THE INFLUENCE OF MOTOR TRAINING ON HUMAN EXPRESS SACCade PRODUCTION

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ABSTRACT

Express saccadic eye movements are saccades of extremely short-latency. In monkey, express saccades have been shown to occur much more frequently when the monkey has been trained to make saccades in a particular direction to targets that appear in predictable locations. Such results suggest that express saccades occur in large number only under highly specific conditions, leading to the view that vector-specific training and motor preparatory processes are required to plan a saccade of a particular magnitude and direction. To evaluate this hypothesis in humans, we trained subjects to make saccades quickly to particular locations, and then examined whether the frequency of express saccades depended on training and the number of possible target locations. Training significantly decreased saccade latency and increased express saccade production to both trained and untrained locations. Increasing the number of possible target locations (2 vs. 8 possible targets) led to only a modest increase of saccade latency. For most subjects, the probability of express saccade occurrence was much higher than that expected if vector-specific movement preparation were necessary for their production. These results suggest that vector-specific motor preparation and vector-specific saccade training are not necessary for express saccade production in humans and that increases in express saccade production are due in part to a facilitation in fixation disengagement or else a general enhancement in the ability of the saccadic system to respond to suddenly appearing visual stimuli.
INTRODUCTION

Saccadic eye movement responses to suddenly appearing visual stimuli have been used frequently as a model system for understanding how sensory responses are processed to create motor commands. In particular, the measurement of saccadic reaction times has been used to gain insight into the sensory, decision-related, and premotor processes involved in the generation of a sensorimotor response.

The minimum reaction time for a saccade elicited by a visual stimulus can, in principle, be calculated from a consideration of the neural delays evident in the shortest pathway leading from the retina to cerebral cortex and down to the oculomotor plant. Saccades of minimal latency (70-100 ms in monkey, somewhat longer in human) have been termed “express saccades” (Boch and Fischer 1986; Boch et al. 1984; Fischer and Boch 1983; Fischer et al. 1984). Evidence that express saccades have a near-minimal latency comes from electrophysiological recordings in the macaque superior colliculus (SC). For longer latency saccades, neurons in the deeper layers of the SC discharge in temporally separate bursts corresponding to visual and pre-saccadic responses (Sparks and Hartwich-Young 1989). For saccades of express latency, however, these bursts of activity are more or less merged in time, suggesting that the visual response immediately triggers the saccade, without any time for lengthy pre-saccadic visual analysis to occur (Dorris et al. 1997; Edelman and Keller 1996; Sparks et al. 2000). Express saccades are much more likely to occur in a gap paradigm, in which the fixation point disappears 100-200 ms prior to target appearance, than when the disappearance of the fixation point and appearance of the visual target occur simultaneously (Saslow 1967). In monkey, the reaction time distribution is often bimodal, with express saccades composing a distinct peak (Dorris et al. 1997; Edelman and Keller 1996; Fischer and Boch 1984; 1983; McPeek and Schiller 1994; Paré and Munoz 1996; Sommer 1994; 1997).
While use of the gap paradigm reduces saccade latency, it does not guarantee prolific express saccade generation. Express saccades have been shown to occur much more frequently when a monkey has had repeated training in a gap paradigm at making saccades with a particular gaze direction and amplitude (Boch and Fischer 1986; Fischer et al. 1984; Schiller and Haushofer 2005). They have also been shown to be more likely to occur when the monkey knows the approximate location at which the target will appear, and, in general, when there are a smaller number of possible target locations (Rohrer and Sparks 1993). This has led to the “motor preparation” hypothesis of express saccade production, which proposes that the preparation of a saccade to a particular region of space is necessary for express saccades to be generated (Dorris et al. 1997; Paré and Munoz 1996). Here, the phrase vector-specific motor preparation will refer to the motor preparatory processes required to plan a saccade of a particular magnitude and direction. Neurophysiological investigations of activity in the superior colliculus suggest that the use of a gap paradigm disengages fixation by reducing activity of neurons that may inhibit saccade generation, in particular the “fixation” neurons located in the rostral pole of the superior colliculus (Munoz and Wurtz 1993; 1992). Although the level of activity of fixation neurons appears to reflect the presence of a visible stimulus at fixation, the extent of the reduction in their activity does not appear to correlate with the probability of making an express saccade. Rather, the probability of express saccade occurrence correlates more closely with the level of low-frequency activity of neurons in the more caudal superior colliculus that codes for the impending saccade (Dorris et al. 1997). One purpose of the current study is to test whether vector-specific motor preparation is necessary for prolific human express saccade production, or whether instead a less spatially specific ability to generate express saccades can be developed.

