

Proof of your article (# J00357-10) from "Journal of Neurophysiology" is available for download

Dear Sir or Madam:

Please refer to this URL address <http://rapidproof.cadmus.com/RapidProof/retrieval/index.jsp>
Login: your e-mail address as listed in the "to" line of this e-mail message
Password: 99ZRbEbMEF29

The file at the URL above contains a single PDF file comprising the following items:

- 1) List of proofing marks; 2) Reprint order form; and 3) Copyedited proof of your article, with query list.

Adobe Acrobat® Reader is available here: <http://www.adobe.com/products/acrobat/readstep.html>.

- 1) Print the file and check the content carefully.
- 2) Clearly mark your corrections in the margin. Substantial changes are subject to evaluation by APS.
- 3) Answer all author queries (AQ1, AQ2, AQ3, etc.) listed on the last page of the PDF file.
- 4) Carefully proofread all/any tables and equations.
- 5) Ensure that any special characters or symbols are correctly represented.

Regarding figure quality: please note that the images in the proof represent the quality of the files you submitted for production. A significant cost has been incurred to set these images into proof, and alterations or substitutions, while not prohibited, are discouraged and subject to evaluation by APS.

To ensure timely publication of your article in the next available issue, please return the corrected set of page proofs **WITHIN 2 BUSINESS DAYS**. Please e-mail your corrections to Barbara A. Meckley (meckleyb@cadmus.com) by attaching a hand-marked digital scan of all proof pages. An itemized summary in the body of the e-mail will be helpful to resolve any ambiguities regarding the corrections you have placed on the proof; however, it remains important to provide corrections on the face of the proof pages and to include all pages in the scanned file (even those pages without corrections). Be sure to retain a copy of the proof with your corrections, for your records.

[Adobe Acrobat editing tools have not proved to be more useful than carefully hand-marked corrections, and so the use of those Adobe Acrobat tools is discouraged.]

As an alternative to e-mail, you may return the proofs via an overnight courier service to APS in Bethesda, Maryland, USA (as listed below). If you have any problems or questions, please contact me. **PLEASE INCLUDE YOUR ARTICLE NO. (J00357-10) WITH ALL CORRESPONDENCE.**

Sincerely,

Barbara A. Meckley, Journal Production Manager, Journal of Neurophysiology (meckleyb@cadmus.com)
Cadmus Communications, DPS Ephrata, 300 West Chestnut St., Suite A, Ephrata, PA 17522-1987 Phone 717-445-8430

REPRINT AND PAGE CHARGES: Please fax your order form and purchase order to 877-705-1373. In lieu of faxing, you may e-mail the order form and purchase order (if available) directly to Pete Brown (BrownP@cadmus.com.) For reprint inquiries, contact Pete Brown (BrownP@cadmus.com.) Mail payment to: Cadmus Reprints, PO Box 822942, Philadelphia, PA 19182-2942 (FEIN #:54-0157890).

*******(Note: Do not send express packages to this PO Box.)*******

Proofreader's Marks

MARK	EXPLANATION	EXAMPLE
	TAKE OUT CHARACTER INDICATED	Your proof.
^	LEFT OUT, INSERT	u Yor proof.
#	INSERT SPACE	# Yourproof.
9	TURN INVERTED LETTER	Your p ^l oof.
X	BROKEN LETTER	X Your pr/of.
eg#	EVEN SPACE	eg# A good proof.
C	CLOSE UP: NO SPACE	Your pro ^g f.
tr	TRANSPOSE	tr A proof good
wf	WRONG FONT	wf Your proof.
lc	LOWER CASE	lc Your proof.
≡ caps	CAPITALS	Your proof. caps Your proof.
ital	ITALIC	Your proof. ital Your proof.
rom	ROMAN, NON ITALIC	rom Your proof.
bf	BOLD FACE	Your proof. bf Your proof.
..... stet	LET IT STAND	Your proof. stet Your proof.
out sc.	DELETE, SEE COPY	out sc. She Our proof.
spell out	SPELL OUT	spell out Queen (Eliz.)
#	START PARAGRAPH	# read. [Your
no #	NO PARAGRAPH: RUN IN	no # marked. → # Your proof.
L	LOWER	L [Your proof.]

MARK	EXPLANATION	EXAMPLE
┌	RAISE	┌ Your proof.
└	MOVE LEFT	└ Your proof.
┐	MOVE RIGHT	┐ Your proof.
	ALIGN TYPE	└ Three dogs. Two horses.
≡	STRAIGHTEN LINE	≡ Your proof.
⊙	INSERT PERIOD	⊙ Your proof.
;/	INSERT COMMA	;/ Your proof.
:/	INSERT COLON	:/ Your proof.
;/	INSERT SEMICOLON	;/ Your proof.
∨	INSERT APOSTROPHE	∨ Your mans proof.
∨ ∨	INSERT QUOTATION MARKS	∨ ∨ Marked it proof.
=/	INSERT HYPHEN	=/ A proofmark.
!	INSERT EXCLAMATION MARK	! Prove it.
?	INSERT QUESTION MARK	? Is it right.
Ⓚ	QUERY FOR AUTHOR	Ⓚ was Your proof read by
[/]	INSERT BRACKETS	[/] The Smith girl
</>	INSERT PARENTHESES	</> Your proof.
1/m	INSERT 1-EM DASH	1/m Your proof.
□	INDENT 1 EM	□ Your proof
▢	INDENT 2 EMS	▢ Your proof.
▣	INDENT 3 EMS	▣ Your proof.

Journal of Neurophysiology 2011

Published by The American Physiological Society

This is your reprint order form or pro forma invoice

(Please keep a copy of this document for your records. This form is not for commercial ordering.)

IMPORTANT Order form must be returned within 48 hours of receipt to avoid late charges. Orders received after 48 hours will be charged an additional fee of 25%. Orders received after 30 days will be charged an additional 50%. It is the policy of Cadmus Reprints to issue only one invoice per order. **Please print clearly. Please return form whether reprints are ordered or not.**

Author Name _____
Title of Article _____
Issue of Journal _____ Reprint # 3668727 Manuscript # J00357-10 Publication Date _____
Number of Pages _____ Color in Article? Yes / No (Please Circle) Symbol JN
Please include the journal name, the reprint number, and the manuscript number on your purchase order or other correspondence.

Order and Shipping Information

Reprint Costs (Please see page 2 of 2 for reprint costs/fees.)

_____ Number of reprints ordered \$ _____
_____ Number of color reprints ordered \$ _____
Subtotal \$ _____
Add appropriate sales tax/GST to subtotal \$ _____
First address included, add \$32 for each additional shipping address \$ _____

Publication Fees (Please see page 2 for fees and descriptions.)

