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The Impact of Saccadic Eye Movement Training on Saccade Accuracy and Latency

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Abstract -- Prosaccades are saccadic eye movements made reflexively in response to the sudden appearance of visual stimuli; those with latencies under 120 milliseconds have been referred to as "express saccades." Antisaccades are saccadic eye movements that are performed volitionally to a location opposite a stimulus. Bibi and Edelman (2009) demonstrated that decreases in reaction time resulting from training express saccades along one axis (horizontal or vertical direction) could transfer to saccades made along the other axis. To help determine the visuomotor processes underlying this facilitation, we trained subjects to make prosaccades and probed their performance on antisaccade trials, as well as trained subjects to make antisaccades and probed their performance on prosaccades. Subjects were trained over several weeks and probed for the effects of training on saccade performance before training, after six sessions of training and after twelve sessions of training). We consider three possible outcomes: 1) A finding that prosaccade training increases error rate in the antisaccade task would indicate that training facilitates visual processes, making it more difficult for reflexive visuomotor processes to be suppressed during an antisaccade trial 2) A finding that saccadic training increases untrained saccade latency would suggest that training suppresses voluntary saccade production with prosaccade training or reflexive saccade production with antisaccade training. 3) A finding that saccadic training decreases untrained saccade reaction time in all tasks would suggest that training has a general effect in facilitating saccade production in reaction time tasks. As in previous work (Bibi and Edelman, 2009), training resulted in the shortening of reaction time,

with a greater percentage of saccades in the express latency range. Subjects exhibited an overall decrease in reaction time in untrained saccades while also showing little, if any, change in error rate. These findings suggest saccadic training has a generalized effect on the saccadic system, allowing it to more quickly generate saccades (pro-and anti) in reaction time tasks.

Introduction

Saccade eye movements and their generation

Saccades are rapid eye movements that involve the shifting of gaze from one point to another to focus images of interest onto the fovea, the portion of the retina with the highest density of photoreceptors (Kowler, 2011). Saccade peak velocity is related to the amplitude of the movement; the greater the amplitude, the greater the peak velocity. This relationship is roughly linear for saccades up to 20°; above this, the relationship becomes increasingly asymptotic with maximum of about 500°/sec for large saccades (80°). Similarly, the duration of the saccade is linearly related to the amplitude of the movement (between 1 to 50°), above a minimum duration of roughly 30 msec. Saccades can be driven by a combination of voluntary and involuntary factors though they are generally driven by visual stimuli, both stable and appearing suddenly in the environment. Mechanisms of inhibition and executive control over the saccadic system can be assessed by observing the generation of antisaccades, which can be performed in the laboratory by instructing subjects to make a saccade in a direction opposite to that of a suddenly appearing stimulus (Hallet, 1978; Bowling et. al., 2011; Condy et al.,2007). (Leigh and Zee, 1999)

The neural components of the saccadic system include various interconnected cortical and subcortical areas. The output of this neural system ultimately projects to the extraocular muscles, which control the rotation of the eyes. These muscles are innervated by the abducens, trochlear nerves, and oculomotor nerve nuclei. Although all ocular motor neurons activity does not depend on the type of eye movement, their recruitment will dependi on the position and rotation of the eye. (Goldberg, 2012; Munoz and Everling, 2004; Johnston and Everling, 2008).

Visual signals important for the generation of saccades are thought to be relayed through the primary visual cortex and extrastriate cortex regions of the posterior parietal cortex. The areas of the visual cortex project to both cortical and subcortical areas involved in producing saccades. From the visual cortex, the information about the position of the stimulus travels to the parietal cortex and parietal eye fields. The parietal cortex has connections to the superior colliculus (SC) and is thought to contain a "priority map," indicating regions of interest in visual space, and is thus associated with visuo-spatial attention processes and transformation of sensory input into motor commands (Colby and Goldberg, 1999; Colby et al.,1996 as cited in McDowel et al., 2008). In humans, the parietal eye fields (PEF) have been associated with the reflexive saccade and triggers saccades by disengaging fixation (Muri and Nyffeler, 2008). (McDowell et al, 2008)

Other cortical areas involved in saccade production include the frontal eye field (FEF) and supplementary eye field (SEF), and the dorsolateral prefrontal cortex (DLPFC), all of which are in frontal cortex. Activity in the FEF has been shown to be involved in volitional saccades and in disengaging fixation (Rivaud et al., 1994; McDowel et al., 2008). The SEF, which has reciprocal connections with the FEF, has been associated with movement generation and is more active in more cognitively complex tasks. Specifically, the SEF is thought to be involved in slowing the buildup of neuronal activity before the generation of an error during an antisaccade (Boxer et al.,2006a; Boxer et al. 2006b, as cited in McDowell et al, 2008), thus playing a role in antisaccade inhibition. Both and FEF and SEF are more active during the antisaccade task than the prosaccade task (DeSouza et al., 2003). The DLPFC is thought to be involved in inhibitory function during the antisaccade task as well. The activity in the DLPFC precedes, and is limited to, correct antisaccades (DeSouza, 2003). (McDowell et al, 2008; Munoz and Everling, 2004; Johnston and Everling, 2008).

Subcortically, the saccadic system relies on the basal ganglia, thalamus and superior colliculus (SC), as well as premotor and motor nuclei. Of these, the SC is of particular importance. The SC receives input from almost all cortical and many subcortical structures controlling the saccadic system. It is involved in the performance of reflexive saccades and its visual response must be inhibited for the generation of antisaccades. This is done, in part, by the basal ganglia which can inhibit the SC so that erroneous saccades are not performed during voluntary visual tasks. The thalamus serves to relay information that ascends from the subcortical areas, both from the retina, and the SC, to the cortex. (Munoz and Everling, 2004; Johnston and Everling, 2008; Goldberg, 2012).

Saccade reaction time in response to a suddenly appearing stimulus is often highly variable, particularly for naïve subjects, but is generally less than 200ms. This amount of variability can generally be explained, at least in part, by the amount of time until threshold is reached in the saccade neurons of the superior colliculus (SC) and frontal eye fields (FEF) upon the appearance of a stimulus (Hallett and Adams, 1980, as cited in Munoz, 2004).

Neural mechanisms underlying antisaccade generation

In order to perform an antisaccade, low-level, “baseline” activity must first be inhibited to prevent the saccade movement threshold from being reached upon presentation of the stimulus. Compared to prosaccades, just prior to saccade generation antisaccades demonstrate an overall increase in activity in fixation neurons in the FEF and SC as well as a decrease in activation in saccade neurons in the same regions. It is this reciprocal activation that causes the increased reaction times observed in this task (Hallett and Adams,1980, as cited in Munoz, 2004). The activity of saccade neurons in the FEF and SC contralateral to the stimulus must first be inhibited to allow the ipsilateral neurons to be activated to drive the movement in the opposite direction of the stimulus; this step is considered the inversion of the target vector into the saccade vector. Once the visual response fails to elicit a saccade, activity can slowly build to induce the volitional antisaccade. Errors in the antisaccade task are usually due to insufficient inhibition of FEF and SC neurons prior to the appearance of the stimulus. This, in addition to the activity caused by the appearance of the stimuli, causes threshold to be reached and a prosaccade to be produced. This can be predicted based on the amount of activity in these neurons. High activity is more likely to lead to an error in the antisaccade task. Despite this, it has been shown that there is no differential activation during an fMRI study in either pro- or antisaccade tasks in response to the stimulus itself, indicating that there is no difference in movement related activity between the tasks (DeSouza et al., 2003; Munoz and Everling, 2004; Everling and Munoz, 2000; Munoz and Wurtz, 1995 as cited in Munoz and Everling, 2004; Dias and Bruce, 1994).

In order for an antisaccade to be performed, the reflexive saccade towards the stimuli (prosaccade) must be suppressed and a saccade in the opposite direction, toward blank space, must be performed voluntarily (Hallett, 1978; Weiler and Heath, 2012). Pro and antisaccades depend on mechanisms that interact, but may well compete. In the antisaccade task, there are two processes that must occur to allow a volitional saccade to be performed in the direction opposite the appearance of a stimulus: the suppression of the reflexive prosaccade and the inversion of the stimulus vector to allow the performance of the antisaccade. Neurons mediating saccades are silent during fixation and fire high frequency action potentials in response to saccades to areas within their response field. In the antisaccade task, however, the activity in these neurons is reduced (Munoz and Everling, 2004). It has also been thought that there is a difference in preparation needed to perform these types of saccades, as differential activation is observed in fMRI studies (DeSouza et al., 2003).

As the location of a stimulus location must be processed to perform a saccade, particularly when performing antisaccades, impairments in the ability of a subject to perform antisaccades can indicate a variety of neurological and psychiatric diseases (Guitton et al., 1985; Everling and Fischer,1998; Munoz and Everling, 2004). An individual must be able to process the location of a stimulus to be able to both inhibit the reflexive saccade to this location and invert the spatial information to an ipsilateral location in the posterior parietal cortex and produce a saccade to the new location. In general, performance in an antisaccade task has higher error rates, is less accurate and results in longer reaction times then prosaccades (Weiler and Heath, 2012) (Knox et. al. 2012). Short latency prosaccades have often been observed in the antisaccade task (Bowling et al., 2011). As with prosaccades, when presented in a gap trial (see below), latencies and error rates are also impacted (Fischer et al., 2000).

The use of a temporal "gap" to reduce saccade reaction time

Experimentally, a temporal "gap" can be used to reduce the reaction time of saccades. This gap involves the presence of a small interval in time between the disappearance of the fixation point and the appearance of the target. A gap tends to reduce reaction time (Bibi and Edelman, 2009). It is thought that the gap functions to release the subject's attention from the fixation point to facilitate saccade generation (Mayfrank et al., 1986). The gap may also be used to train subjects to shorten saccade reaction time. Saccades with short latencies (<120ms) are termed "express" saccades, and occur more frequently with the gap, as well as with training (Bibi and Edelman, 2009). Typically, 75-80 ms is the minimum reaction time of saccades in humans given the anatomical and synaptic constraints of the visual and oculomotor systems.

This study utilized two prosaccade as well as two antisaccade paradigms which will be discussed below: the Gap Prosaccade, Overlap Prosaccade, Step Antisaccade and Gap Antisaccade. This was done to test whether changes in performance were due to general saccadic training, or the use of the gap, which forces disengagement of fixation. In particular, the Gap Antisaccade task is challenging. The gap period is known to facilitate reflexive prosaccades, which potentially increases errors in an antisaccade task

It is possible that training naïve subjects to be more efficient in making prosaccades can have an impact on their ability to perform antisaccades and vice versa. This is possible due to the interconnected mechanisms involved in the production in pro- and antisaccades; by training an individual with a particular task, it is possible that some components of the mechanisms for generating these saccades improves such that saccade performance improves for both saccade types. However, training could also be task-specific, perhaps even resulting in a decrement in performance in untrained saccade types.

Methods

Subjects, eye movement recording and visual stimulus display

Three experiments were conducted. A total of 21 subjects (11 male) that had never taken part in an eye-movement study participated in these studies. Subjects ranged in age from 19 to 25 and included a wide range of racial backgrounds. Experiments were conducted under a protocol approved by The City College of the City University of New York Institutional Review Board. The subjects were seated approximately 60cm from a computer monitor and the head was stabilized through the use of chin and cheek rests. Before data collection, calibration was done using a nine-point (3x3) eye movement calibration procedure. The subject was seated in a fluorescent-lit room and surrounded by a black curtain to help prevent visible reflections on the computer screen.

Eye-movement data were recorded using video-oculography (Eyelink II, SR Research) at a rate of 500 samples/s. Experiments were conducted using a Dell Precision T1600 computer and stimuli displayed on Compaq P1220 monitor with a frame rate of 100 Hz. Visual display generation and data collection were performed using Experiment Builder software (SR Research). Data analysis was performed using custom routines written for MATLAB (Mathworks).

Trial Types – Three trial types were used for most experiments: the Gap Prosaccade, Step Antisaccade and Overlap Prosaccade. An additional trial type was used for only Expt. 3: the Gap Antisaccade. In the Gap Prosaccade task, the trial began with the presentation of a central green square of 0.5° in width. This served as the fixation point and remained on-screen for about 500-800ms before disappearing to reveal a blank screen which served as the "gap." This blank screen was displayed for approximately 150-200ms between the disappearance of the green fixation point and the appearance of the target stimulus. The target stimulus appeared at 10° eccentricity randomly to the left or right of the fixation point and disappeared 300ms after the end of the saccade. After an intertrial interval of 700ms a new trial began.

The Step Antisaccade task was presented in a very similar way, except the central fixation point was red to indicate that the subject should look 180° in direction away from the suddenly appearing stimulus. This task did not incorporate a gap. Instead, the stimulus appeared when the fixation point disappeared. The Overlap Procaccade task was similar to the Gap Prosaccade task as well. In this task, the central fixation point was green once again, however, it remained visible until saccade initiation. The subject was instructed to look in the direction of the stimulus as soon as it appeared on screen rather than wait for the fixation point to disappear. The final task, the Gap Antisaccade task, was similar to the previous tasks in that it utilized a red fixation point as in the Step Antisaccade task and a gap of 150-200ms as in the Gap Prosaccade task. In all tasks, the subjects were informed to perform a saccade as soon as possible upon the appearance of the stimulus to the correct location.

