and all were more correct (9%, SE = 1.57 %, t5 = 4.11, $P < 0.01$) in detecting a brief dot probe when the target location was congruent with the location of the subliminal flicker than when it was incongruent. Note that these results are not subject to speed-accuracy trade-offs: the same conclusions are obtained when we measure the effect via RT efficiency (RT/accuracy): contrast modulation, t6 = 5.59, $P < 0.001$, and probe detection, t5 = 2.70, $P < 0.05$. Thus the congruency effect generalizes to other types of discriminations than the spatial-frequency change.

FIGURE 2

Discussion

We have found that a subliminal, frequency-specific flicker cue (at 50 Hz) causes increased sensitivity and faster RTs to targets presented at cued locations. This provides evidence that exogenous attentional cueing can arise from subliminal and sustained manipulations, extending previous results with abrupt masked cues (22). The effect was mainly due to facilitation by congruent flicker prior to target presentation and was found to be robust across detection tasks (spatial-frequency change, contrast-change, as well as dot-probe) and to occur only at frequencies within the mid gamma-band (50 Hz). In particular, we obtained much smaller (and non-significant) congruency effects with periodic modulations of 25/30 Hz and with aperiodic modulations, whose amplitude was chosen so as to permit a higher flicker detection rate (when tested in isolation, without the change-target stimulus), than that found with 50 Hz flicker (which was at chance). Furthermore, we have shown that this effect shows up even when observers have every incentive to shift their attention away from the cue (if they observe it), indicating that it takes place without awareness and is not contaminated by the perception of the cue in a subset of trials. Finally we find that the congruency effect needs more than 200 ms to build up and that it persists for at least 50 ms after the offset of the flicker but it is short-lived: it disappears after 250 ms.

The speedup in target detection due to the presence of 50Hz flicker at the same location, is consistent with the hypothesis that the flicker triggers modulations in neural activity in the Gamma band (REF), and thus mimics the attentional tag (REF), normally engaged by top down instructions or exogenous cues. The time course of the effect also indicates that it is not the outcome of a simple mechanism based on detectors sensitive to transient contrast changes at the beginning or end of the (flicker) preview period (24), but rather that it involves a continuous increase over a period of time (at least 200 ms). Future work should further investigate the existence of an inhibition component (by flicker incongruent with the probe), which would suggest that, in addition to reproducing the end effect of attention, the 50Hz flicker engages attentional mechanisms that are subject to capacity limitations or mutual inhibition (REF).

The psychophysical method of evoking neural synchrony has limitations in its frequency range. Due to low-pass filtering of the visual system, it is difficult to evoke synchrony in the high-gamma range (16,17). Such neural synchrony (75–150 Hz) has recently also been associated with selective attention (26,27). Further work, with stimulation techniques that directly target cortical circuits, is required to examine the effects of externally modulating synchrony in this frequency range. Specifically, physiological work is needed to clearly establish that (frequency-specific) evoked neural synchrony is causally related to enhanced attentional orienting. One alternative interpretation of our results is that attentional selection is associated not with the Gamma flicker, but simply with the firing-rate fluctuations associated with it, which are likely to exceed those of the ‘non-flickering’ Gabors (that were presented at 100 Hz). If this was the case, however, we would expect that similar congruency effects should obtain with the 30 Hz flicker (here the ‘non-flickering’ Gabors were presented at 120 Hz) or with the aperiodic cues, which are likely to benefit from stronger transients. In our experiments, however, we found null effects with such temporal modulations, when their amplitude was set such as to make detection of the flicker cue difficult, but not as difficult as for 50 Hz flicker. Still, one could argue that this is due to lower amplitude modulations in the relevant (V1) detectors for the 30 Hz and the aperiodic signals. As physiological responses could not be monitored in our experiment, this possibility cannot be ruled out. However, we consider this to be implausible because the strength of neural entrainment is reduced for high frequencies (>40 Hz) due to low-pass filtering (16,17). A parallel reduction in response modulation of linear filters with flicker frequency is assumed in psychophysical models of flicker detection, based on cascading leaky integration (28,29), and accounts of the decrease in flicker sensitivity with frequency (for frequencies higher than 10 Hz). According to such models, the amplitude of the response modulation of the detectors responding to flickering Gabors is the *signal* used to compute their presence (say, by comparing peak with average activation (28)). If this is the case, the higher flicker detection with 30 Hz and with aperiodic signals should correlate with stronger modulations of these detectors. Physiological monitoring of response amplitudes are needed, however, to corroborate the conjecture that flicker detection is monotonic with the amplitude of the entrained oscillations of V1 detectors, and thus confirm that the attentional effects we report can be attributed solely to the frequency of evoked modulations in neural activity, and not to their amplitude.

