The Relationship between Saccadic Suppression and Perceptual Stability

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report

Summary

Introspection makes it clear that we do not see the visual motion generated by our saccadic eye movements. We refer to the lack of awareness of the motion across the retina that is generated by a saccade as saccadic omission [1]: the visual stimulus generated by the saccade is omitted from our subjective awareness. In the laboratory, saccadic omission is often studied by investigating saccadic suppression, the reduction in visual sensitivity before and during a saccade (see Ross et al. [2] and Wurtz [3] for reviews). We investigated whether perceptual stability requires that a mechanism like saccadic suppression removes perisaccadic stimuli from visual processing to prevent their presumed harmful effect on perceptual stability [4, 5]. Our results show that a stimulus that undergoes saccadic omission can nevertheless generate a shape contrast illusion. This illusion can be generated when the inducer and test stimulus are separated in space and is therefore thought to be generated at a later stage of visual processing [6]. This shows that perceptual stability is attained without removing stimuli from processing and suggests a conceptually new view of perceptual stability in which perisaccadic stimuli are processed by the early visual system, but these signals are prevented from reaching awareness at a later stage of processing.

Results

To determine the fate of a saccadically omitted stimulus, we used a visual shape illusion in which the presentation of a line distorts the perceived shape of a subsequently presented ellipse [6] (Figure 1). Our goal was to present the line within 75 ms preceding a saccade—such that the observer would not be aware of it on some trials—and then determine whether such a saccadically omitted stimulus nevertheless retained the ability to change the subsequent perceived shape of an ellipse. The observers first reported whether or not they saw the line, which could be horizontal or vertical and was physically present on only 50% of trials. They then reported the shape of the ellipse that was presented once the eyes had landed. This allowed us to determine the percentage of trials in which they perceived the ellipse to be horizontally elongated. We refer to this as %PHE (perceived horizontal elongation). To quantify the size of the illusion, we presented ellipse stimuli with a physical horizontal or vertical elongation of 10%, 7.5%, 5%, or 2.5% of the diameter (3° of visual angle). A separate cumulative Gaussian was fitted to the %PHE in the horizontal and vertical line conditions. The subjective point of circularity was taken as the physical elongation at which the fitted function reached 50%PHE and the strength of the illusion was defined as the difference between the points of subjective circularity induced by presentation of the horizontal and vertical lines. Subjective circularity is measured in units of percentage of elongation of the diameter of the test circle. We first confirmed that the shape illusion occurs at fixation for briefly flashed stimuli (Figure 2 and Supplemental Results, Experiment 1, available online) and also when an eye movement intervenes in the 250 ms between the presentation of the line and the ellipse (Supplemental Results, Experiment 2). We then analyzed separately the saccade trials in which the subject reported no subjective awareness of the inducing line (saccadic omission was achieved) and those trials in which subjects reported awareness of the inducing line (saccadic omission was not achieved).

Discussion

Our data show that a stimulus that is successfully removed from awareness by saccadic omission is nevertheless processed by...
the visual system. This shows that perceptual stability can be
attained without removing a perisaccadic stimulus from visual
processing. We discuss this finding in light of a number of
debates surrounding perceptual stability and saccadic
suppression.

Early versus Late
The shape contrast illusion we used here has been shown
to survive when the inducing and test stimuli are separated
in space, indicating that the illusion involves an area whose
shape-selective neurons have large receptive fields such as
superior temporal sulcus or inferotemporal cortex [6]. Our
data therefore suggest that saccadically omitted stimuli are
nevertheless processed by such higher visual areas. The fact
that the illusion is reduced in size during omission suggests
that there may be a (possibly early) stage at which the efficacy
of a stimulus is reduced [4]. A modulation, including suppress-
ion, of the visual responses of single cells has been shown as
early as the lateral geniculate nucleus [7].

