

Properties of human eye-head gaze shifts in an anti-gaze shift task

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Abstract

We investigated the metrics and kinematics of human eye-head gaze shifts using the anti-gaze shift task. Surprisingly, no systematic difference was found between peak gaze velocities of large pro- and anti-gaze shifts. In a follow-up experiment that equated perceived stimulus luminance across multiple eccentricities, pro-gaze shifts were consistently faster than anti-gaze shifts. In both experiments, we did not observe any head-only errors where initial head motion dissociates from gaze direction, even though many subjects generated such movements in other paradigms. These experiments confirm the influence of stimulus luminance on comparative movement velocity, and demonstrate that the behavioural set assumed in this task discourages head-only errors.

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1. Introduction

Humans explore their visual environment using gaze shifts that allow successive images to fall upon the fovea. Large gaze shifts frequently require coordination of an eye movement (eye-in-head) and a head movement (head-in-space). Extensive research into saccadic eye movements has produced a refined understanding of the physiology of the oculomotor network when the head is restrained; however, our understanding of the neural mechanisms underlying eye-head gaze shifts is comparatively poor [see Scudder, Kaneko, & Fuchs, 2002 for review].

Exploring the visual environment also requires the ability for context to influence behaviour such that external events do not necessarily elicit orienting responses. The anti-saccade task (Hallett & Adams, 1980) uncouples congruent stimulus–response mappings by requiring subjects

to inhibit an eye movement towards an eccentric stimulus, and generate a saccade to its diametrically opposite position. The anti-saccade task has proven to be a valuable tool for both basic and clinical study of oculomotor control [see Barton et al., 2002; Everling & Fischer, 1998; Fukushima, Fukushima, Miyasaka, & Yamashita, 1994; Fukushima et al., 1990; Guitton, Bachtel, & Douglas, 1985; Munoz & Everling, 2004; Pierrot-Deseilligny, Ploner, Muri, Gaymard, & Rivaud-Pechoux, 2002 for review].

The goal of this study is to investigate the properties of eye-head gaze shifts made in an anti-saccade task. For clarity, we term this task an *anti-gaze shift task* to specify that subjects are free to respond using both their eyes and their head. Of particular interest is whether the characteristics of component eye and head movements during anti-gaze shift trials will demonstrate any systematic differences from pro-gaze shift trials. There are a number of reasons to suspect that this may be the case. First, the coordination of the eyes and head to isometric gaze shifts can be highly variable across a variety of different behavioural contexts. For example, the head moves more and starts earlier when gaze shifts are made to more predictable targets, to auditory targets that

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lack a visual landing point, or when future gaze shifts will be required in the vicinity of the target (Bizzi, Kalil, & Morasso, 1972; Goossens & Van Opstal, 1997; Herst, Epelboim, & Steinman, 2001; Land, 1992; Oommen, Smith, & Stahl, 2004; Zangemeister & Stark, 1982b). Given the lack of a visual anchor on anti-gaze shift trials, and the possibility that more secondary gaze shifts will be required, it is possible that different patterns of eye-head coordination will be used during pro- and anti-gaze shifts. Second, a growing body of behavioural literature demonstrates that the gaze axis and the head have some capacity to orient independently (Corneil & Elsley, 2005; Corneil & Munoz, 1999; Goossens & Van Opstal, 1997; Ron, Berthoz, & Gur, 1993; Ron, Berthoz, & Gur, 1994). Recent neurophysiological evidence has implicated several plausible areas in the frontal cortex and brainstem by which such independence could be realized (Chen, 2006; Chen & Walton, 2005; Corneil, Olivier, & Munoz, 2002b; Cowie & Robinson, 1994; Elsley, Nagy, Cushing, & Corneil, 2007; Gandhi & Sparks, 2007; Pelisson, Goffart, Guillaume, Catz, & Raboyeau, 2001; Quessy & Freedman, 2004; Walton, Bechara, & Gandhi, 2007), and demonstrated that the presentation of a visual stimulus leads to time-locked, short-latency recruitment of neck muscles that turn the head toward the stimulus (Corneil, Olivier, & Munoz, 2004).

Based on these results, we make a number of predictions regarding human performance in the anti-gaze shift task. It is well-documented that anti-saccades have longer reaction times (RTs) and slower peak velocities than pro-saccades, reflecting the additional processes required to generate correct anti-saccades, the lack of stimulus–response congruency, and the absence of a visual stimulus at the goal location (Amador, Schlag-Rey, & Schlag, 1998; Bell, Everling, & Munoz, 2000; Edelman, Valenzuela, & Barton, 2006; Everling & Fischer, 1998; Fischer & Weber, 1992, 1997; Munoz & Everling, 2004; Van Gelder, Lebedev, & Tsui, 1997). Our first two predictions are: anti-gaze shifts will have correspondingly longer RTs and will have slower peak velocities. Furthermore, given the capacity for the head to orient independently from gaze in paradigms like the distractor (Corneil & Munoz, 1999) and countermanding paradigms (Corneil & Elsley, 2005) which set up a competition between potential orienting goals, we sought also to assess whether subjects would generate “head-only errors” on anti-gaze shift trials. This movement sequence (shown in Fig. 1c) is distinct from correct and incorrect anti-gaze shifts directed away from or toward the presented stimulus, respectively (Fig. 1a and b). During head-only errors, the head moves toward the stimulus while gaze remains stable due to the vestibulo-ocular reflex (VOR; Fig. 1c).

To test these predictions, we placed stimuli outside of the typical oculomotor range (in the first experiment, stimuli were placed 60° to the left or right), hence subjects were required to generate coordinated eye-head gaze shifts to complete the task. Portions of these results have been presented previously in abstract form (Chapman & Corneil, 2005).

