19. Kettlewell, H. B. D. & Berry, R. J. The study of a cline. *Heredity* **16,** 403–414 (1961).
20. Mani, G. S. A theoretical study of morph ratio clines with special reference to melanism in moths. *Proc. R. Soc. Lond. B* **B210,** 299–316 (1980).
21. Jain, S. K. & Bradshaw, A. D. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity* **21,** 407–441 (1966).
22. Chevillon, C., Bourguet, D., Rousset, F., Pasteur, N. & Raymond, M. Pleiotropy of adaptive changes in populations: comparisons among insecticide resistance genes in *Culex pipiens*. *Genet. Res. Camb.* **70,** 195–204 (1997).
23. Guillemaud, T. *et al.* Evolution of resistance in *Culex pipiens*: allele replacement and changing environment. *Evolution* **52,** 443–453 (1998).
24. Lenormand, T., Guillemaud, T., Bourguet, D. & Raymond, M. Evaluating gene flow using selected markers: a case study. *Genetics* **149,** 1383–1392 (1998).
25. Lenormand, T., Guillemaud, T., Bourguet, D. & Raymond, M. Appearance and sweep of a gene duplication: adaptive response and potential for a new function in the mosquito *Culex pipiens*. *Evolution* **52,** 1705–1712 (1998).
26. Slatkin, M. Gene flow and selection in a two locus system. *Genetics* **81,** 787–802 (1975).
27. Lenormand, T. & Raymond, M. Analysis of clines with variable selection and variable migration. *Am. Nat.* (in the press).
28. Lenormand, T. & Raymond, M. Resistance management: the stable zone strategy. *Proc. R. Soc. Lond. B* **265,** 1985–1990 (1998).
29. Anderson, D. R., Burnham, K. P. & White, G. C. AIC model selection in overdispersed capture-recapture data. *Ecology* **75,** 1780–1793 (1994).

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Correspondence and requests for materials should be addressed to T.L. (e-mail: lenorm@zoology.ubc.ca).

Illusory shifts in visual direction accompany adaptation of saccadic eye movements

Dan O. Bahcall & Eileen Kowler

Department of Psychology, Rutgers University, Piscataway, New Jersey 08854, USA

A central problem in human vision is to explain how the visual world remains stable despite the continual displacements of the retinal image produced by rapid saccadic movements of the eyes. Perceived stability has been attributed to 'efferent-copy' signals, representing the saccadic motor commands, that cancel the effects of saccade-related retinal displacements[1–6]. Here we show, by means of a perceptual illusion, that traditional cancellation theories cannot explain stability. The perceptual illusion was produced by first inducing adaptive changes in saccadic gain (ratio of saccade size to target eccentricity). Following adaptation, subjects experienced an illusory mislocalization in which widely separated targets flashed before and after saccades appeared to be in the same place. The illusion shows that the perceptual system did not take the adaptive changes into account. Perceptual localization is based on signals representing the size of the initially-intended saccade, not the size of the saccade that is ultimately executed. Signals representing intended saccades initiate a visual comparison process used to maintain perceptual stability across saccades and to generate the oculomotor error signals that ensure saccadic accuracy.

Saccadic adaptation was produced conventionally[7–11]. Subjects made a single saccade to look at a target point that stepped abruptly to an eccentric horizontal location, 228, 240 or 252 arcmin away. The background was dark; only the target was visible. Saccades were accurate, as expected[11,12] (Fig. 1a). In the adaptation trials, which began after 20 baseline step-tracking trials, the target hopped either forwards or backwards by 48 arcmin (about 20% of the size of the original step) during the saccade. (Forward and backward hops, and rightward and leftward saccades, were tested in separate experimental sessions.) Saccades landed near the original (pre-hop) target location during the first few adaption trials (Fig. 1b). Adaptive changes occurred over the ensuing trials, when saccades began to land closer to the target's final, post-hop position (Fig. 1c).