Page Charges: \$70 per journal page \$ _____
Color Figures: \$400 per color figure \$ _____
Hard copy color proof: \$75 per figure \$ _____
Toll-Free Link: \$150 \$ _____

Member No. _____ Member Signature _____
Total Publication Fees \$ _____
TOTAL TO REMIT \$ _____

Shipping Address (cannot ship to a P.O. Box)

Name _____
Institution _____
Street _____
City _____ State _____ Zip _____
Country _____
Quantity _____ Fax _____
Phone: Day _____ Evening _____
E-mail Address _____

Additional Shipping Address* (cannot ship to a P.O. Box)

Name _____
Institution _____
Street _____
City _____ State _____ Zip _____
Country _____
Quantity _____ Fax _____
Phone: Day _____ Evening _____
E-mail Address _____

* Add \$32 for each additional shipping address

Payment and Credit Card Details (FEIN #:540157890)

Enclosed: Personal Check _____
Institutional Purchase Order _____
Credit Card Payment Details _____
Checks must be paid in U.S. dollars and drawn on a U.S. Bank.
Credit Card: ___ VISA ___ Am. Exp. ___ MasterCard
Card Number _____
Expiration Date _____
Signature: _____
Name (please print): _____

Wire Transfer Payment Information:

PNC Bank
Two Tower Center Boulevard
East Brunswick, NJ 08816
Account Name: Cadmus, a Cenveo Company
ABA/Routing #: 031207607
Account #: 8026256369 ; SWIFT Code: PNCCUS33
Reference #: 822942/Invoice Number OR Reprint/Man #

Invoice or Credit Card Information

Please complete as it appears on credit card statement. Cadmus will process credit cards and *Cadmus Journal Services* will appear on the credit card statement. **Please Print Clearly**

Name _____
Institution _____
Department _____
Street _____
City _____ State _____ Zip _____
Country _____
Phone _____ Fax _____
E-mail Address _____

Please **fax** your order form and purchase order to 877-705-1373. Or, in lieu of faxing, you may **email** the order form and purchase order directly to june.billman@cenveo.com. **Checks** should be mailed to address below:

Cadmus Reprints
P.O. Box 822942
Philadelphia, PA 19182-2942

FEIN #:540157890

Note: Do not send express packages to this location, PO Box.

SIGNATURE REQUIRED: By signing this form the author agrees to accept responsibility for the payment of the mandatory page charges of \$70 per page, reprints ordered, as well as any color charges, late payments, and split shipment charges. If the charges are billed to an institution, the author must assume the responsibility for making the necessary arrangements for the issuance of a formal institutional purchase order. Otherwise, it is understood that the author will bear the cost of these charges. Failure to pay any of these agreed-upon charges could jeopardize future submissions.

AUTHOR Signature _____ Fax _____
Telephone _____ E-mail _____

Journal of Neurophysiology 2011

Published by The American Physiological Society

REPRINT AND PUBLICATION CHARGES; Author rates only. Not to be used for commercial ordering

Black and White Reprint Prices

Black and White Pricing, Domestic (USA Only)					
# of Pages	100	200	300	400	500
1-4	\$268	\$373	\$477	\$584	\$688
5-8	\$363	\$547	\$736	\$922	\$1,106
9-12	\$467	\$710	\$960	\$1,201	\$1,446
13-16	\$560	\$885	\$1,211	\$1,537	\$1,865
17-20	\$652	\$1,051	\$1,446	\$1,845	\$2,237
21-24	\$758	\$1,225	\$1,688	\$2,156	\$2,622
25-28	\$850	\$1,400	\$1,947	\$2,494	\$3,041
29-32	\$960	\$1,574	\$2,205	\$2,833	\$3,463

Black and White Pricing, International (non-USA Only)					
# of Pages	100	200	300	400	500
1-4	\$300	\$421	\$545	\$667	\$790
5-8	\$411	\$629	\$851	\$1,071	\$1,289
9-12	\$534	\$825	\$1,129	\$1,417	\$1,716
13-16	\$643	\$1,035	\$1,428	\$1,822	\$2,218
17-20	\$751	\$1,235	\$1,716	\$2,197	\$2,672
21-24	\$872	\$1,439	\$2,007	\$2,575	\$3,143
25-28	\$984	\$1,649	\$2,313	\$2,982	\$3,643
29-32	\$1,107	\$1,860	\$2,626	\$3,390	\$4,154

Minimum order is 100 copies. For orders larger than 500 copies, please consult Cadmus Reprints at 410-943-0629.

Late Order Charges

Articles more than 90 days from publication date will carry an additional charge of \$6.10 per page for file retrieval.

Page Charges

\$70 per journal page for all pages in the article, whether or not you buy reprints.

Color

Reprints containing color figures are available. If your article contains **color**, you must pay subsidized color charges of \$400/fig. (reprint charge is \$1000/fig for those who do not pay promptly), whether or not you buy reprints. These **color charges are waived for APS Members who are the first or last author of the paper**. If you requested a **hard copy color figure proof** when you reviewed your S-proof, the charge is \$75.

Shipping

Shipping costs are included in the reprint prices. Domestic orders are shipped via FedEx Ground service. Foreign orders are shipped via an expedited air service. The shipping address printed on an institutional purchase order always supersedes.

Multiple Shipments

Orders can be shipped to more than one location. Please be aware that it will cost \$32 for each additional location.

State Sales Tax and Canadian GST

Residents of Virginia, Maryland, Pennsylvania, and the District of Columbia are required to add the appropriate sales tax to each reprint order. For orders shipped to Canada, please add 5% Canadian GST unless exemption is claimed.

Color Reprint Prices

Color Pricing, Domestic (USA Only)					
# of Pages	100	200	300	400	500
1-4	\$391	\$622	\$850	\$1,080	\$1,308
5-8	\$487	\$795	\$1,107	\$1,418	\$1,726
9-12	\$591	\$959	\$1,330	\$1,695	\$2,066
13-16	\$684	\$1,133	\$1,585	\$2,032	\$2,485
17-20	\$776	\$1,299	\$1,731	\$2,340	\$2,855
21-24	\$882	\$1,472	\$1,962	\$2,651	\$3,240
25-28	\$973	\$1,647	\$2,208	\$2,990	\$3,662
29-32	\$1,082	\$1,821	\$2,455	\$3,328	\$4,082

Color Pricing, International (non-USA Only)					
# of Pages	100	200	300	400	500
1-4	\$425	\$669	\$918	\$1,163	\$1,411
5-8	\$536	\$878	\$1,225	\$1,569	\$1,912
9-12	\$658	\$1,074	\$1,503	\$1,915	\$2,340
13-16	\$767	\$1,285	\$1,803	\$2,322	\$2,843
17-20	\$877	\$1,485	\$2,092	\$2,697	\$3,298
21-24	\$997	\$1,691	\$2,384	\$3,077	\$3,770
25-28	\$1,111	\$1,901	\$2,691	\$3,485	\$4,270
29-32	\$1,235	\$2,112	\$3,005	\$3,893	\$4,784

TOLL-FREE LINK

A link can be created from a url of your choice to your article online so that readers accessing your article from your url can do so without a subscription. The cost is \$150. This is especially useful if your article contains electronic supplemental material. For more information, please click on this link:

<http://www.the-aps.org/publications/sprooflink.pdf>

Ordering

Please **fax** your order form and purchase order to 877-705-1373. Or, in lieu of faxing, you may **email** the order form and purchase order directly to june.billman@cenveo.com. **Checks** should be mailed to address below:

Cadmus Reprints
P.O. Box 822942
Philadelphia, PA 19182-2942

FEIN #:540157890

Note: Do not send express packages to this location, PO Box.

