

Proof of your article (# JN-00810-2013) 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: 77jKX7amoQ77

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® tools may be used to mark proof; see detailed instructions in this packet.

- 1) Print the file and check the content carefully.
- 2) Clearly mark only necessary corrections (by hand in the margin or electronically).
- 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 any pixel-based images (TIFF, JPEG) have been lowered in quality in this proof to reduce the overall file size. This is done to improve portability and enable faster transmission. Final print and online publication versions of pixel-based images will be representative of the submitted files. 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 Maria Pasho (mpasho@the-aps.org) by attaching a hand-marked digital scan or electronically marked PDF 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.

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. (JN-00810-2013) WITH ALL CORRESPONDENCE.**

Sincerely,

Maria Pasho, Journal Editorial Supervisor, Journal of Neurophysiology, 9650 Rockville Pike, Bethesda, Maryland 20814-3991 (USA) Phone: 301-634-7207, Fax: 301-634-7244, E-mail: mpasho@the-aps.org

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 June Billman (june.billman@cenveo.com.) For reprint inquiries, contact June Billman (june.billman@cenveo.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.)*******

Requesting Corrections on Your PDF Proof

To help us facilitate any necessary late-stage corrections, we encourage authors to use the comments and notes features in Adobe Acrobat. The PDF provided has been "comment enabled," which allows the user to utilize the comments and notes features in Adobe Acrobat, even if using only the free Adobe Acrobat reader (see note below regarding acceptable versions). Adobe Acrobat's Help menu provides additional details on the tools. When you open your PDF, the comments/notes/edit tools are clearly shown on the tool bar. The important features to know are the following:

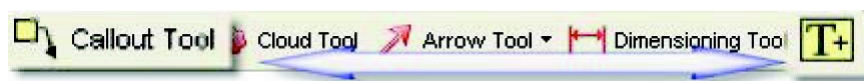
- Note tool (yellow text balloon icon): Click on this feature on the tool bar and then click on a point of the PDF where you would like to make a comment. This feature is useful when providing an instruction to your production contact or to verify a question or change that was posed.
- Text edits ("T" with strike-through and carat icon): The option Insert Text at Cursor allows the user to place the cursor at a point in the text, which will then provide a pop-up box to add the appropriate text to be added to the proof.
- Use the Strike-Out tool to indicate deletions to the text.

As with hand-annotated proof corrections, the important points are to communicate changes clearly and thoroughly, to answer all queries and questions, and to provide complete information for us to make the necessary changes to your article so it is ready for publication.

To use the comments/notes features on this PDF you will need Adobe Reader version 7 or higher. This program is freely available and can be downloaded from <http://www.adobe.com/products/acrobat/readstep2.html>.

Instructions for Annotating Your .PDF Proof

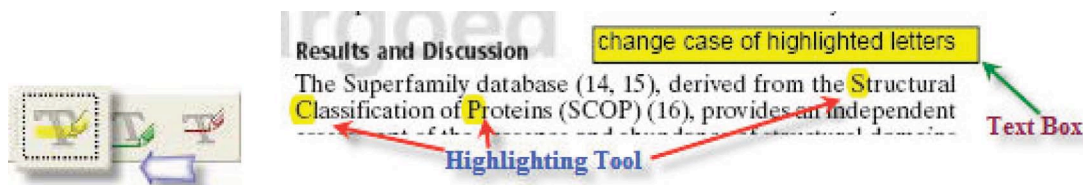
- Use the Text Boxes and the Callout Tool to indicate changes to the text



- Use the Strike-Out tool to indicate deletions to the text.



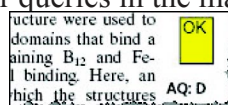
- Use the Highlighting Tool to indicate font problems, bad breaks, and other textual inconsistencies.



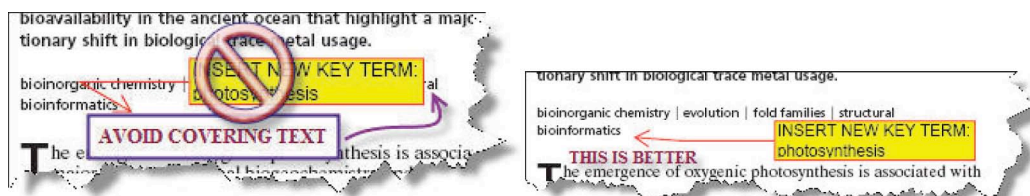
- Clearly indicate where changes need to be made using arrows, lines, and the Call-Out Tool.



- Mark changes and answer queries in the margins and other areas of white space.



- Avoid obscuring the text with corrections.



Proofreader's Marks

MARK	EXPLANATION	EXAMPLE
	TAKE OUT CHARACTER INDICATED	 Your proof f .
^	LEFT OUT, INSERT	u Your proof. ^
#	INSERT SPACE	# Yourproof. ^
9	TURN INVERTED LETTER	Your p ^l oof. ^
x	BROKEN LETTER	x Your pr o of.
eg#	EVEN SPACE	eg# A good proof.
c	CLOSE UP: NO SPACE	Your pro ^g of.
tr	TRANSPOSE	tr A proof ^g ood
wf	WRONG FONT	wf Your proof ^f .
lc	LOWER CASE	lc Your ^f roof.
≡ caps	CAPITALS	Your proof. caps <u>Your</u> proof.
ital	ITALIC	Your proof. ital <u>Your</u> proof.
rom	ROMAN, NON ITALIC	rom Your <u>proof</u> .
bf	BOLD FACE	Your proof. bf <u>Your</u> 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.
└	LOWER	└ [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 <u>proof</u> .
⊙	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 proof ⁻ mark.
!	INSERT EXCLAMATION MARK	! Prove it [!]
?	INSERT QUESTION MARK	? Is it right [?]
②	QUERY FOR AUTHOR	② was Your proof [?] read by
[/]	INSERT BRACKETS	[/] The Smith girl [,]
</>	INSERT PARENTHESES	</> Your proof ¹
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 2014

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 Souto, David & Kerzel, Dirk
Title of Article Ocular tracking responses to background motion gated by feature-based attention
Reprint # 3876054 Manuscript # JN-00810-2013 Publication Date _____
Number of Pages 8 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.)

none Number of reprints ordered \$ _____
none 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: \$75 per journal page \$ 600
Color Figures: \$400 per color figure \$ _____
Hard copy color proof: \$75 per figure \$ _____
Toll-Free Link: \$150 \$ _____
146115

Member No. _____ Member Signature _____
Total Publication Fees \$ 800
TOTAL TO REMIT \$ 800

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 #

822942/JN-00810-2013

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 David Souto
Institution Université de Genève
Department FPSF
Street 40 Boulevard du Pont d'Arve
City Genève State _____ Zip 1205
Country Switzerland
Phone _____ Fax _____
E-mail Address sofia.ferreira@unige.ch

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 cjsreprints@cadmus.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 \$75 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 2014

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	\$275	\$380	\$485	\$590	\$690
5-8	\$370	\$550	\$740	\$925	\$1,110
9-12	\$470	\$715	\$965	\$1,205	\$1,455
13-16	\$565	\$890	\$1,215	\$1,545	\$1,875
17-20	\$655	\$1,055	\$1,450	\$1,855	\$2,250
21-24	\$760	\$1,230	\$1,695	\$2,165	\$2,640
25-28	\$860	\$1,405	\$1,955	\$2,510	\$3,060
29-32	\$965	\$1,575	\$2,215	\$2,850	\$3,480

Black and White Pricing, International (non-USA Only)					
# of Pages	100	200	300	400	500
1-4	\$305	\$425	\$550	\$675	\$800
5-8	\$415	\$635	\$860	\$1,080	\$1,300
9-12	\$540	\$835	\$1,140	\$1,425	\$1,725
13-16	\$650	\$1,044	\$1,440	\$1,835	\$2,225
17-20	\$760	\$1,250	\$1,730	\$2,205	\$2,680
21-24	\$880	\$1,455	\$2,020	\$2,585	\$3,155
25-28	\$990	\$1,665	\$2,325	\$3,000	\$3,655
29-32	\$1,120	\$1,875	\$2,640	\$3,400	\$4,165

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 \$6.22 per page for file retrieval.