After adaptation reached nearly asymptotic levels, 'probe' trials were introduced to assess the perceived relative location of targets flashed before and after the saccade[13–17] (Fig. 1d). A probe trial was run after every three consecutive adaptation trials, thus allowing saccades to remain in the adapted state. The saccadic target in probe trials was flashed for 100 ms. The display remained dark during the saccade to the remembered location of the flash. Two-hundred-and-fifty milliseconds after saccade detection, the post-saccadic probe target was flashed for 100 ms. The subject reported whether the post-saccadic probe was located to the left or to the right of the pre-saccadic target. We used a double-random staircase procedure (see Methods) to select the post-saccadic probe location according to the response on the immediately preceding probe trial, with the goal of 'zooming in' on the location that perceptually matched the remembered location of the pre-saccadic target.

Figure 2 (open symbols) shows the mean sizes of saccades to the right and left over successive blocks of 20 trials for the three subjects (two naive; one author) during forward, backward and no-hop (control) sessions. Saccadic gain (saccade size/target step size) was similar across the three target step sizes (228, 240 and 252 arcmin) so data from the three step sizes was combined (see Methods). Saccadic adaptation reached maximum levels after about 20–60 adaptation trials. The maximum levels of adaptation were less than hop size, and dependent on subject, saccadic direction and hop

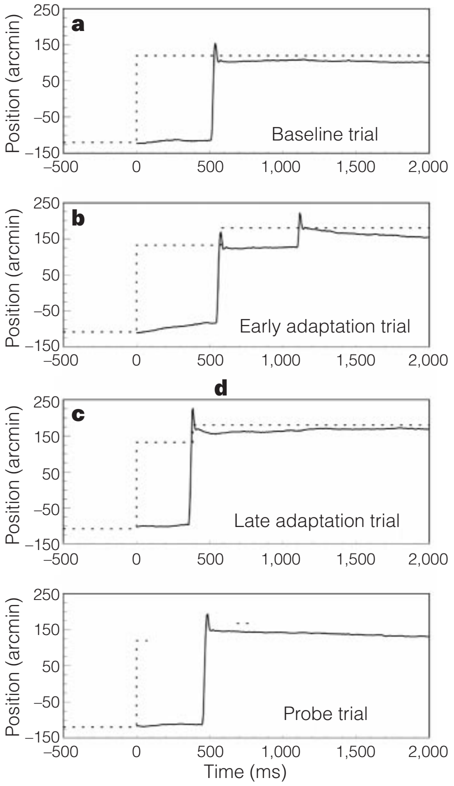

Figure 1 Representative traces of horizontal eye (solid line) and stimulus position (dotted line). Negative values are left of centre. **a**, Saccade in response to a 240-arcmin target step. Saccade size is the difference between pre- and post-saccadic eye position, bypassing the overshoot at the end of the saccade (see Methods). **b**, An early adaptation trial, 48-arcmin forward hop. **c**, A later adaptation trial. **d**, Probe trial, with pre- and post-saccadic flashes to be compared. Because of the intervening saccade, the pre-saccadic target and post-saccadic probe occupied different retinal loci.

direction. Overall, adaptive performance is typical of previous reports[7–11].

Perceptual localization during the same experimental sessions is shown by the average locations of the final 20 post-saccadic probes (filled symbols on right-hand ordinates). An accurate perceptual match of pre- and post-saccadic targets would be shown at 240 arcmin. Matches in the control (no-hop) sessions (circles) were typically accurate[14–16]. The illusory mislocalizations during the adaptation sessions are shown by the differences between post-saccadic probe locations in the adaptation (filled triangles) and no-hop sessions. The mislocalizations were in the same direction as the hops and in the same direction as the adaptive changes in saccades. That is, during forward-hop sessions, where saccadic amplitude adaptively increased, post-saccadic probes located further from the initial fixation position than the pre-saccadic target were seen to be in the same location as the pre-saccadic target. During backward-hop sessions, where saccadic amplitude adaptively decreased, post-saccadic probes located closer to the initial fixation position than the pre-saccadic target were seen to be in the same location as the pre-saccadic target. the illusion was found for all subjects and both saccadic directions. For subject E.K. the illusion was superimposed on a steady-state perceptual misalignment observed during no-hop sessions. Re-testing of the subjects under the same experimental conditions produced the same pattern of results.