Wire Transfer Payment Information:

PNC Bank
Two Tower Center Boulevard
East Brunswick, NJ 08816
Account Name: Cadmus, a Cenveo Company
ABA/Routing #: 031207607
Account #: 8026256369 ; SWIFT Code: PNCCUS33
Reference #: 822942/Invoice Number OR Reprint/Man #

Please direct all inquiries to:

June Billman
866-487-5625 (toll free)
410-943-3086 (direct)
877-705-1373 (FAX)
june.billman@cenveo.com

Reprint Order Forms and Purchase Orders or prepayments must be received 48 hours after receipt of form.

Please return this form even if no reprints are ordered.

Subliminal Gamma Flicker Draws Attention Even in the Absence of Transition-Flash Cues

AQ: 1

Samuel Cheadle,¹ Andrew Parton,³ Hermann J. Müller,^{2,4} and Marius Usher^{2,5}

¹Department of Cell and Developmental Biology, University College London; ²Department of Psychological Sciences, Birkbeck College, London; ³Centre for Cognition and Neuroimaging, Brunel University, Uxbridge, United Kingdom; ⁴Department of Psychology, Ludwig Maximilian University, Munich, Germany; and ⁵Department of Psychology, University of Tel Aviv, Tel Aviv, Israel

Submitted 19 April 2010; accepted in final form 7 December 2010

Cheadle S, Parton A, Müller HJ, Usher M. Subliminal gamma flicker draws attention even in the absence of transition-flash cues. *J Neurophysiol* 105: 000–000, 2011. First published December 8, 2010; doi:10.1152/jn.00357.2010. We recently reported evidence indicating that selective attention is deployed to a target location in a multiobject display, when the target event (a change of one of the objects) is preceded by subliminal flicker in the gamma range. However, concerns have been raised regarding the stimuli used in this study and the possible contribution of an artifactual cue: a “transition flash” between pretarget flicker offset and target onset. Here, we report a series of experiments investigating the existence and potential contribution to selective attention of this transition-flash cue under different presentation conditions. We find that, although the transition flash is a real phenomenon (detection rates $\approx 15\% >$ chance), it cannot, on its own, explain the original effects of gamma flicker on the response time to target detection. Even after eliminating this flash, detection was significantly faster, or more accurate, for targets preceded (vs. not preceded) by flicker. This congruency effect (≈ 15 ms) demonstrates that gamma flicker on its own is sufficient to engage selective attention. This interpretation is further strengthened by a reevaluation of 1) *experiment 7* reported by van Diepen and colleagues and 2) the validity effect experiment reported by Bauer and colleagues. Possible reasons for the discrepant results are also discussed.

AQ: 2

INTRODUCTION

Increased neural synchronization in the gamma-band has been proposed to mediate visual attention (Fries et al. 2001; Niebur et al. 2002; Womelsdorf et al. 2006). Recently, we reported psychophysical results supporting this proposal (Bauer et al. 2009). In a series of experiments, we found that a subliminal 50-Hz flickering Gabor patch, among two nonflickering patches, affects the speed with which one can detect a subtle spatial-frequency (SF) change in one of the patches: detection is faster when the target occurs at the flicker, rather than a nonflicker, location (Fig. 1). Based on the overall pattern of results, we proposed an unconscious attentional account for this congruency effect (CE): the 50-Hz flickering patch engages an attentional mechanism, giving rise to faster detection of subtle changes at its location. We interpreted this as support for the neural-synchrony attention mechanism.

FI

This interpretation has been challenged by van Diepen et al. (2010) who carried out a number of experiments using the same paradigm with some minor variations. Although they

replicated the 50-Hz CE, they argued that this effect is due to a nonsubliminal cue, unrelated to oscillatory neural synchronization: an “illusory transition flash” that occurs at the transition between the 50-Hz flicker preview and the 100-Hz target presentation or, simply, due to the fact that the flicker itself was not truly subliminal. Here we seek to address this important issue. We agree with van Diepen et al. (2010) that a transition flash is “perceptible” during the transition between the flickering 50-Hz preview and the 100-Hz target, although this percept was very weak in our original setup (see DISCUSSION). However, we disagree with the proposal that this flash, or supraliminal flicker, *completely* mediates the CE. To show this, we report new data, free of influences of such cues and replicating the 50-Hz flicker CE. Furthermore, we argue that the results reported by van Diepen and colleagues (2010) are also consistent with our original interpretation.

As explained by van Diepen et al. (2010) in our original experimental paradigm, the target Gabor undergoes a transition from the 50-Hz preview, where the patch is shown at contrast range 0 to A (= maximum contrast), to 100-Hz, where it is shown at contrast $A/2$ (Fig. 1B). This altered contrast range for the target results in the same perceived contrast as that of the other patches (always shown at 100 Hz with contrast $A/2$); at the transition, however, there are two frames (either side of the transition) that sum to a value that is different from $A/2$, causing an illusory transition flash. The effect is subtle and, in our original study, it was not noticed by the experimenters or reported by any participants. In our setup, one can observe it clearly only by fixating on the critical patch. In this task, however, observers fixate the center of the display, which is 6° from each of three patches and therefore randomly fixating on one of the potential target patches would be a nonoptimal strategy. Nevertheless, the presence of this flash (albeit weak) may act as a cue capturing attention. Thus as van Diepen et al. (2010) point out, to know whether the 50-Hz flicker triggers attentional selection as a result of gamma-band neural synchrony entrainment (Bauer et al. 2009) it is crucial to ascertain that the CE we originally reported is observed, even in the absence of such potentially confounding cues. The study by van Diepen et al. (2010) is thus important, both for noticing this illusory transition flash and for motivating further experiments to test whether attentional selection is indeed influenced by gamma-band flicker.