Two types of session were utilized for this study: Training and Probe. A particular trial type was identical in the Probe and Training sessions. The Probe sessions involved the presentation of alternating blocks of pro- and antisaccades. The Training sessions involved the presentation of only one type of trial. This varied between experiments and is described below.

Experiment 1a: The influence of Gap Prosaccade training on antisaccade performance

There were 6 subjects (3 male) in this group. Three Probe sessions, consisting of equal numbers of both Gap prosaccade and Step Antisaccade trials. Probe sessions consisted of 12 blocks of 24 trials. The twelve Training sessions consisted of just Gap Prosaccade trials. Training involved the presentation of only gap trials arranged in 15 blocks of 20 trials. A Probe session was run before training, after six Training sessions, and then after an additional six training sessions. This method of probing and training is similar to previous work (Bibi and Edelman, 2009). The entire process of training and probing took place over a period of 5 weeks.

Experiment 1b: Effect of Gap training on antisaccades and overlap prosaccades

Four subjects (2 male) participated in this experiment. The Probe in this experimental setup was altered to include Overlap prosaccade trials, as well as Gap prosaccade trials and Step antisaccade trials. Each session had a total of 15 trial blocks each consisting of 20 trials. In these Probe sessions there were five blocks each of Gap, Overlap and Antisaccade trials. The addition of the Overlap task was to test whether the subjects became more efficient at disengaging the fixation point when no gap was present. The training in this group remained the same as in Experiment 1a.

Experiment 2: The effect of (Step) Antisaccade training on prosaccades

Six subjects (3 male) participated in this experiment. The probe sessions were the same as in Experiment 1b. The Training Sessions, however, included only Step Antisaccade trials. The experiment was otherwise identical to Experiment 1b.

Experiment 3: Gap Antisaccade training

Six subjects (3 male) participated in this experiment. The Probe sessions were the same as in Experiments 1b and 2. The training in this section involved the use of a new trial type: the Gap Antisaccade. As in the Gap Prosaccade task, saccade instruction was cued with a 0.5° red square which remained on screen for about 500-800ms before disappearing. There was a gap of 150-200ms in between the appearance of the stimulus and disappearance of the fixation point. The cue for this task (red colored fixation point) was the same as the Step Antisaccade task. The gap in this task was implemented to test whether training in this task would improve Gap Prosaccade performance more than Step Antisaccade training.

Data Analysis

Saccade Latency-- Saccade latency was defined as the difference between target appearance and the start of the saccade. The saccade latency was computed by taking the average between all saccades performed. This included only non-anticipatory saccades performed with the correct direction. To test changes in reaction time after training, a t-test was used.

Error and Anticipation Rate— Directional errors were defined as non-anticipatory saccades performed to the incorrect direction. This was compared to the total number of non-anticipatory saccades performed. Anticipatory saccades were defined as those performed in less than 75ms. To find the anticipation rate, the number of anticipatory saccades performed was compared to the total number of saccades performed. To test the improvement in the proportion of errors performed across conditions, a chi square test was performed.

Results

Experiment 1a and b

Reaction Time -- Since both Expts. 1a and 1b examined the effect of prosaccade training on antisaccades, and since, other than the addition of Overlap prosaccades in Expt. 1b the two experiments were identical, we first pooled Expts. 1a and 1b and analyzed the effect of Prosaccade training on antisaccades for the nine subjects. Over the course of Gap prosaccade training, all nine subjects showed an overall decrease in Gap Prosaccade latency during Training (Fig.1).

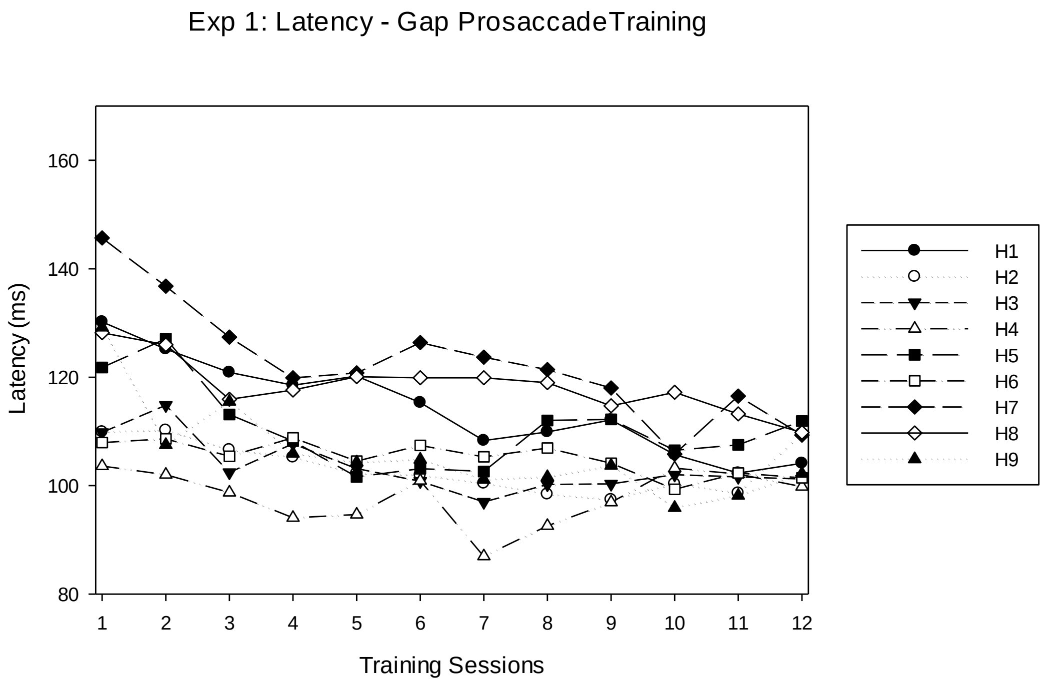

Figure 1: The mean latency over the course of the training period for the 9 subjects trained with the Gap Prosaccade Task.

As shown in Fig. 2a and b, the overall distributions of saccade latencies in the Probe sessions tended to shift with training for all saccade types. In particular, a greater distribution of Gap prosaccades tended to land within the express saccade latency range (75-120ms) after training, as illustrated in the individuals whose data are shown (H6 and H9). In addition, the distributions of antisaccades made appeared to also shift slightly, although not as much as in the Gap Prosaccade task. Additionally, the distributions appear to become less variable overall, with a reduced number of outliers with very long reaction times. Very few, if any, of these saccades fell in the express range. The distribution of Overlap prosaccades was affected similarly, although many more saccades fell within the express saccade range.

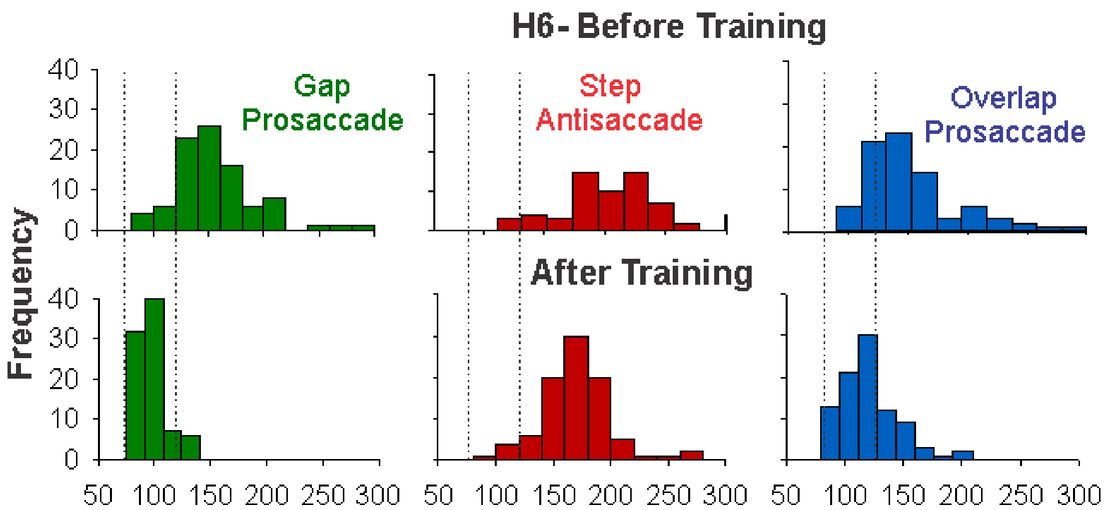

Fig. 2a: The distribution of saccades made before and after training (Probe 1 and 3) for one individual. The two dashed lines indicate the express range (75-120 ms).

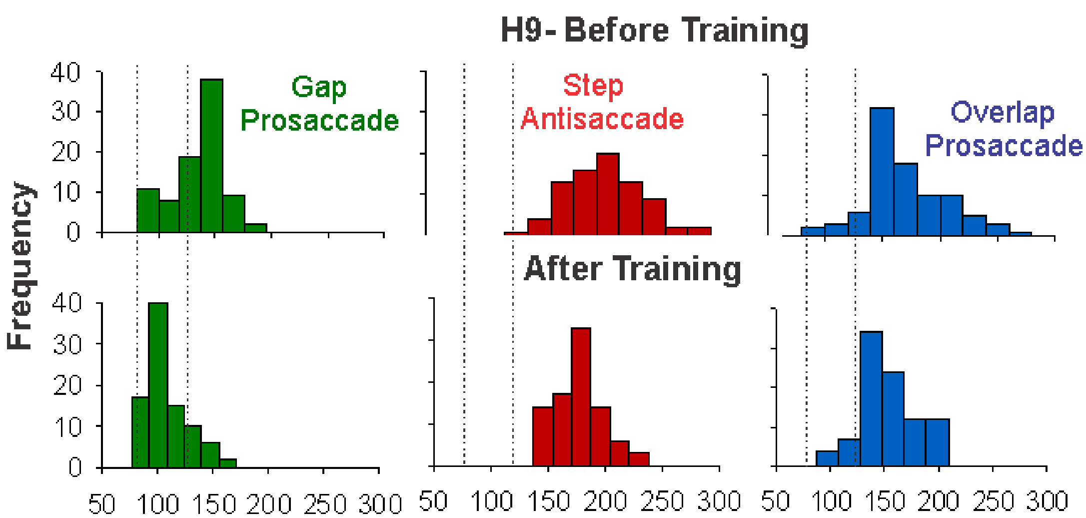

Fig. 2a: The distribution of saccades made before and after training (Probe 1 and 3) for one individual. The two dashed lines indicate the express range (75-120 ms).

The improvement in Gap Prosaccade latency was significant in a t-test ($p<0.05$) in all subjects (Fig.3); subjects also demonstrated an overall latency decrease in both Step Antisaccade and Overlap Prosaccade tasks (Fig. 4 and 5), although not as pronounced as the decrease in Gap Prosaccade latency in Fig. 3. In this experiment, 8/9 subjects demonstrated significant improvement ($p<0.05$) for Step Antisaccade latency and 3/4 subjects demonstrated significant improvement for the Overlap task between the first and final probe.

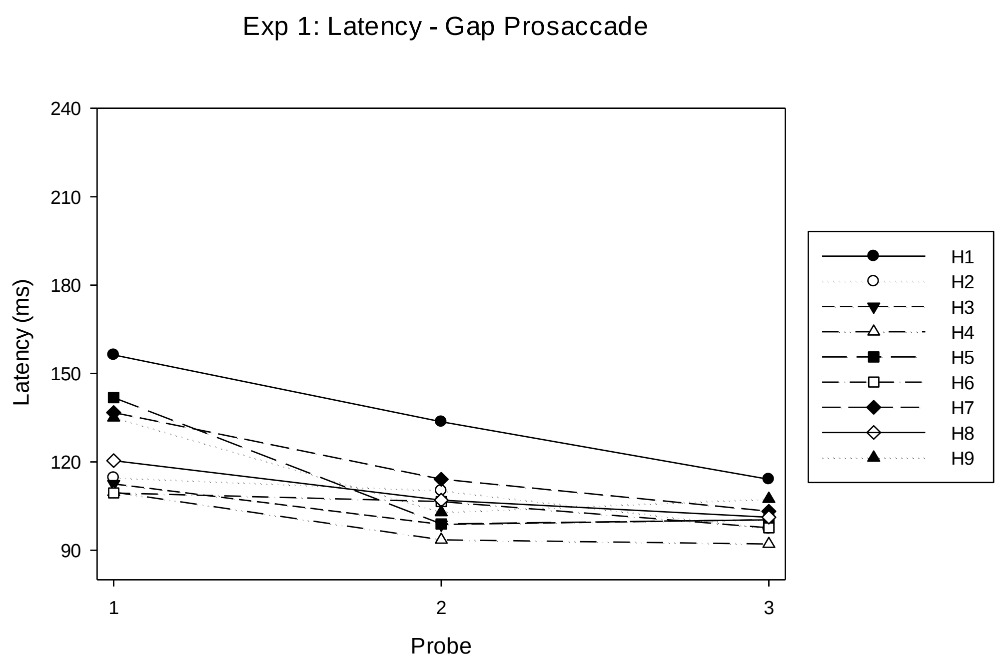

Figure 3: The mean latencies for the 9 subjects in the Gap prosaccade task during all 3 Probe sessions.

