

Adaptation to size affects saccades with long but not short latencies

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Maintained exposure to a specific stimulus property—such as size, color, or motion—induces perceptual adaptation aftereffects, usually in the opposite direction to that of the adaptor. Here we studied how adaptation to size affects perceived position and visually guided action (saccadic eye movements) to that position. Subjects saccaded to the border of a diamond-shaped object after adaptation to a smaller diamond shape. For saccades in the normal latency range, amplitudes decreased, consistent with saccading to a larger object. Short-latency saccades, however, tended to be affected less by the adaptation, suggesting that they were only partly triggered by a signal representing the illusory target position. We also tested size perception after adaptation, followed by a mask stimulus at the probe location after various delays. Similar size adaptation magnitudes were found for all probe-mask delays. In agreement with earlier studies, these results suggest that the duration of the saccade latency period determines the reference frame that codes the probe location.

other system (Goodale, Milner, Jakobson, & Carey, 1991; Goodale, 2011). Psychophysical studies have used visual size illusions to dissociate processing of visual information for perception and for action. The first of these studies used the Ebbinghaus illusion, in which two surrounding disks bias the perception of a center disk (Aglioti, DeSouza, & Goodale, 1995). Subjects were asked to grasp the center disk. Consistent with the two-visual systems hypothesis, action—measured by the anticipatory grip aperture—was not deceived by the illusion. Although several studies have replicated these results (for a review, see Goodale, 2011), others have criticized these results on methodological and conceptual grounds (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Franz, Fahle, Bühlhoff, & Gegenfurtner, 2001). However, Söttinger et al. (2012) reported evidence for dissociation even when taking into account the methodological criticisms.

The duration of the period between the presentation of the target and the initiation of the movement determines whether grasping is affected by visual illusions: While quick movements usually result in a veridical response, delayed movements often follow the illusory target appearance (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu, Eagleson, & Goodale, 1999; Westwood, Heath, & Roy, 2000; Fischer, 2001; Westwood & Goodale, 2003). These studies suggest that the integration of the target information and visual context information takes time to develop. A possible explanation is that targets are coded initially in an egocentric

Introduction

Goodale and Milner (1992) suggested that two distinct visual processing streams exist, one for conscious perception, the other for action. Evidence for this separation comes largely from neuropsychological studies of patients with selective lesions to one or the

Citation: Zimmerman, E., Morrone, M. C., & Burr, D. (2016). Adaptation to size affects saccades with long but not short latencies. *Journal of Vision*, 16(7):2, 1–8, doi:10.1167/16.7.2.

doi: 10.1167/16.7.2

Received November 20, 2016; published May 3, 2016

ISSN 1534-7362



reference frame and are then transformed into an allocentric reference frame. We have recently shown in a series of experiments that the transformation of visual information from a retinal into an allocentric reference frame builds up over a period of up to 500 ms. We argued that spatial position information accumulates over time: If targets are presented only briefly, position information is not strong enough to ensure the detection of spatial displacements (Zimmermann, Morrone, & Burr, 2013).

Studies using visual illusions to deceive saccade targeting have provided mixed evidence: Some studies found that saccade landing positions were affected by the illusion more strongly when latencies were short (Van Zoest & Hunt, 2011; de Grave & Bruno, 2010); others have found the opposite, with strong illusory effects for long latencies (de'Sperati & Baud-Bovy, 2008; Zimmermann, Morrone, & Burr, 2012).

Here we used a new size adaptation method (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Kreutzer et al., 2015a; Kreutzer et al., 2015b) to investigate how adaptation affects the perception of space, and of visually guided action within space. Whereas geometrical illusions work by processing of object context, adaptation methods change the neuronal response properties (Clifford, Wenderoth, & Spehar, 2000). Adaptation techniques are therefore particularly well suited to directly manipulate neural areas responsible for the processing of visual size. Pooresmaeili et al. (2013) showed that adaptation to stationary disks caused stimuli smaller than the adaptors to be perceived as smaller than they were, and larger stimuli to be perceived larger. The adaptation-dependent changes in the BOLD-signal in area V1 revealed a shift in object contour location in the retinotopic map, consistent with the changes in apparent size. These findings are consistent with recent studies that suggest areas as early as V1 may be involved in size perception: The V1 BOLD-response depends on the apparent, rather than physical, size of an object, when apparent size is manipulated by perspective context (Murray, Boyaci, & Kersten, 2006). Sperandio, Lak, and Goodale (2012) reported a similar result, showing that V1 BOLD response changes with apparent distance of the stimulus. Ni, Murray, and Horwitz (2014) further extended these findings by recording from V1 neurons in macaque monkeys while they observed size-distance illusions, showing that V1 neurons shift their receptive fields consistently with the illusory perception of angular size. The involvement of V1 in perceived size is also shown by a correlation between anatomical features of its retinotopic map and the strength of visual illusions (Schwarzkopf, Song, & Rees, 2011; Schwarzkopf & Rees, 2013).