The most important result of our study is the dissociation in performance between flicker detectability and attentional enhancement: while the detection performance of the flicker (without a subsequent target) was higher in the 30 Hz compared with the 50 Hz condition, the effect of the flicker on attentional orienting (as measured by the RT for subsequent target detection) was significant for the 50 Hz condition only. As discussed above, we interpret this to indicate a dissociation of the detection of the flicker and its further attentional effects on visual processing. One possibility is that flicker detectability depends on the response amplitude (28,29) of the corresponding temporal frequency (higher for 30 than for 50 Hz with the stimuli we used), whereas attentional enhancement depends more specifically on the frequency (higher for 40-50 Hz than 30 Hz). The results are consistent with the suggestion that gamma-band neural modulations trigger attentional effects as a result of efficient summation of post-synaptic potentials (30-32), resulting in faster and more accurate responses to stimulus presentation (33).

To conclude, we suggest that, while top-down attentional orienting enhances visual processing through the generation of oscillatory neural activity, a similar enhancement can be obtained without top-down attention by an exogenous flicker cue which evokes gamma activity at the target location. As opposed to endogenous, top-down attentional orienting, the externally evoked gamma response is short-lived (dissipating shortly after the flicker) and does not engage visual awareness, possibly due to the absense of top-down feedback loops needed to sustain it.

Materials and Methods

Apparatus

All experiments were conducted in a dimly lit room. Stimuli were presented using a VSG 2/5 system (Cambridge Research Systems) on a Sony Trinitron Multiscan E450 monitor (800 x 600 pixels). The frame rate was set at either 100 Hz (50 Hz, 25Hz, and aperiodic conditions) or 120 Hz (30 Hz condition). Observers (all with normal or corrected-to-normal vision) maintained their viewing distance (57 cm) via a chin rest and gave their responses through a CT3 four-button response box (Cambridge Research Systems).

Attentional effects of subliminal flicker and frequency specificity

In the first experiment (detection of a spatial frequency change), 20 observers (18 naïve) were tested at 50Hz, and another 20 observers (18 naïve) at 30Hz. In both tests, observers viewed a display consisting of 3 Gabor patches (size 3º, spatial frequency 2 cpd, and deviation 0.45º), which are equally spaced on an invisible circle (radius 6º) around a central black fixation cross (always visible) on a light grey background with the same mean luminance as the Gabor patches (Fig. 1a). At the beginning of a trial, one patch flickered (30/50 Hz) for 1000 ms (preview interval with flicker cue). Following this preview interval a change-detection target, generated by changing the spatial frequency of one of the Gabors (0.14 cpd), was presented for 600 ms. The target location was 50% congruent with the flicker cue, and 50% incongruent. Observers indicated (3AFC) the location of the spatial frequency change by pressing a spatially corresponding button as quickly as possible, and the next trial followed 1000 ms later. Each session consisted of 5 blocks of 50 trials. For the 50 Hz test we used flicker modulation of 10-ms on-off (monitor frequency set at 100 Hz), while for 30 Hz we used a flicker modulation of 16.6 ms on-off (monitor frequency set at 120 Hz). In the 30 Hz condition, the peak-trough contrast value between successive frames was determined individually for each observer, prior to the experiment, using an adaptive staircase procedure that converges approximately at 50% flicker detection (chance level is 33%). For all participants error rates in the change-detection task were lower than 10%. Mean RTs for each observer were computed for correct responses after excluding outliers (i.e. any RTs further than 2.5 SD from the mean).