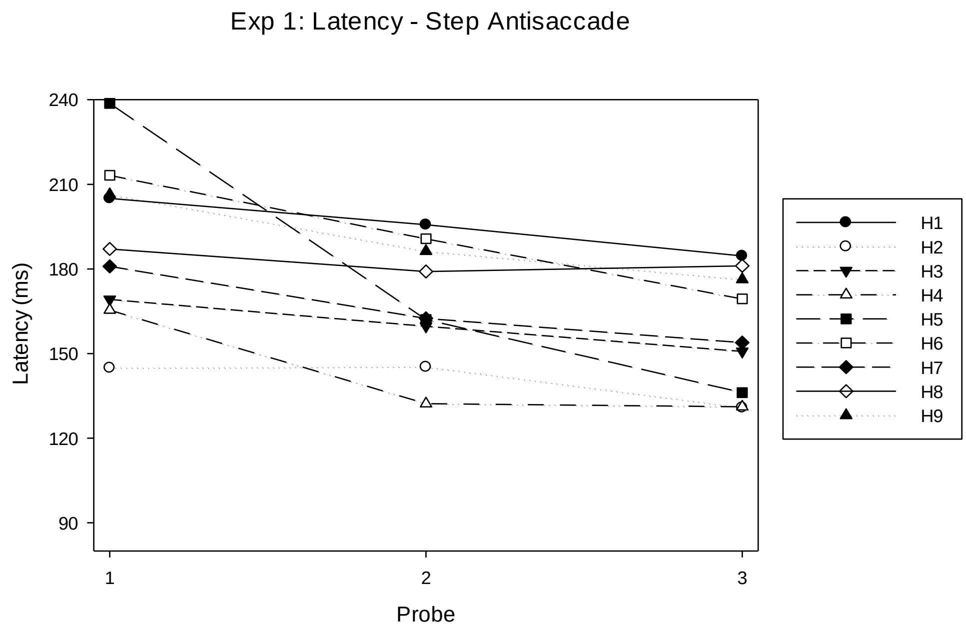

Figure 4: The mean latencies for the 9 subjects in the Step antisaccade task during all 3 Probe sessions.

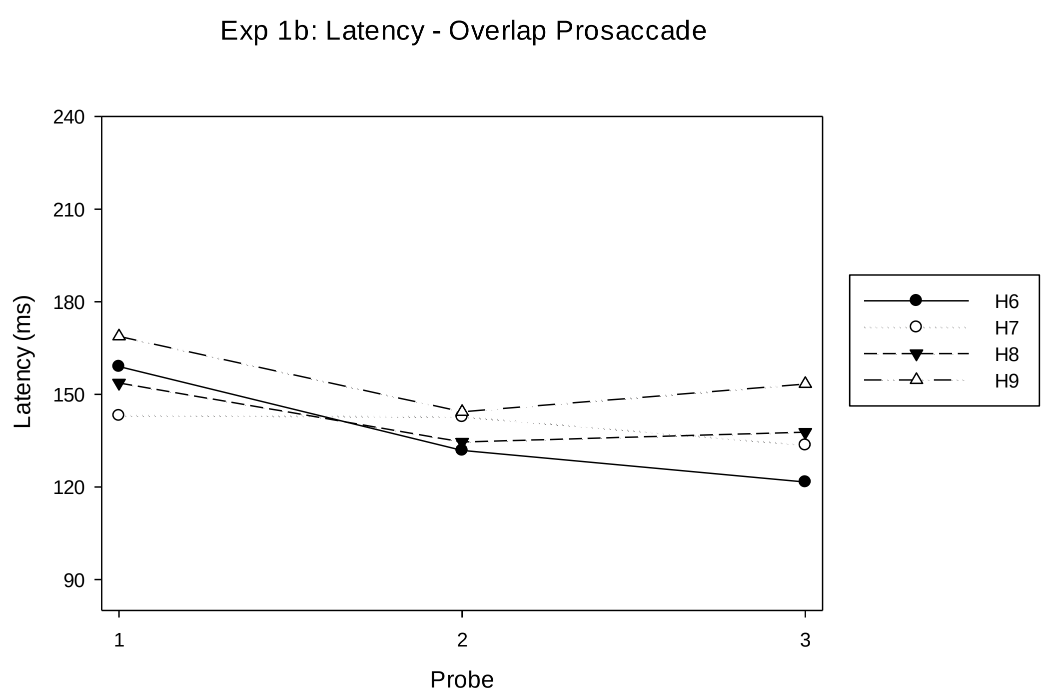

Figure 5: The mean latencies for the 9 subjects who received training in the Overlap prosaccade task during all 3 Probe sessions.

Anticipatory Saccades – In this study, a distinction is made between directional errors and anticipatory errors. Directional errors are those made in an incorrect direction whereas anticipatory errors are defined here as those with reaction time less than 75ms, faster than the minimum time for the oculomotor system to react to the appearance of visual stimulus. After training, subjects tended to make more anticipatory saccades (Fig. 6); in contrast, most tended to make fewer anticipatory saccades in the Step antisaccade task. However, these tendencies seldom reached statistical significance for individual subjects. One individual (H4) made many more anticipatory saccades in both tasks compared to the other subjects. Another individual (H8) made significantly more anticipatory saccades after training.

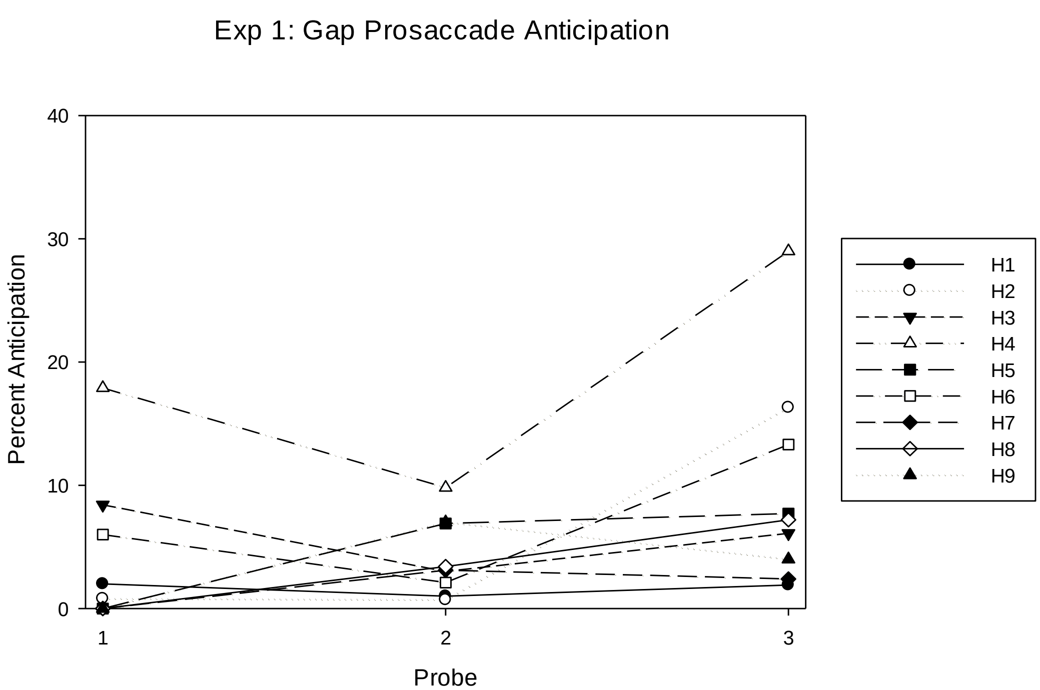

Figure 6: The percentage of anticipatory saccades made during the Gap prosaccade task for 9 subjects.

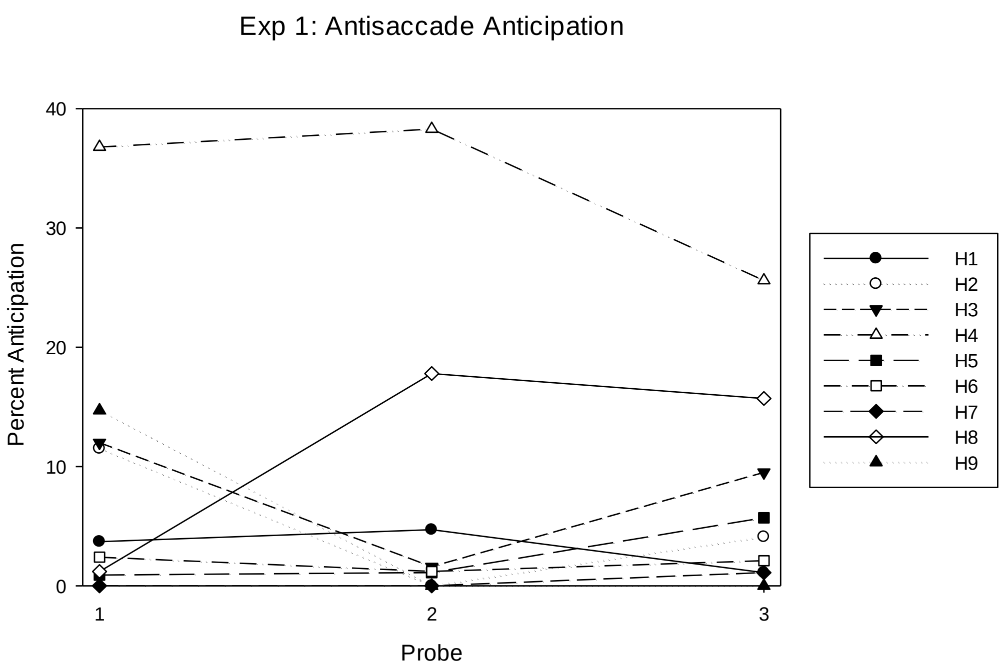

Figure 7: The percentage of anticipatory saccades made during the Step antisaccade task for 9 subjects.

Directional error rate -- The directional error rate here is defined as the percentage of saccades in the incorrect direction (counting only non-anticipatory saccades). The directional error rate in the two Prosaccade tasks did not change significantly due to training for any subject (Fig. 8). The number of errors in these tasks was very low throughout the experiment, however. The trend in the Step antisaccade task (Fig. 9) was more variable, with no subjects showing significant changes in error rate in a chi square test ($p<0.05$). Variability in Antisaccade directional error rate was quite high (Fig. 10).

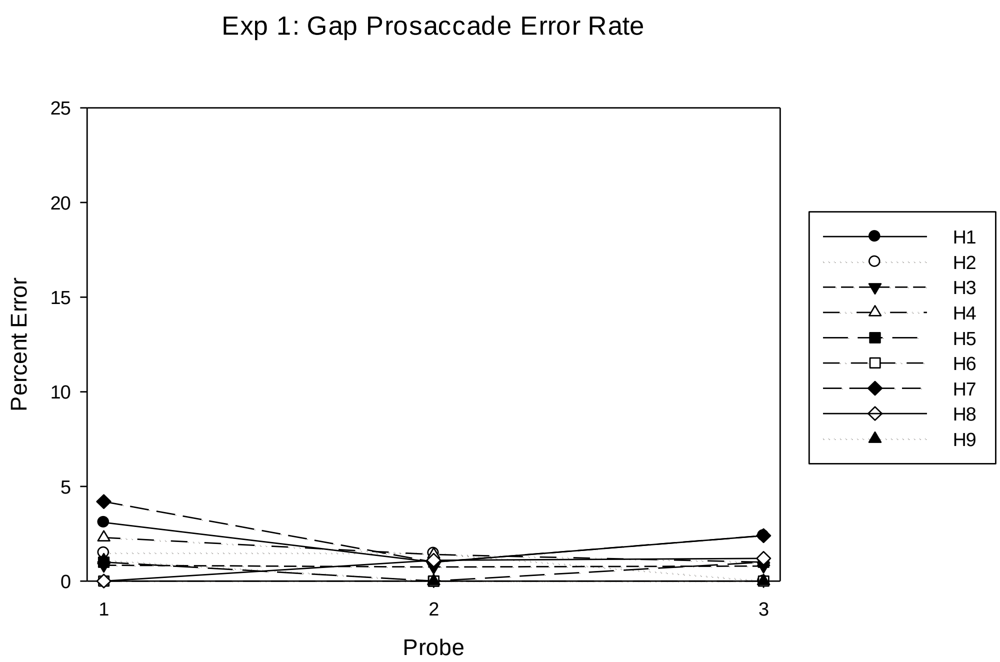

Figure 8: The percent error during the Gap prosaccade task for 9 subjects during all 3 Probe sessions.