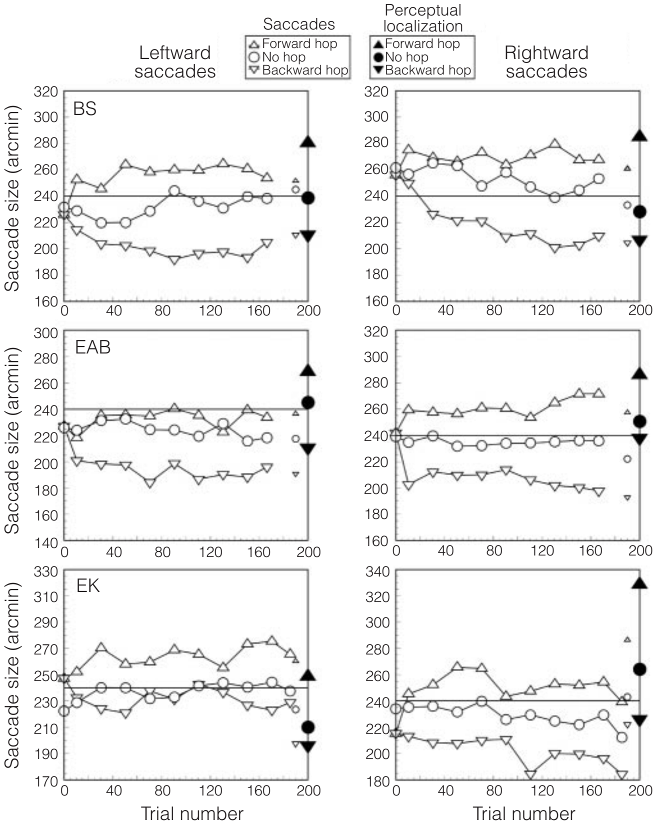

Figure 2 Saccadic adaptation and perceptual localization for each subject. Large open symbols: mean saccade size in blocks of 20 trials as a function of the middle trial in each block. Small open symbols: mean saccade size in probe trials. Data from the three target step sizes (228, 240 and 252 arcmin) were pooled (see Methods). Performance at trial zero is the average of 20 no-hop baseline trials. Standard errors are approximately the size of the large plotting symbols. Filled symbols on right-hand ordinate: post-saccadic probe location (average of final 10 probe trials per staircase; s.e. < 2.5 arcmin). An accurate match of the post-saccadic probe to the pre-saccadic target would be shown at 240 arcmin (horizontal line).

Figure 3 shows a consistent relationship between the magnitude and direction (forward versus backward) of saccadic adaptation and the magnitude and direction of the illusion. Discrepancies between adaptation and the illusion might be expected in light of the different sources of variability that affect motor performance and perceptual judgments[17]. Despite these differences, the correlation between saccadic adaptation and the illusion was 0.9, with most of the discrepancies being due to scatter in the magnitude of the illusion in sessions producing the largest amounts of saccadic adaptation.

In probe trials the display was blank for a brief period of time between the pre-saccadic target and the probe (Fig. 1d) to avoid presenting visual targets near the time of the saccade, when large errors in perceptual localization are expected[13,15,16]. The blank interval was not essential. The illusion was also found when the pre-saccadic target remained on, hopping from its original location to the probe location during the saccade. The illusion was also present when subjects were instructed to saccade 75% of the way to the target in adaptation and probe trials. Saccadic adaptation and the illusion were abolished by briefly (400 ms) removing the target from view during adaptation trials as soon as the saccade was detected. The blank interval during adaptation trials made the hop more apparent[18]. When re-tested in the basic experiment after running adaptation trials containing the blank interval, subject B.S. no longer either adapted or experienced the illusion (the other two subjects continued to adapt and show the illusion). The cessation of adaptation for subject B.S. shows that the presence of the target hops in adaptation trials was not responsible for the illusion. The illusion was tied to the adaptive changes in the saccades.