We asked subjects to perform saccades to the left edge of a diamond-shaped stimulus after they had been

adapted to a smaller diamond. We reasoned that if saccades with low latencies rely on an egocentric representation and saccades with high latencies on an allocentric representation, the former should land close to the veridical target position and the latter at the adapted location. We also tested the effect of processing time in a perceptual task, where the probe was masked after four different delays.

Methods

Eight subjects sat in a dimly lit room, 57 cm from a 22-in. CRT color monitor (Barco Calibrator, Barco GmbH, Karlsruhe, Germany: 120 Hz, 800 × 600 pixels) with head stabilized by chin and head rest, viewing binocularly the 40° × 30° visible field. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Mississauga, Ontario, Canada), which samples gaze position with a frequency of 2000 Hz. The system detected start and end of saccades when eye velocity exceeded or fell below 22°/s and acceleration exceeded $\pm 4000^\circ/\text{s}^2$. Before each session the system was calibrated with the Eyelink 9-point calibration. Each calibration was checked with the Eyelink validation procedure. In all experiments the background was gray and fixation points and saccade targets black.

Experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale, Azienda Ospedaliero-Universitaria Meyer, Firenze) and are in line with the Declaration of Helsinki. Written informed consent was obtained prior to the experiment.

Adaptation to size

In all experiments size adaptation was induced with a black diamond stimulus (6.4° × 6.4°) centered 14° right of the central fixation point (see Figure 1A). The adaptor changed contrast polarity at 30 Hz to prevent formation of an afterimage. The adaptor was displayed for 40 s at the beginning of each session, then again for 3 s before each trial (top-up adaptation period). After a blank period lasting for a random duration between 100 and 800 ms, the probe stimulus, a diamond of 8.5° × 8.5°, was displayed for 17 ms, also centered 14° right of screen center.

Eye movement trials

In eye movement trials, subjects were instructed to saccade to the leftmost corner of this diamond-shaped stimulus as soon as it appeared. The leftmost corner of



Figure 1. (A) Experimental setup for the saccade condition. In adaptation sessions, an adapter stimulus is shown for 3000 ms, followed by a blank interval of random duration between 100 and 800 ms. Then the probe is shown at the same side as the adapter. Subjects were required to perform a saccade to the leftmost corner of the probe stimulus. (B) Experimental setup for the measurement of perceptual size adaptation by matching. Size adaptation of the probe stimulus was induced as described in (A). The probe is shown at the same side as the adapter simultaneously with the reference stimulus at the opposite side. The probe stimulus is larger than the adapter (8.5° compared with 6.4°); the reference stimulus varies in size across trials. Subjects had to indicate in a two-alternative forced choice task which stimulus appeared larger.

the stimulus was at 8° right of fixation. In some sessions the probe appeared with no preceding adaptor; in others subjects were first adapted, as described above (Figure 1A). In order to induce saccades with short latencies, the fixation point was removed after a random duration between 100 and 300 ms before probe stimulus appearance. This procedure—the so-called gap paradigm—is known to elicit express saccade in 11%–34% of trials, depending on the probability with which the target appears in a specific position (Fischer & Ramsperger, 1984). Saccade landing positions were also measured in separate baseline sessions, in which no adaptor was shown. In order to estimate whether there were significant differences in the frequency of express saccades between subjects, we calculated a within-subjects analysis of variance. No significant main effect was revealed.

Perceptual judgments

To test the perceptual effects of size adaptation we measured perceptual adaptation magnitude by forced-choice comparison with a nonadapted diamond-shaped probe centered 14° left of fixation (Figure 1B). The sequence was similar to that during saccades, except that subjects kept fixation throughout the trial. After presentation of the adaptation diamond, the probe stimulus was presented for 17 ms at the same position as the adaptor, together with a reference stimulus on the other side. Subjects had to judge which of the two stimuli appeared larger in a two-alternative forced choice task by pressing the left or the right arrow key on the computer keyboard. The size of the reference varied across trials in seven equiprobable steps. At various durations after the probe disappeared (80, 100, 150, and 200 ms), a mask was presented for 17 ms to curtail processing. The mask comprised six concentric opposite polarity diamonds (see Figure 1), presented for one frame (17 ms) at the same spatial location as the probe stimulus. Baseline and adaptation sessions were run separately.

