Extending the saccadic adaptation paradigm:
Interference of task switching and contraints on mislocalization

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Keywords

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Abstract

The eye is continuously redirected towards relevant targets, by making ballistic movements called saccades. The calibration of these movements can be tuned by surreptitious displacement of targets, leading to systematic overshooting or undershooting of targets. In the current study, we used eye-tracking and a modified version of the double step-target paradigm to induce adaptation of reactive saccades. As a directive aim, we set out to modify this paradigm for use in fMRI. To this end, we explored whether saccadic adaptation can be evoked at low amplitudes, whether it is accompanied by perceptual mislocalization, and the feasibility of on-line monitoring of the time course of this mislocalization. We report three main results: (1) We show that saccadic adaptation can be induced at lower amplitudes than those used in previous studies. Specifically, we successfully elicit both hypermetric and hypometric saccades toward targets at 4 visual degrees from fixation. (2) We found that frequent task switching interferes with saccadic adaptation. Concretely, we observed successful gain modulation when presenting adaptation trials consecutively, but found strong attenuation or complete absence of adaptation with interspersed localization judgments. To our knowledge, this effect has not been reported before. (3) Finally, we observed no transfer of saccadic adaptation to mislocalization of flashed probes during fixation. Previous studies have reported conflicting results with regard to similar post-adaptation localization tasks. We present our results against this controversial background and propose an explanation of the observed differences.

Introduction

Saccadic eye movements are rapid shifts in gaze direction, which serve to redirect the fovea to relevant targets. Due to the brevity of saccades and the masking of intrasaccadic perception by presaccadic and postsaccadic perception (García-Pérez & Peli, 2001), it is apparent that saccade targeting cannot rely on on-line visual feedback, and instead has to be planned in advance. Despite this limitation, saccades remain accurate during aging and growth due to constant modification, commonly referred to as saccadic adaptation. Aside from occurring naturally, saccadic adaptation can be induced artificially by systematically displacing saccade targets while saccades are made, so that they appear to be dysmetric (McLaughlin, 1967).

Subjects do not notice intra-saccadic position changes to visual stimuli, as a result of saccadic suppression of displacement (Bridgeman, Hendry, & Stark, 1975). The resulting dysmetria induces adaptation that is congruent with the direction of the displacement. That is, intrasaccadic reductions of target eccentricity cause systematic undershoots, while outward displacements cause systematic overshoots compared to baseline metrics. The magnitude of the adaptation depends on a multitude of factors, including direction of adaptation (inward or outward; Miller, Anstis, & Templeton, 1981), persistence and magnitude of errors, amplitude, location, timing and saccade type (T Collins, Rolfs, Deubel, & Cavanagh, 2009; Thérèse Collins, Doré-Mazars, & Lappe, 2007; Frens & Opstal, 1994; Hopp & Fuchs, 2004; Pélisson, Alahyane, Panouillères, & Tilikete, 2010; Robinson & Noto, 2003) There are several notable differences between inward and outward adaptation. For example, outward adaptation has a higher rate constant (mean number of trials necessary to induce 66% of terminal saccadic amplitude gain) and remains less stable than inward adaptation (Hopp & Fuchs, 2004). In addition, there is stronger transfer to several higher-order saccade types, such as scanning saccades, after outward than after inward adaptation, suggesting involvement of at least partially different neural mechanisms. In a similar vein, outward, but not inward adaptation causes mislocalization of stimuli during fixation (Schnier & Lappe, 2012). However, this difference is likely driven at least partially by the larger remaining post-saccadic error that remains in outward adaptation, as when post-saccadic error is held constant,

mislocalization can also be induced using inward adaptation (Zimmermann & Lappe, 2010).

Due to such transfer effects to the perceptual domain, it has been proposed that saccadic adaptation induces a "visuotopic remapping of space" (Awater, Burr, Lappe, Morrone, & Goldberg, 2005) or "remapping of the neuronal visual map" (Hopp & Fuchs, 2004). Using fMRI, neural maps of retinotopic space have been found from occipital to parietal regions, with some evidence accumulating for maps in frontal areas. These retinotopic maps comprise orthogonal dimensions of eccentricity and polar angle (with respect to the fovea), and have been mapped primarily using the traveling wave method (Wandell, Dumoulin, & Brewer, 2007), and more recently using population receptive field methods (Dumoulin & Wandell, 2008). If saccadic adaptation does indeed entail neural remapping of visual space, retinotopic maps could provide a fruitful locus to investigate the neural mechanisms of saccadic adaptation. However, the effects of saccadic adaptation on these mappings have, to our knowledge, never been studied.

The present study

In the current study, we have sought to work toward an fMRI-viable design, capable of investigating the effects of saccadic adaptation on retinotopic maps. To this end, several modifications to the standard double-step target paradigm were made, which are detailed below.

Due to an effect called cortical magnification, the strong overrepresentation of low eccentricities in retinotopic maps (Wandell et al., 2007), it is vital that saccadic adaptation can be induced at low amplitudes. This would increase the number of involved voxels and therefore, the sensitivity to picking up retinotopic shifts. As a first subgoal, we tested whether saccadic adaptation could be induced on a much smaller scale of 4 visual degrees, while 12-30° is used in current literature (e.g. Gaveau, Alahyane, Salemme, & Desmurget, 2005; Schnier & Lappe, 2012; Collins, Doré-Mazars, & Lappe, 2007). Succesful adaptation was expected even on this scale, given the wide range in which saccadic adaptation has been induced at higher eccentricities. In addition, partial transfer from higher amplitude saccades has previously been found at 4° (Thérèse Collins et al., 2007), suggesting that saccadic adaptation at lower amplitudes does not operate on fundamentally different principles.