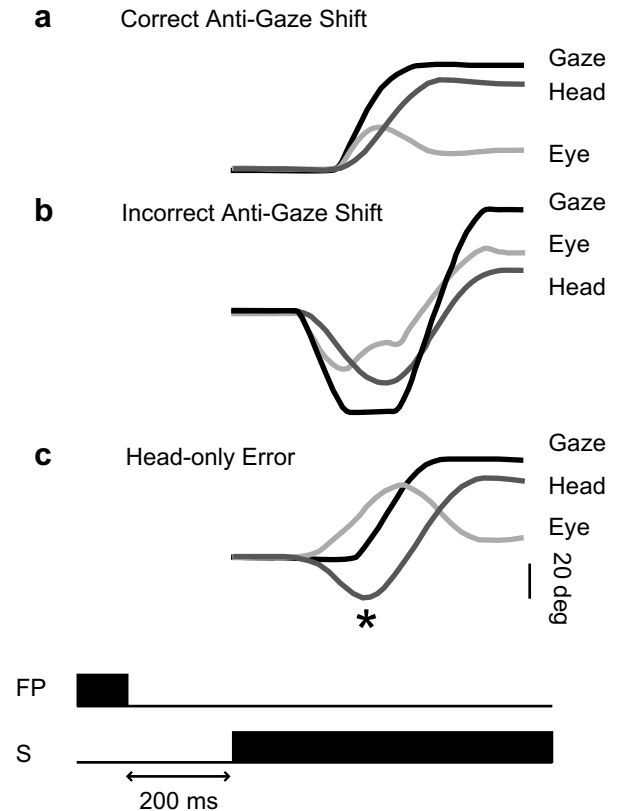


Fig. 1. Classification of predicted movement sequences on anti-gaze shift trials. In all cases, the stimulus was presented to the left hence subjects were instructed to look to the right. (a) A correct anti-gaze shift where gaze is directed correctly away from the stimulus. (b) An incorrect gaze shift where both the eye and head moved incorrectly towards the stimulus, followed by a corrective gaze shift. (c) A head-only error, showing how the head moves (*) towards the stimulus while gaze remains stable due to a compensatory VOR movement. The head-only movement is followed by a correct gaze shift away from the stimulus.

2. Methods

Nine human subjects (seven male, two female, age range 22–33 years) provided consent to participate in two experiments. Experimental procedures were approved by the University Research Ethics Board for Health Science Research at the University of Western Ontario, in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

All subjects reported no record of visual deficiencies (i.e., normal or corrected to normal vision), neurological and musculoskeletal afflictions. Two subjects were authors of this paper; however, no observable differences were identified between these subjects and the rest of the sample. Six of our 9 subjects had head-gains (the ratio of head amplitude to target eccentricity) >0.5 for gaze shifts to targets at 40°, and hence were classified as *head movers* (Fuller, 1992). All subjects were provided with both written and verbal instructions outlining the requirements of the anti-gaze shift task. Participants were instructed to make gaze shifts as quickly and accurately as possible. Subjects were told to use whatever combination of eye and head movements they felt necessary to complete the task. No further instruction or feedback was provided throughout the experiment.

2.1. Pro- and anti-gaze shift task

Subjects were seated on one side of a double layered curtain which prevented any other light source from interfering with the stimuli, which consisted of tri-coloured red/green light emitting diodes (LEDs) driven by 5 V

TTL pulses. The red and green intensities were roughly equiluminant, and measured 110 cd/m^2 (isoluminance was achieved by adjusting the value of an in-series resistor). All LEDs were placed in small black boxes secured on stands that positioned the LEDs 1.2 m from the ground, so that all LEDs lay in a horizontal plane facing the subject. All stands were placed 1.2 m from the subject. One stand was placed directly in front of the subject, and held a single LED which served as the central fixation point. Two stands were placed symmetrically to the left or right at varying eccentricities (see below), and served as the stimuli. As described below, between 1 and 6 LEDs could be illuminated on these stimulus stands.

Each trial started with the presentation of the fixation point. The duration of fixation point presentation was chosen randomly from one of four times (1000, 1166, 1333 and 1500 ms) in order to reduce anticipation. The colour of the fixation point served to instruct the subject about the trial type. A red or green fixation point instructed the subject to generate a pro- or anti-gaze shift gaze shift, respectively, in response to stimulus onset. The stimulus remained illuminated for 1000 ms. In order to decrease reaction times, a 200 ms gap was provided between the offset of the fixation point and the presentation of the stimulus. The 200 ms gap has been shown to reduce reaction times (RTs) for both pro- and anti-saccades (Fischer & Weber, 1992; Saslow, 1967) and to maximize error rates in a variety of behavioural tasks (Fischer & Weber, 1997; Munoz & Corneil, 1995) presumably due to a concession of accuracy for speed. On pro-gaze shift trials, subjects were simply required to make a gaze shift from the fixation point to the stimulus. On anti-gaze shift trials, subjects were required to look to the diametrically opposite position of the stimulus. Each trial was followed by a 1000 ms inter-trial interval to allow participants' time to recenter their gaze before the start of the next trial.

2.2. Experiment 1

In the first experiment, the stimuli consisted of a single LED presented 60° to the left or right. Subjects performed two blocks of 200 trials, for a total of 400 trials each. All possible trial types (e.g., pro- or anti-, stimuli presented to the left or right) were presented an equal number of times within a block. A customized Labview program downloaded onto a PXI controller (National Instruments) controlled the experiment at a rate of 1000 Hz. This program selected the trial type for the upcoming trial in a pseudo-randomized manner (i.e., once a trial was completed it was removed from the list of trials and the ensuing trial type was randomly chosen from the remaining trials until the block was completed).

2.3. Experiment 2

We performed a second experiment where we varied both stimulus eccentricity and luminance. One previous report has established that the difference between pro- and anti-saccade reaction times is diminished when stimulus luminance is low (Doma & Hallett, 1988). It is also known that increasing stimulus intensity reduces the time required for visuomotor processing (Boch, Fischer, & Ramsperger, 1984) and increases the magnitude of stimulus-aligned activity within the oculomotor system [e.g., Bell, Meredith, Van Opstal, & Munoz, 2006]. Our logic in experiment 2 was to roughly equate stimulus luminance across all eccentricities to compensate for the decreased neural tissue devoted to processing peripheral stimuli (Rovamo & Virsu, 1979). Accordingly, in experiment 2, we increased the number of LEDs presented within a stimulus cluster for more eccentric stimuli. The same 9 subjects were used, and the experimental procedures were similar, with the following exceptions. Over a series of six blocks of 80 trials each (40 pro- and 40 anti-gaze shift trials), the stimulus LEDs were placed symmetrically at eccentricities between 10° and 60° in 10° intervals. Within each block, the luminance of the stimulus was adjusted by varying the number of LEDs within a stimulus cluster, so that one LED was presented at 10° , two LEDs at 20° and so on up to presenting six LEDs at 60° . The order of stimulus eccentricity presentation was varied amongst the 9 subjects, and either increased from 10° to 60° or decreased from 60° to 10° in 10° increments.