Results

Saccade latencies

Figure 2A and B show the average latency distributions from the saccade experiment, pooling latency data across participants. Bimodality of the distribution was tested with Hartigan's dip test, which measures departure of the sample from unimodality. The empirical distribution differed significantly from unimodality ($p < 0.05$). Bimodality in saccade latency distributions has been taken as evidence for the generation of two separate saccade modes (Fischer &

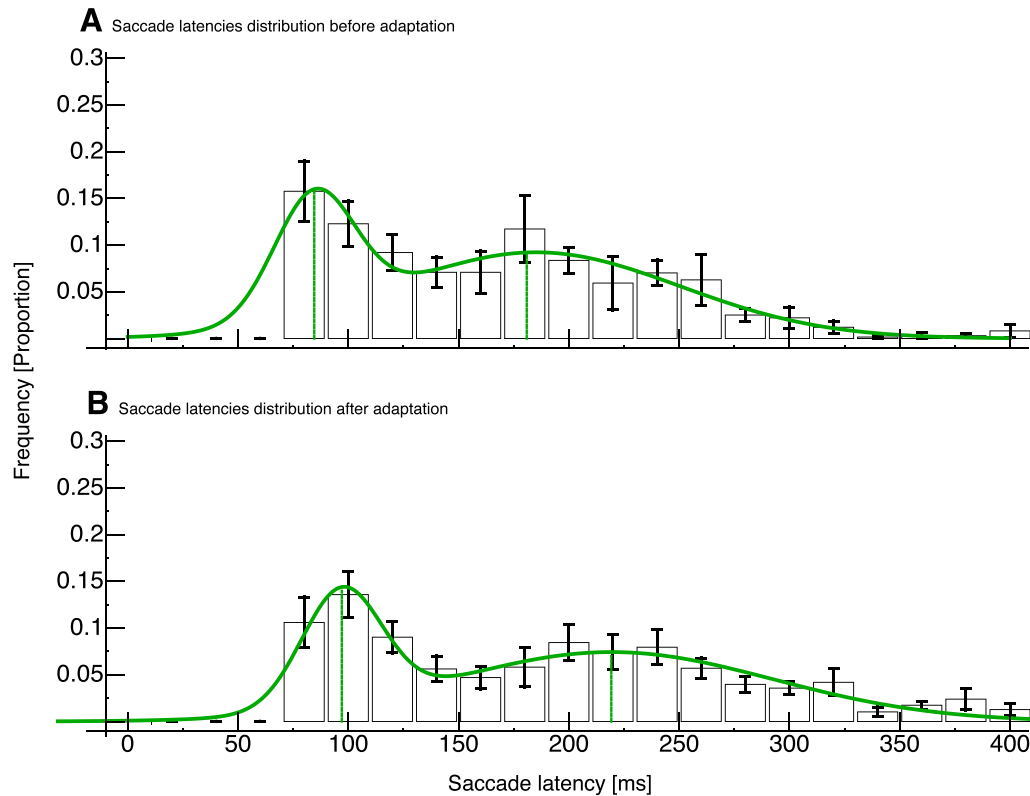


Figure 2. (A) Distributions of saccade latencies from baseline saccade sessions. The short- latency saccade distribution peaks at 85 ms and the long-latency saccade distribution at 181 ms. (B) Distributions of saccade latencies from adaptation saccade sessions. The short-latency saccade distribution peaks at 97 ms and the long-latency saccade distribution at 219 ms.

Ramsperger, 1984). We fitted a mixed model to the average data, which consisted in the sum of two normal distributions each weighted by a constant. The model has six free parameters, which are the two means and standard deviations of the normal distributions and the two weight constants. For baseline trials, the fit showed the first mean to be at 85 ms ($SEM = 18$ ms) and the second mean at 185 ms ($SD = 65$ ms). For adaptation trials the fit revealed the first mean at 95 ms ($SD = 21$ ms) and the second mean at 220 ms ($SD = 75$ ms).