An initial approach to mapping retinotopic shifts would be to induce adaptation first, and to then reconstruct presented stimuli from previously mapped PRFs. To establish accurate mappings despite temporal constraints of fMRI and the inertia of BOLD responses, it is imperative that the perceptual effects of saccade adaptation remain stable for an extended period of time. Consequently, the decay rate of saccade adaptation first needs to be determined. Thus, as our second subgoal, we have investigated the feasibility of on-line monitoring of the time course of adaptation-induced mislocalization by interleaving adaptation and localization. In addition to fMRI benefits, this would be valuable from a psychometric/ophthalmologic perspective, as comparatively little is known about the properties of decay of saccadic adaptation. Previously obtained retention timescales range from 10 minutes (Desmurget et al., 2000) to five days (Alahyane & Pélisson, 2005), with the mechanisms that account for these differences remaining largely unknown (but see Gaveau et al., 2005). Furthermore, rapid interleaving of adapted saccades and localization trials tests the robustness of saccadic adaptation procedures to task switching, which currently remains unexplored.

Third, we have endeavored to develop a reliable metric of mislocalization that does not require the execution of saccades. This is crucial for fMRI applications, to avoid interference from motion related activity. Importantly, this renders unusable the most widely used and best validated method of measuring saccadic adaptation-induced mislocalization, namely peri-saccadic mislocalization. This is because in this method, localization takes place directly after making a saccade (e.g. Awater et al., 2005; Collins et al., 2007; Schnier, Zimmermann, & Lappe, 2010). This problem, too, is relevant from a psychometric/ophthal- mological perspective, since uncertainty remains about the extent to and conditions under which saccadic adaptation evokes perceptual effects in addition to its motor effects. Authors have reported visuotopic remapping of space in peri-saccadic localization judgments (Awater et al., 2005; Collins et al., 2007). However, arguments have also been made in the opposite direction (Wallman & Fuchs, 1998), and conflicting results have arisen when localization judgments were made in the absence of saccades (e.g. no transfer: Awater et al., 2005; partial transfer: Moidell & Bedell, 1988; complete transfer: Zimmermann & Lappe, 2010). It was expected that if our design produced measurable mislocalization, this mislocalization would be exclusive to outward adaptation and remain absent in inward conditions, consistent with previous results (Schnier & Lappe, 2012; Zimmermann & Lappe, 2010).

Methods

Participants

5 participants (2 female) with a mean age of 24.8 years (SD=2.5) were included in the final analyses of this study. Participants received a monetary reward of 8 euros per hour and had normal or corrected-to-normal vision. Participants were healthy and had no reported sight or hearing problems. All subjects underwent all experimental conditions.

Experimental setup

Stimuli were presented on a 22-inch CRT monitor (LaCie Electron 22BLUE IV) at a resolution of 1024x768 pixels with a vertical refresh rate of 120Hz. During the entire experiment, participants were seated with the head stabilized by a chin rest at a distance of 60 cm from the stimulus monitor. The experiment was carried out in a dark room, barring illumination from the stimulus monitor.

Stimuli

All stimuli were designed and presented using OpenSesame (Mathôt, Schreij, & Theeuwes, 2012). Visual stimuli were circles with a radius of 8 pixels, with a transparent 2-pixel radius center. A black circle was used for saccade trials, which turned green during localization trials. Localization probes were purple. All visual stimuli were presented against a gray background, to prevent artefacts induced by phosphor persistence (see Groner, Groner, Müller, Bischof, & Lollo, 1993). Auditory stimuli were fixed-frequency sine waves with a duration of 100 ms.
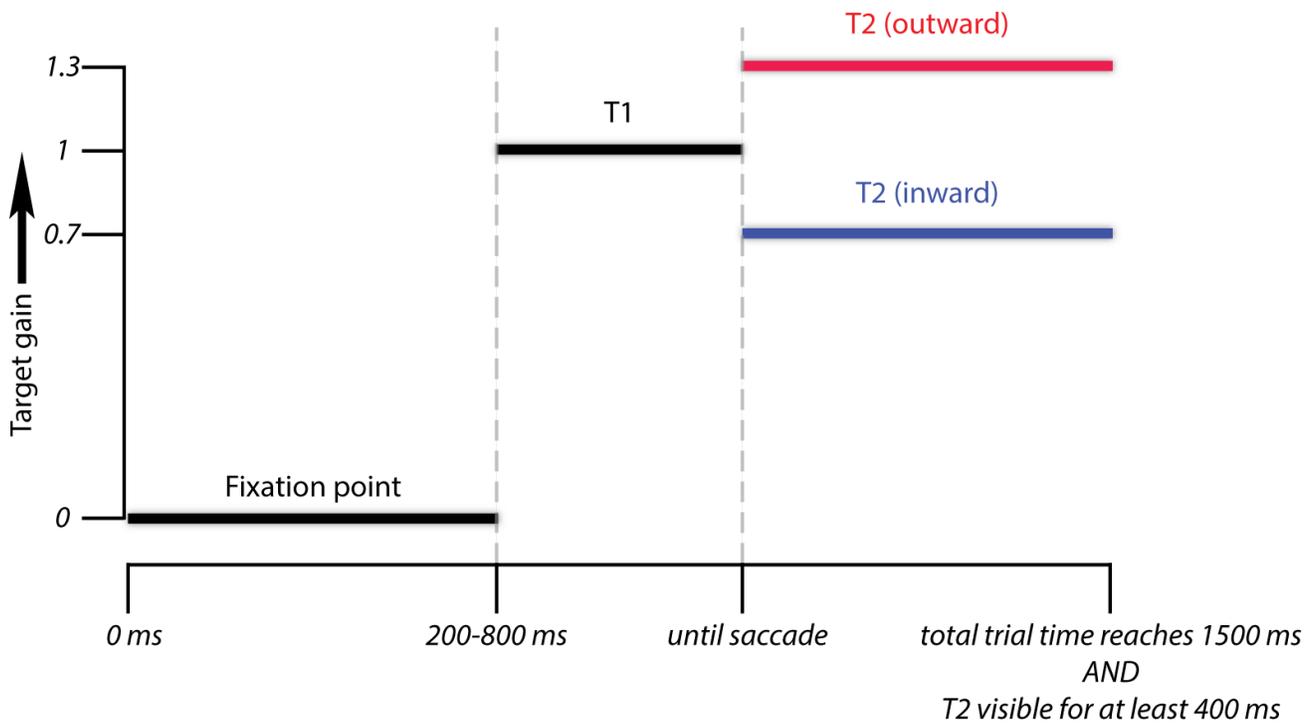
Figure 1: Time course for the events that comprise a single saccade trial. Black lines represent events that occur in every condition, while events in red are specific to outward conditions and blue events are present only in inward conditions. Saccade trials always started with fixation. The fixation point remained on screen for a random interval between 200 and 800 ms. Simultaneous with the offset of fixation, T1 became visible. T1 disappeared when a saccade was detected, which was defined as when gaze position exceeded 30% of the distance between fixation and T1. When this occurred, T1 was immediately displaced to position T2, prompting a corrective saccade. T2 would remain visible for at least 400 ms and until the total trial time reached 1500 ms. Afterward, T2 would serve as the fixation point for the next trial, which took place in the opposite direction if it was another saccade trial. For an overview of target positions, see Figure 3.