2.4. Data collection and analysis

Horizontal eye movements were measured using bi-temporal DC electro-oculography (EOG) with a P122 AC/DC preamplifier (Grass Instruments). Horizontal head rotation was measured using a baseball helmet attached to a low-torque potentiometer that was anchored behind the subject. The potentiometer signal was first calibrated to known angles of rotation. Subjects were then asked to maintain fixation upon the central fixation point while they turned their heads. The gain of the EOG signal was adjusted to be equal to that of the potentiometer signal. Horizontal eye and head movements were filtered (100 Hz, low pass filter), amplified, and digitized at a rate of 500 Hz onto the PXI controller. Digitized data was then transferred to a PC computer and subsequent off-line analyses were performed using customized Matlab (The MathWorks) programs. Horizontal gaze (eye-in-space) position was constructed off-line by adding eye and head signals. Eye, head and gaze movements were analyzed via a customized Matlab Graphical User Interface. Movement onsets and off-sets were identified by an automarking program, which detected crossing of velocity thresholds ($50^\circ/\text{s}$ for eye and gaze, $25^\circ/\text{s}$ for head). Velocities were differentiated from position traces and filtered with a second-order low-pass Butterworth filter ($f_s/f_c = 17$). These automarks were used as guides for the placement of interactive marks by a data analyst. Interactive marks were then reviewed by a second analyst. Trials where gaze or head RTs were $< 80 \text{ ms}$ were catalogued as anticipatory and excluded from analysis (Corneil & Munoz, 1996). Trials with gaze RTs exceeding 600 ms were also excluded due to presumed lack of subject alertness.

3. Results

3.1. Experiment 1

Over 3600 eye-head gaze shifts were collected from the 9 subjects who participated in experiment 1. We found no significant differences between leftward and rightward movements, and therefore collapsed all data across the side of stimulus presentation. For clarity, we will refer to the direction of anti-gaze shifts in reference to the goal, hence a “correct” anti-gaze shift is one that moves gaze away from the presented stimulus.

3.1.1. Comparative timing of pro- versus anti-gaze shifts

The distribution of pro and anti-gaze shift reaction times (RTs) is presented for both a representative individual and our sample of 9 subjects in Fig. 2a and b, respectively. Subject-by subject data has been provided in Table 1. Some features are readily apparent in the RT frequency histogram of the representative subject (Fig. 2a). First, anti-gaze shifts were generated at significantly longer latencies than pro-gaze shifts [for this subject, pro-gaze RT: $207 \pm 32 \text{ ms}$ (means \pm SD), anti-gaze RT: $225 \pm 38 \text{ ms}$; *t*-test, $P < .001$]. This trend was consistent across our sample (Fig. 2b), with anti-gaze shifts being initiated on average $\sim 40 \text{ ms}$ later than pro-gaze shifts (paired *t*-test, $P < .01$; mean difference = $39 \pm 24 \text{ ms}$). Second, the few incorrect gaze shifts that were generated on anti-gaze shift trials (downward, filled histograms in Fig. 2a) were initiated at relatively short RTs in the range of the shortest RTs on pro-gaze shift trials. Across our sample, the reaction times of incorrect anti-gaze shifts were $\sim 35 \text{ ms}$ shorter than the RTs of correct anti-gaze shifts (paired *t*-test, $P < .01$; mean