The illusory misalignment of pre- and post-saccadic targets accompanying saccadic adaptation indicates that the perceptual system is not using a signal representing the actual size of the saccade. Had such a signal been available, pre- and post-saccadic targets would have been perceived as accurately aligned, independent of the adaptive state of the saccadic system. Instead, the illusory misalignment indicates that the perceptual system was unaware of the adaptive changes in saccadic magnitude. The pre- and post-saccadic targets were aligned according to a signal that corresponded to the magnitude of the original displacement of the target, and the originally intended saccade, rather than to the

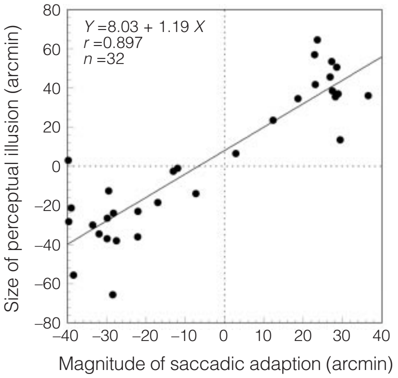

Figure 3 Magnitude of saccadic adaptation plotted against the size of the perceptual illusion. The magnitude of adaptation was estimated by the difference between average saccade size in the last 100 trials of the hop and no-hop sessions. The magnitude of the illusion was estimated by the difference between average probe locations (last 20 probe trials) in hop and no-hop sessions. Positive values indicate adaptation or localization forwards of the pre-saccadic target. The 32 points show data for two hop directions (forward, backward), two saccadic directions (left, right) and three replications for subjects E.A.B. and E.K. and two for subject B.S.

saccade that was actually made (see refs 14, 19 and 20 for related suggestions). Such a signal could be created by re-calibrating a representation of the final (post-adaptation) saccadic command. A simpler solution would be for the perceptual system to tap into the generation of the saccadic command at a high level, before the site of the adaptive changes. This high-level signal may be related to the efferent-copy signals that produce changes in neural activity[21] and shifts in the receptive field locations[22] of single neurons in parietal cortex.

What is the advantage of relying on a high-level efferent copy signal that is likely to be an imperfect representation of the actual saccade? The advantage may lie in the process of saccadic adaptation itself. Evidence indicates that saccadic adaptation is localized fairly late in the motor-processing stream, probably involving the cerebellum[23–26]. A useful error signal for adaptation can be generated as a result of a dissociation between a high-level efferent copy signal, which predicts the content of the future foveal image, from the metrics of the executed saccade. With such a dissociation, any deviation of the actual from the predicted foveal image can be attributed to events at lower levels of the oculomotor system, downstream from the initial coding of the intended saccade. The failure to attain the predicted foveal image produces perceptual mislocalizations, such as those we observed, but, more importantly, it can provide an unambiguous error signal to trigger subsequent adaptive modifications of saccades. Adaptation would then continue until saccade size changed sufficiently so that the post-saccadic image matched, within some criterion, the pre-saccadic prediction.

The illusory mislocalizations accompanying saccadic adaptation show that the perceptual system is not making use of signals representing actual, executed saccades, as is often assumed[1–6]. Signals representing initial saccadic intentions, generated before the site of adaptation, can initiate a visual comparison of pre- and post-saccadic images that would both contribute to stable percepts and ensure accurate saccades. □

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Methods

Subjects. The subjects were E.A.B. and B.S., naive as to the purpose of the experiment, and E.K., an author. All had previous experience as eye-movement subjects.

Eye moment recording. Movements of the right eye, with the head stabilized, were recorded by a Generation IV SRI Double Purkinje Image Tracker (sensitivity <1 arcmin)[27]. Tracker output was filtered (50 Hz) and sampled every 5 ms[12,28].