Page Charges

\$75 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	\$400	\$630	\$855	\$1,085	\$1,310
5-8	\$495	\$805	\$1,115	\$1,425	\$1,745
9-12	\$600	\$970	\$1,345	\$1,715	\$2,105
13-16	\$700	\$1,150	\$1,605	\$2,100	\$2,545
17-20	\$780	\$1,315	\$1,765	\$2,375	\$2,930
21-24	\$900	\$1,500	\$2,000	\$2,700	\$3,340
25-28	\$995	\$1,675	\$2,255	\$3,045	\$3,780
29-32	\$1,105	\$1,855	\$2,510	\$3,395	\$4,220

Color Pricing, International (non-USA Only)					
# of Pages	100	200	300	400	500
1-4	\$450	\$675	\$930	\$1,175	\$1,420
5-8	\$545	\$890	\$1,240	\$1,580	\$1,920
9-12	\$665	\$1,085	\$1,515	\$1,930	\$2,350
13-16	\$775	\$1,300	\$1,815	\$2,340	\$2,850
17-20	\$890	\$1,500	\$2,110	\$2,720	\$3,310
21-24	\$1,010	\$1,705	\$2,400	\$3,100	\$3,780
25-28	\$1,120	\$1,915	\$2,710	\$3,510	\$4,285
29-32	\$1,245	\$2,130	\$3,025	\$3,920	\$4,800

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 cjsreprints@cadmus.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 Cenvo Company
ABA/Routing #: 031207607
Account #: 8026256369 ; SWIFT Code: PNCCUS33
Reference #: 822942/Invoice Number OR Reprint/Man #

Please direct all inquiries to:

Reprints
866-487-5625 (toll free)
410-943-0629 (direct)
877-705-1373 (FAX)
cjsreprints@cadmus.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.

AQ: 1

Ocular tracking responses to background motion gated by feature-based attention

David Souto¹ and Dirk Kerzel²

¹*School of Psychology, University of Leicester, Leicester, United Kingdom; and* ²*Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, Genève, Switzerland*

Submitted 13 November 2013; accepted in final form 6 June 2014

AQ: 2

Souto D, Kerzel D. Ocular tracking responses to background motion gated by feature-based attention. *J Neurophysiol* 112: 000–000, 2014. First published June 11, 2014; doi:10.1152/jn.00810.2013.—Involuntary ocular tracking responses to background motion offer a window on the dynamics of motion computations. In contrast to spatial attention, we know little about the role of feature-based attention in determining this ocular response. To probe feature-based effects of background motion on involuntary eye movements, we presented human observers with a balanced background perturbation. Two clouds of dots moved in opposite vertical directions while observers tracked a target moving in horizontal direction. Additionally, they had to discriminate a change in the direction of motion ($\pm 10^\circ$ from vertical) of one of the clouds. A vertical ocular following response occurred in response to the motion of the attended cloud. When motion selection was based on motion direction and color of the dots, the peak velocity of the tracking response was 30% of the tracking response elicited in a single task with only one direction of background motion. In two other experiments, we tested the effect of the perturbation when motion selection was based on color, by having motion direction vary unpredictably, or on motion direction alone. Although the gain of pursuit in the horizontal direction was significantly reduced in all experiments, indicating a trade-off between perceptual and oculomotor tasks, ocular responses to perturbations were only observed when selection was based on both motion direction and color. It appears that selection by motion direction can only be effective for driving ocular tracking when the relevant elements can be segregated before motion onset.

smooth pursuit eye movements; feature-based attention; attention; motion; eye movements

A CENTRAL QUESTION IN UNDERSTANDING how perception and action may be articulated is whether perceptual selection and eye movement control rely on similar filtering mechanisms (for a review Kowler 2007; Schutz et al. 2011). Involuntary ocular tracking eye movements offer a good opportunity for understanding early filtering mechanisms given that their initiation can involve relatively few processing steps (for a review, see Masson and Perrinet 2012).

Among involuntary tracking eye movements, ocular following is a quasireflexive response to motion covering a large part of the visual field (Kawano 1999; Miles et al. 1986), which is believed to reflect the unfolding of visual motion processing that provides a window on the link between neural computation and behavior (Ilg 1997; Lisberger et al. 1987; Masson and Perrinet 2012). Ocular following depends on first-order motion signals, with little input from higher order motion processing (Hayashi et al. 2008), suggesting that attention may have a

minor role. However, this latter aspect is poorly understood, especially in relation to feature-based attention, the ability to select a specific feature dimension (e.g., motion, color, and shape), or value (upward vs. downward motion) across the visual field. In the context of voluntary and involuntary tracking eye movements, feature-based attention may have a role in helping integrate motion information across space, as for tracking surfaces occluded by objects in the foreground (e.g., Grossberg 1998; Mestre and Masson 1997; Murasugi et al. 1989).

Feature-based attention has been shown to modulate motion processing. Arman et al. (2006) showed that the motion aftereffect is stronger for motion in an attended direction even when the test appears at a nonattended location, indicating enhancement of motion processing by selection of same-direction motion signals. In a similar vein, Lankheet and Verstraten (1995) elicited a motion aftereffect in a direction opposite to an attended motion layer, even when the stimulus motion was balanced by showing two clouds of dots moving in opposite directions. However, it is unclear whether feature-based attention modulates involuntary eye-movements, since recent research indicates that perception and slow eye movements rely on partially different networks or on information arising from the same networks but read out in different ways (Simoncini et al. 2012; Spering and Carrasco 2012; Spering and Gegenfurtner 2007b; Spering et al. 2011; Tavassoli and Ringach 2010). Recently, Spering and Carrasco (2012) showed that pursuit eye movements spontaneously follow the direction of the attended motion in dichoptic plaids, suggesting that feature-based attention can determine which motion direction is pursued and perceived. However, their paradigm was not suited to assess the importance of feature-based involuntary eye movements, as there was no fixation point and no incentive to maintain fixation.

With respect to involuntary eye movements in response to background motion, we know that the optokinetic nystagmus, whose early phase shares neural substrates with ocular following (Kawano 1999), can be reduced to some extent by paying attention to stationary elements (Mestre and Masson 1997; Murasugi et al. 1989). However, those studies confounded feature-based and spatial attention. We adapted established paradigms (Miura et al. 2009; Suehiro et al. 1999) to investigate the role of feature-based attention in gating motion signals that drive involuntary ocular responses to background motion. When the background moves orthogonally to the pursuit direction, its motion causes a brief involuntary eye movement in the direction of the perturbation. To obtain responses due to feature-based attention, we presented a balanced motion per-

AQ: 3

AQ: 6

Address for reprint requests and other correspondence: D. Souto, School of Psychology, Henry Wellcome Bldg., Univ. of Leicester, Leicester LE1 9HN, United Kingdom (e-mail: ds572@le.ac.uk).