Design

Saccade trials

Experiments always started with a saccade trial block. Saccade trials began with the presentation of the fixation dot. After a variable delay of 200-800 ms (all stochastic parameters drawn from continuous uniform distributions), the fixation dot disappeared. Simultaneously, the initial saccade target appeared at 4 degrees left or right of fixation (T1) and a 1000 Hz sine wave was played for 100 ms, indicating that the participant should make a saccade. Sound cues and variable interval lengths were used to ensure that saccades were reactive instead of planned. When the saccade detection threshold was met (gaze position exceeded 30% of the distance between fixation and T1), T1 disappeared and immediately reappeared 1.2 degrees inward or outward, depending on experimental condition (T2). It remained here for a minimum of 400 ms or until the total trial time reached 1500 ms. After this, T2 served as fixation for the next trial, with the transition being undetectable if the next trial was another saccade trial. Thus, during saccade trial blocks, participants alternated between leftward and rightward saccades. Importantly, it follows that the number of adaptive saccades in a single direction was always half the current total number of adaptive saccade trials. A visual overview of saccade trials is given in Figure 1.

Localization trials

In order to demarcate a clear transition between saccade and localization trials, transitions to localization blocks were marked by three subsequent beeps of increasing pitch, the fixation dot turning green, the mouse cursor becoming visible and an extra 500 ms delay before the next trial started. The fixation dot remained visible and stationary during localization blocks. Participants were instructed not to make any eye movements and to maintain fixation at all times while the fixation dot was green. During localization trials, a probe (purple circle) was flashed for 60 ms after a variable delay of 200-400 ms.

Massed condition

Baseline — Core

Interspersed condition

Baseline — Core
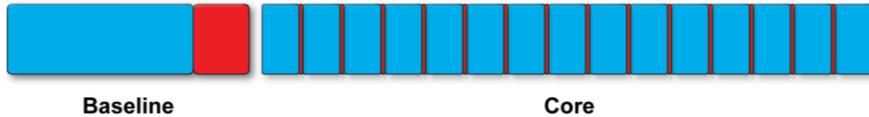
Figure 2: Visualisation of block length conditions. blue: saccade trials, red: localization trials. Bar width is directly proportional to number of trials in that block.
Above: in the massed condition, the core phase consists of a single block of 300 saccade trials, followed by 30 localization trials.
Below: in the interspersed condition, the core phase is subdivided into 15 blocks of 20 saccade trials, each followed by 2 localization trials

Probe eccentricity was 3.6-4.4 degrees, with direction randomized such that probes appeared to the left and right of fixation an equal number of times within each block. Participants had to indicate the perceived location of the flashed probe by moving the cursor and clicking the left mouse button. The next trial started when a position had been indicated, the mouse cursor was moved to the bottom of the screen, and a minimum of 2000 ms had passed since trial onset. In total, 82.9% of trials concluded in exactly their minimum duration (mean deviation: 61.5 ms). Transitions to saccade blocks were demarcated by three subsequent beeps of decreasing pitch, the fixation dot becoming white, the disappearance of the mouse cursor and an extra 500 ms delay before the next trial.

Procedure

During their first session, each participant completed a practice block of 50 gain 1 saccade trials (i.e. without target displacement), followed by a localization block of 30 trials. All subjects indicated that they understood and were comfortable with the task after the practice block. Data from the practice block was not recorded.