Stimulus. The stimulus was a single point, 2 log units above the absolute light-adapted foveal threshold, refreshed every 20 ms, shown on a Tektronix 608 display monitor (fast-decay P4 phosphor) located directly in front of the right eye. Except for the target point the room was totally dark. The stimulus was viewed through a collimating lens that placed it at optical infinity.

Adaptation trials. Subjects fixated a single point located either 108, 120 or 132 arc min (selected randomly) to the left (for testing rightward saccades) or right (for leftward saccades) of straight ahead and started trials by pressing a button when ready. Two-hundred milliseconds later the target point stepped 228, 240 or 252 arcmin (selected randomly). Subjects aimed a single saccade at the pre-saccadic target, keeping the latency long enough to avoid compromising accuracy, and not trying to reach the target with a sequence of two or more saccades. These instructions produce accurate saccades and reduce extraneous behavioural variability[12,28]. When the saccade was detected on-line (position change of 12–15 arcmin in 5 ms) the target hopped 48 arcmin forwards or backwards or not at all, and remained at its new location for the remainder of the 2-s trial. Each session began with 20 no-hop baseline trials followed by 172 adaptation trials for E.A.B. and B.S., and 190 for E.K. Forward, backward and no-hop trials, and rightward and leftward saccades were tested in separate sessions. The order of testing hop conditions within a replication (3 hop conditions × 2 saccadic directions) was random; saccadic direction (left or right) was alternated from session to session.

Perceptual probe trials. Probe trials (34 per session for E.A.B. and B.S. and 40 trials per session for E.K.) began after the first 70 adaptation trials and were tested after every third adaptation trial thereafter. The target for the saccade was flashed for 100 ms. The display was dark until 250 ms after saccade detection when a single point (the probe) was flashed for 100 ms. The subject pressed a button to indicate whether the probe was to the right or to the left of the initial target flash. A double random staircase procedure determined probe location[29]. Specifically, if the subject indicated that the probe was to the left of the saccadic target, the next probe in the staircase would be shifted to the right; responses of 'right' shifted the next probe to the left. Probes were shifted by 15 arcmin for the first 5 probe trials, 10 arcmin for the next 7 trials and 5 arcmin thereafter. Two independent randomly interleaved staircases were run, one starting to the right of the saccadic target and the other to the left. Data were pooled over the three target step sizes by calculating localization error (probe location minus presaccadic target location) on each trial.

Analysis. Saccades were detected off-line by an acceleration criterion. Saccade size was the distance between the mean position of the eye at the start of the trial and the position at the end of the saccade, bypassing the overshoots[12,28]. Overshoots are in part genuine characteristics of saccades and in part due to the Dual Purkinje Eyetracker's sensitivity to movements of the lens during saccades[30]. Data from the three target step sizes (228, 240 and 252 arcmin) were pooled after multiplying saccadic gain (saccadic size/target step size) by the middle step (240 arcmin).