In human, the existence of a distinct population of express saccades as a class of true sensory-driven movements, rather than anticipatory responses, remains controversial.
Whereas some investigators have reported that a separate population of express saccades exists, as evident in a saccade latency histogram (Carpenter 2001; Fischer and Ramsperger 1984; Fischer et al. 1993; Juttner and Wolf 1992), others have failed to observe the bimodality seen in humans, and find very fast responses (< 110 ms) only when subjects can anticipate where and when the target will appear (Fischer et al. 1993; Kalesnykas and Hallett 1987; Kingstone and Klein 1993b; Reuter-Lorenz et al. 1991); still others find unimodality in the absence of target predictability (Edelman et al. 2007; Trottier and Pratt 2005; Wenban-Smith and Findlay 1991). An early study of express saccades in human examined the effects of vector-specific training and motor preparation on express saccade production, showing that latencies decreased over several sessions of training, including saccades with vectors that were not specifically trained (Fischer and Ramsperger 1986). However, these results are difficult to interpret as their latency cutoff for classifying an express saccade was 135 ms, much later than would be considered analogous for express saccades in monkey, and probably too long to be driven by a visual-related burst of discharge in the superior colliculus.

A recent study in our lab using video-oculography, which allows the monitoring of both horizontal and vertical components of eye position with high fidelity, demonstrated that well-trained subjects make numerous express saccades (latencies as low as 80 ms) to one of six unpredictable positions across a wide variety of directions in a gap task (Edelman et al. 2007). However, in that study the two subjects who were adept at generating express saccades had extensive training with the gap task over the course of weeks or months, leaving uncertain whether human express saccades only emerge after long periods of training in a laboratory setting.

It is possible that training humans to make short latency saccades is less arduous than training monkeys. Humans are easier to motivate and are likely to respond more quickly to behavioral feedback to improve their performance. In the present study we explored whether
humans naïve to oculomotor experiments could make express saccades with only modest periods of training, and do so even in a task where saccade target location was highly unpredictable. We reasoned that training to reduce saccade latency could result in a generalized increase in the sensitivity of the saccadic system to the sudden appearance of visual stimuli, rather than shorter latencies only for saccades of a particular vector. This increased sensitivity could prove useful to the saccadic system by providing flexibility in responding to targets regardless of their location or of previous experience making saccades of a particular vector.

METHODS

Nine 18- to 21-year-old subjects who were naïve to the purpose of this experiment and who had never taken part in an eye movement study participated. Experiments were conducted under a protocol approved by The City College of the City University of New York Institutional Review Board (IRB).

White squares (100 cd/m²) were presented on a computer monitor at 85 Hz controlled by the Vision Shell (Raynald Comtois) video display software package running on a Macintosh G4. The luminance level of the background was set to its minimum. Eye movement data were collected using video oculography (Eyelink II – SR Research) at a rate of 500 samples/s. Subjects were seated comfortably at a distance of 60 cm from the computer monitor. Each subject’s head was stabilized during each experimental session by the use of cheek and chin rests. Experimental sessions were preceded by a 9-point (3 x 3) eye movement calibration procedure. Subjects sat in a room lit from above with fluorescent light and enclosed within a black curtain. The monitor had a low-reflectance screen and care was taken to minimize visible reflections.
Experimental Design

We examined whether training subjects to make express saccades with directions either along the horizontal or vertical axis would enhance subjects’ ability to make express saccades in other directions. Our approach was first to test subjects’ saccade latencies in both horizontal and vertical directions, then train them to make either horizontal or vertical saccades, then examine how this training affected horizontal, vertical, and diagonal saccades. Two types of experimental sessions were conducted: Probe sessions and Training sessions. (Fig. 1)

Probe sessions assessed saccade latencies of various directions before, during, and after training. They consisted of trials in which subjects first were required to fixate a small square point (0.30°) in the center of the display for 500-800 ms, after which the fixation point disappeared; 150-200 ms later, a 2° square target appeared. Subjects were instructed to make a saccade to the target as quickly and accurately as possible. The target remained present until 300 ms after the end of the saccade. Subjects were required to hold fixation at the target until it disappeared. After a 700-ms intertrial interval, the next trial began.