AQ: 6

turbation in a dual task situation. That is, two clouds of dots moved in opposite directions (transparent motion paradigm) and observers had to pay attention to one of the clouds to discriminate a change in direction. Feature-based attention was expected to gate motion signals in the attended direction, creating an imbalance between motion signals that would result in a tracking response. In separate experiments, we manipulated the dimension on which the motion of one of the clouds could be selected. Selection could be based on both color and direction of motion (*experiment 1*), only on the direction of motion because color was uniform (*experiment 2*), or on color because motion direction was unpredictable (*experiment 3*). We finally compared ocular tracking results against a control condition in which there was only one group of dots.

METHODS

Participants

Undergraduate psychology students at the University of Geneva participated in the experiments for class credit ($M = 24$ -yr-old, 18–42). The procedure was approved by the local ethics committee. All subjects reported normal or corrected to normal vision. The number of subjects per experiment is given in Table 1. No participant ran more than one experiment.

Apparatus and Stimuli

The stimuli were presented on a 21-in. (diagonal) CRT with a resolution of 1,280 (H) \times 1,024 (V) pixels at a refresh rate of 85 Hz. The participants' head position was stabilized with a chin rest at 50 cm from the screen center. Eye movements were recorded with a desktop-mounted, video-based eye tracker (EyeLink 1000; SR-Research, Ontario, Canada) at a sample frequency of 1,000 Hz. The experiment was run in a dimly lit room.

A sketch of the stimuli and procedure is shown in Fig. 1. All stimuli had a luminance of 20.5 cd/m² and were presented on a black background. The pursuit target, a light gray bull's eye with a diameter 0.7°, moved horizontally at 11.2°/s for 1 s. The trajectory was centered on the midpoint of the screen. The background consisted of 80 dots (squares, side length of 0.2°) that moved at the same horizontal velocity as the target. For placing dots, the screen was divided in a matrix of 10 columns and 8 lines, and a dot was placed within each cell. The dot position within the cell was randomly jittered. Half of the dots were green, and the other half was red. Dot lifetime was only limited by the borders of the screen. The temporal structure of each trial is illustrated in Fig. 1C. The dots started moving vertically

306 ms after target motion onset at 33.6°/s for 200 ms. The vertical motion was added to the horizontal motion, resulting in diagonal motion on the screen. However, dot motion was experienced as vertical because the eye moved at the same horizontal velocity as the dots. The two clouds of dots moved in opposite directions in a retinal reference frame centered on the horizontally moving pursuit target. Dots that left the screen at the edges reappeared on the other side. One cloud slightly changed its vertical direction of motion 94 ms after onset of vertical motion. Instead of moving vertically all along, the motion path deviated by $\pm 10^\circ$ angle from vertical. Dots that were closer than 2° to the pursuit target were not presented.

Task and Procedure

Experiment 1: selection by motion and color. The experiment started with two single task blocks, in which observers were asked to pursue the target and to ignore the background. No mention of a change in motion direction during the vertical motion pulse was made. The two single task blocks, our control condition, were run before the two dual task blocks to avoid carry-over effects of attentional set. In two dual task blocks, observers were asked to pursue the target and to report whether the vertical motion of dots in a designated color deviated to the left or to the right. The color of the attended dots was fixed for each participant. The vertical direction of the attended color changed between blocks, while the horizontal direction of target motion varied randomly from trial to trial. The attended color and the vertical direction of motion of the attended dots in the first block were counterbalanced across participants. There were 64 control trials in the control condition (2 \times 32) and 96 trials in the attention condition (2 \times 48). The control condition had a third less trials than the attention condition because less eye movement variability was expected when participants' eye movements are driven exogenously as opposed to when they need to shift attention according to instructions.

An error message was displayed when the participant blinked during pursuit target motion, when a vertical saccade $> 1^\circ$ occurred, or when the distance covered by the eye from motion onset to offset was $< 70\%$ of the target's trajectory.

Experiment 2: selection by motion. The methods were as in *experiment 1* with the following exceptions. All dots had the same color, which did not change in the course of the experiment for individual observers but was counterbalanced between red and green across observers. In dual task blocks, observers were instructed to report the horizontal deviation of the cloud of dots moving in a specified direction. The relevant vertical direction was indicated before each of the two dual task blocks. The order of vertical motion directions was counterbalanced across participants. The experiment started with two single task blocks using the same stimuli as the dual task blocks.

Table 1. Number of excluded participants, excluded trials, and perceptual performance among participants included in the analyses

	Experiment 1	Experiment 2	Experiment 3	Experiment 4
N participants				
Included	13	13	8	15
Excluded: eye movement criteria	1 of 15	7 of 21	6 of 16	5 of 20
Excluded: perceptual criterion	1 of 15	1 of 21	3 of 16	–
Trials				
Valid: attention	74 (49–89)	67 (46–89)	66 (34–91)	39 (15–57)
Valid: control	37 (14–51)	34 (13–57)	34 (15–55)	25 (12–41)
Pursuit error	4% (1–11%)	6% (0–23%)	5% (1–19%)	2% (0–8%)
Saccade error	25% (13–40%)	31% (9–49%)	30% (16–38)	50% (33–76%)
Perceptual task				
Percent correct	91% (76–98%)	86% (63–98%)	79% (65–93%)	–

Participants were excluded if there were < 12 valid trials in any condition (eye movement criteria), or if perceptual performance was $< 60\%$ correct, to ensure that observers were paying attention to the perceptual task target. Blinks during the critical interval were very rare (0–1%) and are therefore not detailed in the table.