Following the change detection experiment observers were tested on the detection of flicker without a subsequent change-detection. In the flicker detection task, observers viewed 180 trials of flickering cues identical to the first 1-second preview interval of the change detection experiment, and they were instructed to indicate which patch appeared different (in flicker or any other visual property) in a 3AFC. To maintain motivation throughout this difficult task, 10% of trials contained a more detectable half-frequency flicker; such trials were excluded from analysis. Participants whose detection rate exceeded 55% were discarded, leaving a total of 20 observers that satisfied these constraints, per group.

50 Hz, 25 Hz, and aperiodic flicker within-design

8 observers (6 naïve) took part in the experiment; stimuli, task, and procedure were identical to experiment 1, except that three conditions where randomly intermixed: 50 Hz, 25 Hz, and aperiodic flicker. To permit random intermixing of the 50 Hz and 25 Hz conditions, the monitor frequency was set at 100 Hz. In the non-oscillatory (aperiodic) temporal modulation (see Fig. 1d), 'temporal events' (consisting of a 10 ms contrast increment followed by a 10 ms decrement) were positioned randomly within the 1 second cue interval. The placement method was as follows: An array representing each frame of the display sequence was assigned an event with 0.06 probability, resulting in a stochastic sequence of 6 events (on average) per 100 frames (representing the 1 second cue interval). Sequential placement of events was prevented. As in experiment 1, for the 25 Hz and the aperiodic condition, the peak-trough contrast value between successive frames was set so as to permit a 50% flicker detection rate (chance level is 33%).

Discrimination thresholds

7 observers (5 naïve) performed 5 interleaved staircases with congruent/incongruent-cue trials, in a task that required them to discriminate between an increase/decrease in the spatial frequency of one of the 3 Gabor patches. The changed patch was presented for 100 ms after the flicker cue preview interval, after which all of the stimuli disappeared. The response was non-speeded: observers had to press the left button of the response box for a frequency decrease and the right button for an increase, independently of the target location. Frequency increases and decreases were equiprobable ($P = 0.5$) on a trial. The staircases started with a large spatial-frequency change value, and used a 2/1 protocol that converged at a 71%-correct level. Each interleaved staircase resulted in two thresholds (one for congruent and one for incongruent locations), which were computed by averaging the value of the frequency change across the last 6 (out of 8) reversals. For each observer, the 5 congruent and 5 incongruent threshold estimates were then averaged. Finally, the congruent/incongruent threshold ratio was computed in order to standardize the threshold differences.

Time-course of the attentional effect: flicker duration and flicker-target interval (ISI)

7 (duration experiment, 5 naïve) and, respectively, 11 (ISI experiment, 9 naïve) observers performed 9 blocks (450 trials) using stimuli and procedures matched to those described above for the first experiment's 50 Hz condition, apart from the following details: The duration experiment started with the presentation of the 3 non-flickering Gabor patches for a variable duration of 900, 800, 700, or 600 ms, followed by an interval during which one patch flickered, for a duration of 100, 200, 300, or 400 ms, respectively, so that the total preview interval (before the target was presented) was 1 sec. The ISI experiment employed a variable cue-target inter-stimulus interval (50, 250, or 500 ms), with non-flickering Gabor patches presented between the 50 Hz flicker cue (of 1 sec) and the target.

Contrast modulation and dot probe experiments

7 (contrast modulation, 5 naïve) and, respectively, 6 observers (dot probe, 4 naïve) performed 5 blocks (250 trials) using stimuli and procedures matched to those described above for the first experiment's 50 Hz condition, apart from the following details: For the contrast modulation experiment, the target was defined as a Gabor patch changing in contrast every 100 ms. The total target duration was equal to the previous experiments (600 ms). For the dot probe experiment, the target consisted of a briefly presented (50 ms) white dot (diameter 0.2º) that appeared in the center of one Gabor patch.