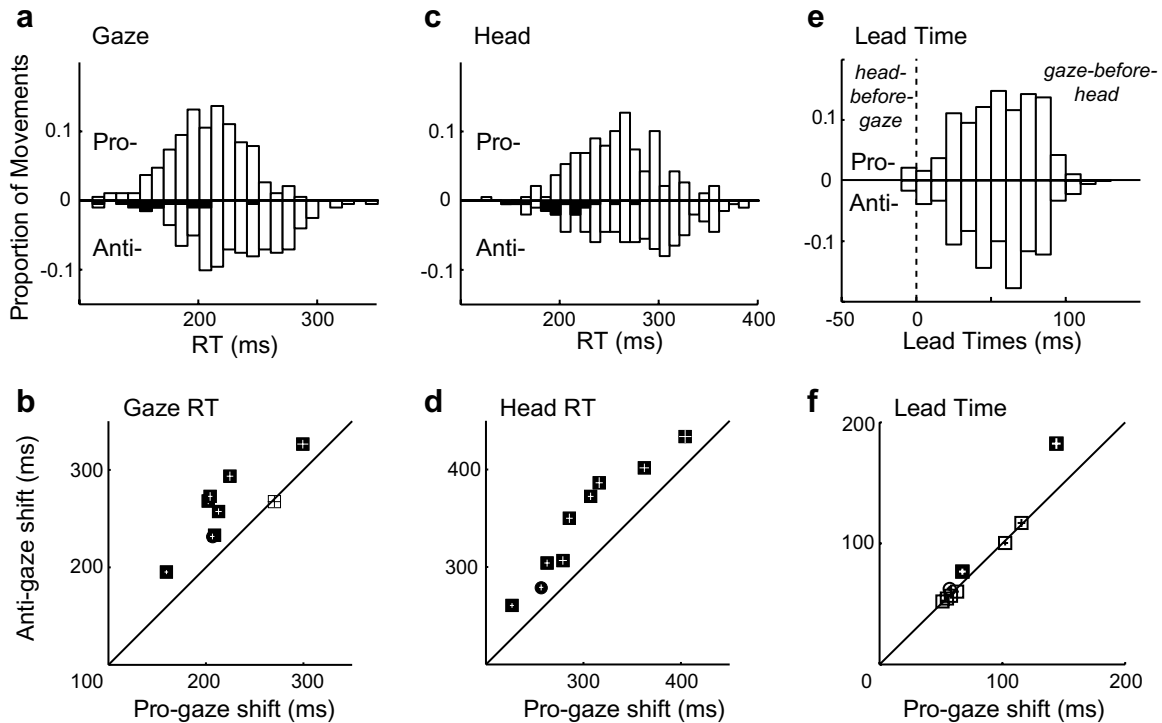


Fig. 2. Reaction times during pro- and anti-gaze shift trials in experiment 1. Here, the stimuli were placed at 60° to the left or right. The data has been collapsed across direction. (a and c) Frequency histograms of gaze (a) and head (c) RTs on pro- (upward histogram) and correct anti- (inverted, empty histogram) gaze shift trials, for one representative subject. Shaded inverted histograms represent the RTs of incorrect anti-gaze shifts. (b and d) Summary of gaze (b) and head (d) RTs across different trial types for all 9 subjects. Each square shows data for a single subject. The circular data point denotes the representative subject from a, c, and e. Filled or empty squares represent instances where the differences between RTs on pro- versus anti-gaze shift trials reached significance or not, respectively. Error bars within each symbol represent the standard error of the mean. (e) Frequency histograms of gaze-head lead time, with upward and inverted histograms representing data from pro- versus anti-gaze shift trials, respectively. Observations to the right of the zero line represent trials where gaze shift onset led the initiation of the head movement. (f) Summary of lead-time across all 9 subjects. Same format as b. Note: Data from 2 subjects overlap considerably in b.

difference = 35 ± 25 ms). Both of these features have been reported previously in head-restrained anti-saccades.

In Fig. 2c and d, we repeat these RT analyses on the head movement component of the gaze shift. As expected given its heavier inertial load, head RTs were significantly longer than gaze RTs (head RTs on pro- and anti-gaze shift trials were 79 ± 30 and 83 ± 39 ms longer than gaze RTs, respectively; paired *t*-tests; $P < .01$ for both comparisons). Consistent with the features observed for gaze RTs, head RTs were significantly longer on anti- versus pro-gaze shift trials (Fig. 2c; head RTs on pro-gaze shift trials: 302 ± 60 ms, anti-gaze shift trials: 349 ± 69 ms; *t*-test, $P < .001$; Fig. 2d: paired *t*-test, $P < .01$; mean difference = 43 ± 18 ms), and head RTs on incorrect anti-gaze shift trials were ~ 45 ms shorter than head RTs on correct anti-gaze shift trials (paired *t*-test, $P < .01$; mean difference = 47 ± 38 ms).

We also examined the difference between the onset of the gaze shift (equivalent to the onset of the high-velocity eye movement) and the onset of the head movement across pro- and anti-gaze shift trials. Across our sample, we saw no evidence that this lead-time metric was systematically different across pro- and anti-gaze shift trials (Fig. 2e; lead-time on pro-gaze shift trials = 55 ± 25 ms; lead time

on anti-gaze shift trials = 54 ± 26 ms; *t*-test; $P = .81$, Fig. 2f: paired *t*-test; $P = .26$; mean difference = 5 ± 13 ms; note that subjects retained the same lead times on pro- and anti-gaze shift trials). Negative lead-times, signifying that head onset preceded gaze shift onset, were rarely observed on either pro- or anti-gaze shift trials.

3.1.2. Comparative kinematics of pro- versus anti-gaze shifts

A comparative analysis of the peak velocity of pro- and anti-gaze shifts, somewhat surprisingly, revealed little systematic difference. For our representative subject (Fig. 3a), the peak velocities for both gaze and head movements overlapped substantially for pro- and anti-gaze shift trials (Fig. 3a; peak gaze velocity on pro-gaze trials = $513 \pm 112^\circ/\text{s}$ peak gaze velocity on anti-gaze shift trials = $531 \pm 93^\circ/\text{s}$; $P = .61$. Fig. 3c: peak head velocity on pro-gaze trials = $270 \pm 42^\circ/\text{s}$; peak head velocity on anti-gaze shift trials = $278 \pm 40^\circ/\text{s}$; $P = .07$). Although significantly faster peak gaze velocities were observed on pro- versus anti-gaze shift trials in 5 of 9 subjects (filled squares lying below the line of unity in Fig. 3b), peak gaze velocities were significantly faster on anti- versus pro-gaze shift trials in 2 subjects, and not significantly different in the remaining 2 subjects (Fig. 3b; paired *t*-test, $P = .11$; pro-gaze

Table 1
Reaction times and velocities are provided for each subject in experiment 1 and 2

Subject	Experiment 1				Experiment 2			
	Pro-gaze shift RT (ms)	Anti-gaze shift RT (ms)	Pro-gaze shift velocity (°/s)	Anti-gaze shift velocity (°/s)	Pro-gaze shift RT (ms)	Anti-gaze shift RT (ms)	Pro-gaze shift velocity(°/s)	Anti-gaze shift velocity (°/s)
Subject 1	207	225	513	531	177	218	708	637
Subject 2	224	277	533	495	153	198	602	605
Subject 3	270	272	367	300	225	295	384	372
Subject 4	202	275	379	369	153	193	448	399
Subject 5	213	248	531	531	N/A	N/A	N/A	N/A
Subject 6	159	195	487	509	93	137	510	507
Subject 7	299	338	395	375	283	320	591	475
Subject 8	204	291	387	370	121	184	479	477
Subject 9	208	264	741	668	159	186	630	591
Means ± STD	221 ± 40	265 ± 40	481 ± 119	460 ± 115	170 ± 59	216 ± 61	544 ± 106	507 ± 96

Sample for experiment 2, data is only shown at the 60 degree eccentricity. Data is pooled across direction for all subjects. Subject 5 was unavailable to participate in experiment 2.