The main results that led van Diepen et al. (2010) to a negative conclusion regarding a role of 50-Hz flicker for attentional selection were the following: 1) they found that observers are able to detect the transition flash at a level higher

AQ: A

Address for reprint requests and other correspondence: S. Cheadle, Laboratory of Neurobiology, Department of Cell and Developmental Biology, University College London, London, WC1 E6BT, UK (E-mail: s.cheadle@ucl.ac.uk).

AQ: A

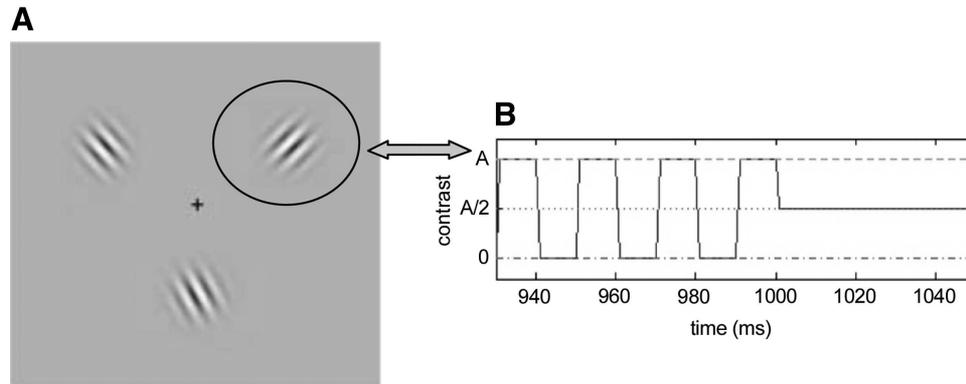


FIG. 1. Experimental setup used in Bauer et al. (2009). *A*: the stimulus, 3 Gabors of random orientation, are presented for a 1-s preview, after which one of the Gabors undergoes a subtle change in spatial frequency (SF) for another 600 ms and observers have to report its location as fast as possible. *B*: the temporal modulation (50-Hz flicker) that is applied to one of the 3 Gabors during the 1-s preview (A = maximum contrast); only the last 7 frames of the flicker sequence are shown, spanning the period 930–1,000 ms. The other 2 Gabors are not modulated (i.e., they are presented at the screen refresh rate of 100 Hz, with constant contrast = $A/2$; the monitor is gamma corrected). The target (SF change) can appear either at the same location as the flickering Gabor (congruent) or at a different location (incongruent).

than chance (54%, with chance level being 33%); 2) they found that observers were also able to detect the 50-Hz flicker (in the absence of a transition flash) better than chance (40%; they suggest that the reason that our observers did not achieve this level was related to the lack of feedback in our tests and to the mixing of easy and difficult trials within the same block); 3) they found a null CE (2 ms, nonsignificant) when the transition flash was prevented by making the 50-Hz flickering patch continue to flicker (at 50 Hz) during target presentation. It should be noted, though, that such a null CE was *not* obtained in *experiment 7* of the same study, when the flicker was made truly subliminal (70 Hz) and the transition flash was also prevented. In this case, van Diepen et al. (2010) reported a reduced but significant CE of 11 ms, which they attributed to nonattentional processes.

Before examining the existence of a gamma-induced CE in the absence of flash cues, it is apt to consider the only discrepancy between the results reported by van Diepen et al. (2010) and those of Bauer et al. (2009). This concerns *experiment 5* of van Diepen et al. (2010), which showed that, with a 100-ms flicker interval preceded by 900 ms of nonflicker (100-Hz) preview and followed by the (nonflicker) change target, one obtains a robust CE. For the same condition, Bauer et al. (2009) reported a null effect. Having retested this condition, we concur that indeed a robust CE effect takes place, consistent with van Diepen et al. (2010). We have now verified that the null effect reported in Bauer et al. (2009) was actually obtained with a preview of a 100-ms flicker interval without being preceded by a 900-ms static preview, which was erroneously reported in Bauer et al. (2009). However, we believe that neither display procedure is informative regarding the role of gamma flicker: the large CE reported by van Diepen et al. (2010) may be due to the presence of a “double transition flash” (two transition flashes may sum to produce a stronger signal), whereas our null effect (with the 100-ms preview) could be due to masking of the flicker by strong onset transients.

To further examine the nature of the CE, we report here a number of critical tests. First, we report an examination of flicker-detection accuracy (*experiment 1*), with and without the transition flash, in the same experimental setup we used in our original experiments, but using the protocol (error feedback

and no mixing of easy/difficult trials) that van Diepen et al. (2010) suggested as being more stringent for assessing the ability to detect the flicker. Second, we report tests (*experiments 2* and *3*) that examine the presence of (50-Hz flicker) CE effects in two flash-free variants of the task. Some of the observers who participated in *experiment 2* had also participated in *experiment 1*, the two experiments being performed within the same 1-h session. For reasons of clarity, we report them separately. In all the experiments, we followed van Diepen et al. (2010) in using paired, two-tailed *t*-tests to test for significant differences between conditions.

AQ: 3

METHODS

Experiment 1: flicker and flash detection in the original setup

The first detection condition, labeled *no-transition*, corresponds to detection of the flicker in our original study, which involves a 1-s presentation of one of the three Gabors flickering at 50 Hz and the other two at 100 Hz; this condition is free of a transition flash (because there is no transition to a subsequent display in which all Gabors flicker at 100 Hz) and designed to measure detectability of the 50-Hz flicker on its own. We report this here to test whether, with our experimental setup [the same apparatus and stimuli as those in Bauer et al. (2009), but with error feedback as in van Diepen et al. (2010)], the flicker *itself* is subliminal. The second condition, labeled *transition*, examines detectability with the flash present; this condition involves the same 1-s preview as that in the previous condition, followed by a 600-ms period in which all three Gabors flicker at 100 Hz. No spatial-frequency (SF) change of any of the Gabors took place in this (flicker and flash detection) experiment.

PARTICIPANTS. A group of 26 observers (11 female) with normal, or corrected-to-normal, vision were tested in both conditions. All observers (mainly students from Birkbeck and nearby colleges) voluntarily signed up for the experiment using the Birkbeck subject recruitment system (<https://psyc-bbk.sona-systems.com>). Their informed consent was obtained prior to running the experiment and it was explained to them that they could withdraw at any time. The experiment was carried out under ethical guidelines approved by the Department of Psychological Science, Birkbeck College (University of London). All observers were naïve as to the purpose of the experiment.