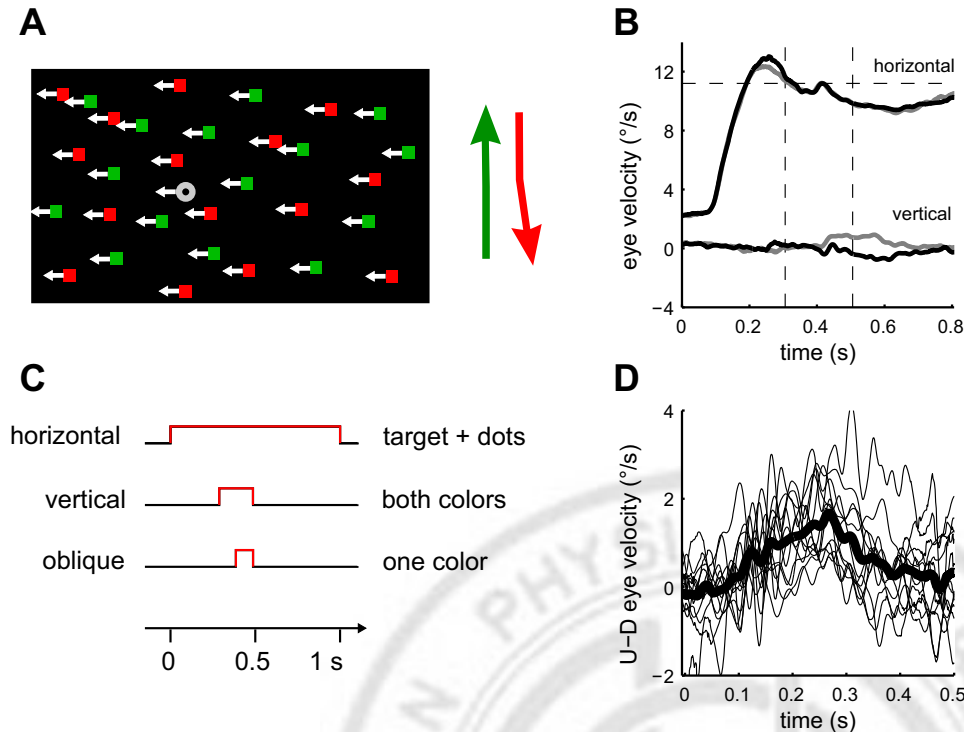


Fig. 1. Experimental procedure and results from *experiment 1*. *A* and *C*: target and background dots moved horizontally for 1 s (first line in *C*). After 306 ms, the dots moved vertically for 200 ms (second line in *C*). Dots of different colors moved in opposite vertical directions at 33.6°/s. The to-be-attended dots moved to the left or right from vertical relative to a reference centered on the pursuit target (oblique motion, third line in *C*). The pictogram to the right of the stimulus indicates the vertical trajectory of red and green dots in 1 particular condition. *B*: mean horizontal and vertical eye movement velocity (group averages) locked to pursuit target motion onset. Gray lines indicate upward dot motion, and black lines indicate downward dot motion. Vertical broken lines delimitate background motion duration. Note that there is a horizontal eye movement of $\sim 2^\circ/\text{s}$ at the start of the target motion, since target onset and trajectory could be anticipated. *D*: U-D eye velocity in the first 500 ms after the onset of vertical motion, obtained by subtracting vertical eye velocity with attention to the downward (D) moving dots from vertical eye velocity with attention to the upward (U) moving dots. A positive value indicates ocular tracking in the direction of background motion. Thin lines represent individual average traces and the thick line the group average.

Experiment 3: selection by color. The methods were as in *experiment 1* with the following exceptions. The vertical direction of motion of each cloud (red or green) changed randomly from trial to trial. In dual task blocks, observers were instructed to focus on the color indicated at the start of each block. As in *experiment 1*, this color did not change for a given observer but was counterbalanced between green and red across observers. The same stimuli were used in the initial single task blocks.

Because of the brevity of the motion signal, it is unlikely that feature-based attention could be voluntarily deployed in time to enhance motion signals if selection was based on motion direction; therefore, we consider that selection was based on color in this experiment.

Experiment 4: classic response. The first two blocks of the experiment were as in *experiment 1*. That is, the direction of motion of each color stayed the same in a block of trials and dots of two colors were overlaid. In the following two blocks, only half of the dots were shown with a single color and direction of motion. For instance, observers saw the red dots moving upward in block three and downwards in block four. There was always a horizontal deviation in the vertical motion pulse of one cloud (as in *experiment 1*), but the change was task irrelevant. As there was no opposite motion, this experiment should reveal the maximal response to the stimulus that was attended in *experiments 1–3*.

Data Analysis

To identify saccades we used the output of the EyeLink 1000 eye movement parser. The criterion used to detect saccade onset was acceleration $>4,000^\circ/\text{s}^2$ and velocity $>22^\circ/\text{s}$. Trials with errors detected online (blinks, vertical saccades, low gain horizontal pursuit, see above) were discarded from further analysis (see eye movement criteria in Table 1). A large number of ocular errors indicated that the participant was unable to maintain smooth pursuit in the presence of distracting stimuli or that the position signal was poor. Observers whose perceptual task performance was $<60\%$ were excluded from analysis to ensure that all subjects were paying attention to the stimulus. For offline analysis, we also removed trials in which a

saccade was detected during a temporal window going from vertical cloud motion onset to 500 ms after that, ensuring that this most informative period was not contaminated by a saccadic component. Our only criterion to exclude subjects was that there were >12 trials per condition (motion direction \times attention task).

Ocular following is a relatively small response, even though it is enhanced when performing a pursuit eye movement (Miura et al. 2009). Therefore, it is customary to improve the velocity signal by subtracting the average response to an upward motion signal to the response to a downward motion signal, and given it is a slow response, by filtering the velocity data with a low cutoff frequency (e.g., Hayashi et al. 2008; Miura et al. 2009). Velocity traces were filtered with a second-order Butterworth filter with a 25-Hz cutoff frequency. We ensured that no saccades were present in the velocity traces during an interval going from 0 to 0.5 s after onset of vertical motion. Furthermore, we extended the definition of a saccadic episode by adding 40 ms after the end of a saccade and 25 ms before its start. Because the vertical direction of motion was blocked, we also tested whether there was anticipation of the vertical motion pulse by analyzing the interval from vertical motion onset until 80 ms thereafter, which is too early for a visually driven response.

RESULTS

Table 1 summarizes the criteria used for analyzing the data, the number of excluded participants in all experiments, percent discarded trials, and average perceptual performance. The number of discarded trials is rather high (about 30–35% in *experiments 1–3*), especially in *experiment 4* ($>50\%$), due to a large number of saccades executed during the interval of interest where they are more likely to be triggered as retinal slip increases (de Brouwer et al. 2002). Because we wished to focus on the well-described slow eye movements following background motion, we had to exclude saccadic episodes.

Figure 1D shows the difference in vertical eye velocity between attending upwards and downwards motion in *experiment 1*, which we refer to as U-D response. Upward and

downward movements of the eye were given positive and negative signs, respectively. U-D values result from subtracting attention to downward motion from attention to upward motion. Therefore, positive U-D values indicate responses in the direction of attended background motion.

The individual U-D responses in Fig. 1D show a deflection in the direction of the attended motion in *experiment 1*. Figure 2A also shows a clear effect of the direction of attended dot motion on the averaged data that peaks at 222 ms [95% confidence interval (CI): 165–280 ms] after motion onset. Figure 2D shows that the peak occurred earlier when only a single cloud was shown in *experiment 4* (135 ms, 95% CI: 125–144 ms). The U-D peak amplitude was 1.67°/s in *experiment 1* (95% CI: 1.21–2.14°/s). With only a single cloud in *experiment 4*, the peak amplitude was 4.82°/s (95% CI: 3.67–5.97°/s). That is, the feature-based response was 34% of the classical response to unidirectional background motion; over the same time, the U-D response in the control condition without instruction to attend to one of the two clouds was close to zero (*experiment 1*: 0.04°/s; *experiment 4*: –0.28°/s). Statistical significance of the difference between attention and control conditions was evaluated by two-tailed *t*-tests over a large temporal window, going from 80 to 400 ms postvertical motion onset; we had no a priori reason for choosing a narrower temporal window for the effect of feature-based attention. This showed a significantly larger U-D eye velocity in the attend condition compared with the control condition in *experiment 1* (0.87 vs. 0.03°/s), $t(12) = 5.792$, $P < 0.0001$, but not in *experiment 2* (0.19 vs. 0.08°/s) and *experiment 3* (0.30 vs. 0.14°/s), $P > 0.4$. Furthermore, there was a significant difference between attention and control in *experiment 4* (1.08 vs. –0.12°/s), $t(14) = 5.743$, $P < 0.0001$.

It should be noted that observers anticipated the horizontal motion of the target, as the horizontal eye velocity at motion onset was $\sim 2^\circ/\text{s}$ (see Fig. 1B). Because the target always moved from an eccentric position toward the center of the screen, target motion was highly predictable and this explains the anticipatory eye movement. There was also evidence of anticipation in the response to the vertical dot motion when they were displayed in a single direction (*experiment 4*; Fig. 2D). We tested for an anticipatory component in the vertical ocular response by carrying out paired *t*-tests on the initial 80 ms after motion onset. During this period, only U-D eye movements in *experiment 4* were significantly different from zero, $t(14) = 3.919$, $P = 0.0015$ (other $P > 0.42$), with an average of 0.62°/s (95% CI: 0.31–0.93°/s).