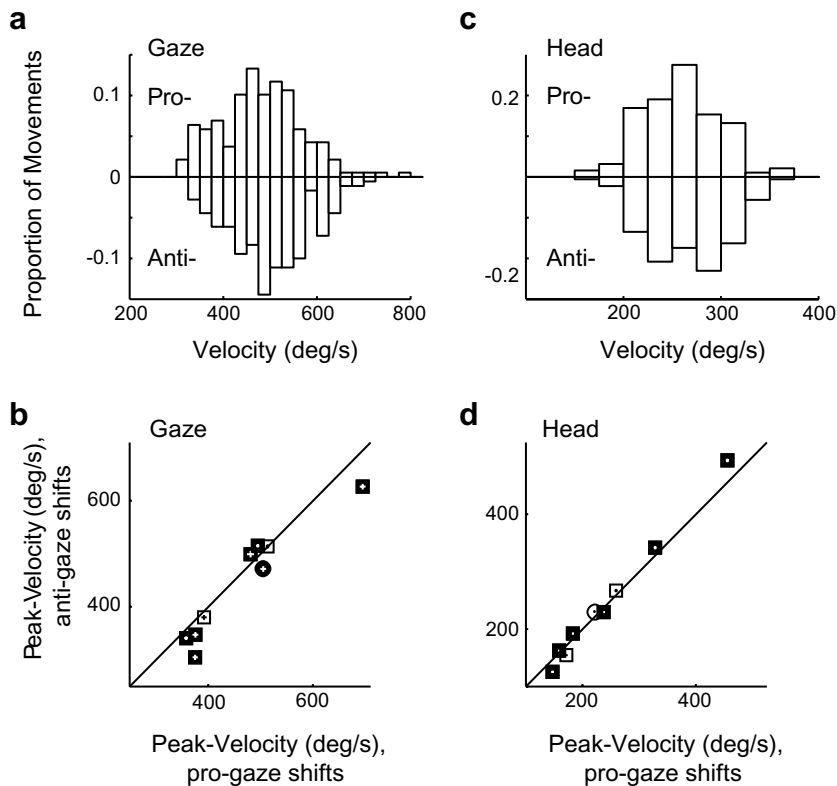


Fig. 3. Peak gaze (a and b) and head (c and d) velocities for pro- and anti-gaze shifts, shown as a frequency histogram for a representative subject (a and c), and across our sample of 9 subjects (b and d). Same format as Fig. 2.

shifts were on average = $20 \pm 33^\circ/\text{s}$ faster than anti-gaze shifts). We also observed no evidence for head movements to reach higher peak velocities for pro- versus anti-gaze shift trials (Fig. 3d; paired t -test, $P = .51$; mean difference = $4 \pm 17^\circ/\text{s}$).

We also compared a variety of metrics for pro- and anti-gaze shifts across each subject (for simplicity, these data are not shown). For example, the time to reach peak velocity did not differ between pro- and anti-gaze shift trials for both gaze (paired t -test, $P = .48$: time to peak gaze velocity

on pro-gaze shift trials = 48 ± 20 ms, time to peak gaze velocity on anti-gaze shift trials = 48 ± 15 ms) and head movements (paired t -test, $P = .48$: time to peak head velocity on pro-gaze shifts = 54 ± 14 ms, time to peak head velocity on anti-gaze shift trials = 54 ± 14 ms). Further, the time of peak gaze velocity occurred relatively early in the gaze shift, coinciding with the time of peak eye velocity. The amplitude of the gaze shift did not differ significantly across trial type (paired t -test; $P = .1$: pro-gaze shift amplitude = $56 \pm 6^\circ$, anti-gaze shift amplitude = $57 \pm 10^\circ$),

although gaze shift amplitudes on anti-gaze shift trials exhibited significantly larger scatter (paired *t*-test; $P < .01$). We also observed no systematic trends for total head movement amplitude across trial type (paired *t*-test; $P = .48$ head amplitude on pro-gaze shift trials = $40 \pm 11^\circ$, head amplitude on anti-gaze shift trials = $40 \pm 13^\circ$), or how much the head contributed to a gaze shift (paired *t*-test; $P = .2$: head contribution to pro-gaze shifts = $26 \pm 11^\circ$, head contribution to anti-gaze shifts = $28 \pm 15^\circ$).

3.1.3. Incidence rates

As described in the Introduction (see also Fig. 1), we expected three sequence of eye-head coordination on anti-gaze shift trials. The incidence rates for each sequence are provided in Table 2 for each subject, and averaged across our sample. We have not shown the comparative incidence rates for pro-gaze shift trials because subjects generated correct gaze shifts at a high rate (averaging $>97\%$), and generated relatively few error trials (incorrect pro-gaze shifts = 2.1% ; incorrect head-only errors = 0.6%). By comparison, subjects generated more errors on anti-gaze shift trials, but still performed the task relatively well, performing correctly on $\sim 93\%$ of all anti-gaze shift trials. Most errors on anti-gaze shift trials consisted of incorrect gaze shifts ($\sim 6\%$ of all anti-gaze shift trials) and, contrary to our expectations, the incidence rate of head-only errors was very low ($\sim 1\%$ of all anti-gaze shift trials). Importantly, 6 of our 9 subject participated previously in a countermanding experiment which required them to cancel a planned gaze shift (Corneil & Elsley, 2005), where they generated an appreciable amount ($\sim 13\%$) of head-only errors (see rightmost column; Table 2; stop trials were presented on 1/3 of the trials in the countermanding task). This demonstrates that our anti-gaze shift results are not due to the sensitivity of the equipment, nor to differences in stimulus properties.

3.2. Experiment 2

We were surprised by two findings in experiment 1. First, we did not observe the expected difference in pro-versus anti-gaze shift peak velocities. Second, the incidence rate of head-only errors was much lower than expected. One potential reason for these results is that the perceived luminance of the stimulus was low, given its relatively large eccentricity. In experiment 2, we investigated the importance of stimulus luminance and eccentricity by roughly equating stimulus luminance for eccentricities ranging between 10° and 60° (see Methods). Eight of our 9 subjects participated in experiment 2, generating over 3900 gaze shifts.