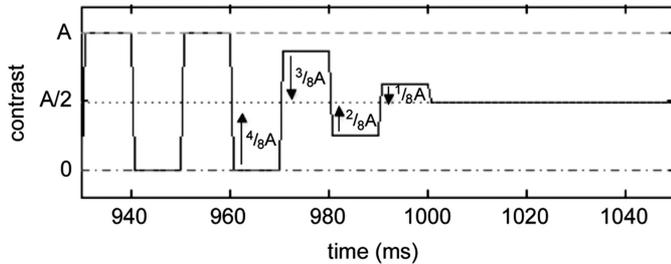


FIG. 2. The temporal modulation for the ramp condition. The last 7 frames of the flicker sequence spanning the period 930–1,000 ms. Note that the modulation amplitude decreases from $4A/8$ through $3A/8$ and $2A/8$ and to $A/8$.

APPARATUS AND MATERIALS. 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 (gamma corrected; screen resolution 800×600 pixels), with the frame rate set at 100 Hz. Observers maintained their viewing distance (57 cm) via a chin rest and gave their responses through a CT3 four-button response box (Cambridge Research Systems).

STIMULI. Displays consisted of three Gabor patches (size 3° , spatial frequency 2 cpd, deviation 0.45°) that were equally spaced on an invisible circle (radius 6°) around a central black fixation cross (always visible) on a light gray background of the same mean luminance as that of the Gabor patches (51.1 cd/m^2 ; Fig. 1). The luminance range of the 50-Hz flickered (cue) patch ranged from 6.7×10^{-3} (black) to 103 cd/m^2 (white).

PROCEDURE. Two versions of the flicker-detection task were tested: 1) a “no-transition” version, in which one patch maintained a 50-Hz flicker throughout the (1-s) display time (whereas the others were presented at 100 Hz); and 2) a “transition” version, which contained an additional interval (600 ms) displaying all elements at 100 Hz (and therefore contained the transition flash). The two versions of the task were blocked, with 180 trials each, and with self-paced breaks every 50 trials. In both tasks, the observers were instructed to indicate which patch appeared different (in flicker or any other visual property, except for orientation) in a three-alternative forced-choice (3AFC) response. Feedback was given in the form of a beep for incorrect responses. A 50-trial practice block was given to each observer before starting the tasks. Participants were also told that this task is difficult, but they could use the error feedback to improve, and they were instructed to do their best and to guess if they were not sure. The task was not sped up. This is the same procedure as that used by van Diepen et al. (2010).

Experiments 2 and 3: congruency effects in flash-free, flicker-primed change detection

STIMULI AND PROCEDURES. In the SF change-detection task, the stimulus was the same as that used in *experiment 1*, with the exception that following the preview interval, a target was presented, generated by increasing or decreasing the spatial frequency (SF) of one of the Gabors by 0.14 cpd; the SF change was done repeatedly in *experiment 2* (a change occurred every 100 ms, for a total of 600 ms) and only once in *experiment 3* (followed by 600 ms of static Gabor display). There were two variations of this general procedure: a “ramped” condition and a “continuous” condition. In the *ramp* condition, the flicker in the 1-s preview was ramped down, smoothing the transition to the 600 ms of nonflicker, which contained the target SF change (Fig. 2).

In the *continuous* condition, the flicker of the Gabor continued throughout the entire 1,600 ms (i.e., during both the preview and the SF target change presentation). In all conditions, the target location was congruent with the flicker cue in 50% of the trials and incongruent

in the other 50%. Observers indicated (using a 3AFC procedure) the location of the SF change by pressing a spatially corresponding button as quickly as possible. The next trial followed 1,000 ms later. Each experimental condition consisted of three blocks of 50 trials (150 trials in total). The main focus of interest was on the CE in SF change detection for observers who were unable to detect the flicker. We followed the same method as that used by van Diepen et al. (2010) for estimating CEs on the basis of (individual observers’) median RT after elimination of responses faster than 100 ms and slower than 1 s (Fig. 3).

F3

CHANGE-DETECTION TASK. For the continuous condition group, the flicker-detection task involved the no-transition condition from *experiment 1*; for the *ramp* group, it involved a similar 1 s of flicker preview, which was ramped out in the last three frames, followed by 600 ms of no-flicker. Both versions did not include SF changes. Each subject completed 120 trials per condition.

In both *experiments 2* and *3*, all the participants were tested first on SF change detection (without flash) and only then in a flicker-detection task. The flicker-detection task was always performed after the change-detection task, to ensure (on an individual basis) that the CEs were not mediated by strategic use of either flash or flicker detection (as could have been the case if the reverse order was used).

EXPERIMENT 2. Participants. In all, 14 observers (6 female) were tested under the continuous condition and 17 (9 female) under the ramp condition. All 14 observers in the continuous condition were also tested in *experiment 1* (both tasks being run within the same session). The continuous flicker-detection data are, in fact, part of the data (14 of 26 subjects) reported in the no-transition condition of *experiment 1*. We report this condition again because our emphasis here is on CE effects of the observers that were at chance at flash/flicker detection.

EXPERIMENT 3. The continuous stimulus presentation from *experiment 2* was used, with the exception that the target consisted of a *single* SF change and that the magnitude of the SF change was individually calibrated (prior to the experiment proper) using a staircase procedure.

Participants. In all, 11 observers (4 female) were tested under the continuous condition.

RESULTS

Experiment 1

We found a detection rate of 37% (range: 21–47%) in the no-transition condition, which increased to 45% in the transition condition (range: 33–60%). The difference between the two conditions is significant [$t(25) = 3.75, P = 0.001$],

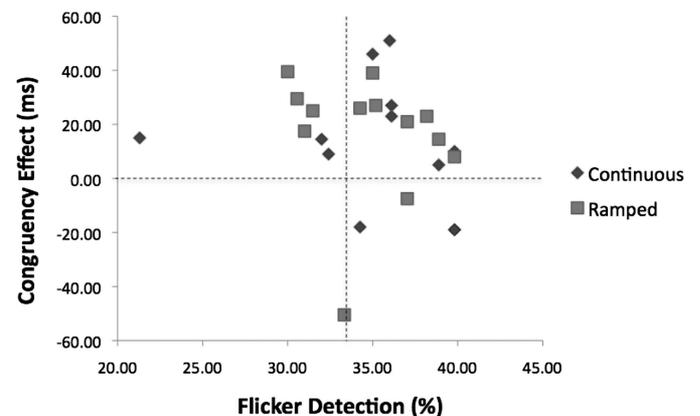


FIG. 3. Scatterplot of congruency effect in reaction times (RTs, in ms) vs. detection rate for the continuous and ramped conditions.

F2

providing an estimate of the contribution of the flash to detection performance. In the no-transition condition, only 4 (of the 26) observers had a detection rate $>40\%$; after eliminating these observers (as was also done in our original study), the mean detection rate decreased to 35% (not significantly different from chance). On this basis, we maintain that the 50-Hz flicker of the Gabor patch (without the transition flash) is subliminal for most of the observers in the setup used in our original experiments.