The possible target locations in a block of trials during a Probe session depended on the trial type. Horizontal blocks consisted of trials in which targets appeared randomly in two possible locations, either at 8° to the right or left relative to the center of the screen. Vertical blocks consisted of trials in which targets appeared randomly in one of two vertical positions 8° above or below relative to the center of the screen. Eight-location blocks consisted of trials in which targets appeared randomly at an 8° eccentricity at one of eight cardinal and diagonal directions relative to the center of the screen.

If a saccade occurred sooner than 60 ms or later than 400 ms after target appearance, or if a saccade landed outside a circular region 4° radius centered on the center of the target, a beep sounded and the screen blanked until the next trial. Each Probe session consisted of 12 blocks of twenty-four trials per block: 3 Horizontal Blocks, 3 Vertical Blocks, and 6 Eight-location
Blocks. A Probe session was performed before the first session, after six Training sessions and, for almost all subjects (see below), upon completion of all twelve Training sessions. To help reduce saccade latency and increase the awareness of a subject’s performance, after each trial a number appeared next to the target location that indicated the saccade’s reaction time. (Kingstone and Klein 1993b).

Training sessions had trials identical in temporal format as those in the Probe sessions, but only a single block type (Vertical or Horizontal) was used for all 12 blocks (288 trials) within the session. All subjects, except one (described below), participated in twelve Training sessions and three Probe sessions. Five subjects were trained on horizontal saccades and four were trained on vertical saccades.

Both Probe and Training sessions lasted approximately 20 minutes.

Data analysis
Saccade latency

To compute the latency (reaction time) of each saccade, we first calculated saccade radial velocity by differentiating the horizontal and vertical components of the eye position trace using a central difference algorithm implemented in Matlab (MathWorks) and then using the Pythagorean Theorem to calculate the saccadic speed as a function of time. To determine saccade onset, we identified in the eye position trace the time at which velocity first exceeded 35 deg/s after target onset; the start time was defined as the first prior point during which velocity fell below 10 deg/s. Saccade latency was defined as the difference in time between target appearance and the start time. As stimuli were presented on a CRT, we took the vertical stimulus position into account when calculating saccade latency.

The Wilcoxon ranksum test was performed on differences in median reaction time between conditions within a particular subject. To test differences in proportions of express
saccades between conditions, or to test whether a proportion was significantly higher than a particular value, the z-test on proportions was used. Finally, paired t-tests were used to compare reaction time metrics across the entire subject pool.

Data inclusion and definition of “express saccade”

In rough agreement with previous results (Edelman 2007; Trottier and Pratt 2005), we found that saccades with latencies less than 70 ms tended to be directed at random locations rather than toward the visual target. Therefore, to be conservative, saccades with latencies less than 75 ms were excluded from the data analysis. Such anticipatory saccades were relatively rare, comprising only 6.2% of all saccades (see Results for additional details). In keeping with previous research (Kalesnykas and Hallett 1987) (Edelman et al. 2007; Kingstone and Klein 1993b), the latency histograms for the vast majority of our subjects did not reveal bimodality (i.e., express saccades and longer latency peaks).

In the current study, we define express saccades as those with latencies spanning 75 ms to 110 ms. Our upper bound of 110 ms is quite arguably conservative and, to the best of our knowledge, a smaller value than that used in any other study of human saccades (reviewed in Delinte et al. 2002) (e.g. Fischer and Ramsperger 1986; Fischer and Ramsperger 1984) (Fischer et al. 1993);(Weber et al. 1995). An argument for setting the upper limit to 110 ms can be made from consideration of monkey saccade latencies in the gap task, which often have an upper limit of approximately 100 ms and a lower limit of 65-70 ms (Dorris et al. 1997; Edelman and Keller 1996), approximately 10 ms faster than we define in humans. Moreover, in both monkey and human, when bimodality is observed, the span of the first saccade latency peak is typically 30-40 ms, even accounting for variation in minimum latency (Carpenter 2001; Fischer and Boch 1984; Fischer et al. 1984; Fischer and Ramsperger 1986; Fischer et al. 1993; Suzuki and Hirai 2000). Similarly, models of neural generators for separate modes in saccade latency
histograms also suggest a distinct latency span of around 30 ms in duration (Gezeck et al. 1997). Thus, the latency span of 75-110 ms defined in the current study corresponds well with previous monkey and human data. Although any individual saccade identified here as “express” may not, in fact, arise from immediate activity in the superior colliculus, our cutoff offers a useful statistic for characterizing the saccade latency distribution and provides information on the overall reliance of immediate collicular generation for a sample of saccades.