3.2.1. Comparative timing of pro- versus anti-gaze shifts across stimulus eccentricity

The gaze and head RTs for pro- and anti-gaze shifts are shown for a representative subject in Fig. 4a and c, respectively, across all stimulus eccentricities. The RTs of both pro- and anti-gaze shifts tended to increase for larger stimulus eccentricities, consistent with previous reports (Kalnesnykas & Hallett, 1994). Across our sample, gaze RTs were consistently shorter on pro- versus anti-gaze shift trials, with the difference between gaze RTs on pro- and anti-gaze shift trials decreasing only slightly (~ 10 ms) at larger stimulus eccentricities (Fig. 4b). In contrast, the head RTs tended to be shorter for larger stimulus eccentricities (e.g., Fig. 4c), consistent with the head playing a larger role for larger gaze shifts. Across our sample, head RTs were generated at consistently shorter RTs on pro-gaze shift trials than on anti-gaze shift trials, and also this difference tended to increase slightly for larger stimulus eccentricities (Fig. 4d). Overall, these comparative RT findings resemble those observed in experiment 1; the overall shortening of RTs in experiment 2 versus experiment 1 is significant (paired *t*-tests; $P < .05$ for both pro- and anti-gaze shift

Table 2

Incidence rates of correct anti-gaze shifts, incorrect anti-gaze shifts and head-only errors for experiment 1 and 2

Subject	Experiment 1			Experiment 2			Countermanding experiment Head-only errors (%)
	Correct anti-gaze shifts (%)	Incorrect anti-gaze shifts (%)	Head-only errors (%)	Correct anti-gaze shifts (%)	Incorrect anti-gaze shifts (%)	Head-only errors (%)	
Subject 1 ^a	89.80	8.20	3.00	95.00	0.00	5.00	11.00
Subject 2 ^a	93.90	6.10	0.00	87.20	10.30	2.60	9.70
Subject 3	85.40	10.50	4.10	92.50	5.00	2.50	N/A
Subject 4 ^a	99.00	0.50	0.50	85.00	15.00	0.00	18.00
Subject 5 ^a	90.50	7.50	2.00	N/A	N/A	N/A	11.00
Subject 6 ^a	90.50	9.00	0.50	94.90	5.10	0.00	19.00
Subject 7	96.50	1.50	2.00	89.70	10.30	0.00	6.20
Subject 8	90.90	8.10	1.00	92.50	5.00	2.50	N/A
Subject 9 ^a	96.00	4.00	0.00	100.00	0.00	0.00	N/A
Sample mean	92.50	6.20	1.30	92.60	5.90	1.50	12.50

For the data from experiment 2, data is shown only for the 60° stimulus eccentricity. Data is pooled across direction for all subjects. Pro-gaze shift incidence rates are not shown as all participants approached or reached 100% correct during these trials. Incidence rates of head-only errors during the countermanding task are provided for 6 subjects that participated in both the anti-gaze shift and countermanding experiments.

^a denotes head movers as defined in Section 2.

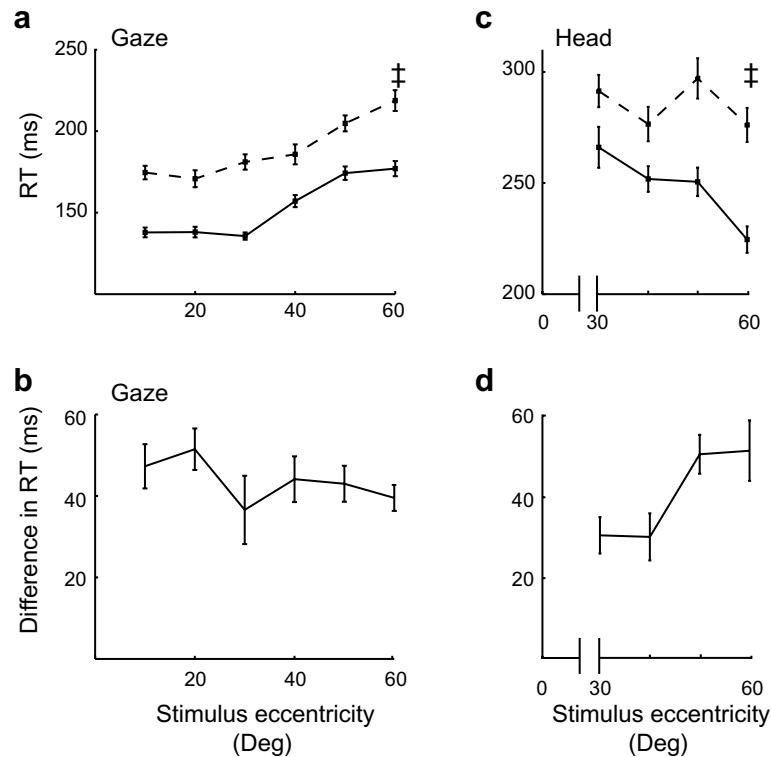


Fig. 4. (a and c) Mean gaze (a) and head (c) RT across stimulus eccentricity, for one representative subject in experiment 2. RTs on pro-gaze shift trials are represented by solid lines, RTs on anti-gaze shift trials are represented by a dashed line. Error bars denote the standard error of the mean. (b and d) To represent these data across the sample of 8 subjects, we derived a difference curve between RTs on pro- and anti-gaze shift trials at each eccentricity for each subject, and subsequently averaged these difference curves across the sample. Error bars denote standard error of the mean. (‡) Represents comparisons made with only one LED.

RTs) is consistent with previous studies which have varied stimulus luminance (Doma & Hallett, 1988; Pins & Bonnet, 1996).

3.2.2. Comparative dynamics of pro- versus anti-gaze shifts across stimulus eccentricity

To examine the effects of eccentricity and increasing stimulus luminance on pro- and anti-gaze shift dynamics, we constructed main sequence plots of peak velocity versus movement amplitude for both gaze shifts and head movements (shown for a representative subject in Fig. 5a and c, respectively). If the similarity in peak velocities observed in experiment 1 was due to decreased stimulus luminance, then increasing stimulus luminance should lead to faster peak velocities on pro- compared to anti-gaze shift trials across all eccentricities. Consistent with this interpretation, a comparison of the main sequence plots for gaze shifts made on pro- and anti-gaze shift trials revealed that the peak velocities of pro-gaze shifts remained consistently elevated above that for anti-gaze shifts. To analyze this feature across our sample, we first derived the difference between the main sequence plots for pro- and anti-gaze shifts for each subject, and subsequently averaged these difference curves across all subjects. The results of this analysis are shown in Fig. 5b, and demonstrate that peak gaze velocity remained consistently elevated on pro- versus

anti-gaze shift trials across all amplitudes [repeated 1-tailed *t*-test were significant ($P < .01$) at all amplitudes except 30°]. Although both pro- and anti-gaze shift velocity increased in experiment 2, a larger increase in pro-gaze shift velocity was observed when compared to pro- and anti-gaze shift velocities in experiment 1 [increase in pro-gaze shift velocity = 63°/s, increase in anti-gaze shift velocity = 47°/s; both increases were significant ($P < .05$) via paired *t*-tests]. Because head contribution was negligible for gaze shifts to 10°, the differences noted at this amplitude are consistent with findings from the head-restrained literature.