We concede, however, that although detection of the flash is not easy (45% in the transition condition), it is nevertheless possible and can increase the accuracy with which the critical Gabor is picked out (12% above chance level on average, with 15 of the 26 observers exhibiting a detection rate $>40\%$). Because a detection rate of this order could contribute to the CE (faster response to targets at the location of previous flicker, compared with targets at nonflicker locations), it is critical to determine whether the presence of flicker can trigger the CE even when detection of the flash, or of the flicker, is not possible. We examine this in *experiments 2 and 3*.

Experiments 2 and 3

In the two experiments that follow, we examined whether the 50-Hz flicker preview of one of the Gabors generates a congruency effect (CE) in spatial frequency (SF) change detection when the transition flash is eliminated. Elimination of the transition flash was achieved in two ways, with different groups of observers. In the first, *continuous* condition (group 1), the flickering patch continues to flicker at 50 Hz during target presentation (i.e., the condition does not involve a transition from 50 to 100 Hz); this approximately replicates the “continuous” procedure for eliminating the transition flash, introduced by van Diepen et al. (2010) (but see *experiment 3*). The second, *ramped* condition (group 2) involves a gradual decrease in 50-Hz flicker amplitude during the last three frames at the end of the preview (before the presentation of the target), to remove the abrupt transition (see Fig. 2). We introduced this additional condition (in *experiment 2* only) to distinguish between potential effects of the flicker before and after target presentation (also see the DISCUSSION on methodological differences between *experiments 2 and 3*).

The difference between *experiments 2 and 3* concerns a minor variation to target presentation, which relates to a subtle difference between our original experimental setup [used in most of the experiments reported in Bauer et al. (2009)] and the one used by van Diepen (2010).¹ In our original setup, we presented a *repeated* SF change (increase and decrease every 100 ms) for a total time of 600 ms, in which a single SF change was subtle. This allowed us to make the SF change difficult to detect, with a single presentation, so that the task was attention dependent, while at the same time maintaining high accuracy and avoiding a more complex analysis based on two dependent variables, reaction time (RT) and accuracy (with possible trade-offs), both of which could show attention effects. With this setup, accuracy was high (observers had more opportunities to detect the change) and the attentional CE was effectively collapsed in the RTs.

In van Diepen et al. (2010) the SF change occurred only once. If the change is subtle (i.e., detection is attention dependent), this could result in both RT and accuracy effects [van Diepen et al. (2010) did not report the accuracy effects]. In one of the experiments reported in Bauer et al. (2009) we did actually use a single (nonrepeated) SF change; the detection response was not sped up and we used an accuracy, rather than RT, measure (SF thresholds for 71% correct detection). This experiment revealed a CE effect of 50-Hz flicker; that is, observers' discrimination thresholds were significantly lower for the incongruent compared with those of the congruent presentations [$t(6) = 4.01, P < 0.01$]. Given this, we believe that the difference between the single and the repeated versions is not critical for the results, as long as the change remains subtle enough for detection to be attention dependent. Given this, we believe that the difference between the single and the repeated versions is not critical to the results, as long as the change remains subtle enough—involving a form of time-limited processing—for the detection to be attention dependent; time-limited presentation would probe early perceptual, rather than later response-related, processes (Santee and Egeth 1982), and thus be more likely to disclose attentional effects in this paradigm.

However, since the accuracy experiment of Bauer et al. (2009) was not flash-free and to obtain more uniformity with the procedure used by van Diepen et al. (2010), we carried out *experiment 3*. This used the same procedures as those used by van Diepen et al. (2010; the SF change applied only once), except that the magnitude of the change introduced was individually predetermined, for each participant using a staircase (with nonflickering Gabors), before the actual change-detection experiment (with congruent/incongruent flicker), to permit a detection rate of about 71% to be achieved. Both accuracy and RT effects were measured for the SF change-detection task with congruent/incongruent flicker.

The flicker-detection rates were 38% ($n = 17$) for the *ramp* condition and 37% ($n = 14$) for the *continuous* condition (the average detection rate for these 14 observers happens to be the same as the detection rate of the larger group ($n = 26$), which includes these 14 observers, reported in *experiment 1*). Of the 17 observers who performed the *ramp* (flicker detection) condition, 4 reached a detection level exceeding 40%. When these observers are eliminated, the detection rate decreased to 35% (not significantly different from chance; $P = 0.14$). The average CE effect for these 13 observers was 16 ms and is significantly larger than zero [$t(12) = 2.5, P = 0.03$]. Of the 14 observers who performed the *continuous* condition, 3 exhibited detection rates that exceeded 40%. When these 3 observers were eliminated, the detection rate (of the remaining 11 observers) became 35% (not significantly different from chance; $P = 0.39$). The CE effect for these 11 observers, in the continuous condition, averaged 15 ms and was also significantly larger than zero [$t(10) = 2.2, P < 0.05$].

Both of these results indicate that the detection of a subtle change in a property (SF) of one of the Gabors is sped up when the same Gabor had flickered at 50 Hz, compared with when another Gabor had flickered at 50 Hz, even for observers who were unable to detect the flicker. Because the detection criterion of 40% that we introduced for observer elimination is somewhat arbitrary, we inspected (for the 11 observers in the continuous condition and the 13 observers in the ramp condi-

¹ Having reexamined our METHODS section (Bauer et al. 2009), we realize that this procedural detail was not clearly set out. Thus, van Diepen et al. (2010) were well justified when they interpreted our methods in this way.

tion) the correlation between the change-detection CEs and the flicker-detection rates. If residual flicker detection contributes to the congruency effect in change-detection RTs, we should expect a positive correlation: observers exhibiting larger flicker-detection scores should show larger congruency effects. The result of the correlation was $r(22) = -0.14$, $P = 0.52$, which suggests that the 50-Hz flicker CE in these participants is not mediated by a residual ability to detect the flicker and use it as a cue.

The average flicker-detection rate over the 11 observers was 38%. Of these observers, 3 exhibited detection rates that exceeded 40%. When these 3 observers were eliminated, the detection rate (of the remaining 8 observers) became 34.9% (not significantly different from chance; $P = 0.14$). For accuracies, the average CE for these 8 observers was 3.3%, which was significantly larger than zero [$t(7) = 2.0$, $P \leq 0.05$]. For the response time data, although RTs were numerically faster (8 ms) for congruent than for incongruent stimuli, this difference was nonsignificant. The results, however, demonstrate a CE in accuracy without a speed-accuracy trade-off. Furthermore, a scatterplot of the CE against detection scores (Fig. 4) shows no consistent relationship between the variables, indicating that the effect is not attributable to a few observers that were able to detect the flicker slightly better than chance.