Flicker congruency and target-location validity in opposition

6 observers (4 naïve) were tested in 12 blocks (600 trials) using a task and procedure based on the first experiment. However, in this experiment, only two Gabor patches were presented, one to the left and one to the right of the fixation cross (distance 5.91º). Observers were informed that the change target would appear at the location opposite to that of the flicker with a probability of 0.8 and that sometimes the flicker would be easily detectable and at other times harder. If they could not detect the flicker, they should still react as fast as possible to the change target. Thus, they knew the flicker cue indicated that the target was likely to appear at the opposite location, rather than at the location of the cue. In 20% of trials, the target appeared at the same location as the cue (invalid condition); and in 80%, it appeared at the opposite location (valid condition). Observers were tested in two (randomly intermixed) frequency conditions: 50 Hz and 25 Hz.

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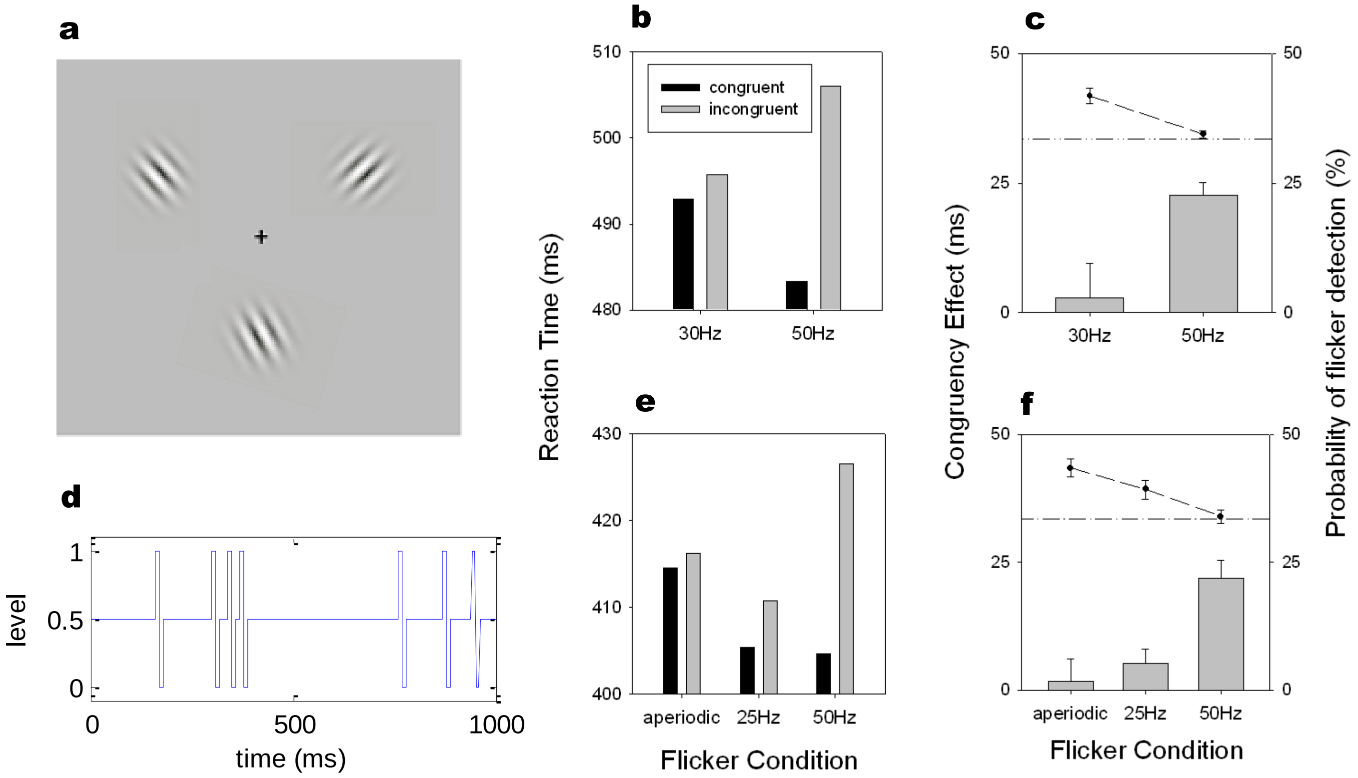
a
b
c
d
e
f
congruent
incongruent
Reaction Time (ms)
510
500
490
480
30Hz
50Hz
430
420
410
400
aperiodic
25Hz
Flicker Condition
Congruency Effect (ms)
Probability of flicker detection (%)
50
25
0
level
1
0.5
time (ms)
500
1000