After practice, each participant performed a total of 4 experiments over 2 sessions. Experimental conditions varied across 2 dimensions: block length and displacement direction. One session always comprised a single block length and both displacement directions (one per experiment). The order of sessions and of displacement directions within sessions was randomized across participants.

Course of experiments

Each experiment started with a baseline phase that was identical for all conditions. The baseline phase consisted of 100 gain 1 saccade trials without target displacement, followed by 30 localization trials. Afterwards, the core

phase started, which varied depending on experimental condition (see paragraphs 'Block length' and 'Displacement direction' below for details).

After finishing the first experiment of a session, participants could rest, during which they were allowed to remove their head from the chinrest and close their eyes. When ready, they started a de-adaptation block which consisted of 200 saccade trials with gain 1 and no target displacement. This block was added to prevent remaining saccadic adaptation from the previous experiment from contaminating the second experiment. The de-adaptation block was not recorded. After completing de-adaptation, participants could rest again. When ready, they started the second experiment, which was identical to the first, but with reversed displacement direction. Time between the first and second sessions varied between participants. If the second session took place within five hours of the first, it was preceded by another de-adaptation block, to eliminate potential leftover adaptation. The eye-tracker was recalibrated before each experiment.

Block length

The two levels of block length were massed and interspersed. In the massed condition, participants performed 300 consecutive saccade trials, followed by 30 localization trials, resulting in a single block of saccade trials, followed by a single block of localization trials in the core phase. In the interspersed condition, the core phase consisted of 15 runs, each consisting of 20 saccade trials, followed by 2 localization trials. Thus, the total number of saccade and localization trials was identical between massed and interspersed conditions, but the trial order was not. This design is visualized in Figure 2.

Displacement direction

During saccade trials in the core phase, T2 always had a
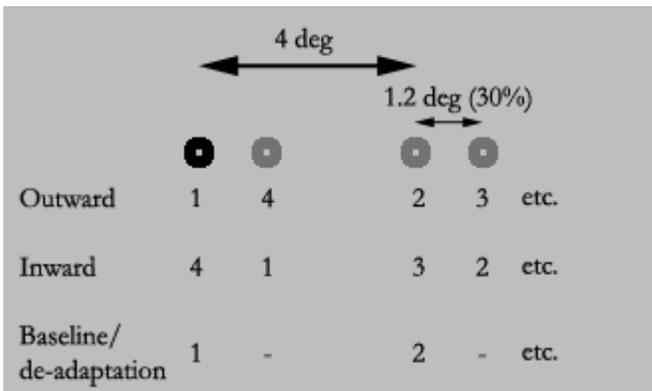
Figure 3: Stimulus locations and appearance order per condition. During saccade trials, visual stimuli were displayed at four locations. For example, an outward condition trial could start with fixation at the first position from left. T1 would then appear at the third position, and would shift to the fourth position as soon as a saccade was detected. This position would then serve as the starting point for the next trial, in which T1 would appear at the second position and T2 at the first position, closing the circle. Note that in the actual experiment, only one stimulus was present at a time during saccade trials. Colors, stimulus shapes and relative distances between stimuli displayed here are veridical.

displacement of 30% gain (with respect to a normetric saccade to T1 from fixation), the maximum displacement under which complete saccadic suppression is maintained (Bridgeman et al., 1975). In the outward condition, this displacement was in the same direction as the saccade, increasing the length of the desired saccade vector. In the inward condition, the target was displaced in the opposite direction of the saccade, shortening desired saccade length. An overview of possible stimulus locations is given in Figure 3.

Eye movement recording & pre-processing

Gaze positions were sampled with an EyeLink 1000 eye tracker at 1000 Hz. Viewing was binocular, but only one eye was recorded. All subsequent data analysis was performed using a custom written Python package. For every saccade trial, saccades made between T1 appearance and 160 ms post-T2 appearance were calculated using the Engbert & Mergenthaler algorithm (Engbert & Mergenthaler, 2006). From all saccades detected in this window, the saccade with the largest amplitude was selected for analysis. Saccade trials were rejected when there was a blink between T1 appearance and saccade offset, when the amplitude or velocity of the saccade were more than 3 standard deviations from their respective means across all trials for that participant, when the saccade gain was below 0.5 or exceeded 1.5, or when the starting gaze position was more than 1 degree from fixation.

Data analysis

Hypothesis testing was done using a bootstrapping method, since sample sizes were too small to infer normality or allow for parametric testing. In addition, this method is more robust against variations in trial rejection rates over participants, increasing signal-to-noise ratio compared to drawing a single statistic from each participant.

In order to compute adaptation strength, 1000-fold bootstrapping was performed over subjects. Within each fold, five participants were sampled with replacement. Adaptation magnitude was then computed by taking the difference between start and end points of a power law fit to the median saccade gain over permuted subjects, resulting in a power law divergence outcome.

For localization trials, datasets were first transformed by averaging over every two subsequent trials in interspersed conditions, eliminating differences in temporal dependency between successive data points. Then, for interspersed conditions, power law divergences were computed following the above procedure. In this context, power law divergence represents the mislocalization that was built up over the course of the experiment.

For all saccade trials and for interspersed localization trials, one-sided p-values were calculated as the proportion of powerlaw divergence values smaller than or equal to 0 for inward conditions or larger than or equal to 0 for outward conditions.

For massed conditions, all localization trials took place after the saccade trials, rendering the power law divergence metric meaningless. In these conditions, data was bootstrapped from randomly permuted participants as per the above procedure, but instead of fitting a power law to this data, a single median saccade gain value was computed within each fold.