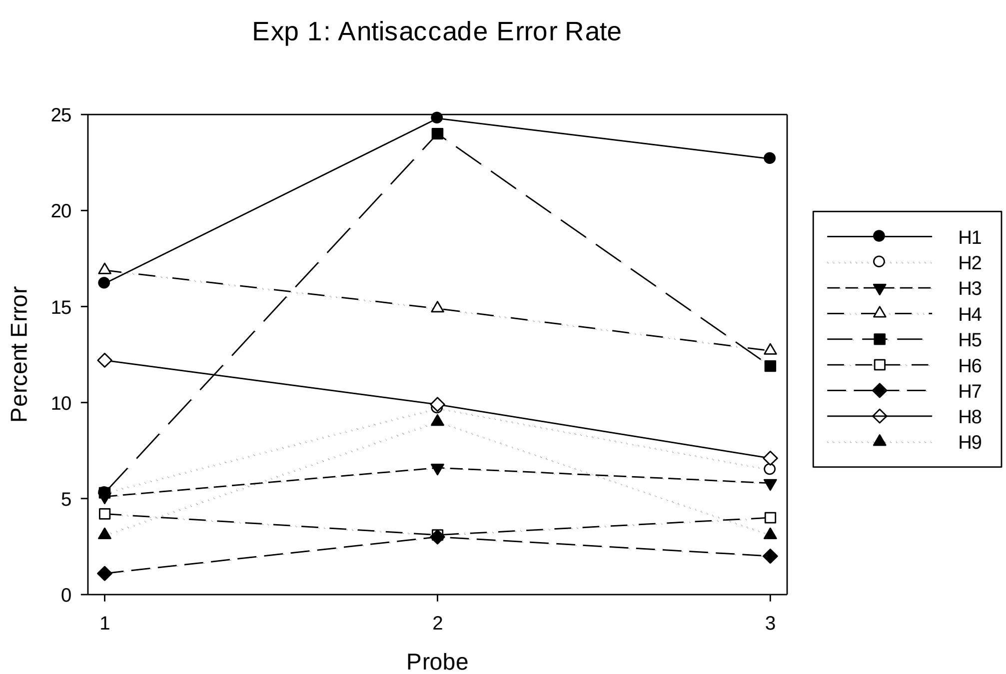

Figure 9: The percent error during the Step antisaccade task for 9 subjects during all 3 Probes sessions.

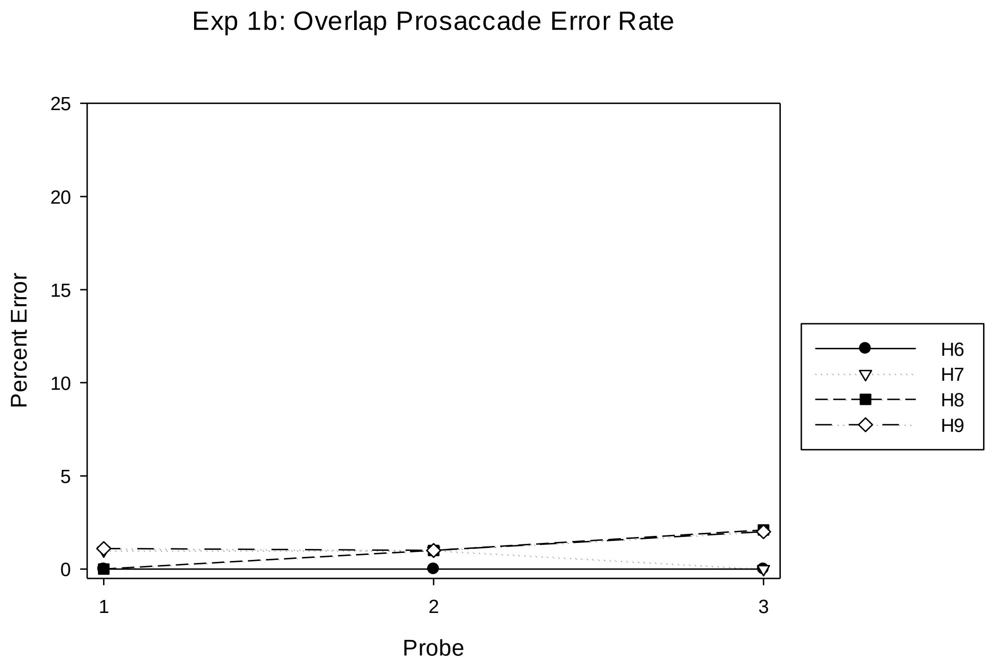

Fig. 10: The percent error during the Overlap prosaccade task for 4 subjects during all 3 Probe sessions.

Experiment 2 – The effect of Step Antisaccade training

Reaction Time -- Not surprisingly, training on the Step antisaccade task led to reductions in saccade latency (Fig. 11). This trend is the same as the one in Expt.1.

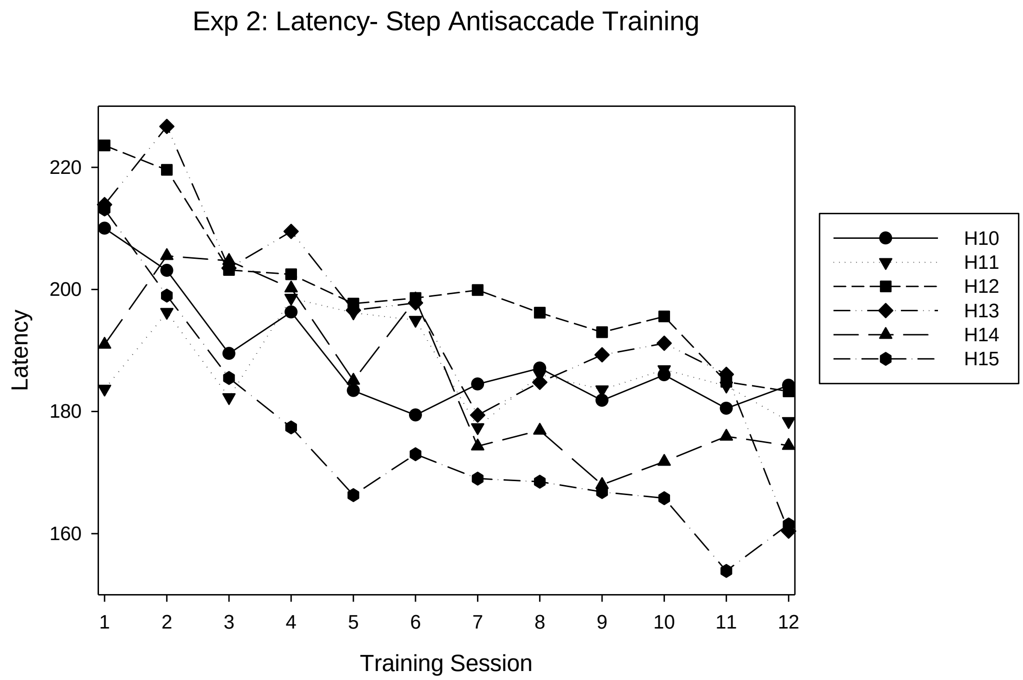

Fig. 11: The mean latency over the course of the training period for the 6 subjects trained with the Step antisaccade task.

The overall distributions of saccades made for two individuals (H12 and H13) before and after training is displayed in Figure 12 a and b. As in Figure 2 a and b, the overall distribution of saccades in the Gap Prosaccade task shifted to lower reaction times; more of these saccades fall within the express latency range (75-120 ms) after training. These individuals also showed an overall increase in overlap latency after training despite improvements in Gap Prosaccade and Step Antisaccade latency.

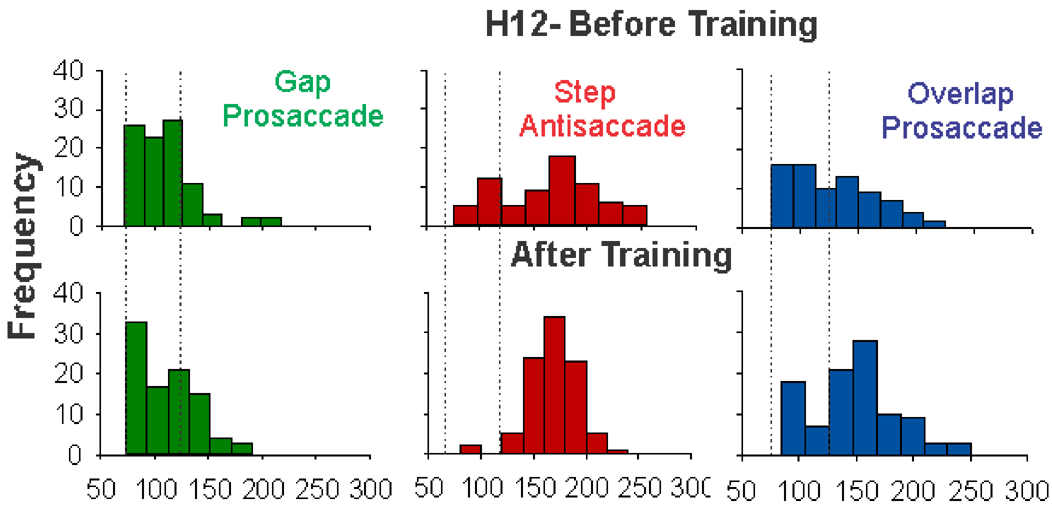

Fig. 12a: The distribution of saccades made before and after training (Probe 1 and 3) for one subject. The two dashed lines indicate the express range (75-120 ms).

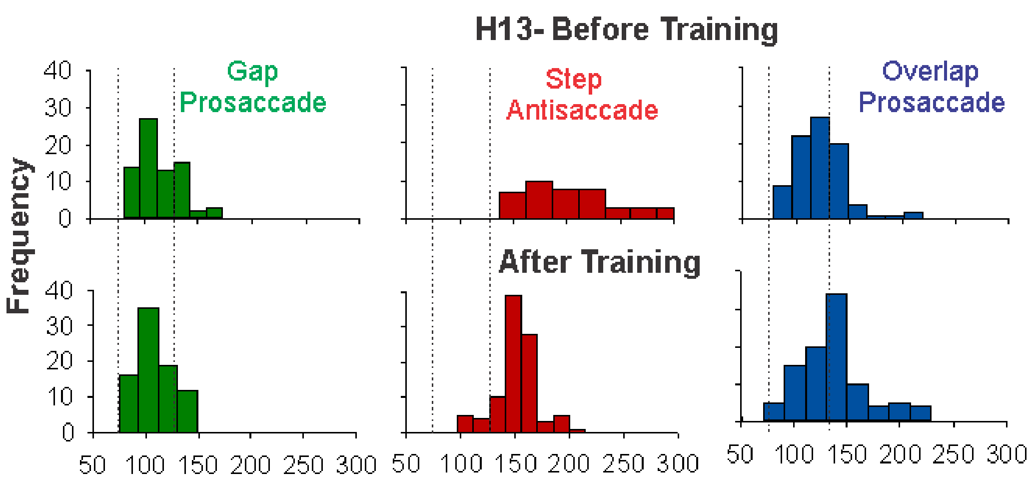

Fig. 12b: The distribution of saccades made before and after training (Probes 1 and 3) for one subject. The two dashed lines indicate the express range (75-120 ms).

The improvement in antisaccade performance was evident across Probe sessions (Fig. 14). As in Expt. 1, this improvement in the trained saccade performance did not come at the expense of large decreases in untrained saccade performance, though improvements in performance did not generalize completely. In particular, latency in the Gap Prosaccade task decreased significantly (P<0.05) for 3/6 subjects, while 2/6 showed small, non-significant increases (Fig.13). Unlike the previous cases, antisaccade training tended to increase Overlap prosaccade latency (Fig. 1). This was significant (p<0.05) in 3/6 subjects. Only one subject showed a significant decrease in reaction time.

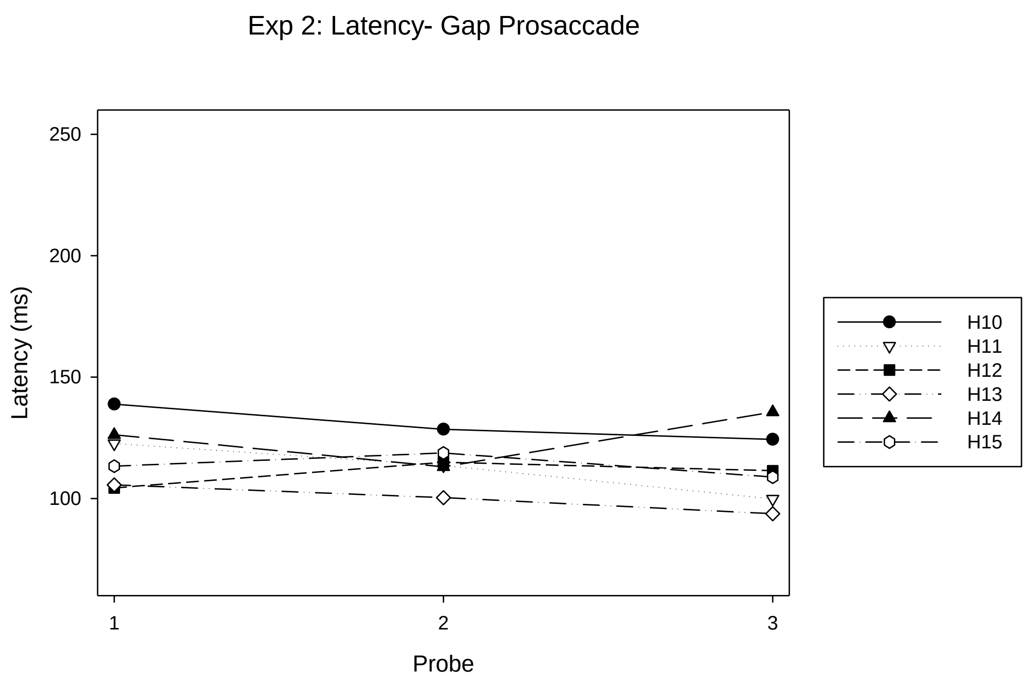

Fig. 13: The latencies for the 6 subjects in the Gap prosaccade task during all 3 Probe sessions.