Saccadic amplitudes

Figure 3A and B show saccade landing errors for a representative subject, divided into short-latency saccades (≤ 140 ms) at left, and long-latency saccades (> 140 ms) at right. In baseline sessions, short-latency saccades landed on average 0.6° short of the target, and for long-latency saccades 1.2° short of target—typical undershooting for these saccade amplitude sizes (Gillen, Weiler, & Heath, 2013). As the probe stimulus was larger than the adapter, it should appear larger than it actually is (Pooresmaeili et al., 2013), causing even greater undershoot. For the subject shown in Figure 3, both types of saccades showed greater

undershoot (negative errors) after adaptation, but the effect was much stronger for long-latency than short-latency saccades. Long-latency saccades undershot by 3.7° (2.5° more than baseline) while short-latency saccades only by 2.1° (1.5° more than baseline).

The effect of adaptation on saccade landing was calculated by subtracting mean landing in the post-adaptation sessions from mean landing in the pre-adaptation sessions. Figure 3C shows individual data for all eight subjects, plotting average landing positions short-latency (≤ 140 ms) against long-latency (> 250 ms) saccades. The data of six out of eight subjects are positioned above the equality line, implying a greater reduction in saccadic amplitude for short- compared with long-latency saccades. The red triangle shows the average results: The effect for long-latency saccades was $M = 1.11$ ($SEM = 0.16$), while that for short saccades was only $M = 0.21$ ($SEM = 0.35$). A paired test confirmed a significant difference in saccade landing between short- and long-latency saccades.

Perceptual effects of adaptation

To investigate whether the difference in saccade landing for short- and long-latency saccades reflects a

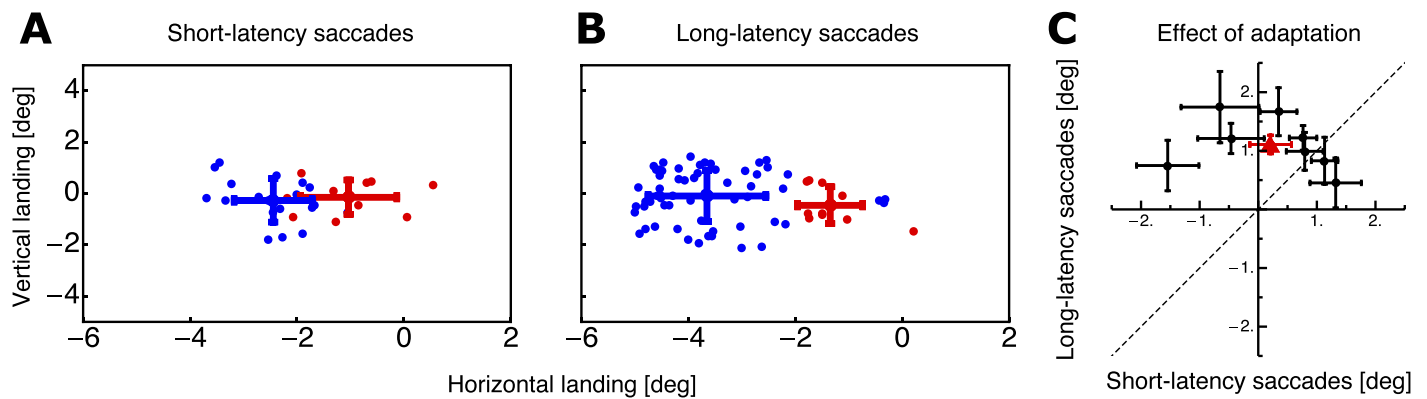


Figure 3. (A) Short-latency (≤ 140 ms) saccade data from a representative subject. The x-axis origin is aligned to the saccade target position. Saccades from the baseline sessions are shown in red and those from the adaptation sessions in blue. The centers of the crosses represent the mean landing positions, and the bar lengths *SEM*. (B) Long-latency (>140 ms) saccades for the same subject. Same conventions as in (A). (C) Adaptation effects of long-latency saccades plotted against adaptation effects of short-latency saccades, for all subjects. Error bars represent *SEM*. The red triangle shows average results.

genuine difference in oculomotor processing, or results from the brief visual perception for the shorter saccades, we measured the effect of size adaptation on perceptual judgments. To mimic the time available for visual processing with short and long saccade latencies, we presented a mask in the same spatial location as the probe stimulus at one of four possible durations after probe offset. Figure 4A and B shows two psychometric functions from two representative subjects, for masks

80 ms after the probe presentation (purple symbols), and for masks 200 ms after probe (orange symbols). Both subjects overestimated the probe size, indicating adaptation of size. Importantly, the psychometric functions for both probe latencies were virtually identical for both subjects. Figure 4C shows the results averaged across all subjects. Clearly there is no effect of mask latency, confirmed by a one-way repeated measures analysis of variance, which revealed no