In contrast to the persistent differences in peak gaze velocities for pro- and anti-gaze shifts across all stimulus eccentricities, a similar analysis revealed little if any differences between peak head velocities across trial type [Fig. 5c and d; repeated 1-tailed *t*-test were not significant at all amplitudes ($P > .15$)].

3.2.3. Incidence rates

Increasing the luminance of the stimulus had a negligible effect on the incidence rates of the three expected sequences of eye-head coordination on anti-gaze shift trials. The overall incidence rates were very similar to those observed in experiment 1, with only a marginal increase in head-only error rate. Although the data shown from experiment 2

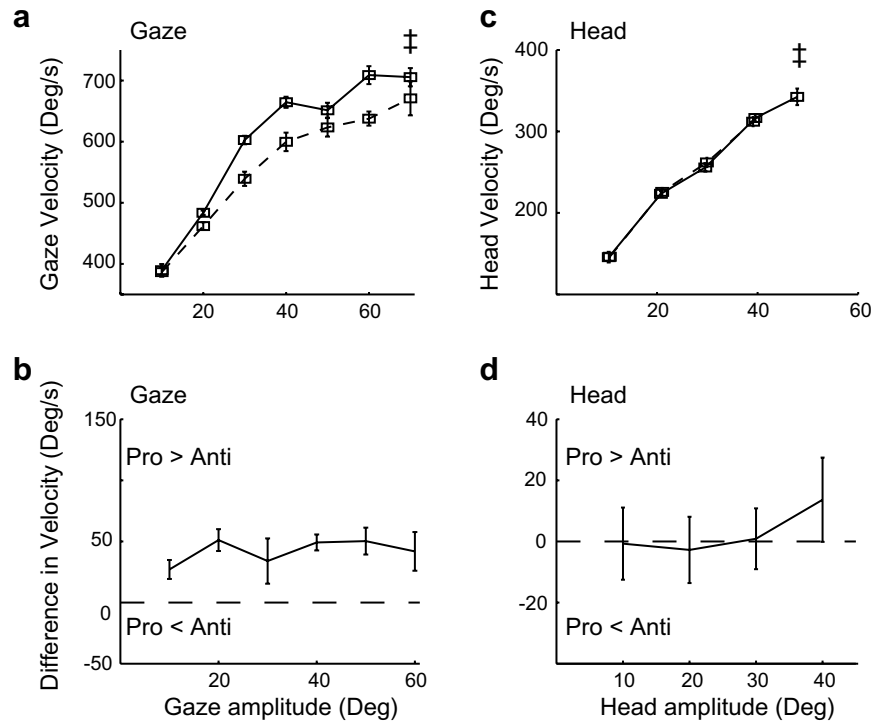


Fig. 5. Peak gaze (a and b) and head (c and d) velocities as a function of movement amplitude, from experiment 2. Same format as Fig. 4.

in Table 2 is taken only from when the stimuli were placed at 60°, we never observed head-only error rates greater than 1.5% at any eccentricity. Although increasing the luminance of the stimulus did effect the peak velocity of gaze shifts on pro- versus anti-gaze shifts, increasing stimulus luminance did not increase the rate of head-only errors on anti-gaze shift trials.

4. Discussion

Previous research has produced a refined understanding of the neural mechanisms underlying the generation of anti-saccades [see Munoz & Everling, 2004 for review]. To our knowledge, ours is the first study to systematically examine the metrics, dynamics, and coordination patterns of anti-saccades generated to locations that necessitate head motion (termed anti-gaze shifts, in order to be distinguished from anti-saccades made with the head restrained). Although many of our results were straightforward (e.g., longer RTs for anti-gaze shifts, regardless of stimulus eccentricity), the dependence of differences in peak gaze velocity on stimulus luminance, and the paucity of head-only errors were unexpected. Here, we relate these findings to previous results in the literature, and speculate on the neuromuscular patterns of neck muscle recruitment during anti-gaze shift trials.

4.1. Comparative timing and dynamics

One of our consistent findings was that the RTs of both gaze shifts and head movements were prolonged on anti-

compared to pro-gaze shift trials. These differences reflect the increasing demands during anti-gaze shift trials. Correct anti-gaze shifts require suppression of the inappropriate movement to the stimulus and vector inversion, in addition to the processes of stimulus detection and movement initiation common to both pro- and anti-gaze shifts. We did not observe any systematic difference in the lead time metrics, which measures the relative timing of gaze and head movement initiation. Indeed, given that head motion usually lagged gaze onset on both pro- and anti-gaze shift trials, we can surmise that the inertial lag of the head was the dominant factor in determining lead time regardless of trial type.

A number of reports in both humans and monkeys have shown that anti-saccades typically have slower peak velocities than pro-saccades (Amador et al., 1998; Bell et al., 2000; Smit, Van Gisbergen, & Cools, 1987; Van Gelder et al., 1997), although some variability in the results of individual subjects has been reported (Fischer & Weber, 1992) consistent with what we observed in experiment 1 (see Fig. 3b). Previous work has demonstrated that differences in reaction times between pro- and anti-saccades diminish with less luminant stimuli (Doma & Hallett, 1988), and differences in peak velocity diminish when a visual stimulus is provided at the goal location for anti-saccades (Edelman et al., 2006). The persistent differences in peak gaze velocities for pro- versus anti-gaze shifts observed in experiment 2 (Fig. 5a and b), where stimulus luminance was increased by increasing the number of LEDs within a stimulus cluster, attest to the importance of stimulus luminance in dictating differential peak velocities. More luminant stimuli

presumably lead to earlier and larger activation within the oculomotor system [e.g., see Bell et al., 2006], which would selectively speed gaze velocity for congruent pro-gaze shifts.