Figure 1

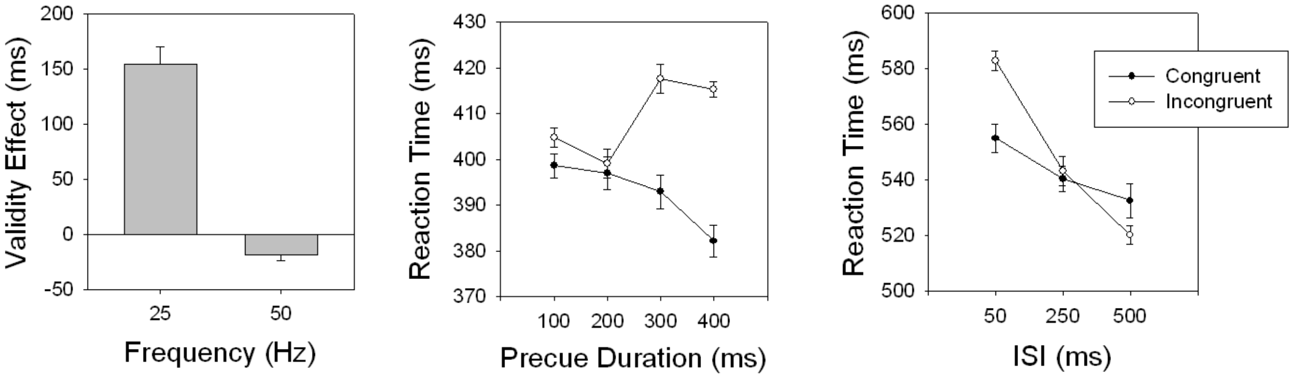
Validity Effect (ms)
200
150
100
50
0
-50
25
50
Frequency (Hz)
Reaction Time (ms)
430
420
410
400
390
380
370
100
200
300
400
Precue Duration (ms)
Reaction Time (ms)
600
580
560
540
520
500
50
250
500
ISI (ms)
Congruent
Incongruent

Figure 2

Figure Captions

Figure 1

a) Example of a stimulus display. Two groups of 20 observers each were tested at each of the two modulation frequencies (50/30 Hz). Each group was tested on two tasks: i) detection of a change-target following the flicker interval, and ii) detection of the flicker (without any additional change-target), in separate blocks (see Method). b) Reaction times on congruent and incongruent trials. c) Congruency effect (bars, left scale) and flicker detection rate (symbols and line, right scale); the horizontal dotted/dashed line corresponds to the chance level (33%) of flicker detection. A second comparison of the 50 Hz modulation to i) a 25 Hz flicker and, ii) an aperiodic temporal modulation was made using a within participant design (with trials, corresponding to 25/50 Hz or aperiodic modulations, randomized within each block). d) example waveform showing the contrast modulation of the cue, over a 1 second interval, in the aperiodic condition. RTs are depicted in panel (e); the corresponding congruency effects and detection rates in panel (f). Error bars (in this and subsequent figures) denote 1 SE (standard error), and where applicable the SE has been adjusted for within subject designs (21).

Figure 2

(a) Results of the opposition experiment. A positive validity effect is obtained in the 25 Hz condition, whereas the validity effect is negative in the 50 Hz condition. (b) RTs for congruent and incongruent trials as a function of (50 Hz) flicker preview duration. The congruency effect develops only after at least 200 ms flicker duration. (c) RTs for congruent and incongruent trials with a constant flicker preview duration (1000 ms), but varying change target onsets (ISI) after flicker preview offset. While there is still a congruency effect 50 ms after flicker offset, the effect vanishes after 250 ms and produces an ‘inhibition of return’ effect after 500 ms.