One-sided p-values were then calculated by testing the bootstrapped distribution against the median gain in the baseline phase.

For all conditions, a 95% confidence interval was determined by taking the 25th and 975th permilles of bootstrap outcomes as lower and upper bounds, respectively.

Power law fits were chosen as a model for saccadic

adaptation as they incorporate multiple time constants, whereas exponential fits express only a single time constant (Shmuelof & Krakauer, 2014). Conceptually, this matches saccadic adaptation, which is thought to be composed of separate components with differential timescales (Hopp & Fuchs, 2004; M. A. Smith, Ghazizadeh, & Shadmehr, 2006)

Results

Saccadic adaptation

Figure 4 shows the data and fits for saccade trials, averaged over all participants. In massed conditions, there is significant outward adaptation (p=0.031) and inward adaptation (p=0.002), indicating that over the course of 300 saccade trials with target displacement, saccade length had significantly increased or decreased, respectively. Power law divergences used for hypothesis testing are displayed in a violin plot in Figure 4. An example bootstrapping result is given in Figure 5. This visualisation displays the power law fit to the mean data and powerlaw fits to bootstrapped permutations of the data, which were used for hypothesis testing. A complete overview of statistical outcomes is given in Table 1

Transfer to mislocalization

Figure 6 displays the data and fits for localization trials, averaged over all participants. For massed conditions, no main effects were found, indicating that after 300 saccade trials with target displacement, localization accuracy did not significantly differ from baseline. For interspersed conditions, mean values of trial pairs are analyzed to eliminate differences in intertrial interval length between localization trials, as localization trials always occurred in pairs, with a block of saccade trials between each localization pair. In interspersed conditions, power law divergence was not significant, indicating that localization gain was not significantly altered over the course of the experiment. Differences of medians for massed conditions and power law divergences for interspersed conditions are displayed in a violin plot in Figure 6. A complete overview of statistical outcomes is given in Table 2.
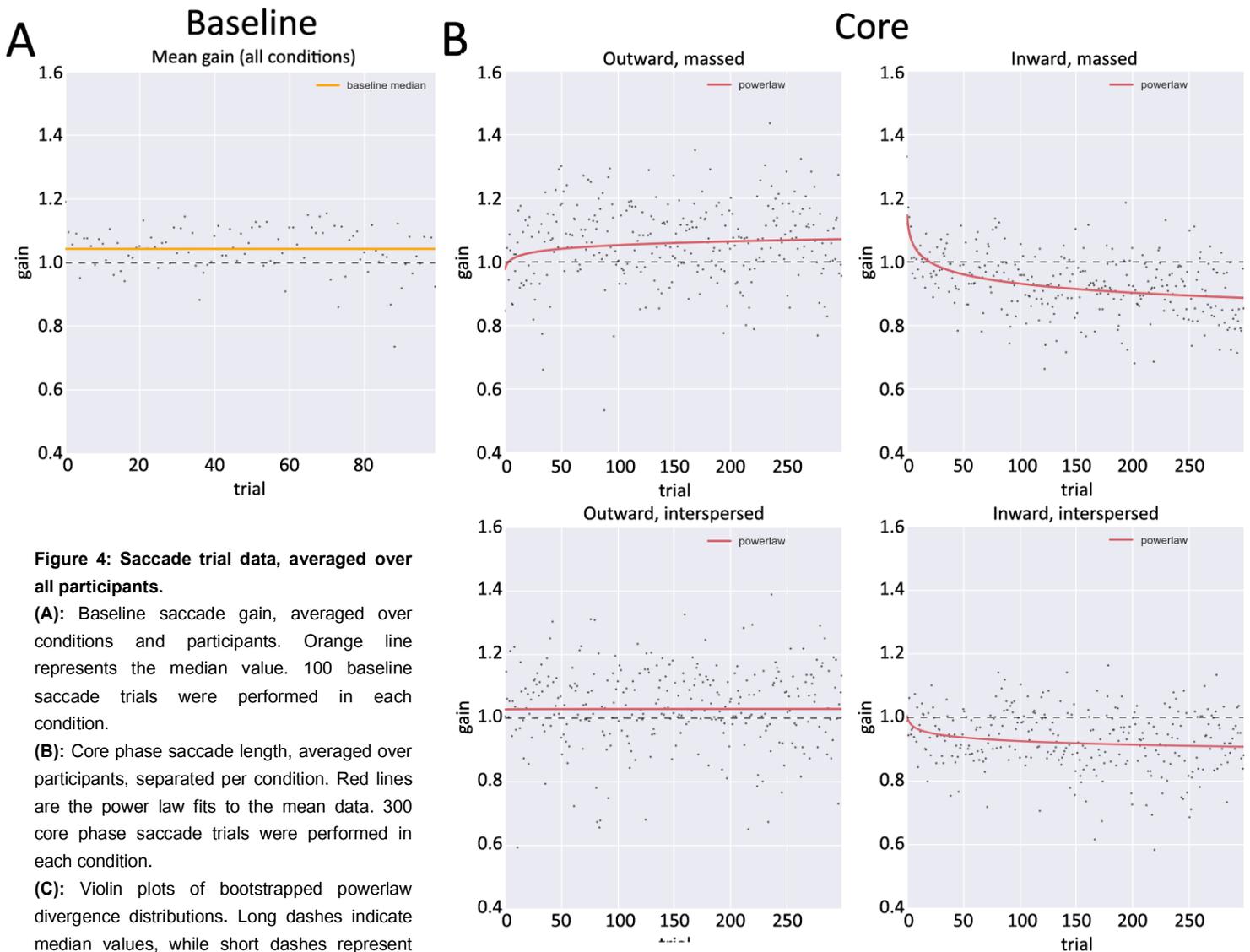
Figure 4: Saccade trial data, averaged over all participants.