While this mechanism could explain our comparative results on peak gaze velocity, we observed that the peak head movement velocities were equal across trial type, regardless of stimulus luminance. We suspect that the lack of any difference in head movement velocity may relate to the comparative nature of the neuromuscular drive to the head compared to that of driving high-velocity gaze shifts. For example, movement-related activity on neck muscles during orienting head movements far outlasts the duration of gaze shifts (Corneil et al., 2004; Zangemeister & Stark, 1982a), as do the bursts of putative head pre-motor neurons in the brainstem (Isa & Sasaki, 2002; Pathmanathan, Cromer, Cullen, & Waitzman, 2006; Walton et al., 2007). We speculate that the additional neuromuscular drives that are recruited to move the more inertial head presumably do not differ across pro- and anti-gaze shift trials.

4.2. Possible mechanisms explaining the lack of head-only errors

Based on previous results, we expected that subjects would occasionally generate head-only errors on anti-gaze shift trials. Head-only errors have been observed with a frequency of ~10–20% in a variety of tasks, such as the countermanding and distractor task (Corneil & Elsley, 2005; Corneil & Munoz, 1999), and indicate a degree of independence between the neural mechanisms initiating gaze shifts and orienting head movements. In both versions of the anti-gaze shift task presented here, the rate of head-only errors rarely exceeded 3% in any subject, and averaged ~1.5% overall. The rarity of head-only errors is noteworthy given that some of our subjects commonly generated head-only errors in a countermanding task at a much higher rate (e.g., subjects four and six essentially generated no head-only errors on the anti-gaze shift trials, but generated such sequences on ~13% of countermanding trials).

Why then are head-only errors so rare in the anti-gaze shift task? Oculomotor behaviour in paradigms like the countermanding and distractor tasks has been modeled as a race between two competing motor command signals to threshold (Hanes & Schall, 1996; Logan & Cowan, 1984), using a rationale adapted from double-step tasks (Lisberger, Fuchs, King, & Evinger, 1975). In such models, programs for alternative responses race to a threshold, with the ensuing behaviour being determined by which program “wins” the race. Such a conceptual architecture has recently been extended to model eye-head gaze shifts in a countermanding task, whereby head-only errors occurred when the motor program surpassed a lower head-movement threshold but did not surpass the threshold for evoking gaze shifts (Corneil & Elsley, 2005). While the anti-gaze shift task shares some features in common with the countermanding and distractor task, such as the availability of

two potential motor responses, recall in the anti-gaze shift task that subjects are put into an “anti-gaze shift mode” based on the colour of the fixation point at the start of the trial. We speculate that this mechanism, which is present on anti-gaze shift trials but not present on trials in the countermanding or distractor task, accounts for the diminished incidence of head-only errors, as well as the relatively low rate of gaze errors [gaze error rates were ~6.5% here, compared to 32% and 30% reported previously in the countermanding and distractor experiments, respectively (Corneil & Elsley, 2005; Corneil & Munoz, 1999)]. The overall ratio of head-only errors to gaze errors is slightly lower in the anti-gaze shift task (1.5% versus 6%) than in the countermanding (13% versus 32%; stop trials were presented on 30% of all trials) or distractor tasks (19% to 30%; distractor trials were presented on half of all trials), but it is difficult to draw significant conclusions from these comparisons.

The instruction for human subjects to adopt the “anti-gaze shift mode” may be associated with increasing activity of fixation neurons in the rostral superior colliculus (SC) and in the frontal eye fields (FEF), as observed in monkeys (Munoz & Everling, 2004). Recent evidence has demonstrated that movement neurons in the SC can be classified into categories such as gaze-related or head-only neurons (Walton et al., 2007). Head-only neurons have enhanced activity preceding head motion which persists until movement offset. Inhibition of these SC head-only neurons, perhaps associated with the increased activity of SC and FEF fixation neurons, may be at least partly responsible for the lack of head-only errors in the anti-gaze shift task. However, we do not believe the engagement of the oculomotor fixation network directly inhibits head movements by co-contracting neck muscles. Electrical stimulation of the rostral SC recruits a weak head turning synergy rather causing neck muscle co-contraction (Corneil, Olivier, & Munoz, 2002a), and stimulation of the brainstem omni-pause neurons exerts little effect on on-going head motion even though gaze shifts are arrested in mid-flight (Gandhi & Sparks, 2007).

Recent results have demonstrated that presentation of a visual stimulus leads to time-locked recruitment of a head turning synergy that would serve to turn the head to the stimulus, presumably via signals relayed from the SC (Corneil et al., 2004). Given that neurons in the SC emit time-locked visual responses in response to stimulus presentation on anti-saccade trials (Munoz & Everling, 2004), it seems plausible that stimulus onset on anti-gaze shift trials should lead to recruitment of a head turning synergy that would turn the head in the wrong direction, and our preliminary evidence in monkeys supports this prediction [monkeys also generate few head-only errors; (Chapman & Corneil, 2007)]. Why then would the head not move toward the flashed stimulus on anti-saccade trials? First, any neck muscle recruitment favouring head movement toward the stimulus on anti-gaze shift trials may be insufficient to overcome the head's inertia. Alternatively, subjects may

be co-contracting neck muscles bilaterally prior to stimulus onset on anti-gaze shift trials, effectively stiffening the head plant, or have adopted a strategy whereby any stimulus-locked recruitment is quickly counteracted by recruitment of muscles on the opposite side, thereby preventing head motion. It remains an open question whether any of these strategies would be associated with increased fixation activity within the oculomotor system.

In conclusion, we found that perceived stimulus luminance at large eccentricities affects comparative peak gaze shift velocity in an anti-gaze shift task. In addition, although our preliminary results in monkeys demonstrate stimulus-locked neck muscle recruitment, the paucity of head-only movements in the anti-gaze shift task means that other oculomotor paradigms will be better suited to study the behavioural dissociation of the gaze and head.

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