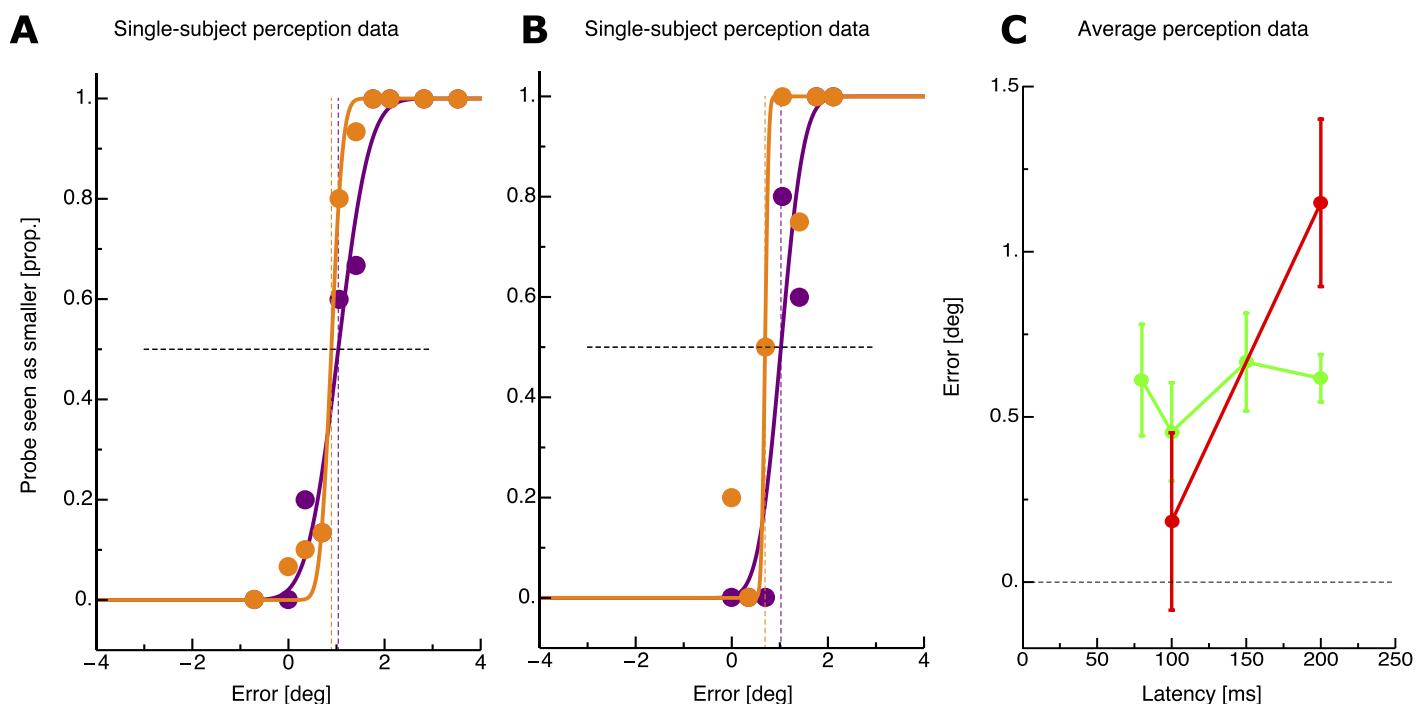


Figure 4. (A–B) Psychometric functions from the size adaptation experiment from two representative subjects. Zero refers to veridical matching. Data shown in purple derive from trials with a short temporal delay between probe and mask stimulus and data shown in orange with a long temporal delay. (C) Average results from the saccade task (shown in red) and from the perceptual task (shown in green) as a function of latency. Error bars represent *SEM*.

significant difference between the different probe-mask distances.

For comparison, the red symbols of Figure 4C show the average results for the saccade experiment (taken from Figure 3C), expressed as a function of average saccade latency. There the effect of latency is clear: The magnitude of the adaptation effect clearly increased with saccade latency.

Note that the main aim of comparing saccadic localization of the probe border with the visual estimation of the probe size was to test whether the dependency of saccadic errors on latency may arise from differences visual processing. Figure 4C clearly shows that this effect is only seen in the saccade data, indicating that it arises from oculomotor processing. It is difficult to compare absolute adaptation magnitudes between the saccade and the perceptual conditions since the tasks are quite different. Whereas in the saccadic task localization of an absolute position is required, in the perceptual task the size between two stimuli has to be compared.