DISCUSSION

We agree with van Diepen et al. (2010) that our original test (Bauer et al. 2009) was subject to a transition-flash “cue.” Although detectability of this flash is lower in our setup than that in their setup, it was nevertheless essential to examine whether the expedited response to the spatial-frequency (SF) change at the flicker (relative to a nonflicker) location remains when this potentially confounding cue is eliminated. Using two procedures (ramped and continuous conditions), we found this to be the case. In *experiment 2*, we showed that although the congruency effects (CEs) measured using reaction times (RTs) were slightly smaller compared with those of our original condition (15 and 16 ms, compared with 21 ms), the effect remains significant, in both protocols, after the elimination of the transition flash. In *experiment 3*, we showed similar CE

effects using an accuracy measure. Although we reported CEs in terms of RT in *experiment 2* and in terms of accuracy in *experiment 3*, we argue that both measures reflect perceptual limitations in the detectability of the target; that is, they are both accuracy dependent because they are obtained under time-limited viewing conditions and the target change is subtle. With regard to *experiment 2*, the repeated target presentation will result in RT measures across trials reflecting detection of the SF change at each of several discrete presentations. Previous research has shown that there are tasks that dissociate between accuracy measures in time-limited viewing paradigms versus RT measures in time-unlimited paradigms (Santee and Egeth 1982), the former tapping into early perceptual processes and the latter more into response selection processes. Thus if anything, compared with our accuracy-based measures, the pure RT measure used by van Diepen et al. (2010) is more likely to reflect influences of response-related processes due to the higher visibility of their (single) change target.

Our results differ from those reported by van Diepen et al. (2010) who obtained a nonsignificant CE, albeit in the predicted direction, in their continuous condition, which eliminates the transition between the 50-Hz preview and the 100-Hz target display. One possible source of this discrepancy may be the procedural difference previously discussed. When the SF change is made only once, one has to examine both RT and accuracy costs (unless the SF change is so large as to be easily detectable, without requiring attentional processing). As shown in our *experiment 3*, where we used a subtle SF change, a CE effect is found in accuracy, with a nonsignificant effect in RT (again, though, in the predicted direction, indicating that the accuracy CE is free from a speed-accuracy trade-off). Importantly, van Diepen and colleagues (2010) did not report the accuracy data, so we cannot tell whether their pattern of results was indeed similar to ours. Furthermore, we maintain that accuracy-based measures are in any case more sensitive because they better tap into the perceptual (rather than response-related) processes that are enhanced by selective attention.

The conclusion that the 50-Hz flicker-induced CE is not an outcome of a supraliminal flicker cue is further supported by the results of the validity effect experiment in our original article (Bauer et al. 2009), which was designed to directly address this issue. In that experiment (which van Diepen and colleagues did not address), the flicker “cue” and the target (SF change) were set in opposition to each other, such that in 80% of the trials the target appeared on the side opposite to the flicker; this experiment was performed with only two Gabor patches, one positioned to the left and the other to the right of fixation, and with two types of flicker: 25-Hz (supraliminal) and 50-Hz (subliminal). Furthermore, participants were informed at the start of the experiment that either an easy (25-Hz) or a hard (50-Hz) flicker cue was present in one patch on each trial and that the SF change would most likely occur in the opposite patch. They also received error feedback. We reasoned that if observers can detect the flicker, they should be able to reorient attention to the other side, showing a positive validity effect (and a negative CE); by contrast, if they are unable to do so and attention is automatically attracted toward the 50-Hz flicker without conscious detection, strategic redeployment of attention would not take place and a negative validity effect (positive CE) would be found (cf. McCormick 1997). The results were clear-cut: a strong positive (154 ms)

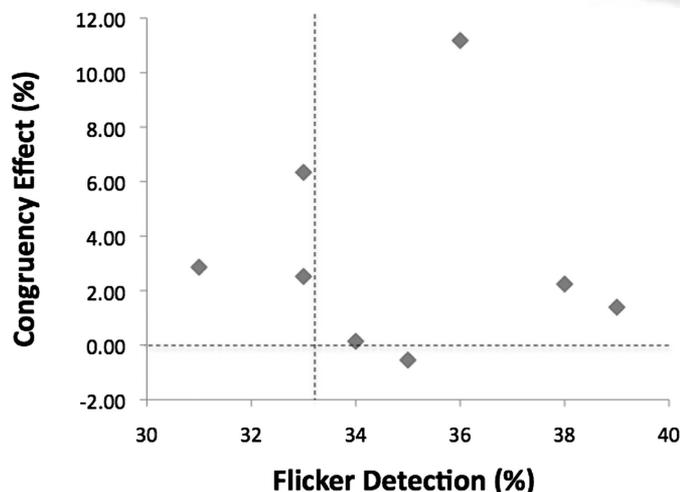


FIG. 4. Scatterplot of congruency effects in accuracy vs. flicker-detection rates for the 8 observers included in the continuous condition.

validity effect for the supraliminal 25-Hz flicker and a smaller but significant negative validity effect (-19 ms) for the 50-Hz flicker. Together with the results reported here, we believe that this dissociation strongly supports the conclusion that the CE we reported is not mediated by conscious detection of the flicker cue.

Furthermore, we believe the conclusion—that truly subliminal flicker (free of any visible cues) speeds up SF change detection—is further supported by the results of *experiment 7* reported by van Diepen et al. (2010), where a subliminal flash-free 70-Hz flicker (continuous condition) enhanced RTs to SF change targets at congruent locations. This effect was somewhat smaller (11 ms) than that in our original paradigm (21 ms), but highly significant [$t(9) = 3.96$; $P = 0.005$]. van Diepen et al. (2010) took the diminished magnitude of this effect as one argument against the role of gamma-band entrainment for attentional selection. We concede that the diminished effect magnitude might indicate that the detection of a transition flash partially contributed to the larger CE in our original studies. However, there are two other factors that may have resulted in a diminished CE with the 70-Hz flicker, which relate to the considerations that led us to select the 50-Hz flicker frequency in our experiments. Although the 70-Hz flicker falls within the frequency range of gamma-band attentional modulations in humans (Vidal et al. 2006), maximum power has been reported at 50 Hz (Figs. 1 and 2 in Fries et al. 2001). Due to the low-pass filtering properties of the visual system, a 70-Hz flicker is predicted to generate a lower magnitude of response modulation in visual cortex. This predicts a diminished effect of the 70-Hz flicker. Arguably, the existence of this smaller-magnitude effect at a gamma-band frequency therefore provides further support for our original proposal. Finally, we note that significant RT effects of this magnitude have often been found and interpreted in studies of visuospatial attention (for a review, see Wright and Ward 2008).