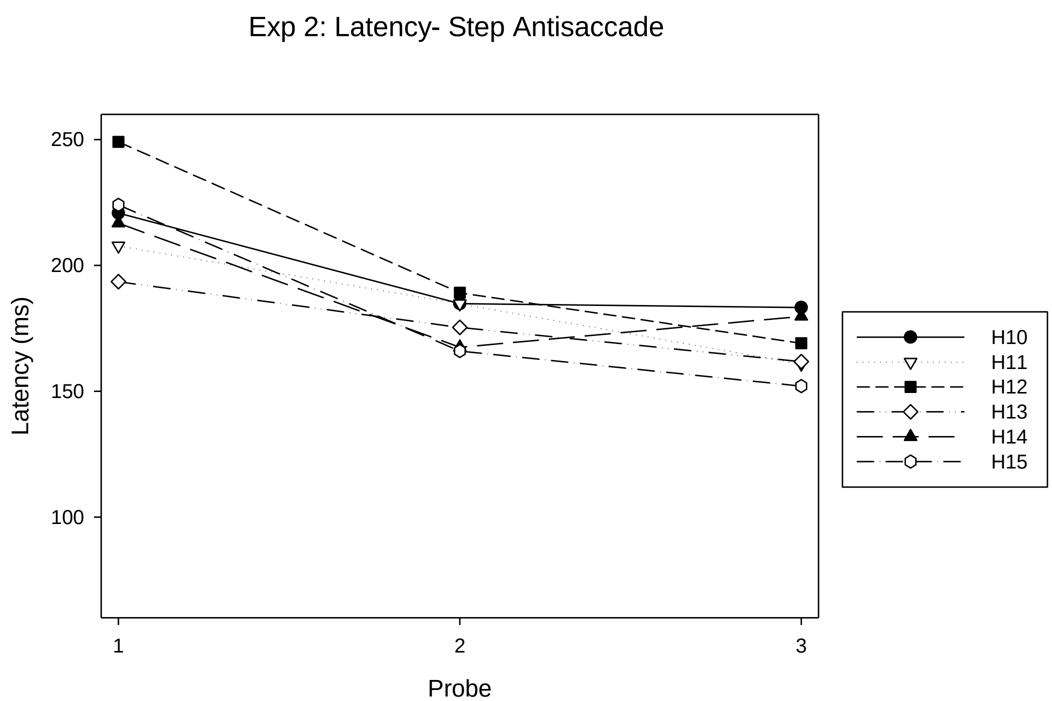

Fig. 14: The latencies for the 6 subjects in the Step antisaccade task during all 3 Probe sessions.

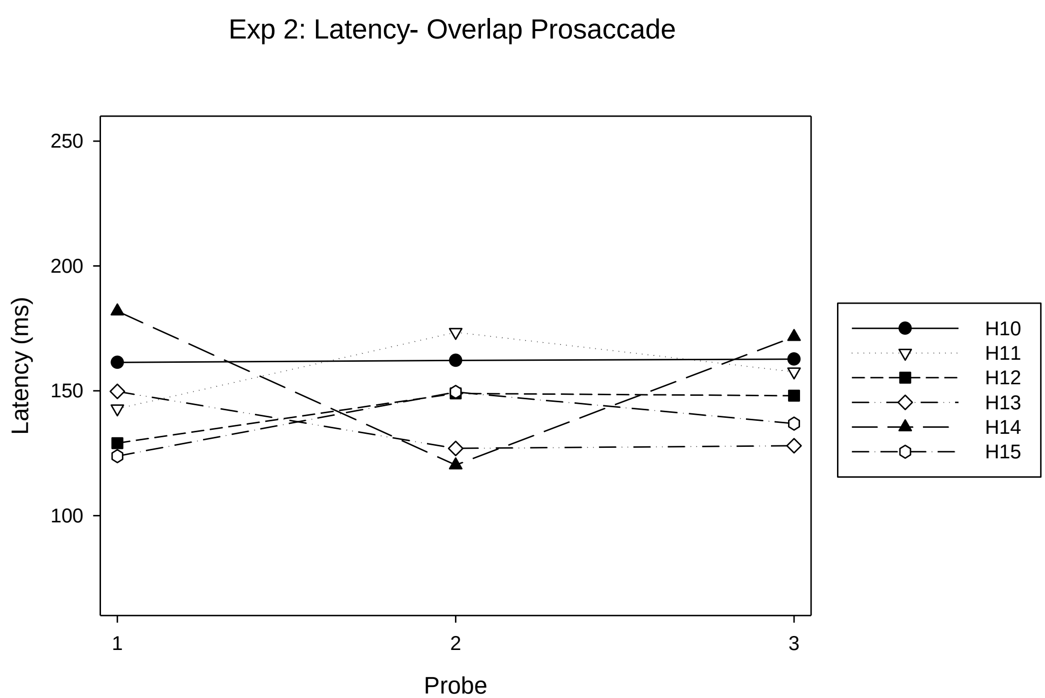

Fig. 15: The latencies for the 6 subjects in the Overlap prosaccade task during all 3 Probe sessions.

Anticipatory saccades -- Surprisingly, antisaccade training led to an overall increase in anticipation in the Gap Prosaccade task (Fig 16), though one subject (H12) showed an overall decrease in anticipatory saccades. There was no change in anticipation for the step antisaccade task (Fig. 17), however, two individuals (H12 and 15) showed an increase in anticipation. This is similar to the findings of Expt. 1 (Fig.5 and 6).

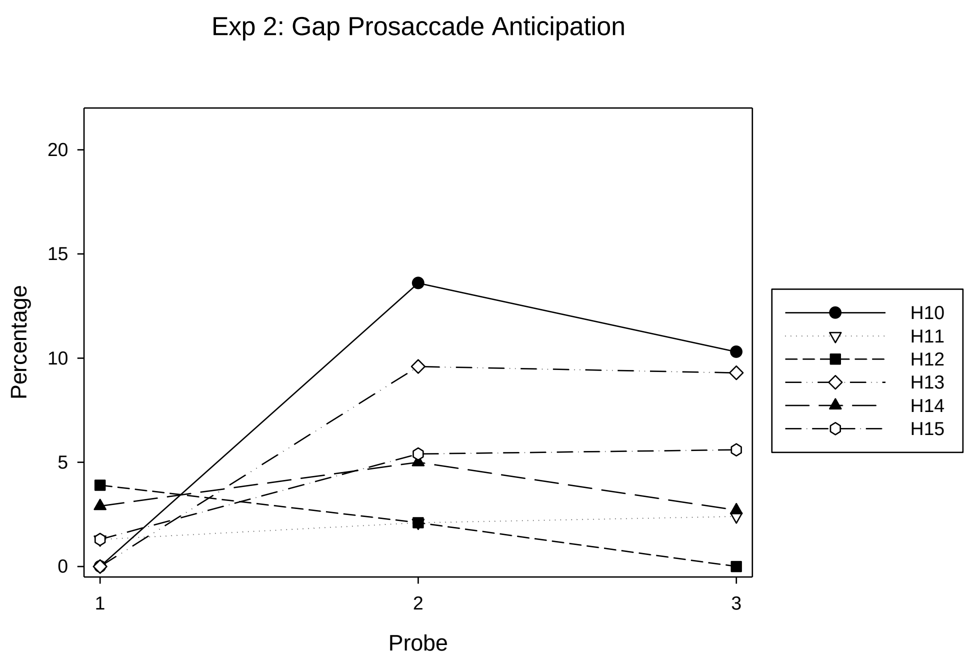

Fig. 16: The percentage of anticipatory saccades made during the Gap prosaccade task for 6 subjects.

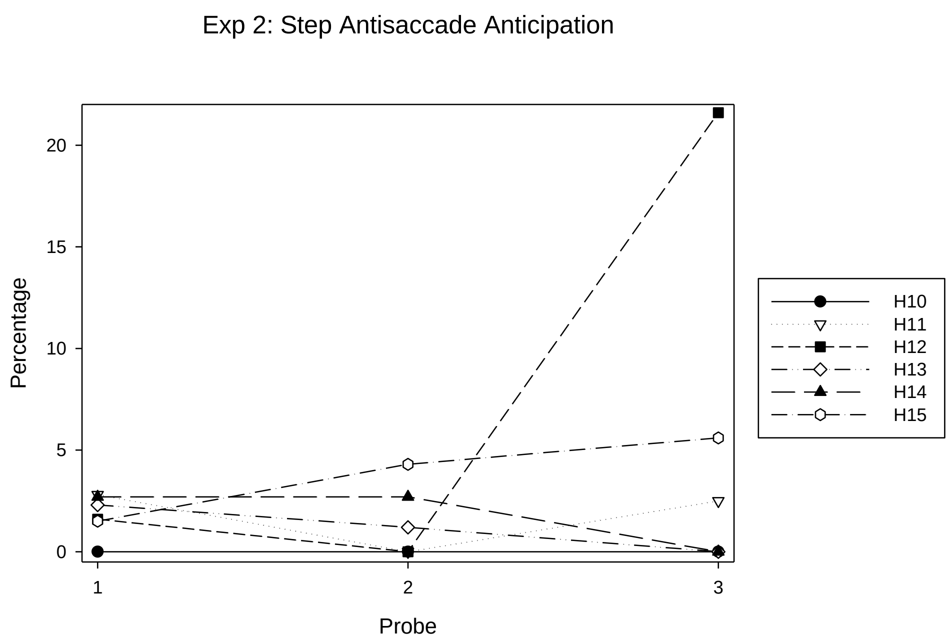

Fig. 17: The percentage of anticipatory saccades made during the Step antisaccade task for 6 subjects.

Directional error rate -- There was an overall reduction in Directional Error rate (Fig 18). In addition, individuals appeared to have higher error rates when the saccade latency was lower.

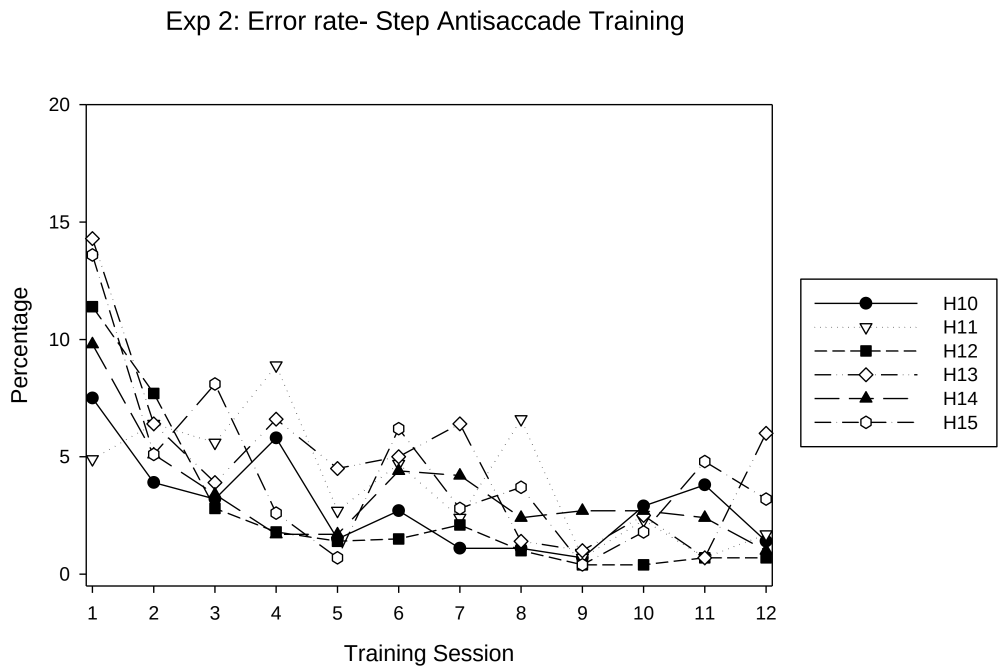

Fig. 18: The percent error over the course of the training period for the 6 subjects trained with the Step antisaccade task.