Retinal versus Extraretinal
Two main mechanisms of saccadic suppression have been
proposed. The first relies on an extraretinal signal that prepares
the visual system to discount the upcoming high velocity peri-
saccadic retinal motion. The second is a form of masking
whereby the perisaccadic stimulus is “wiped out” by the stable,
fixed stimuli before or after the saccade. Both of these
mechanisms are thought to occur early in the visual processing
hierarchy to stabilize the visual world by removing the intrusion
of the perisaccadic stimulus into the stable representation of
fixated scenes [3]. The extraretinal component of saccadic
suppression suppresses mainly low-spatial-frequency, lumi-
ance-defined stimuli [4], which are considered the domain of
the magnocellular visual pathway, and does not appear to
affect judgments involving isoluminant chromatically defined
stimuli, which are processed mainly by the parvocellular
pathway [4].

In our experiments the inducing line was presented just
before the eye movement, a time at which the extraretinal
mechanism of suppression is known to operate. Moreover,
the luminance-modulated line was flashed briefly and would
likely activate the magnocellular pathway. Masking mecha-

nisms will also be activated by the background luminance of
the CRT screen and by presentation of the ellipse after the
eye movement. Hence, our experiments do not allow us to
distinguish between extraretinal and masking mechanisms
of suppression, but it is likely that both mechanisms were
operating and therefore both were only partially effective in
removing the stimulus from processing even when omission
was complete.

Dorsal versus Ventral
The shape contrast illusion reported here presumably arises
from interactions in the ventral stream. Hence, one could
hypothesize that complete omission with incomplete suppres-
sion is a phenomenon that is unique to the ventral stream. Or,
stated differently, that the dorsal stream undergoes suppres-
sion and omission, while the ventral stream only undergoes
omission. Such a distinction is consistent with behavioral
data that show that saccadic suppression mainly targets
stimuli that drive the magnocellular stream, which, in turn,
mainly projects to the dorsal stream. The neural evidence,
however, suggests that saccadic reductions in firing rate can
be found in both magnocellular and parvocellular cells of the
lateral geniculate nucleus [7] and in both dorsal [8, 9] and
ventral [10] cortical areas. Hence, it seems unlikely that ventral
areas undergo no suppression. Conversely, it is also unlikely
that suppression is complete in dorsal areas; the perisaccadic
reversal of direction preference reported by Thiele et al. [8],
for instance, suggests that saccadic suppression is more
complex than simply not responding to perisaccadic stimuli.

Our data, together with the extensive literature on perisacca-
dic changes in neural response properties, lead us to rethink
the purpose of saccadic suppression. We speculate that perisacca-
dic signals are useful; the visual motion signals generated by the
eye movement, for instance, are excellent indicators of the size
and speed of the eye movement. These signals could be used to
improve perceptual stability as long as they do not directly
enter visual awareness. This suggests that perisaccadic pro-
cessing leading to saccadic omission consists of three concep-
tually different components: a (possibly early visual) reduction
in sensitivity (saccadic suppression) and a component that
processes perisaccadic signals to extract information useful
for visual stability (saccadic information extraction). Addition-
ally, perceptual stability requires a conceptually separate
component that prevents the perisaccadic signals from reaching awareness (saccadic omission).

Most research whose purported goal is to investigate the neural mechanisms of saccadic omission has only looked for signatures of the first component. Even though some studies did indeed find neural correlates of a reduced perisaccadic sensitivity [11–15], others have reported complex changes in perisaccadic activity that are difficult to reconcile with a mere suppression of visual processing [7–9, 15–17] (see [3] for a review). Within our framework, however, complex changes in activity are expected because the visual system tries to extract information from the perisaccadic visual inputs or because the system processes the information while keeping it hidden from awareness. Importantly, our data show that even if a neural correlate of the change in sensitivity could be found in early visual areas, then we would still not understand the neural basis of saccadic omission and how it leads to perceptual stability. Our conceptualization, therefore, provides a useful framework to guide further research and interpret findings about the neural basis of perceptual stability.