RESULTS

Effect of training on saccades in the trained orientation. Saccade latencies decreased substantially over the 6-12 sessions of training. For one subject, reaction times decreased rapidly over three sessions to ~100 ms and thereafter decreased only slightly (see Fig. 4), suggesting that a latency floor had been reached; thus, training of this subject was halted after six sessions. Improvement took longer for the other subjects, so they were trained for the entire twelve sessions. Figure 2 shows for two subjects latency histograms in the first, sixth, and twelfth (final) training sessions; saccade latency decreased dramatically after twelve sessions with a large percentage of saccades in the express range. Final session results for the other seven subjects appear in Figure 3.

As can be seen in Figure 4, the median saccade latency decreased and the percentage of express saccades increased significantly (p < 0.05) from the first to the last session of training for all subjects. Whereas no subject made significantly more than 50% express saccades in the first session, a majority of subjects (4/5 trained horizontally, 2/4 trained vertically) made significantly more than 50% express saccades in the last session. The average median saccade latency decreased across sessions from 124 ms to 102 ms for subjects trained horizontally, and from 136 ms to 107 ms for subjects trained vertically. The average percentage
of express saccades more than doubled with training, increasing overall from 32.9% to 70% for subjects trained horizontally and from 14.3% to 53.3% trained vertically.

Anticipation, direction and trial ordering effects. Anticipatory saccades comprised only 6.2% of all saccades across the nine subjects (minimum: 1.1%, maximum: 11.6%) and their frequency changed little across the training sessions (mean first session: 4.9%, last session: 6.5%). For saccades along a particular axis (horizontal or vertical), there was perhaps a slight tendency for saccade latencies to depend less on direction after training (left vs. right in horizontal training, up vs. down in vertical training). For subjects trained to make horizontal saccades, the average latency of rightward saccades decreased from 119 ms in the first session to 99 ms in the last session, whereas the latency of leftward saccades decreased from 130 ms to 105 ms. For subjects trained vertically, upward saccade latency decreased from 135 ms to 107 ms, whereas downward saccade latency shortened from 142 ms to 104 ms.

Carpenter (2001) found that saccades had shorter latencies when preceded by saccades of the opposite direction, suggesting that the return saccade back to the fixation point primed the generation of saccades in the same direction. However, we failed to find a substantial effect of trial order in the current study (see also Dickov and Morrison 2006; Kurata and Aizawa 2004). Across training sessions, the average latency was 114 ms when the saccade on the preceding trial was in the same direction, and 109 ms when it was in the opposite direction. This difference was 11 ms in the first training session and 3 ms in the final session.