As was the case for Expt. 1, there was little to no change in Gap Prosaccade directional error rate (Fig 19), but there were very few errors regardless of training. In contrast, there was a clear improvement in error rate in the Step Antisaccade task (Fig. 20). This was significant in a t-test ($p<0.05$) for 4/6 subjects. The remaining 2/6 subjects performed few errors overall. As in Expt. 1, error rate in the Overlap Prosaccade task showed little to no change with training (Fig. 21).

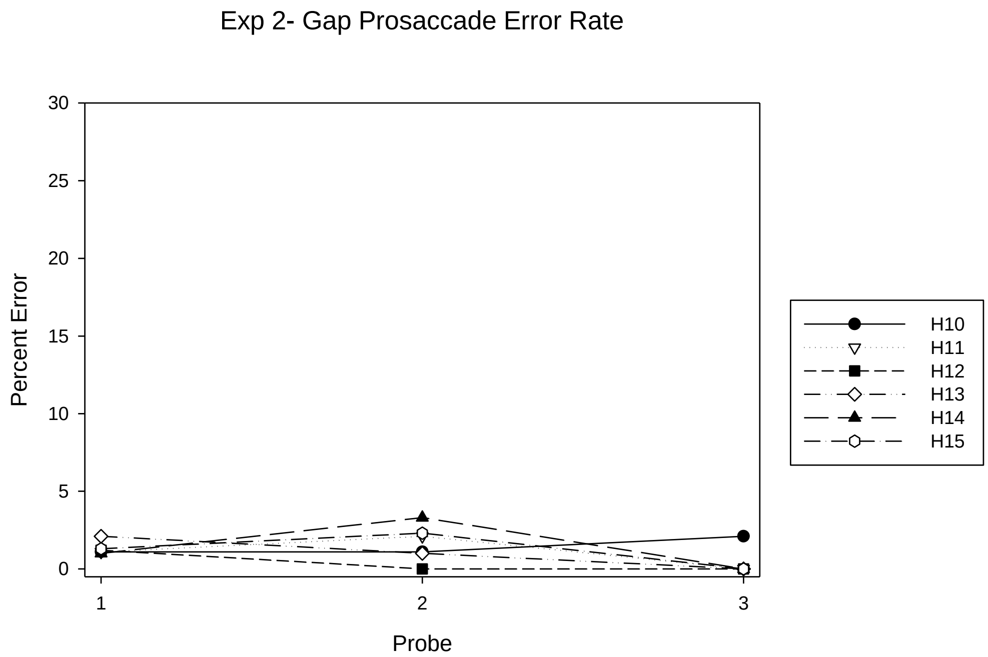

Fig. 19: The percent error during the Gap prosaccade task for 6 subjects during all 3 Probe sessions.

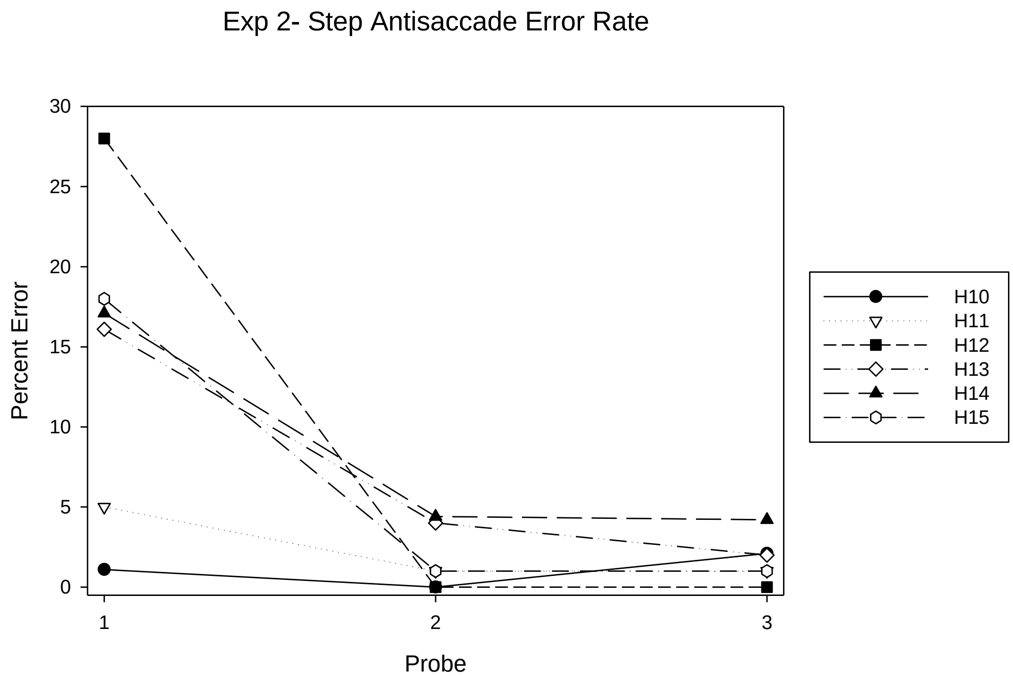

Fig.20: The percent error during the Step antisaccade task for 6 subjects during all 3 Probe sessions.

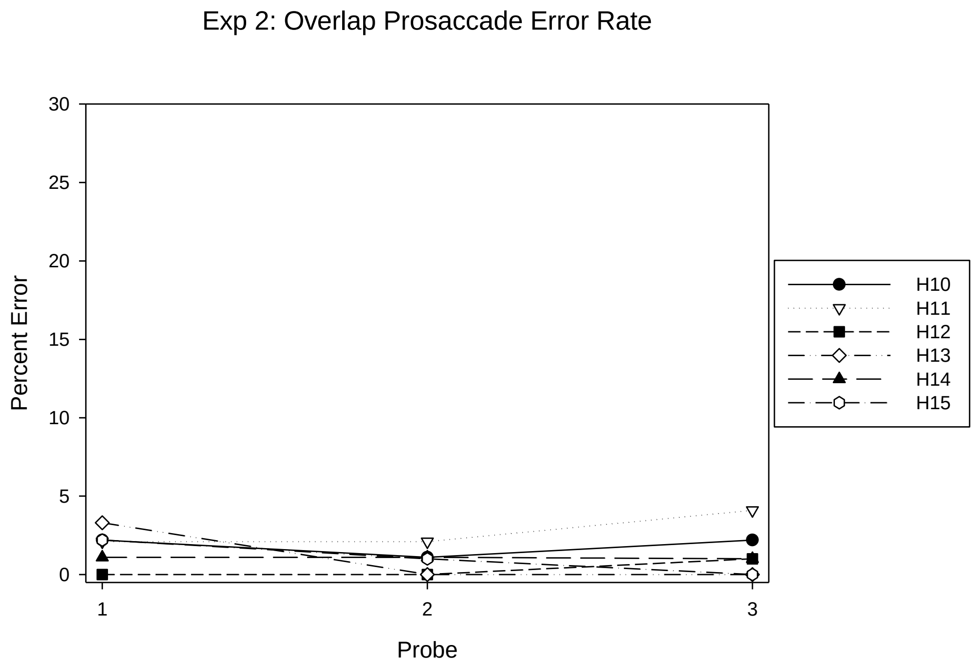

Fig. 21: The percent error during the Overlap prosaccade task for 6 subjects during all 3 Probe sessions.

Experiment 3 – The effect of Gap Antisaccade training

Reaction Time -- In Experiment 3, we examined whether training on a Gap Antisaccade task would improve performance on the Gap Prosaccade more than training on the Step Antisaccade task did. Note that the Gap Antisaccade is particularly challenging, as the gap period is known to facilitate reflexive prosaccades, thus potentially increasing errors in an antisaccade task. As in Expt. 1 and 2, the overall distribution for the trained saccade (Gap Antisaccade in this case) showed decreases in mean latency (Fig.22). Overall, the group performed better with training, as did the subjects who received Gap Prosaccade training (Expt. 1) and Step Antisaccade training (Expt. 2).

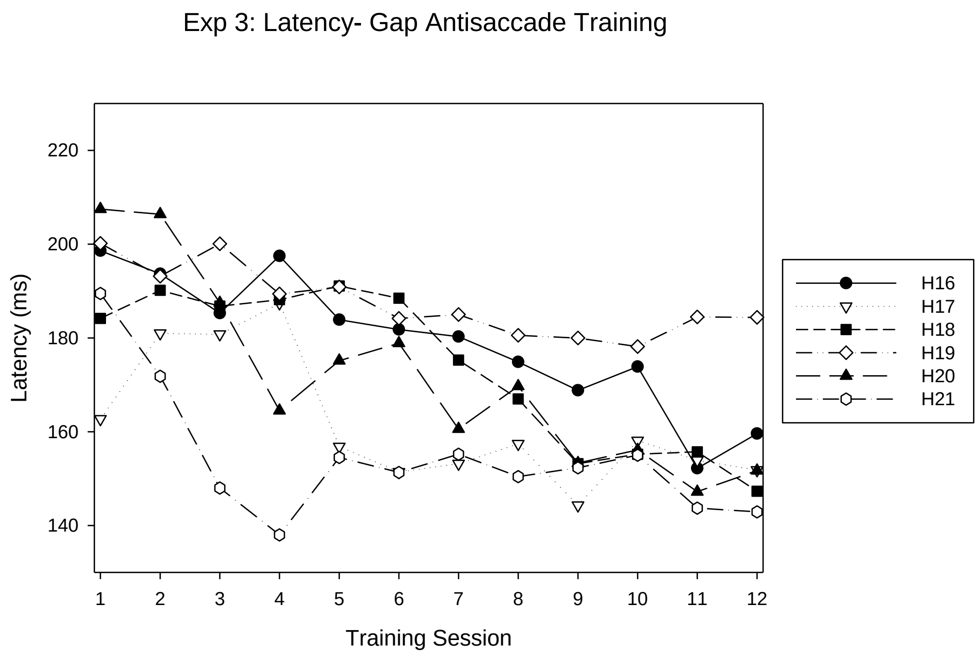

Fig. 22: The latency over the course of the training period for the 6 subjects trained with the Gap Antisaccade task.

As in the previous experiments, the distributions for the saccades performed for two individuals is displayed in Figure 23a and b. In both individuals, the distribution of the Gap prosaccades performed appears to shift and a greater proportion are within the express range. The distribution of the Step antisaccades performed also appear to shift towards lower latencies; overlap prosaccades latency also appears to shift slightly, though to a much smaller degree than the other tasks.

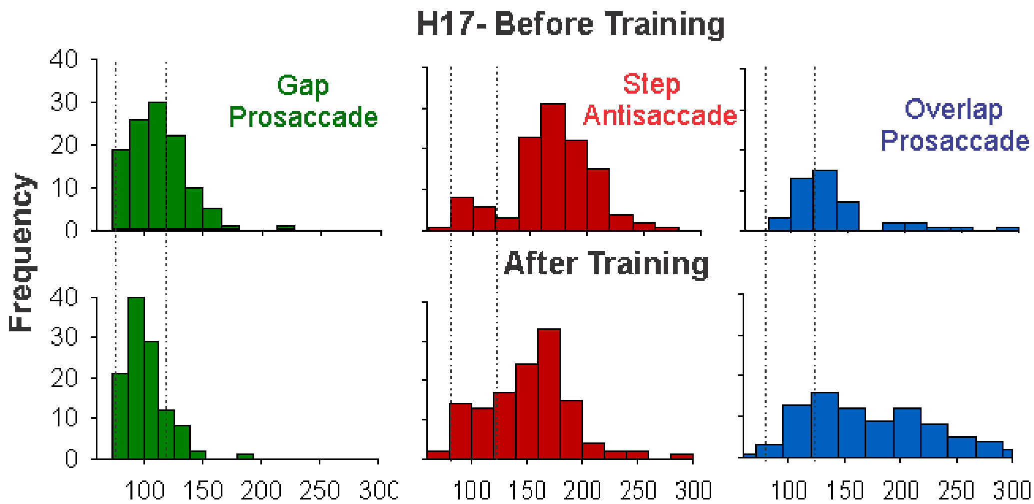

Fig. 23a: The distribution of saccades made before and after training (Probe 1 and 3) for one individual. The two dashed lines indicate the express range (75-120 ms).