Experimental Procedures

Subjects

All conditions were completed by four naive participants and one experimenter. The four naive participants received remuneration and all had normal or corrected to normal vision.

Visual Stimuli

The stimuli consisted of a bar and a ring. Both were presented with half cosine profile luminance graduated edges against a background luminance of 45 cd/m² and a peak luminance of 47 cd/m². The inducing line was 7 × 1° of visual angle, whereas the circle had a diameter of 3° of visual angle and an outline line width of 0.8° of visual angle. The bar was present on the screen for 16 ms, and the ring was present for 100 ms. The ring was always presented 250 ms after the onset of the inducing line.

Apparatus

Stimuli were presented on a Sony FD Trinitron (GDM-C520) CRT monitor with a resolution of 1024 × 768 pixels at a refresh rate of 120 Hz. Stimuli were generated with Neurostim (http://neurostim.sourceforge.net). Eye movements were measured with a head-mounted Eyelink II eye tracker (SR Research, Mississauga, Canada). The pupil of the left eye was tracked at a sample rate of 500 Hz and a spatial resolution of 0.1°. Participants were seated in a darkened room at a 57 cm distance from the display. Head movements were restricted via individually molded bite bars.

Procedure

**Experiment 1**

For testing the basic shape contrast illusion with stimuli optimized for saccadic suppression, experiment 1 was carried out without eye movements and all stimuli were presented at the center of the screen. The inducing bar could be either horizontal or vertical but was only presented on half of all trials while the test stimuli were presented with a horizontal or vertical elongation of 10%, 7.5%, 5%, and 2.5% of the diameter. All possible pairings of bar and ring orientation were presented in a randomized order and 40 trials were collected for each, making a total of 640 trials.

Participants were made aware that only half the trials contained a line stimulus and were asked to report the orientation of the elongation of the ring stimulus via a key press once the stimulus had appeared around the location of the now invisible upper fixation point. This timing aimed to present the inducing bar to the participant within the window of saccadic suppression but before the eye had started the saccade. The ring stimulus was then presented at the location of the saccade target 250 ms after presentation of the inducing bar. Participants were required to achieve fixation of this target at least 100 ms prior to presentation of the ring stimulus. This fixation requirement ensured that the ring stimulus always landed on a stationary retina.

Participants reported whether they saw the inducing bar and the axis of elongation of the ring. Both tasks were carried out via a key press after the completion of the eye movement.

An additional set of trials were carried out with the same procedure; however, the inducing line was presented 2050 ms after initial fixation was achieved. This ensured that the inducing line was presented well before the saccadic suppression window and provided an estimate of participants’ miss rate for the inducing line.

**Data Analysis**

**Experiments 1 and 2**

A separate cumulative Gaussian distribution was fit to the reported perceived axis of elongation of the ellipse during trials with a vertical inducer, trials with a horizontal inducer, and trials without an inducer. The Psgnifit toolbox for Matlab [18, 19] was used for this analysis. The threshold at 50% was considered the point of subjective circularity under each different inducing condition. As a test of significance, we used the bootstrapping methods of the Psgnifit toolbox to test the null hypothesis that the cumulative Gaussians for vertical and horizontal bars could be generated by the same underlying distribution.

**Experiment 2**

Trials during which appropriate fixation was not achieved were automatically discarded. Additionally, we selected only those trials in which the test stimulus was presented during the 75 ms before an eye movement was initiated. Additional to the separation of trials according to orientation of the inducing bar, trials were also grouped according to participants’ responses about its visibility.

**Supplemental Data**

Supplemental Data include Supplemental Results and five figures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01051-3.

**Acknowledgments**

The authors are grateful to Kai Schreiber and Adam Morris for comments on the manuscript and thank the Human Frontiers Science Program (T.L.W.) and the Pew Charitable Trusts (B.K.) for financial support.

Received: March 10, 2009
Revised: April 10, 2009
Accepted: April 20, 2009
Published online: May 28, 2009

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