Transfer of training to other directions in Probe Sessions. We found that training of saccades in one orientation (vertical or horizontal) generally shortened saccade latencies in untrained orientations, whether diagonal or orthogonal. Indeed, analysis of data in Probe sessions for Eight-target blocks (see Figs. 5, 6) revealed that training substantially increased the
number of express saccades made in untrained orientations, though this was less evident for vertical express saccades after horizontal training. With vertical training, all but one subject showed a significant reduction in horizontal saccade reaction time, both in latency (mean initial Probe session: 141 ms, mean final Probe session: 102 ms, p < 0.05, Wilcoxon ranked sum test) and in the proportion of express saccades (initial: 27%; final: 70%), improvement comparable to that found in the trained (vertical) orientation (initial: 152 ms; final: 114 ms) (note that overall the latencies are slightly higher than that seen in the Training sessions, because the Probe sessions discussed here include eight possible target locations). Vertical training had an equivalent effect on diagonal saccades, with all but one subject showing significant improvement in saccade latency (initial: 146 ms; final: 105 ms) and percentage of express saccades (initial: 13.9%; final: 63.5%). The lone subject (V3) revealing no transfer coincidentally showed a high percentage of both horizontal (45%) and diagonal (29%) express saccades prior to training. Interestingly, the effect of training horizontal saccades transferred substantially, but not completely, to vertical saccade performance in the Eight-target Probe blocks. Although four of five subjects significantly decreased their vertical (untrained) saccade latency (initial: 146 ms; final: 124 ms), the 22 ms decrease amounted to only 69% of the reduction achieved in the horizontal (trained) directions (initial probe: 136 ms, final probe: 101 ms). Only two of five subjects showed significantly more express saccades (initial: 6.7%; final: 19.9%). Still, only one subject (H4) showed no transfer of horizontal training in latency to vertical saccades. Overall, transfer of training appeared to be more evident for raw saccade latency than for percentage express saccades because vertical saccade latency was longer before training, so that the decrease in saccade latency after training did not bring most vertical saccades into our defined express saccade range. This is seen most dramatically for subject H2 for which the decrease in latency of vertical saccades was generally not sufficient to meet the criterion for
express saccades. By contrast, horizontal training had a strong effect on both aspects of performance of diagonal saccades, with all subjects showing a significantly reduced median latency (initial: 135 ms; final: 112 ms) and three of five subjects significantly elevating the percentage of express saccades (initial: 12.4%; final: 44.5%; with a 4th subject just missing significance, p = 0.06).

Effect on saccade latency of number of possible target locations. Across the nine subjects, saccade latency was modestly, but significantly, slower when the display contained eight possible targets (Eight-target blocks) than when it contained only two (Fig. 7). The median latency difference between conditions was on average 4.8 ms for horizontal saccades (Horizontal target blocks, paired t-test, p = 0.004, minimum: 0 ms, maximum: 11 ms) and 7.6 ms for vertical saccades (paired t-test, p < 0.001, minimum: 3 ms, maximum: 13 ms). The small differences may be due in part to a floor effect produced as a function of training, with performance approaching a plateau regardless of the number of possible targets.

Overall percentage of express saccades after training. We used data from the Probe sessions to evaluate the motor preparation hypothesis, namely, the view that express saccades are limited by the vector-specific motor operations that can be prepared in advance. We restricted our evaluation of the hypothesis to a “vector-specific” view of motor preparation, consistent with discussions by Pare and Munoz (1996) and Dorris et al. (1997), thereby eschewing the issue of how many movements could be simultaneously prepared (see Basso and Wurtz 1997). Without prior knowledge of target location, the hypothesis predicts that with vector-specific motor preparation and two possible target locations 50% of saccades will have express latencies. We found that significantly more than 50% of saccades were in the express latency range for the majority of subjects (6/9) during the last session of training. The findings were stronger for horizontal saccades than for vertical saccades: Eight of nine subjects made
horizontal express saccades with a frequency significantly greater than 50%, whereas only five of nine subjects did so for vertical saccades.

A similar analysis can be applied when eight target locations are possible. Here, though, motor preparation could facilitate fast saccade production across a region of visual space that may span more than one target location (see Pare and Munoz, 1996). To formulate a conservative estimate, we took a quadrant as the unit of visual space affected by vector-specific motor preparation, with two of eight possible target locations lying within the region. Accordingly, to generate a saccade with a specific vector the motor preparation hypothesis predicts a maximum of 25% express saccades. Once again, the results of the current study disconfirm the hypothesis: The number of subjects who made express saccades at a frequency significantly greater than 25% was 9/9 for horizontal saccades, 3/9 for vertical saccades, and 7/9 for diagonal saccades (which were only tested in blocks with eight possible targets). In sum, our findings suggest that vector-specific motor preparation is not strictly necessary for express saccade generation.