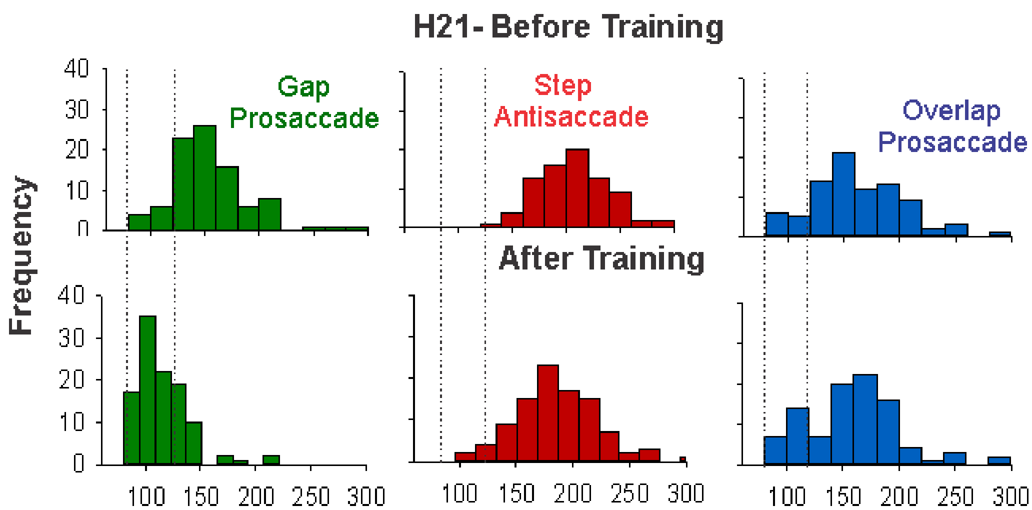

Fig. 23b: The distribution of saccades made before and after Gap Antisaccade training (Probe 1 and 3) for one individual. The two dashed lines indicate the express range (75-120 ms).

A similar trend to the previous two experiments was also observed in this experiment. The overall latency of saccades in the Gap Prosaccade task decreased with training (Fig. 24); this was significant in a t-test ($p<0.05$) for 4/6 subjects. The latency of saccades in the Step Antisaccade task showed significant ($p<0.05$) improvement in all subjects after training (Fig.25).

This is the same trend as seen in both Expt. 1 and 2, in which not only did the trained saccade latency improve in all subjects, but the untrained saccade (except the Overlap Prosaccade task) demonstrated overall improvement as well. In contrast, there was no trend in the Overlap task (Fig.26). Within this group, 2/6 showed significant ($p<0.05$) decreases and 2/6 showed significant ($p<0.05$) increases in latencies after training. Similar to Expt. 2, there was no clear trend in the change in latency observed in the overlap task.

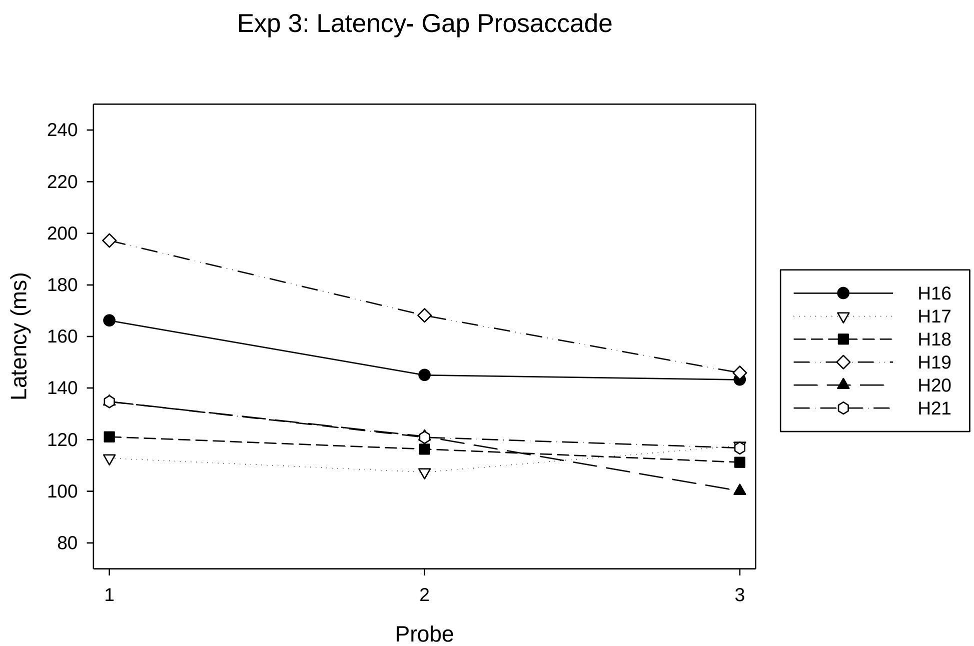

Fig. 24: The latencies for the 6 subjects in the Gap Prosaccade task during all 3 Probe sessions.

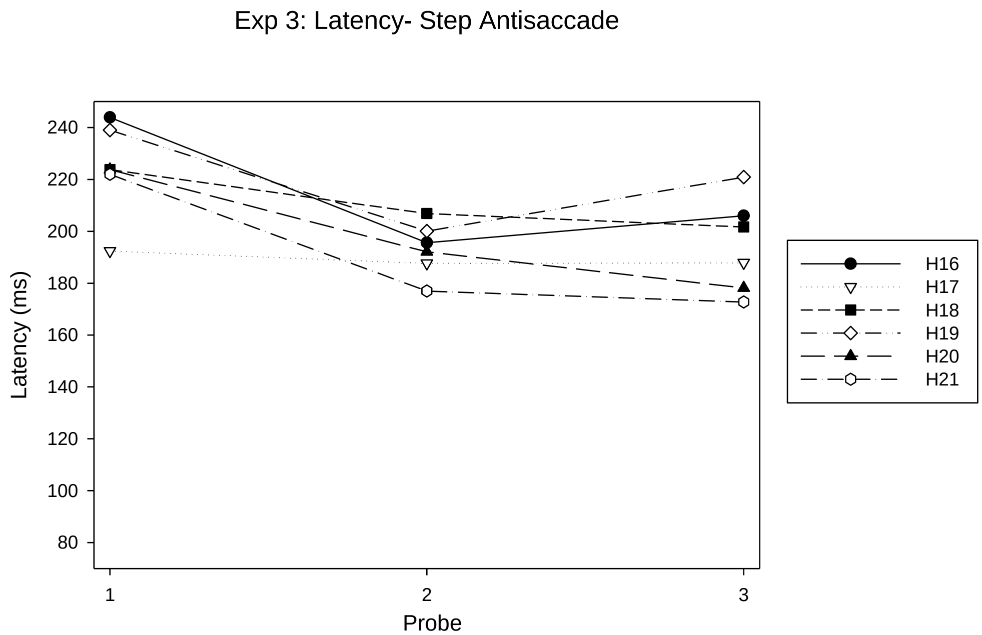

Fig. 25: The latencies for the 6 subjects in the Step Antisaccade task during all 3 Probe sessions.

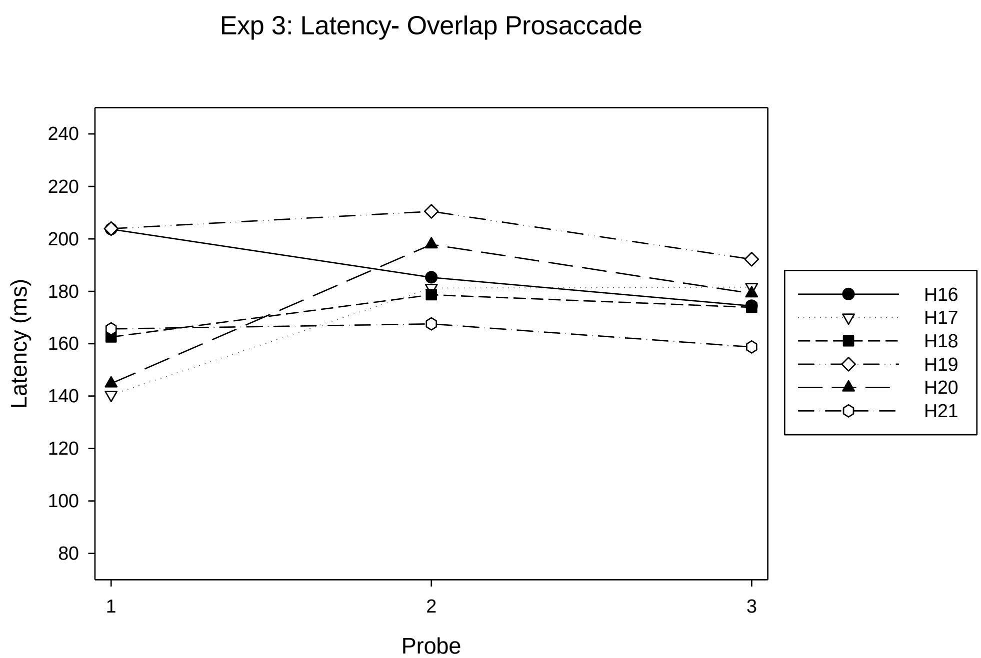

Fig. 26: The latencies for the 6 subjects in the Overlap Prosaccade task during all 3 Probe sessions.

Anticipatory Saccades -- In addition to changes in latencies and error rates, the subjects in this experiment also showed overall more anticipation after training (Fig. 27). This change was also much more pronounced than the change shown in the previous experiments. Additionally, as in Expt. 2, there was a greater change in Gap Prosaccade anticipation after training than the trained antisaccade. With the exception of one individual (H18), all subjects performed more anticipatory saccades in this task. There was no overall change in antisaccade anticipation (not shown due to low numbers of errors).

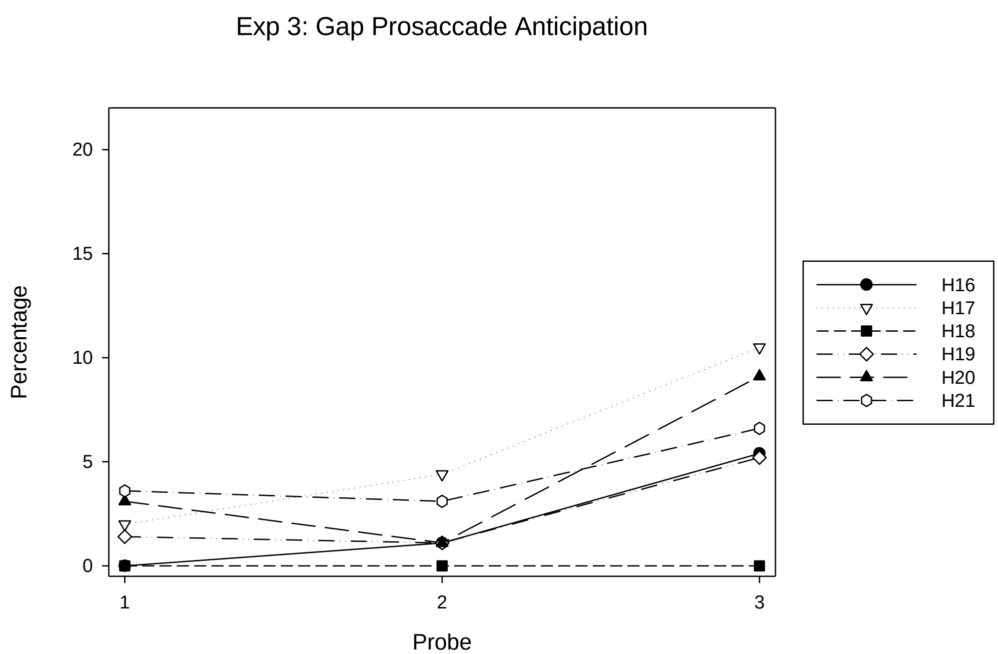

Fig. 27: The percentage of anticipatory saccades made during the Gap prosaccade task for 6 subjects.

Directional Error rate -- As in Expt. 1 and 2, there were overall decreases in error rate (Fig. 28). It can also be noted that during sessions with lower latencies, there is generally a larger error rate. This applies to individual subjects as well; those with overall slower latencies tend to have lower error rates and vice versa.

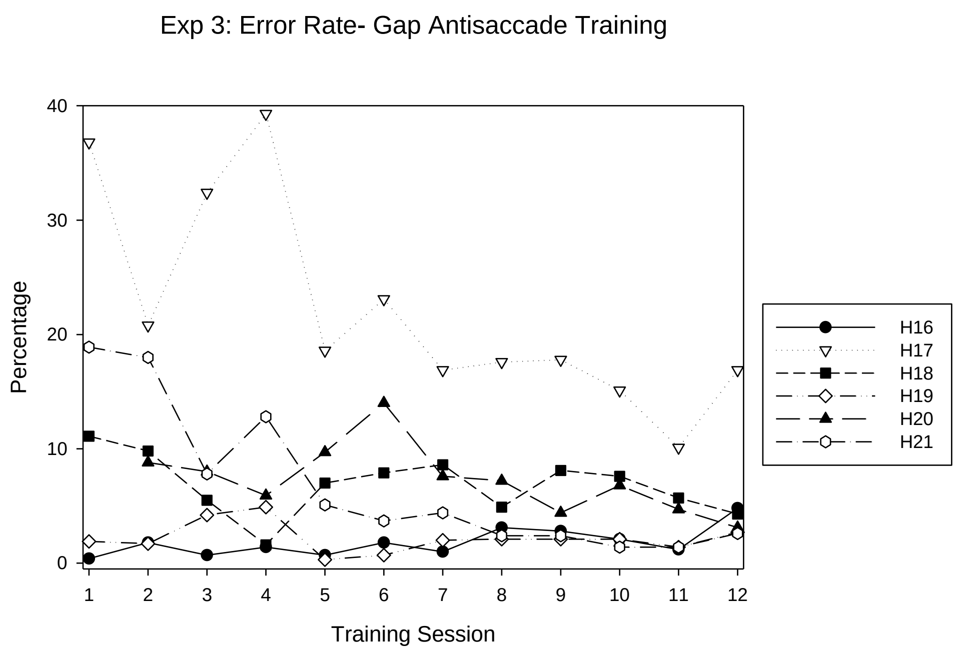

Fig. 28: The percent error over the course of the training period for the 6 subjects trained with the Step antisaccade task.