(A): Baseline saccade gain, averaged over conditions and participants. Orange line represents the median value. 100 baseline saccade trials were performed in each condition.

(B): Core phase saccade length, averaged over participants, separated per condition. Red lines are the power law fits to the mean data. 300 core phase saccade trials were performed in each condition.

(C): Violin plots of bootstrapped powerlaw divergence distributions. Long dashes indicate median values, while short dashes represent the interquartile range. Violin widths are kernel density estimations. In massed conditions, there is significant inward (p = 0.002) and outward (p = 0.031) adaptation. In interspersed conditions, there is no saccadic adaptation.
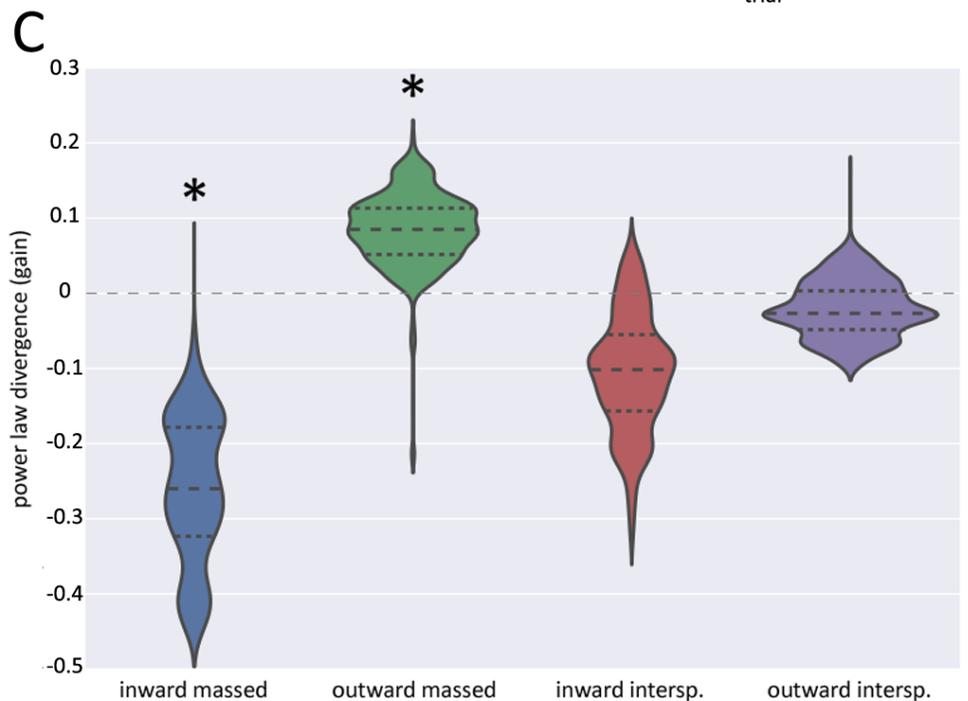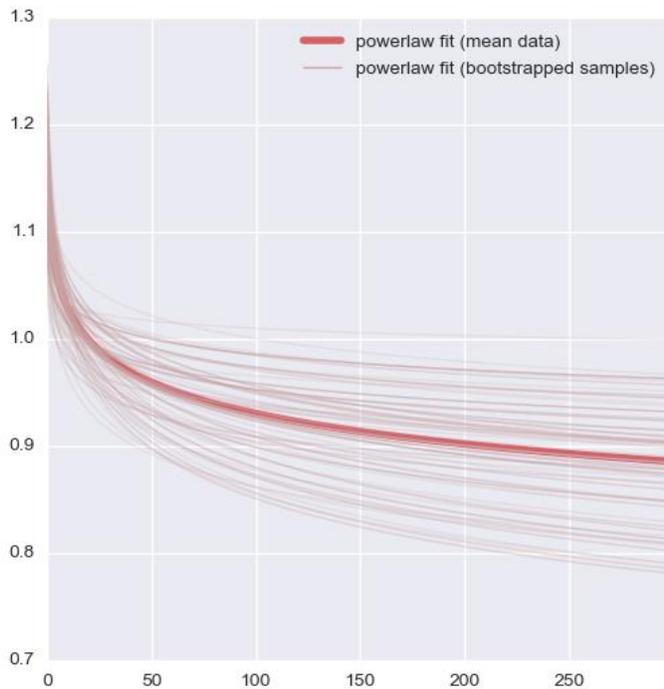
Figure 5: Example bootstrapping result. Plotted data is for the inward, massed condition. The thick red line represents the power law fit to the mean data, while the thin red lines represent power law fits to bootstrapped data permutations. For visualization purposes, only 100 bootstrapped fits are plotted.

Table 1: Statistics for saccade trials.