Focusing on the attention condition, multiple comparisons between experiments over the same critical interval (80–400 ms postmotion onset) gave statistically significant differences between *experiments 1* and 2, $t(24) = 3.369$, $P = 0.0025$; between *experiments 1* and 3, $t(19) = 2.771$, $P = 0.0122$; but not between *experiments 1* and 4, $t(26) = 1.273$, $P = 0.214$. *Experiment 4* was also significantly different from *experiment 2*, $t(26) = 4.287$, $P = 0.0002$, and from *experiment 3*, $t(21) = 3.437$, $P = 0.0025$. There was no statistical difference between *experiments 2* and 3, $P = 0.806$. *Experiment 4* yielded an early peak and then a response opposite to the attended motion. Hence, the comparison of average U-D velocity over a large temporal interval does underestimate the strength of the response, which prompts us to compare *experiments 1* and 4 by their peak response. Peak responses in *experiments 1* and 4

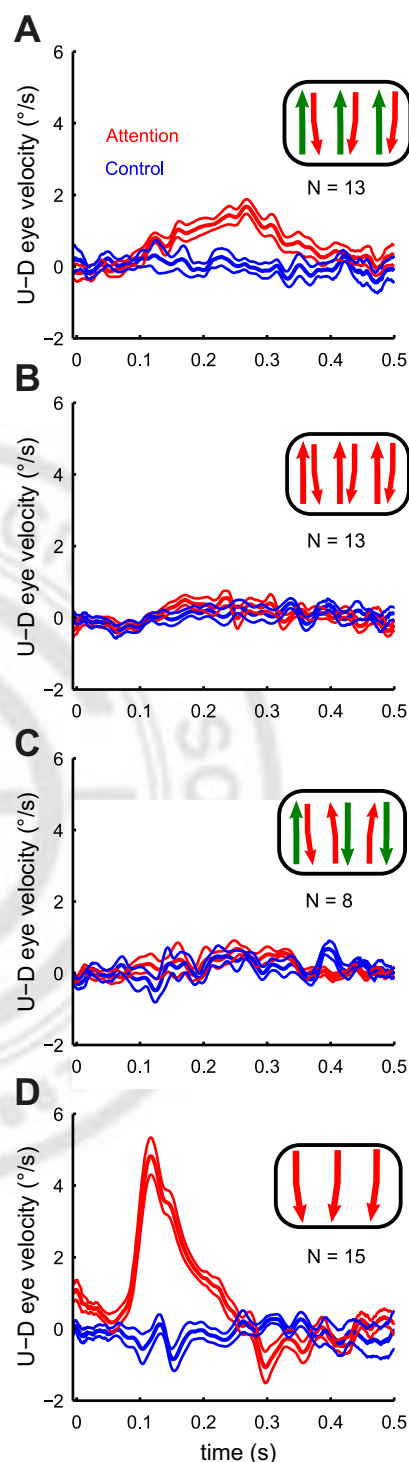


Fig. 2. Vertical eye velocity in *experiments 1–4* locked to vertical motion onset. *Insets*: experimental condition by showing the direction of the clouds of dots and how they change from trial to trial. *A*: both color and direction of the motion to discriminate are kept constant within a block (color + direction selection). *B*: direction is kept constant (direction selection). *C*: color is kept constant (color selection). *D*: only 1 cloud of dots is displayed (classic effect). Note that in this experiment the “attention condition” is an exogenous attention condition in which there is only 1 cloud of dots that is task irrelevant. *A–D*: thick lines represent the group average. Thin lines represent means \pm SE.

were significantly different (1.67 vs. 4.82°/s), $t(26) = 4.287$, $P < 0.0001$. Statistical significance levels was also reached when comparing open-loop responses from 90–180 ms post-vertical motion onset (0.62 vs. 3.27°/s), $t(26) = 11.144$, $P < .0001$.

We were also interested in testing whether there was a significant response during the open-loop response phase. The fastest open-loop responses may occur within a time window going from 90–180 ms (following Hayashi et al. 2010). Measured over this time window we obtained significantly larger responses in the attended compared with the unattended conditions (0.67 vs. 0.16°/s) in *experiment 1*, $t(12) = 2.521$, $P = 0.0268$, and in *experiment 4* (3.32 vs. $-0.35^\circ/\text{s}$), $t(14) = 11.298$, $P < 0.0001$. Other experiments yielded no significant differences, $P > 0.2$.

Perceptual performance between groups was compared as an indication of task difficulty (see Table 1). Perceptual performance between *experiments 1* to 3 was compared by running multiple comparisons using a nonparametric test, the Wilcoxon rank sum test. Perceptual performance was higher with direction and color being constant (*experiment 1*: 91%) than with color alone (*experiment 2*: 86%) or direction alone (*experiment 3*: 79%) being constant. The difference between *experiments 1* and 3 was statistically significant, $z = 2.609$, $P < 0.01$, but neither between *experiments 1* and 2, $z = 0.822$, $P = 0.4108$, nor between *experiments 2* and 3, $z = 1.340$, $P = 0.1800$. This suggests that the task was either easier in *experiment 1* compared with *experiment 3* or that observers may have engaged less in the perceptual task in *experiment 3*, which would explain the lower perceptual accuracy and the absence of attentional modulation of the vertical tracking response. If there was less engagement in the perceptual task in *experiment 3* than in *experiment 1*, horizontal smooth pursuit gain should have suffered less from the dual task situation.

We therefore analyzed the eye movement gain for the horizontal component of smooth pursuit eye movements within the first 500 ms after the onset of vertical motion. Figure 3 shows that horizontal eye movement gain is lower in the attention condition compared with the control condition across experiments (0.95 and 1.04, respectively). An ANOVA taking

experiment as a between-subjects factor (*experiments 1–4*) and task as a within-subjects factor (attend to cloud, control) confirmed that there was no effect of experiment, $F(3,45) = 0.316$, $P = 0.814$, or an interaction between experiment and task condition, $F(3,45) = 0.993$, $P = 0.405$, but an effect of task, $F(1,45) = 32.827$, $P = 0.001$. Hence, there was no evidence that attentional engagement was reduced in *experiment 3*. It must be noted that there was no explicit instruction to attend background motion in *experiment 4*, but it is likely that attention was engaged exogenously in that experiment, resulting in a similar reduction in gain.