As an alternative to an attentional account of their (70-Hz flicker) CE, van Diepen et al. (2010) suggest that the RT facilitation observed with subliminal flicker results from an enhancement of perceptual/motor processing. However, van Diepen and colleagues (2010) do not provide an explanation of how such a perceptual/motor enhancement would differentially influence responses to targets at flickered versus nonflickered locations (resulting in a CE). Furthermore, it is difficult to see how a perceptual/motor enhancement would explain the fact that flicker-induced CEs were obtained not only in terms of reaction times (sped up response task), but also in signal detectability (i.e., detection thresholds) in a task that did not require sped up responses (Bauer et al. 2009). Nevertheless, in an attempt to positively establish that the CE is nonattentional in nature, van Diepen et al. (2010) carried out a similar SF change-detection experiment with a single element presented at fixation—the question being whether, in the absence of distractors (where there may be less need for selective attention), detection would still be sped up by a flickering of the target patch prior to the relevant change. The result, contrary to their perceptual/motor-enhancement account, was now negative: targets preceded by a 70-Hz flicker were responded to 9 ms more slowly, rather than faster, than those preceded by a 140-Hz flicker. This negative CE is interesting, but requires further work to be understood.

Two possibilities need to be considered. First, as suggested by van Diepen et al. (2010) with a single patch presented at fixation, attentional processes may play only a minor role; this should be the case if the change-detection task is easy, as indicated by the high accuracy (94%) reported on this task (see *experiment 8* in van Diepen et al. 2010). In this case, the most plausible interpretation of the negative CE might be in terms of interference of the flicker with the detection of the SF change. However, this would imply that the 11-ms CE obtained with three patches is an underestimation of the true CE (observers are faster to detect targets at the flickering patch, despite the interference).

Second, even if the central task is attentionally engaging, we believe that it is difficult to predict exactly what impact the 70-Hz flicker would have. In the multiple-Gabor-patch task (unlike the task with a single, centrally presented patch), the endogenously generated (top-down) attentional activity produced in accordance with the “attention-by-synchrony” hypothesis (Fries et al. 2001) should be fairly weak because there is no single location to which attention can be advantageously directed. Consequently, externally elicited flicker-related gamma activity (at either 50 or 70 Hz) will tend to dominate induced endogenous activity in multiple-Gabor-patch tasks. By contrast, in a central-fixation single-patch task, previous studies indicate there will be increased power induced across a wide range of gamma frequencies from 40 to 80 Hz (Vidal et al. 2006). The interaction of endogenous activity with that elicited by the stimulus flicker at 50 and 70 Hz (and occurring at random phase to the endogenous synchronization) means that it is hard to make simple behavioral predictions of their effects. It thus appears that, although the positive 70-Hz-flicker CE, with multiple-patch displays, is consistent with the “attention-by-synchrony” hypothesis, no firm conclusions (either for or against it) can be derived from the central-patch task. We thus believe that the attentional explanation offers the best account for the flicker-induced CE with multiple patches. Accordingly, the entrained synchronous gamma oscillations may promote a type of “winner-takes-all” dominance of one cell coalition, representing the attended location, over competing assemblies, representing to-be-ignored locations (Lee et al. 1999; Niebur et al. 1993). Nevertheless, alternative explanations should be examined, such as the idea that the flicker, rather than engaging the attentional system, sets in place some type of location or object priming, making the system more sensitive to the detection of subsequent targets.²

Fn2

To conclude, we agree that an illusory transition flash occurred in our original experiments. The report by van Diepen et al. (2010) is important for noting this phenomenon and raising critical questions. However, we believe that the data we report here, as well as data from the 70-Hz flicker experiment in van Diepen et al. (2010), provide support for the claim that detection of this flash (or of the flicker itself) does not account for *all* of the CE, in either RT or accuracy measures. We believe that attentional selection via neural entrainment remains the most plausible explanation for these data, which are

² The existence not only of significant costs but also of benefits (Bauer et al. 2009) suggests that priming is unlikely to explain the results of Bauer et al. (2009): priming is likely to result in a significant benefit component only. Future studies are needed to examine costs–benefits for (transition-flash) cue-free stimuli.

consistent with neurophysiological data (Fries et al. 2001; Womelsdorf et al. 2006).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

REFERENCES

- Bauer F, Cheadle SW, Parton A, Müller HJ, Usher M.** Gamma flicker triggers attentional selection without awareness. *Proc Natl Acad Sci USA* 106: 1666–1671, 2009.
- Fries P, Reynolds JH, Rorie AE, Desimone R.** Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291: 1560–1563, 2001.
- Lee DK, Itti L, Koch C, Braun J.** Attention activates winner-take-all competition among visual filters. *Nat Neurosci* 2: 375–381, 1999.
- McCormick PA.** Orienting attention without awareness. *J Exp Psychol Hum Percept Perform* 23: 168–180, 1997.
- Niebur E, Hsiao SS, Johnson KO.** Synchrony: a neuronal mechanism for attentional selection? *Curr Opin Neurobiol* 12: 190–194, 2002.
- Niebur E, Koch C, Rosin C.** An oscillation-based model for the neuronal basis of attention. *Vision Res* 33: 2789–2802, 1993.
- Santee JL, Egeth HE.** Do reaction time and accuracy measure the same aspects of letter recognition? *J Exp Psychol Hum Percept Perform* 8: 489–501, 1982.
- van Diepen RM, Born S, Souto D, Gauch A, Kerzel D.** Visual flicker in the gamma-band range does not draw attention. *J Neurophysiol* 103: 1606–1613, 2010.
- Vidal JR, Chaumon M, O'Regan K, Tallon-Baudry C.** Visual grouping and selective attention induce gamma-band oscillations at different frequencies in human MEG signals. *J Cogn Neurosci* 18: 1850–1862, 2006.
- Womelsdorf T, Fries P, Mitra PP, Desimone R.** Gamma band synchronization in visual cortex predicts speed of change detection. *Nature* 439: 733–736, 2006.
- Wright RD, Ward LM.** *Orienting of Attention*. Oxford, UK: Oxford Univ. Press, 2006.



AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES

1

AQ1— Suggested short running title OK? If not, please provide.

AQ2— Please note that JNP style does not allow full reference entries in the Abstract.

AQ3— The text has been rearranged to preserve JNP's usual style of INTRODUCTION, METHODS, RESULTS, and DISCUSSION. Please verify placement of text under these headings.

AQA— Please verify the accuracy of your e-mail address or delete it if you do not wish it included. Please check all Tables and Equations carefully for presentation and accuracy. All tables and display equations (those set off from running text) are set by hand during the composition process. I have edited all of these slightly. As you check the page proofs, please indicate all necessary changes to tables and equations. The text in the DISCLOSURES section reflects your data entry into the Peer Review submission. Is this still complete, relevant, and accurate?