Condition	Powerlaw divergence (gain)	CI (95%)**	p-value
Outward, massed	0.0821	-0.04 – 0.17	0.031*
Inward, massed	-0.2640	-0.43 – -0.11	0.002*
Outward, interspersed	-0.0186	-0.09 – 0.05	0.666
Inward, interspersed	-0.1106	-0.26 – 0.04	0.128

* indicates significant results.
** confidence intervals represent estimates of population value of powerlaw divergence

Table 2: Statistics for localization trials

Condition	Powerlaw divergence (gain)	Difference of medians (gain)	CI (95%)**	p-value
Outward, massed	-	0.0206	-0.07 – 0.12	0.357
Inward, massed	-	0.0095	-0.12 – 0.08	0.794
Outward, interspersed	0.0261	-	-0.13 – 0.17	0.321
Inward, interspersed	-0.0265	-	-0.19 – 0.10	0.762

* indicates significant results.
** confidence intervals represent estimates of population value of difference of median between bootstrapped data and mean data for massed conditions. For interspersed conditions, confidence intervals represent estimates of powerlaw divergence.

Figure 6: Localization trial data, averaged over all participants.

(A): Mean data across conditions in baseline phase. Orange line represents median value over trials.

(B): Core phase mean localization gain per trial, averaged over participants. Blue lines represent median values. Red lines are power law fits to data pairs. For massed conditions, no power law fits were made, as all localization trials took place subsequent to saccade trials. Thus, no saccadic adaptation was induced over the course of these trials. Conversely, for interspersed conditions, no median is plotted, since each trial pair is interjected with a block of saccade trials, which may evoke saccadic adaptation with transfer effects to localization accuracy.

(C): Violin plots of bootstrapped divergences from null for localization trials. Long dashes are median values, while short dashes represent the interquartile range. Violin widths represent kernel density estimations. For massed conditions, y-axis values is the difference of medians (bootstrapped minus baseline), while for interspersed conditions, y-axis values represent power law divergence. No conditions yielded significant results, indicating that there was no transfer to mislocalization in any condition.

Discussion

The aim of this study was to answer three main questions, which will be discussed separately in the sections below.

Adaptation of low-amplitude saccades

The first was whether it is possible to induce saccadic adaptation using the double-step target paradigm at very low amplitudes. Indeed, our results confirm that the double-step target paradigm can be used to induce both hypermetric and hypometric saccades to saccade targets with an azimuth of 4 visual degrees. Adaptation was stronger for inward displacements than for outward displacements (see Table X1), which is consistent with previous findings (e.g. Hopp & Fuchs, 2004; Schnier & Lappe, 2011; Zimmermann & Lappe, 2010).

Effects of task switching

Second, we have investigated the feasibility of on-line monitoring of the time course of adaptation-induced mislocalization by interleaving saccade trials and localization trials. An unexpected result was that when trial types alternated in short blocks, no saccadic adaptation was found in either direction (inward/outward). This finding cannot be easily attributed to deficiencies in experimental design, because (1) significant adaptation was found in both directions in massed conditions and (2) massed conditions were identical to interspersed conditions in all respects, except for the frequency of switches in trial type. To the author's knowledge, this effect has never been reported before.

Transfer to mislocalization

Third, we have measured the extent to which the adaptation of saccades transferred to mislocalization. Notably, localization judgments were made during fixation, which has led to mixed results in previous studies (cf. Collins et al., 2007; Moidell & Bedell, 1988; Zimmermann & Lappe, 2010). In the present study, no mislocalization was observed, regardless of experimental condition.

Implications

Task switching

Our results suggest that there is an effect of task switching on saccadic adaptation, which is unaccounted for by the current literature. Moreover, previous designs that test for saccadic adaptation-induced mislocalization have generally used adaptation blocks with a minimum of 200 saccades (e.g. Schnier & Lappe, 2012; Schnier et al., 2010; Zimmermann & Lappe, 2010). Notably, however, some peri-saccadic mislocalization designs have succesfully built up saccadic adaptation while subjects performed localization judgments at every trial (Awater et al., 2005; Collins et al., 2007). Thus, it could be hypothesized that saccadic adaptation can be induced despite increases in task complexity, but is interfered with by top-down task switching, especially when task switches are unpredictable (i.e. don't occur at every trial). An interesting comparison to make is with earlier findings which show that the gain of volitional saccades is modulated separately from and does not interact with the gain of reactive saccades (Deubel, 1995; Gaveau et al., 2005). It may be argued, then, that the diminished predictability of the task and the requirement to monitor whether saccades should be inhibited, as was the case in localization trials, led to the involvement of the volitional system, or, conversely, that the volitional system is recruited not just for volitional saccades, but more generally when the task presents higher top-down involvement. Indeed, previous accounts have proposed a general dichotomy between reactive and higher-order saccades operating on separate neural architectures (Hopp & Fuchs, 2004; Srimal & Curtis, 2010). The extents to which these volitional and higher-order networks are generalizable and overlap with each other constitute an interesting topic for future research. Furthermore, it has been estabilished that while natural and experimental modifications of saccadic gain have drastically different time courses (Hopp & Fuchs, 2004), these differences disappear in a controlled experimental context (Scudder et al., 1998). The present study contributes to the outstanding question of which differences between real-life and laboratory settings account for the observed differences in time courses, with the finding that task switching demands appear to impair effective saccadic gain modulation. This mechanism provides a possible explanation for the large differences in retention that have previously been observed (c.f. Alahyane & Pélisson, 2005; Desmurget et al., 2000), which may be attributable to variations in the engagement of separate saccade systems between sessions, contexts and participants. In addition, clarifying the functional segregation of saccade systems may contribute to the development of more focused

rehabilitation following ophthalmoplegia or similar oculomotor debilitations.