Finally, we sought to characterize eye movement velocity on a trial-by-trial basis in *experiment 1*. This analysis is relevant to distinguish between rival conceptions of feature-based attention effects. A priming account predicts a buildup of effects across trials due to the repetition of the attended feature. Therefore, feature-based effects are expected to be absent at the beginning of the experiment and to increase over trials. A feed-forward selection account claims that feature-based attention selects the relevant feature before stimulus onset. Therefore, the effects should be present from the first trial onward without any changes over trials. Since signal variability did not allow for an accurate calculation of velocity profiles in every trial (this can be appreciated in Fig. 4A), we took the peak velocity latency of the group as a reference for comparing velocity across trials (i.e., the peak of the thick line in Fig. 1D). Therefore, velocity was averaged over a 50-ms time window centered on the group peak latency. On the first trial, the attention condition yielded statistically significant larger responses compared with the control condition, $t(12) = 2.845$, $P = 0.0148$. The subsequent analysis was restricted to the first 30 trials to avoid missing data in the attention condition. We observed that the U-D eye velocity fluctuated around a constant level across trials, as indicated by the slopes of the best-fitting least-squares linear regression in attention and control conditions (see Fig. 4B). Individually, regression lines in the attention condition had a negative slope in five subjects (from -0.001 to -0.09), indicating decreasing U-D velocity across trials; in 8 of them slopes were positive (from 0.025 to 0.23). The slope of the group average was 0.04, which was not statistically different from zero (Wilcoxon rank sum test, $z = 1.041$, $P = 0.1677$). The fact that feature-based effects were present on the first trial and did not increase over the course of the experiment is inconsistent with the priming account and favors feed-forward selection.

To sum up, when moving dots are displayed alone (*experiment 4*) or when one of the two clouds of dots is selected by its color and direction of motion (*experiment 1*), observers involuntarily track the attended motion direction. This effect depends on feature-based attention since vertical motion is otherwise balanced, as indicated by the absence of differences when the dots are unattended (i.e., single task condition), and that selection by location is unlikely because presentations time was short, the dots were relatively dense and not shown in the fovea. Trial-by-trial analysis indicates that performance fluctuates around a constant level in the first 30 trials.

DISCUSSION

We asked whether background motion signals generate an ocular tracking response depending on feature-based attention.

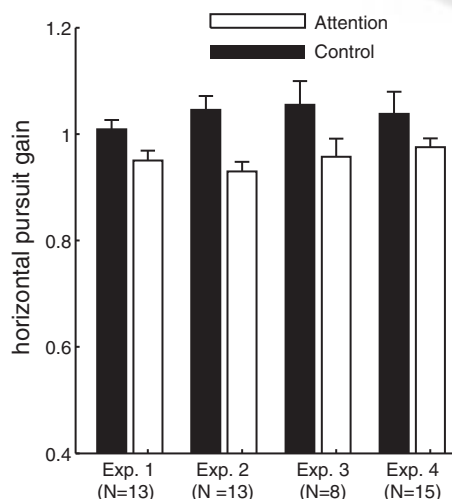
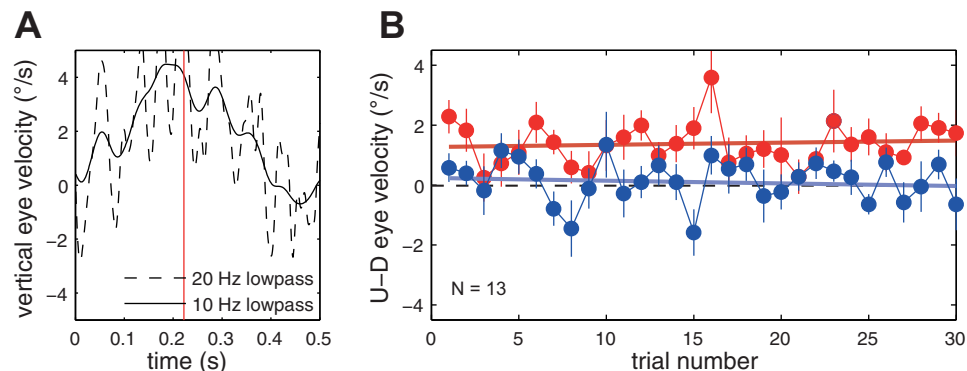


Fig. 3. Horizontal eye movement gain averaged across subjects in the 4 experiments (time window: 0–500 ms after vertical motion onset). Error bars represent means \pm SE.

Fig. 4. Trial-by-trial analysis of ocular response in *experiment 1*. **A**: Vertical eye velocity in response to a target moving upwards on the 1st trial in 1 observer. A 10-Hz low-pass filtered version is shown with the original trace (20-Hz low pass) for clarity. The latency of the group peak velocity is shown as a vertical red line. This was the reference for comparing U-D vertical eye velocity across trials in **B**, showing control (blue) and attention conditions (red) and respective regression lines. Error bars represent means \pm SE.



Participants pursued a target moving horizontally, while attending to a designated cloud of dots in the background. A vertical ocular tracking response occurred in response to the attended dot motion when selection could be based on specific feature values along two feature dimensions: motion and color. The amplitude of the attention-based tracking response was $\sim 30\%$ of the tracking response elicited in a single task with only one direction of background motion and $\sim 20\%$ if we consider not the peak response but an estimate of the open-loop response.

In two other experiments, we tested the effect of the perturbation when selection was based on color while motion direction varied unpredictably (color selection, see *experiment 3*) or when selection was based on motion direction because all dots had the same color (direction selection, see *experiment 2*). Although the decrease of horizontal pursuit gain indicated that observers across experiments were equally engaged in the perceptual task, ocular responses to perturbations depended on the combination of color and motion selection. In *experiment 3*, we assumed that selection of one of the clouds is too slow when its motion direction is unpredictable. Previous research has shown that it takes at least 300 ms to see the perceptual benefits of selecting a layer of dots based on direction of motion (Andersen and Muller 2010; Liu et al. 2007), but vertical motion only lasted 200 ms in our experiments.

We noted no significant feature-based response when selection was based on the color of the dot layer or when selection could only be made by attending to a given motion direction. We may think of this pattern of results as a multiplicative effect of combining selection by color with selection by motion. We take this as an indication that selection by motion direction can only be effective for driving involuntary ocular tracking when the relevant layer can be segregated before the motion starts, on the basis of any object feature, such as color, or depth plane (Mestre and Masson 1997).

The ocular responses that we recorded were always in the direction of the motion perturbation. Regarding the direction of the response, we note that there is a discrepancy in the literature. Some studies report an ocular response opposite to the background perturbation whereas others report an ocular response in the same direction. However, there is an essential difference in those studies. Studies that present background motion orthogonal to the pursuit direction show a response in the same direction (Lindner et al. 2001; Miura et al. 2009; Suehiro et al. 1999), with the exception of Sperling and Gegenfurtner (2007a), probably because of their relative low background velocity (Miura et al. 2009).

Our results indicate that although ocular tracking responses are often characterized as low-level responses to motion energy, they can nonetheless be modulated by feature-based attention. At the same time, we show that this effect is limited to specific conditions. Next, we consider a number of alternative interpretations to our results. Is the response we recorded in *experiment 1* due to the gating (or enhancement) of motion signals by feature-based attention or is it secondary to attentional tracking? Short presentation times and high velocities were supposed to discourage attentional tracking as an efficient way of performing the direction discrimination task. Latencies can help disentangle those two interpretations. Although we observed longer peak response latencies in *experiment 1* compared with the classical effect in *experiment 4*, the most informative analysis concerns the early, open-loop response. Because of high variability on single trials (see Fig. 4A), we could not estimate response onsets reliably. However, we can analyze early average responses. The *feature-based tracking hypothesis* would state the ocular response was initiated by tracking a particular feature by a covert movement of attention, rather than by the gating of first-order motion signals by feature-based attentional selection (*gating hypothesis*). It was shown that feature-based tracking and luminance-based motion are independent (Cavanagh 1992; Lu and Sperling 1995). Feature-based tracking implies that the eye movement will start after attentional tracking starts, which can only happen with some delay after onset of first-order motion. Consequently, the earliest response to feature-based tracking is necessarily delayed relative to the response to first-order motion. In contrast, the gating hypothesis allows for preemptive selection of motion signals according to a particular defining feature, for instance, by enhancing the weight given to responses coming from a subset of motion detectors. Further, studies indicate that the open-loop response of tracking eye movements is a response to first-order motion (Wilmer and Nakayama 2007), as is initial ocular following (Sheliga et al. 2005). Our data showed a response during the open-loop period in the attention compared with the control condition in *experiments 1* and *4*, favoring the gating hypothesis. A caveat of this analysis is that the motion direction of the relevant cloud of dots could be anticipated, contaminating the supposedly open-loop response. However, our analysis indicated no anticipatory component in *experiment 1*. An anticipatory component is only observed in *experiment 4* (Fig. 2). A further argument against feature-based tracking is that when motion direction was constant and there was no color cue, we did not observe a feature-based attention based response. To sum up, we suggest that the ocular tracking

response reflects preemptive feature-based selection rather than attentional tracking.