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1. von Helmholtz, H. *Treatise on Physiological Optics* vol. 3 (1910) (trans. Southall, J. P. C.) (Dover, New York, 1963).
2. von Holst, E. & Mittelstaedt, H. Das Reafferenzprinzip. *Naturwissenschaften* **37,** 464–476 (1950).
3. MacKay, D. M. in *Handbook of Sensory Physiology* vol. VII/3: Central Processing of Visual Information (ed. Jung, R.) 307–331 (Springer, Berlin, 1973).
4. Matin, L. in *Handbook of Sensory Physiology* vol. VII/4: Visual Psychophysics (eds Jameson, D. & Hurvich, L. M.) 331–380 (Springer, Berlin, 1972).
5. Skavenski, A. A., Haddad, G. M. & Steinman, R. M. The extraretinal signal for the visual perception of direction. *Percept. Psychophys.* **11,** 287–290 (1972).
6. Skavenski, A. A. in *Eye Movements and Their Role in Visual and Cognitice Processes* (ed. Kowler, E.) 263–287 (Elsevier, Amsterdam, 1990).
7. McLaughlin, S. C. Parametric adjustment in saccadic eye movement. *Percept. Psychophys.* **2,** 359–362 (1967).
8. Deubel, H. Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Res.* **35,** 3529–3540 (1995).
9. Miller, J. M., Anstis, T. & Templeton, W. B. Saccadic plasticity: parametric adaptive control by retinal feedback. *J. Exp. Psychol. Hum. Percept. Perform.* **7,** 356–366 (1981).
10. Erkelens, C. J. & Hulleman, J. Selective adaptation of internally triggered saccades made to visual targets. *Exp. Brain Res.* **93,** 157–164 (1993).
11. Carpenter, R. H. S. *Movements of the Eyes* 2nd edn (Pion Press, 1992).
12. Kowler, E. & Blaser, E. The accuracy and precision of saccades to small and large targets. *Vision Res.* **35,** 1741–1754 (1995).
13. Matin, L. & Pearce, D. G. Visual perception of direction for stimuli flashed during voluntary saccadic eye movement. *Science* **165,** 1485–1488 (1965).
14. Lennie, P. & Sidwell, A. Saccadic eye movements and visual stability. *Nature* **275,** 766–768 (1978).
15. Dassonville, P., Schlag, J. & Schlag-Rey, M. Oculomotor localization relies of a damped representation of saccadic eye displacement in human and nonhuman primates. *Vis. Neurosci.* **9,** 261–269 (1992).
16. Sperling, G. in *Eye Movements and Their Role in Visual and Cognitive Processes* (ed. Kowler, E.) 307–351 (Elsevier, Amsterdam, 1990).
17. Goodale, M. A., Pelisson, D. & Prablanc, C. Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* **320,** 748–750 (1986).
18. Deubel, H., Schneider, W. X. & Bridgeman, B. Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res.* **36,** 985–996 (1996).
19. Ludvigh, E. Control of ocular movements and visual interpretation of environment. *AMA Arch. Ophthalmol.* **48,** 442–448 (1952).
20. Pola, J. in *Eye Movements and Psychological Processes* (eds Monty, R. A. & Senders, J. W.) 245–254 (Erlbaum, Hillsdale, New Jersey, 1976).
21. Andersen, R. A., Essick, G. K. & Siegel, R. M. Encoding spatial location by posterior parietal neurons. *Science* **230,** 456–458 (1985).
22. Duhamel, J.-R., Colby, C. L. & Goldberg, M. E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255,** 90–92 (1992).
23. Optican, L. M. in *Adaptive Mechanisms in Gaze Control* (eds Berthoz, A. & Melvill-Jones, G.) 71–79 (Elsevier, Amsterdam, 1985).
24. Goldberg, M. E., Musil, S. Y., Fitzgibbon, E. J. ,Smith, M. & Olson, C. R. in *Role of the Cerebellum and Basal Ganglia in Voluntary Movements* (eds Mano, M., Hamada, I. & DeLong, M. R.) 203–211 (Elsevier, Amsterdam, 1993).
25. Frens, M. A. & Van Opstal, A. J. Monkey superior colliculus activity during short-term saccadic adaptation. *Brain Res. Bull.* **43,** 473–483 (1997).
26. Desmurget, M. *et al.* Functional anatomy of saccadic adaptation in humans. *Nature Neurosci.* **1,** 524–528 (1998).
27. Crane, H. D. & Steele, C. S. Accurate three-dimensional eyetracker. *Appl. Opt.* **17,** 691–705 (1978).
28. McGowan, J., Kowler, E., Sharma, A. & Chubb, C. Saccadic localization of random dot patterns. *Vision Res.* **38,** 895–909 (1998).
29. Cornsweet, T. The staircase method in psychophysics. *Am. J. Psychol.* **75,** 485–491 (1962).
30. Leigh, R. J. & Zee, D. S. *The Neurobiology of Eye Movements* 82 (F. A. Davis, Philadelphia, 1991).

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Correspondence and requests for materials should be addressed to E.K. (e-mail: kowler@rci.rutgers.edu).