**DISCUSSION**

Results of the current study demonstrate that for naïve human subjects a modest amount of training to make short-latency saccades to suddenly appearing targets significantly decreases reaction time and dramatically increases the production of express saccades. Indeed, for most of our subjects, the quantity of express saccades was significantly greater than would be expected if express saccades required preparation to a specific location. Furthermore, training saccades of a particular vector (combination of amplitude and direction) transferred well to the production of express saccades in other directions, particularly the horizontal and diagonal. The number of possible target locations (two vs. eight) also had a significant (though small) effect on motor preparation, with an average increase of 6 ms in
saccade latency. These findings are consistent with the notion that training the saccadic system
to produce short-latency saccades has a general effect of increasing the responsiveness of the
saccadic system to the sudden appearance of visual stimuli and that vector-specific saccade
training and motor preparation are not necessary for prolific express saccade production.
The necessity of motor training and motor preparation for express saccade production

Although the gap paradigm tends to reduce saccade latency, a large number of
oculomotor studies using the paradigm have failed to elicit an appreciable number of express
Pare and Munoz (1996) found that monkeys produced large quantities of express saccades in
the gap paradigm only when vector-specific training was combined with high predictability of
target location. Similarly, for humans it has been demonstrated that large numbers of express
saccades occur when target location has both high temporal and high spatial probability
(Fischer and Ramsperger 1984).

Several factors may account for the discrepancy between our findings and those of
previous researchers. First, it is possible that our use of explicit behavioral feedback, displaying
reaction times after every trial, enabled our subjects to better calibrate their oculomotor strategy,
thereby speeding their saccade latencies. Perhaps more importantly, our training regimen
required subjects to generate saccades in opposite directions along a particular axis (horizontal
or vertical), which may have encouraged a strategy of rapidly disengaging fixation or else a
more global, less spatially specific preparation to make a saccade. By contrast, previous
studies generally involved the training of saccades of one particular vector or a narrow range of
vectors, which may have encouraged those subjects to adopt a more vector-specific strategy.
To be sure, motor preparation clearly can play a role in increasing express saccade production
or anticipatory saccades. Whether a movement is “stimulus driven” or anticipatory may simply
depend upon whether preparatory activity in saccade-related structures reaches an intensity
sufficient for triggering a saccade prior to the appearance of the visual stimulus. Humans, almost certainly more so than monkeys, have a tremendous propensity to anticipate target appearance, initiating saccades before the target is visible (Shelhamer and Joiner 2003). In the current study, we reduced the number of anticipatory saccades by always keeping the target location uncertain.

With respect to express saccade production we found evidence of vector-specific effects when comparing the results of horizontal to vertical training. Training vertical saccades transferred almost completely to saccades in other directions. However, training of horizontal saccades did not transfer completely (70%) to vertical or diagonal saccades. It is thus possible that the training of horizontal saccades relied somewhat more on vector-specific mechanisms than did vertical saccades.

The influence of target location probability on saccade latency

We found a statistically significant, yet surprisingly small (~6 ms), dependence of saccade latency on the number of possible target locations. The effect was far less than the effect due to training, even that on untrained vectors. This pattern is consistent with our conclusion that the training regimen adopted here resulted in a weak reliance on vector-specific motor preparation, with less priority accorded any specific stimulus location. Of course, it also is possible that our subjects reached a floor in saccade latency, so that factors beyond training could have little influence on reaction time.

Previous research on the effects of location probability on saccade latency has yielded conflicting results. Several studies have examined whether saccade latency follows Hick’s Law, which states that motor response latency increases proportionately to the logarithm of the number of stimulus-response alternatives (Hick 1952). The dependence of saccade reaction time on the number of possible target locations appears to faithfully follow Hick’s law when stimulus locations are mapped to motor responses in some non-trivial way, such as when
making a saccade to a particular location on the basis of the color change of a fixation point (Lee et al. 2005), or in an antisaccade task (Kveraga et al. 2002). But, the effect of target location uncertainty on latency is greatly reduced or non-existent if there’s a direct, spatially specific relation between visual stimuli and saccade responses, as when a saccade is made to a suddenly appearing stimulus (Kveraga et al. 2002; Lawrence et al. 2008). Indeed, Hick’s law actually may be reversed when the number of potential targets is very low (e.g., two) because here subjects betray a greater tendency to anticipate, and counteract this tendency by being less responsive when the visual stimulus actually appears (Lawrence et al. 2008). Although our use of a gap paradigm could have further increased this tendency to anticipate, anticipation was minimal in our study. This suggests that differing levels of anticipation contributed little to the small latency dependence on the number of possible targets observed in this study. In any case, our study extends previous findings relating to violations of Hick’s law to express saccades.