The idea that selection could be based on motion when target motion direction is held constant within a block presupposes that we can deploy “preparatory attention” to motion. However, this is a contentious issue in the literature (e.g., Fannon et al. 2007). Recently, Theeuwes (2013) made a case for distinguishing between postselection and feed-forward selection processes in feature cueing effects. He proposed that features can be primed in a bottom-up manner when there is a match with the target on previous trials but that features cannot be voluntarily selected by directing attentional resources towards a target feature. Our data do not lend support to the bottom-up (priming) account, since this would predict a buildup of the tracking response across trials. Not only did some observers show a strong response in the attended direction on the first trial, but on average, the best fitting linear trend indicated a constant response across trials.

Was task difficulty a factor explaining the absence of ocular tracking in some conditions? The perceptual task was easier when the target was defined by two rather than by one constant feature, as indicated by the percentage of correct trials, at least when comparing *experiments 1* and *3*. We also observed that involuntary tracking was absent when there was only one constant feature, opening the possibility that the task might have been too difficult in those conditions or that observers were less engaged in the task. However, performance in the oculomotor task (horizontal tracking) does not support the idea of differential attentional engagement. The availability of attention to a secondary task trades-off with ocular performance, especially when the perceptual task requires a motion judgment (Kerzel et al. 2008, 2009; Kowler and Zingale 1985). If observers engaged in the secondary task similarly across experiments, we should see that the pursuit task performance was reduced equally across experiments in the attention condition compared with the control condition. The analysis of smooth pursuit gain confirms an equal reduction of gain in all attention conditions, suggesting that the absence of involuntary ocular tracking was not due to a lack of engagement in the perceptual task. Overall, however, it remains possible that the pattern of eye movements was explained by task difficulty, at least when comparing *experiment 1* (constant motion and color) and *experiment 3* (constant color). That is, perceptual performance suggests that it was easier in *experiment 1* to selectively attend to a specific dot-field despite that the velocity of horizontal eye movements confirms the same level of engagement as in the other experiments.

Finally, did anticipatory pursuit contaminate our estimation of open-loop ocular following since motion direction was predictable? Since the predictability of motion direction across trials was a precondition for observing an effect, we cannot exclude this possibility; however, there is no indication that this is the case. There was no significant response that would have been clearly anticipatory (0–80 ms postmotion onset) in *experiment 1*. Also, the ocular tracking response in *experiment 1* showed no discontinuity that would characterize the presence of anticipatory pursuit together with a visually driven response, as both responses have different accelerations (Kao and Morrow 1994). The anticipatory component observed in *experiment 4* was actually clearly separated from the visual response (Fig. 2D). Furthermore, in *experiment 2* the ocular effect was

not observed even though motion direction was held constant, ruling out anticipation of motion as a sufficient factor.

Neural Mechanisms

Electrophysiological evidence points to the implication of cortical motion processing (MST, V1) in driving ocular following, the dorsolateral pontine nucleus (DLPN) acting as a relay passing motion information to the cerebellum, where the motor command is elaborated (Kawano 1999; Masson and Perrinet 2012; Miles et al. 1986).

The maximal magnitude of the ocular tracking effect (color and motion selection) that we observed was 30% of the effect with a single dot layer. This number can represent the bias towards the attended layer resulting from enhancement of the attended surface and from suppression of the unattended surface. Feature-based attention modulation of neural responses in MT when motion is attended was found to be 13%, by comparing attention towards a same direction of motion outside the receptive field to the null direction response (Masson and Perrinet 2012; Treue and Martinez Trujillo 1999); 20% increment for blood oxygen level-dependent signal in hMT+ (Beauchamp et al. 1997). We also note that attentional modulation appears stronger from lower to higher level visual areas, in the order of 10% in V1 to about 30–40% in hMT+ when motion (or color) matched the direction at the attended location (Saenz et al. 2002). Modulation by spatial attention was stronger in MST than in MT (40 vs. 20%, respectively) (Treue and Maunsell 1996). Taking into account differences between paradigms and measures, our results are roughly compatible with how feature-based attention gates motion information in MT–MST.

Functional Role

Mestre and Masson (1997) have pointed out the significance of feature-based attention in singling out a depth plane for controlling the optokinetic nystagmus. In their study attention to a given flow field was sufficient to segregate signals for perception and for tracking. Our present contribution adds that under some conditions feature-based attention can help in segregating motion signals lying on the same depth plane for driving ocular tracking, but this has to be qualified by the weakness of the feature-based response compared with a single direction response. The question of why we are unable to selectively enhance a motion direction for driving ocular tracking without the help of another cue (color) requires further investigation, as it might reveal the involvement of attention in form and motion interactions whose major function could be segregating an object from its background (Grossberg 1998) and especially a dissociation between ocular and perceptual tasks. Finally, we would like to point out that the relatively weak effect of feature-based attention on smooth pursuit is matched by relatively weak effects on perception during saccadic eye movements (Born et al. 2012, 2013; Jonikaitis and Theeuwes, 2013). However, it remains to be proven that spatial attention has a larger effect than feature-based attention on ocular tracking responses.

ACKNOWLEDGMENTS

We thank Uwe Ilg and Nancy Carlisle for insightful comments.

GRANTS

The work was supported by the Swiss National Foundation (SNE 100014_135374, PDFMP1_129459).

DISCLOSURES

AQ: 5 No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: D.S. and D.K. conception and design of research; D.S. performed experiments; D.S. and D.K. analyzed data; D.S. and D.K. interpreted results of experiments; D.S. and D.K. prepared figures; D.S. and D.K. drafted manuscript; D.S. and D.K. edited and revised manuscript; D.S. and D.K. approved final version of manuscript.