As in the previous experiments, there was very little overall change in the Gap Prosaccade error rate for all subjects (Fig. 29), however, few errors were made overall as in the previous experiments. In the Step Antisaccade task, 5/6 subjects showed significant improvement in a chi square test ($p<0.05$) for the number of errors performed (Fig.30). One individual (H19) did not perform many errors throughout the experiment. Interestingly, few errors were observed in the Overlap Prosaccade as well (Fig. 31), but there were more errors performed in this task than in the Gap Prosaccade task, albeit slight.

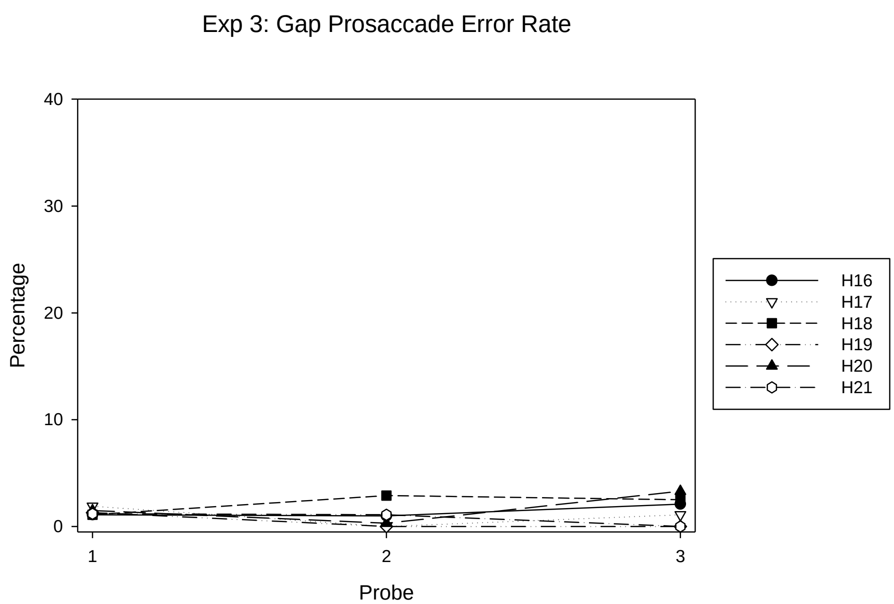

Fig. 29: The percent error during the Gap prosaccade task for 6 subjects during all 3 Probe sessions.

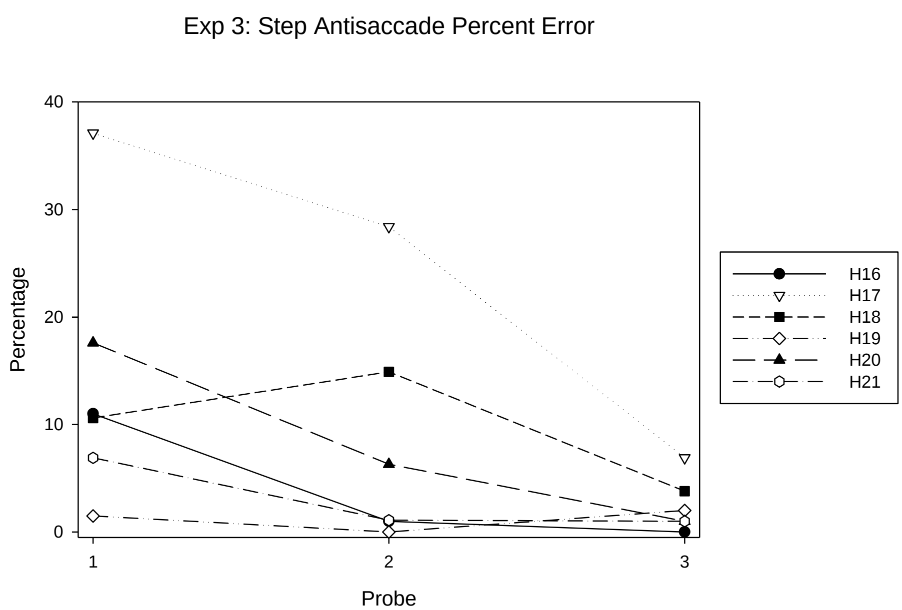

Fig.30: The percent error during the Step antisaccade task for 6 subjects during all 3 Probe sessions

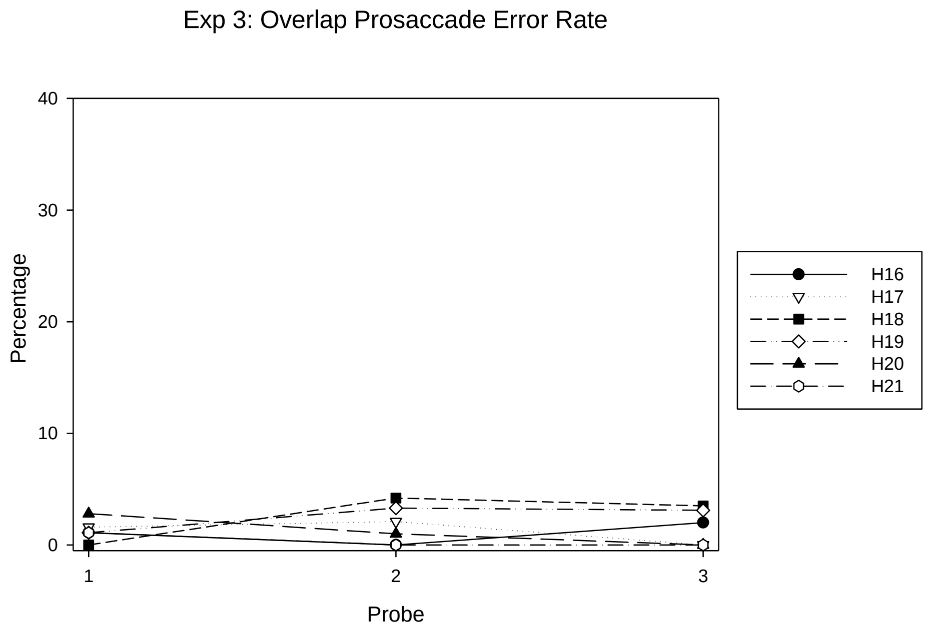

Fig. 31: The percent error during the Overlap prosaccade task for 6 subjects during all 3 Probe sessions.

Discussion

Our results showed that in virtually all cases subjects showed significant improvement after twelve training sessions in the saccade task on which they were trained (Gap Prosaccade in Expt.1, Overlap Antisaccade in Expt. 2 and Gap Antisaccade in Expt. 3). This improvement agrees with previous observations (Bibi and Edelman, 2009) which showed that training in a gap saccade task led to improvements in performance. This is evident both in the change in latencies during Training (Figs. 1, 11 and 22), as well as the improvement in error rates (Figs. 12 and 23). Moreover, there was often a generalized improvement, training either improved or had little change on untrained saccade types. The improvement in the trained saccade reaction time are larger than those for untrained saccades, indicating that transfer may be incomplete. Incomplete transfer was particularly evident for Overlap Prosaccades, with latency increasing significantly with training ($P<0.05$) for 3/6 subjects after Step Antisaccade training in Expt. 2 (Fig. 16) and for 2/6 subjects after Gap Antisaccade training in Expt. 3 (Fig. 27). However, 2/6 individuals experienced significant ($P<0.05$) improvements in Overlap Prosaccade latency with Gap Antisaccade training, but only 1/6 with Step Antisaccade training.

Improvements in performance also did not generally come at the expense of large increases in errors of saccade direction, where the saccade was made in a direction opposite to that dictated by the task. Antisaccade training did not increase errors on Prosaccade tasks, though these tended to be very low prior to training. With the exception of one subject, individuals trained with the Gap Prosaccade task (Expt.1) did not show any significant change in error rate in any task. Individuals trained with the Antisaccade task (Expt. 2 and 3) demonstrated significant ($p<0.05$) improvement in antisaccade error rate while showing little to no change in Prosaccade tasks. Overall, 4/6 and 5/6 individuals demonstrated significant ($p<0.05$) improvement in antisaccade error rate in the experiments involving antisaccade training (Expts 2 and 3). More surprising is that despite this antisaccade-specific training, directional errors in the Prosaccade task tended to remain low.

Contrary to the observations in this study, other studies have observed a decrement in both antisaccade latency and error rate with prosaccade training (Dyckman and McDowell, 2005). It is possible that such studies observed this as a result of less training. This study implemented a longer period of training with more trials per session. It is also possible that having a longer time in between sessions (1-2 days between sessions compared to daily practice) allowed the subject to adjust to the training better.

One possibility for the overall decrease in latencies in this experiment is that over the course of several training sessions, the subjects become more comfortable with the experimental procedure and the general ability to make saccadic eye movements in a laboratory task. It is possible that this ability transferred to the subjects' ability to produce untrained saccades. Based on the decrease in latency of the saccade types that were not trained (specifically the Gap Prosaccade and Step Antisaccade), it is likely that a general effect of facilitation in saccade production occurred. As more improvement was seen in Overlap Prosaccade task in the group trained with the Gap Antisaccade (Expt. 3) compared to that trained with the Step Antisaccade (Expt. 2), it may be that the use of the gap allows subjects to learn to lower fixation related activity. It would then follow that the Overlap improvement in Expt. 1 was due to the combination of training with both the gap and the pro-direction. Overall, untrained Gap Prosaccades were affected similarly by Step Antisaccade and Gap Antisaccade training, with reaction times decreasing modestly, suggesting that the addition of the gap to the antisaccade training protocol had little impact. In particular, Step Antisaccade training (Expt.2) resulted in a significant ($p<0.05$) increase in 3/6 subjects compared to the 4/6 after Gap Antisaccade training (Expt. 3).

If training on Gap Prosaccades resulted in increases in visual activity, or more specifically, visual inputs into the motor system, then antisaccade performance in Expt. 1 should have worsened, since increases in visual responses would have increased error rates. Likewise, if training on Step or Gap Anticasccades caused decreases in visual inputs to the motor system then training in Expts. 2 and 3 should result in increases in reaction time in prosaccades. Other than a slight increase in latency in some subjects in the Overlap task in Expts. 2 and 3, these patterns of generalized excitation and inhibition did not occur, suggesting that the visual interface into the motor system was not the locus of changes due to the training protocol used here. As inputs from visual and parietal cortices to the SC provide most of the visual input to the saccadic system, it is thus likely that these cortical areas are little affected by training.

It is possible that the results reported here are due at least in part to improvements in the ability to disengage fixation. The absence of a gap in Expt. 2 seemed to allow for the improvement of latency in both the Gap Prosaccade and Step Antisaccade tasks, but not for the improvement in Overlap Prosaccade latency. It may be that training here led to an improvement in the ability to generate a saccade, but not in the ability to disengage, which then delays saccade execution. It is uncertain whether the presence of the gap caused an improvement in fixation, however, as only 2/6 subjects in this experiment demonstrated significant ($p<0.05$) Overlap Prosaccade improvement (Fig. 27). In Experiment 1, it is likely the combination of both the gap and saccade training enabled an improvement in all 3 tasks.

One unintended side effect of an increased ability to disengage fixation is an increased tendency to generate anticipatory saccades. In all three experiments, the percentage of anticipatory Gap Prosaccades increased after training. Anticipatory saccades were evident mostly in the Gap Prosaccade task, but also in the Step Antisaccade task. Interestingly, more anticipatory saccades were observed in the Step Antisaccade tasks in Expt. 1 and 2 than were in Expt.3 when the subjects had been trained with Gap Antisaccades. The percentage of anticipatory saccades performed varied greatly between subjects (between 0 and 36.8% across all individuals). The presence of the gap increases adaptation since subjects are more likely to anticipate target location when no stimulus is present on the screen.

If fixation disengagement is being improved in Expt. 1 and 3, it is possible that neurons in the FEF, an area which has been shown to be involved in disengaging fixation (Dias and Bruce, 1994), are becoming more efficient with gap training (see also Bibi and Edelman, 2008). Such an improvement may be sufficient to improve the overall latency of saccade generation regardless of trial type as shown here. Moreover, previous work has shown that in the FEF, greater activity has been shown to be associated with faster reaction times during saccade generation (Everling and Munoz, 2000). Another area which has been associated with reaction time include the SC, however, it is thought to be related to reflexive saccade generation; greater activity in this area is also thought to correlate with reduced latencies (Neggers et al., 2005). Given the importance of the FEF for saccade generation, it is possible that the training studied in this paper has an effect on this area of the frontal cortex.

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