The dependence of express saccade frequency on saccade direction

The effects of training were uneven in this study, with a greater number of horizontal saccades than vertical saccades falling in the express range after training. One source may be intrinsic differences in saccade direction: Horizontal saccades tend to have shorter latencies than vertical saccades (Goldring and Fischer 1997). It is not clear what is at the heart of this difference, as it may reflect some combination of differences in sensory latency, saccadic programming, and the interface between sensory and motor areas. Whatever the source of the differences in latency between directions, a latency criterion specific to express saccades in the vertical direction may be more appropriate. An analysis of the latency histograms for the last session of training may justify setting a higher cutoff for vertical express saccades, as latencies for horizontal saccades trailed off by 110 ms, whereas those for vertical saccades did so only by 120 ms (see Figures 2 and 3).
Neural mechanisms underlying express saccade generation

Edelman and Keller (1996) and Dorris et al. (1997) showed evidence that express saccades were elicited immediately by the arrival of a visual response in neurons in the intermediate layers of the superior colliculus, which was known to have temporally separate bursts of activity for longer-latency saccades (Sparks and Hartwich-Young 1989). It was speculated that for longer latency saccades this visual response could be considered a saccade trigger that failed (Edelman and Keller 1996) (Sommer 1994).

It is thought that fixation disengagement reflects a decrease in activation of neurons dedicated to keeping the eye fixating or making very small saccades (Hafed and Krauzlis 2008; Munoz and Wurtz 1993), and that the disappearance of the fixation point in the gap paradigm releases fixation or attention from the current position of gaze, thus disinhibiting the saccadic system prior to the appearance of a peripheral target (Mayfrank et al. 1986). Indeed, there are neurophysiological correlates of this fixation disappearance: Activity in the rostral pole of the superior colliculus increases, while activity of some neurons in the frontal eye fields decreases (Dorris and Munoz 1995; Dorris et al. 1997). Dorris et al (1997) found, however, that trial-to-trial fluctuations in rostral pole activity may not predict the occurrence of an express saccade, but that express saccade occurrence, correlated more strongly with the level of low-frequency activity in the caudal superior colliculus, (see also Dorris and Munoz 1998). This spatially localized low-frequency activity is thought to be the neural correlate of a preparatory process to make a saccade of a particular vector (Dorris and Munoz 1998; Dorris et al. 1997), in line with the behavioral findings of Paré and Munoz (1996) showing that vector-specific motor preparation and motor training are prerequisites for express saccade production.

In contrast to previous findings, our data suggest that with a modest amount of training express saccades can be made frequently to untrained locations where stimuli appear with a low probability. This raises the question of whether the mechanism underlying the increased
express saccade production that we observed is different from that observed by Dorris et al (1997). One possibility is that with training in the gap task human subjects learn to lower their fixation-related (rostral) activity sufficiently to make low-frequency caudal buildup unnecessary to trigger express saccades. In this case one may find that the probability of express saccades depends inversely on fixation-related activity in a saccade motor map, in contrast to the results of Dorris et al (2007). But, the lowering of fixation-related activity is not the only neural mechanism by which subjects could increase express saccade production in such a non-spatially specific way. Additionally, a portion of the gap effect on saccade latency may result from fixation disappearance serving as a general warning signal (Reuter-Lorenz et al. 1995; Kingstone and Klein 1993a; Pratt et al. 2000; Ross and Ross 1980), which might increase generalized, non-spatially specific motor preparatory processes. Low frequency, non-spatially selective (caudal) activation of a large portion of the collicular saccade motor map would also enable short latency saccades to a large portion of the visual field (see Basso and Wurtz 1997; Dorris and Munoz 1998). If thus seems plausible that applying a version of our training protocol to monkeys may yield a generalized ability to make express saccades, perhaps even to uncertain target locations (also see Schiller et al. 2004).

Implications for the presence of express saccades in natural visuomotor behavior

It is still not clear that express saccades are a frequent occurrence during primate behavior in the natural world. Sommer (1994) showed that monkeys frequently make saccades in a scanning task in which visual stimuli appear suddenly. However, the saccades that had the highest likelihood of being express were also those that recurred in a particular monkey’s scanpath (Sommer 1994; 1997), suggesting that vector-specific motor preparation increased the likelihood of express saccade production. In contrast, naïve human subjects can make saccades with average latencies bordering on the express range to targets of unpredictable
If vector-specific training or motor preparation were required for express saccade production then it is unlikely that express saccades would be commonplace during natural visuomotor behavior in humans. It is unclear how frequently vector-specific motor training occurs in real life, other than possibly for reading, where saccades are of small amplitude, are almost always made in one direction, and are not made to suddenly appearing visual stimuli. Moreover, it is unclear how useful vector-specific preparation would be for natural behavior, except perhaps in tracking visual items moving in straight trajectories at high speeds, each saccade of similar direction and amplitude priming the next (Anderson et al. 2008). Given these considerations, a finding that express saccades were contingent on vector-dependent processes would seem to be most consistent with the view that such processes represent a laboratory artifact.