Another factor that may have played a role in the observed effects of task switching is provided by a recent study that showed that the magnitude, speed and retention of saccadic adaptation depend on the amount of attention required by saccadic targets (Gerardin, Nicolas, Farnè, & Pélisson, 2015). Specifically, they find that when a perceptual judgment must be made about adaptive saccade targets, targets that demand more attention to solve the task induce greater changes in saccadic gain. Relating this to the present study, it could be reasoned that increasing the difficulty of monitoring current task requirements would shift some attention from extrinsic cues to endogenous processes, attenuating the magnitude of saccadic adaptation. One problem with this account, however, is that it fails to generate specific hypotheses. For example, it may just as well be used to predict that frequent task switching would increase saccadic adaptation, for example by reducing boredom effects. Evidently, this is not the case.

Mislocalization

The absence of mislocalization observed in our experiment leaves open the question why some previous studies did observe mislocalization during fixation, while others did not. Integrating our findings with previous studies, two potential causes for this discrepancy can be identified.

First, it has been proposed that differences in saccadic adaptation-induced mislocalization between inward and outward adaptation are based on differences in target acquisition or planning stages (Schnier & Lappe, 2012). From this perspective, it's possible that disparities observed between the present study and Awater et al. (2005) on one hand, and Schnier & Lappe (2012) and Zimmermann & Lappe (2010) on the other are caused by differences in the delay between probe presentation and the onset of localization judgments. Whereas Awater et al. and the present study used immediate localization judgments, Schnier & Lappe and Zimmermann & Lappe's designs had a 925-1325 ms delay between probe onset and the appearance of the mouse cursor. Thus, it is conceivable that in order for transfer to hand movements to occur, an extended planning phase is required.

The second explanation is the presence of visual references. Awater et al. (2005) found no transfer to mislocalization during fixation. It should be noted that in their design, fixation remained visible during localization judgments, providing a visual referent. These results are similar to those of the present study, which also provided a visual referent and found no mislocalization. This differs from the designs used by Zimmermann & Lappe and Schnier & Lappe, who eliminated the fixation point during these trials and instead instructed participants to maintain fixation in the absence of a fixation marker. In addition, the present study presented stimuli against a gray background and Awater et al. employed a red background, both of which provided visual referents at the screen borders. By contrast, in the studies performed by Zimmermann & Lappe and Schnier & Lappe, black backgrounds were used, with the screen and its borders covered by a dark foil, eliminating potential visual references. In light of these differences, it seems plausible that the absence of visual references is required for the induction of saccadic adaptation-induced mislocalization. This view is consistent with the classic finding that without additional experimental manipulations, saccadic adaptation does not appear to distort visual metric judgments (Mclaughlin, Kelly, Anderson, & Wenz, 1968). Instead, the most parsimonious explanation appears to be that saccadic adaptation is in the main an oculomotor process, which can display transfer to other motor systems in the absence of perceptual context, with the proportion of motor transfer and differences between displacement directions most likely being related to the magnitude and persistence of visual error (Schnier & Lappe, 2012). Lending support for such an account is the striking observation that all current studies that report saccadic adapatation-induced mislocalization (both peri-saccadic and during fixation) employ designs in which localization judgments are accompanied by motor activation, be they hand movements or saccades. It seems plausible, then, that motor involvement is a requirement for the induction of mislocalization transfer effects. A similar motor-dependent effect exists for the mislocalization of flashed probes during smooth pursuit eye movements. Notably, this effect is also strongly diminished by the presence of visual landmarks (Brenner, Smeets, & van den Berg, 2001). In light of these similarities, it is possible that saccadic adaptation-induced and smooth pursuit-induced mislocalization operate on similar mechanisms, which incorporate both perceptual and motor information, and in

which perceptual information takes precedence when visual landmarks are available to inform judgment. A potential link between such findings is given by the premotor theory of attention, which posits that planning a goal-directed action is both sufficient and necessary for a shift in spatial attention (Rizzolatti, Riggio, & Sheliga, 1994; but see Smith & Schenk, 2012).

It should be noted, however, that current designs are ultimately uninformative of whether saccadic adaptation-induced mislocalization is a perceptual effect or a motor transfer effect, since mouse localizations entail both perceptual target registration and motor activation. An alternative interpretation that cannot be ruled out based on current findings is therefore that perceptual remapping of space does take place in saccadic adaptation, but only in the complete absence of visual context. For conceptual purity, then, it should first be established whether this mislocalization is due to motor transfer, or due to perceptual changes. For example, a future study could eliminate motor involvement by adapting only a single hemifield and testing localization using a psychometric staircase, in which participants are presented with a flashed probe in both the adapted and unadapted hemifields at every iteration (without a visible fixation point and with asynchronous probe presentations to eliminate visual landmarks), for which they judge which probe was closer to fixation. If saccadic adaptation-induced mislocalization is a perceptual effect, this should evoke mislocalization, whereas if it is a motor effect, localization judgments should remain veridical. Subsequently, if it turns out mislocalization is perceptual, this would be a strong indicator for the involvement of retinotopic maps. However, the possibility that retinotopic maps are involved cannot be discarded even if motor involvement is required. For example, parietal areas contain overlapping maps for hand movements and saccades (Hagler, Riecke, & Sereno, 2007), which could be selectively adapted in lieu of system-wide changes. Further experiments are also required to disentangle the roles of planning time and visual references in saccadic adaptation-induced mislocalization, although it should be noted that these accounts are not mutually exclusive.

Acknowledgements

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