REFERENCES

- Andersen SK, Muller MM. Behavioral performance follows the time course of neural facilitation and suppression during cued shifts of feature-selective attention. *Proc Natl Acad Sci USA* 107: 13878–13882, 2010.
- Arman AC, Boynton GM, Ciaramitaro VM. Effects of feature-based attention on the motion aftereffect at remote locations. *Vision Res* 46: 2968–2976, 2006.
- Beauchamp M, Cox R, DeYoe E. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J Neurophysiol* 78: 516–520, 1997.
- Born S, Ansorge U, Kerzel D. Feature-based effects in the coupling between attention and saccades. *J Vis* 12: 27, 2012.
- Born S, Ansorge U, Kerzel D. Predictability of spatial and non-spatial target properties improves perception in the pre-saccadic interval. *Vision Res* 91: 93–101, 2013.
- Cavanagh P. Attention-based motion perception. *Science* 257: 1563–1565, 1992.
- de Brouwer S, Missal M, Barnes G, Lefèvre P. Quantitative analysis of catch-up saccades during sustained pursuit. *J Neurophysiol* 87: 1772–1780, 2002.
- Fannon SP, Saron CD, Mangun GR. Baseline shifts do not predict attentional modulation of target processing during feature-based visual attention. *Front Hum Neurosci* 1: 7, 2007.
- Grossberg S. How is a moving target continuously tracked behind occluding cover. In: *High-Level Motion Processing: Computational, Neurobiological, and Psychophysical Perspectives*, edited by Watanabe T. Cambridge, MA: MIT Press, 2008, p. 1–30.
- Hayashi R, Miura K, Tabata H, Kawano K. Eye movements in response to dichoptic motion: evidence for a parallel-hierarchical structure of visual motion processing in primates. *J Neurophysiol* 99: 2329–2346, 2008.
- Hayashi R, Sugita Y, Nishida S, Kawano K. How motion signals are integrated across frequencies: study on motion perception and ocular following responses using multiple-slit stimuli. *J Neurophysiol* 103: 230–243, 2010.
- Ilg UJ. Slow eye movements. *Prog Neurobiol* 53: 293–329, 1997.
- Jonikaitis D, Theeuwes J. Dissociating oculomotor contributions to spatial and feature-based selection. *J Neurophysiol* 110: 1525–1534, 2013.
- Kao GW, Morrow MJ. The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Res* 34: 3027–3036, 1994.
- Kawano K. Ocular tracking: behavior and neurophysiology. *Curr Opin Neurobiol* 9: 467–473, 1999.
- Kerzel D, Born S, Souto D. Smooth pursuit eye movements and perception share target selection, but only some central resources. *Behav Brain Res* 201: 66–73, 2009.
- Kerzel D, Souto D, Ziegler NE. Effects of attention shifts to stationary objects during steady-state smooth pursuit eye movements. *Vision Res* 48: 958–969, 2008.
- Kowler E. Attention and eye movements. In: *The New Encyclopedia of Neuroscience*, edited by Krauzlis RJ. Amsterdam, The Netherlands: Elsevier, 2007.
- Kowler E, Zingale C. Smooth eye movements as indicators of selective attention. In: *Attention and Performance XII*, edited by Posner MI, Marin OS. Hillsdale, NJ: Erlbaum, 1985.
- Lindner A, Schwarz U, Ilg UJ. Cancellation of self-induced retinal image motion during smooth pursuit eye movements. *Vision Res* 41: 1685–1694, 2001.
- Lisberger SG, Morris EJ, Tychsen L. Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annu Rev Neurosci* 10: 97–129, 1987.
- Liu T, Stevens ST, Carrasco M. Comparing the time course and efficacy of spatial and feature-based attention. *Vision Res* 47: 108–113, 2007.
- Lu ZL, Sperling G. Attention-generated apparent motion. *Nature* 377: 237–239, 1995.
- Masson GS, Perrinet LU. The behavioral receptive field underlying motion integration for primate tracking eye movements. *Neurosci Biobehav Rev* 36: 1–25, 2012.
- Mestre DR, Masson GS. Ocular responses to motion parallax stimuli: the role of perceptual and attentional factors. *Vision Res* 37: 1627–1641, 1997.
- Miles F, Kawano K, Optican L. Short-latency ocular following responses of monkey. I. Dependence on temporospatial properties of visual input. *J Neurophysiol* 56: 1321–1354, 1986.
- Miura K, Kobayashi Y, Kawano K. Ocular responses to brief motion of textured backgrounds during smooth pursuit in humans. *J Neurophysiol* 102: 1736–1747, 2009.
- Murasugi C, Howard I, Ohmi M. Human optokinetic nystagmus: competition between stationary and moving displays. *Percept Psychophys* 45: 137–144, 1989.
- Saenz M, Buracas G, Boynton G. Global effects of feature-based attention in human visual cortex. *Nat Neurosci* 5: 631–632, 2002.
- Schutz AC, Braun DI, Gegenfurtner KR. Eye movements and perception: a selective review. *J Vis* 11: 9, 2011.
- Sheliga BM, Chen KJ, Fitzgibbon EJ, Miles FA. Initial ocular following in humans: a response to first-order motion energy. *Vision Res* 45: 3307–3321, 2005.
- Simoncini C, Perrinet LU, Montagnini A, Mamassian P, Masson GS. More is not always better: adaptive gain control explains dissociation between perception and action. *Nat Neurosci* 15: 1596–1603, 2012.
- Spering M, Carrasco M. Similar effects of feature-based attention on motion perception and pursuit eye movements at different levels of awareness. *J Neurosci* 32: 7594–7601, 2012.
- Spering M, Gegenfurtner KR. Contextual effects on smooth-pursuit eye movements. *J Neurophysiol* 97: 1353–1367, 2007a.
- Spering M, Gegenfurtner KR. Contrast and assimilation in motion perception and smooth pursuit eye movements. *J Neurophysiol* 98: 1355–1363, 2007b.
- Spering M, Pomplun M, Carrasco M. Tracking without perceiving: a dissociation between eye movements and motion perception. *Psychol Sci* 22: 216–225, 2011.
- Suehiro K, Miura K, Kodaka Y, Inoue Y, Takemura A, Kawano K. Effects of smooth pursuit eye movement on ocular responses to sudden background motion in humans. *Neurosci Res* 35: 329–338, 1999.
- Tavassoli A, Ringach DL. When your eyes see more than you do. *Curr Biol* 20: R93–94, 2010.
- Theeuwes J. Feature-based attention: it is all bottom-up priming. *Philos Trans R Soc Lond B Biol Sci* 368: 2013.
- Treue S, Martinez Trujillo JC. Feature-based attention influences motion processing gain in macaque visual cortex. *Nature* 399: 575–579, 1999.
- Treue S, Maunsell JH. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382: 539–541, 1996.
- Wilmer JB, Nakayama K. Two distinct visual motion mechanisms for smooth pursuit: evidence from individual differences. *Neuron* 54: 987–1000, 2007.

AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES

1

- AQ1— AU: Please read entire Proof (including Query page), answer queries, and make essential corrections in Proof margins; return Proof via e-mail or by 1- or 2-day carrier WITHIN TWO BUSINESS DAYS. Please include Query page. IMPORTANT: e-mail (mpasho@the-aps.org) an itemized list of requested changes (these should be essential data error changes and not cosmetic changes, which will not be implemented at this late stage in production). Please do not undo what may have been copy-edited to conform to APS journal style (use of hyphens, quotation marks, italics for certain phrases, non-use of italics for Latin phrases and for emphasis, etc.).
- AQ2— AU: Please note that the author list in the abstract line represents the form in which these names will appear in many online databases, such as the NCBI/NIH/NLM Pubmed database. Check this carefully, be sure there are no misrepresentations. Please make a note on the proof, if any corrections are needed.
- AQ3— AU: Lankheet and Verstraten (1995) are not on the reference list. Please add to the reference list or delete in-text reference.
- AQ4— AU: Please define M in M = 24 yr old.
- AQ5— AU: ANPCYT correctly defined as Agencia Nacional de Promoción Científica y Tecnológica in the GRANTS section?
- AQ6— AU: Please verify accuracy of your e-mail address in the address for correspondence, or delete e-mail address if you do not want it included. (Note: This material is listed as a footnote at bottom of left column of text, on the first page).
-