Instead, our results indicate that subjects can make express saccades as a consequence of learning how to increase the responsiveness of the saccadic system to the sudden appearance of visual stimuli, and are thus consistent with the possibility that express saccades are part of natural visuomotor behavior. Maintaining the saccadic system in a sensitized state through some combination of disengagement of fixation and spatially non-specific motor preparation would allow suddenly appearing salient visual stimuli to quickly generate a movement. Whether such short-latency saccades would specifically be of express saccade latency remains unclear.

REFERENCES


FIGURE LEGENDS

Fig. 1. Schematic of protocols used for training and testing of subjects. Five subjects were trained to make horizontal saccades and four were trained to make vertical saccades. All subjects participated in the Probe sessions.

Fig. 2. Saccade latency histograms for two subjects for the first, sixth, and twelfth Training sessions. Subject H3 was trained to make horizontal express saccades and V1 was trained to make vertical express saccades. Downward directed bars represent saccades that went in the wrong direction. Such saccades always had latencies less than 75 ms. Vertical lines are placed at 75 ms and 110 ms (indicating what we consider, respectively, the minimum and maximum latency of express saccades).

Fig. 3. Saccade latency histograms for the final Training session for the seven subjects whose data are not portrayed in Fig. 2. Otherwise, conventions are identical to that of Fig. 2.
Fig. 4. Median saccade latencies (top) and the percentage of all saccades that were express saccades (bottom) as a function of training session are shown for the nine subjects.

Fig. 5. *Eight target blocks* -- Median saccade latencies in the *Probe* sessions are shown for all nine subjects, as well as averages for the subjects trained horizontally and the subjects trained vertically. Data shown are from the *Eight Target blocks*, in which the targets could appear at any of the eight cardinal or diagonal directions. Grey bars indicate averages across all saccades for the particular *Probe* session. Letters (H, V, D) indicate whether there was significant transfer of training with respect to median saccade latency for horizontal, vertical, and diagonal saccades, respectively. Average interquartile ranges are shown for each probe session for each subject.

Fig. 6. *Eight target blocks* -- The percentage of all saccades that were express saccades in the *Probe Sessions* are shown for all nine subjects, as well as averages for the subjects trained horizontally and the subjects trained vertically. Letters (H, V, D) indicate whether there was significant transfer of training with respect to percentage of express saccades for horizontal, vertical, and diagonal saccades, respectively. One subject (H1) showed an increase in the percentage of express saccades in the diagonal orientation that bordered on statistical significance. Other conventions as in Fig. 5.

Fig. 7 -- *Final Probe session* -- Comparison of average median saccade latencies (left) and percentage express saccades (right) for trials in which there were two possible targets (*Horizontal* and *Vertical* blocks) and in which there were eight possible targets (*Eight Target* blocks).
blocks). Data are from the final *Probe Session* for each subject. Errors indicate standard
deviation of median saccade latencies across the subject pools.
Probe Sessions:
- 3 block types
- 2 target locations horizontal
- 2 target locations vertical
- 8 target locations

Training Sessions:
- Single block type
- 2 target locations horizontal or vertical
Figure 3
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Final Training Session

Subjects trained horizontally

Subjects trained vertically

Number of saccades

Saccade latency (msec)
Figure 4
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Subjects trained horizontally

Subjects trained vertically

Median saccade latency (msec)

Percentage express saccades

Training session

H1
H2
H3
H4
H5

V1
V2
V3
V4
Figure 5
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Subjects trained horizontally

Subjects trained vertically

Median saccade latency (msec)

H1  V,D  H2  V,D

H3  V,D  H4  D

H5  V,D  Average

Initial  Middle  Final

Initial  Middle  Final

Average

Horiz.
Vert.
Diag.