Discussion

We investigated whether adaptation to visual size influences processing of visual space information for action. We found that size adaptation affected saccadic landing positions toward the edge of a diamond-shaped stimulus. However, the effects on saccadic landing were strong only for saccades with latencies longer than 140 ms: Short-latency saccades were affected much less. Analysis of the saccade latency data of our subjects suggests that the distribution is bimodal, with distinct peaks at 100 and 200 ms. This supports the notion of two distinct classes of saccades, rather than a continuum. Adaptation did not change the distribution, showing that it does not affect latencies directly (see Figure 2).

There are (at least) two possible explanations for why short-latency saccades are unaffected by the illusion: Either the size adaptation effect takes more time to develop than is required for the generation of short-latency saccade, or the mechanism generating short-latency saccades relies on a representation that is not affected by size adaptation. Our results for size adaptation with brief, temporally masked stimuli suggest that there is no significant development of the illusion over time, consistent with the idea that size adaptation occurs in early visual processing (Pooresmaeili et al., 2013). Stimuli masked 80 or 100 ms after presentation (well within the latency range of short-latency saccades) showed the same degree of mislocalization as stimuli masked 150 or 200 ms after presentation. Thus, size adaptation is equally effective

for probe stimuli that are masked briefly and for those that are masked later after presentation.

It seems more likely that the generation of short-latency saccades does not take into account information about the adapted size of the probe stimulus. This interpretation finds support in the literature. For example, de'Sperati and Baud-Bovy, (2008) looked at the effect of target motion on deviation of saccade landing and found a strong effect only for saccades of long latency. Zimmermann et al. (2012) reported that saccades with latencies under 130 ms stereotypically went to the mean position of possible probe locations, whereas longer latency saccades were shifted in the direction of motion. It has been proposed that short-latency saccade planning circumvents higher cortical areas and uses a direct pathway from V1 to the superior colliculus (Isa, 2002). This pathway may be unaffected by adaptation in V1. On the other hand, it has been reported recently that lateral intraparietal area neurons are modulated during short-latency saccade planning (Chen, Liu, Wie, & Zhang, 2013). It is still far from clear whether short-latency saccades are mediated by a separate pathway or mediated in an accelerated manner by the same pathway that mediates long-latency saccades.

The level where certain illusions occur in the visual hierarchy might explain why some illusions affect visually guided action when others do not (Milner & Dyde, 2003). Our adaptation method modulates neural responses in early visual areas (Pooresmaeili et al., 2013), but still we found a dissociation between very quick and normal saccade responses. We argue that the quick responses rely on signals that are uninformed by adaptation. This supports studies suggesting that the latency of actions determines whether stimuli are coded in an egocentric or an allocentric frame of reference (Gentilucci et al., 1996; Hu, Eagleson, & Goodale, 1999; Fischer, 2001; Westwood et al., 2000; Westwood & Goodale, 2003). Other studies have found that saccades with short latencies are deceived by the Müller–Lyer illusion while saccades with long latencies are not (de Grave & Bruno, 2010; van Zoest & Hunt, 2011). However, the Müller–Lyer illusion arises at later stages in the visual hierarchy (Weidner & Fink, 2007; Walter & Dassonville, 2008; Plewan, Weidner, Eickhoff, & Fink, 2012), even involving dorsal stream areas (de Brouwer, Smeets, Gutteling, Toni, & Medendorp, 2015). A recent study has found that presentation duration, not saccade reaction time, determines whether action and perception are deceived by the illusion: Longer presentation durations resulted in smaller effects (de Brouwer, Brenner, Medendorp, & Smeets, 2014). This finding is consistent with results by our lab, where saccadic suppression of displacement, another illusion that deceives perception but not action,

decreases as a function of presentation duration (Zimmermann et al., 2013).

In conclusion, we demonstrate that size adaptation affects long- but not short-latency saccades. These results suggest that the transformation of the stimulus representation into a format that takes into account the adaptation takes time to develop. This is consistent with earlier studies indicating that that suparetinal representations are not automatic and immediate, but build up actively over time.

Keywords: size adaptation, saccades, action/perception dissociation

Acknowledgments

This study has been supported by the Italian Ministry of University and Research (FIRB 2013), by European Community Projects Space Time and Number in the Brain (STANIB) and Early Cortical Sensory Plasticity and Adaptability in Human Adults (ECS-PLAIN) (FP7 ERC Advanced grant) and by the Deutsche Forschungsgemeinschaft, DFG (ZI 1456/3-1).

Commercial relationships: none.

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