# ABSTRACT

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| Title of Document: | HEAD-EYE COORDINATION DURING A NATURAL TAPPING TASK |
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This thesis describes the research of Herst et al. (2001) who examined the coordination of head and eye movements while participants searched for targets under natural conditions in which the head was free to move. This investigation was done because, while the technical difficulties in measuring these patterns of head-eye coordination in humans have been overcome, the results obtained over the last 35 years have yet to show what the typical pattern of head-eye coordination looks like. Herst et al. (2001) described the 'natural' temporal coordination of head and eye of four participants who tapped a sequence of targets arranged in 3D on a worktable in front of them. The results were not expected based on prior studies of head-eye coordination performed under less natural conditions. This thesis reinterprets the original (2001) findings and draws new conclusions in the light of new research on head-eye coordination conducted since then.

# HEAD-EYE COORDINATION DURING A NATURAL TAPPING TASK

By

Andrew Neal Herst

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Professor Michael R. Dougherty, Ph.D, Chair
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# Chapter 1: Introduction

## Section 1 Head-eye coordination

The maintenance of stable gaze relies on effective coordination of head and eye movements. And having control of gaze is necessary for gathering any visual information with high spatial frequency. As a result, understanding how the head and eyes are coordinated as we search our environment is a topic of interest in the oculomotor literature. Of more practical importance, the relationship between eye movements and information processing has been of interest for at least 145 years (Steinman & Levinson, 1990). Normally, the head and eyes move about freely and coordinate together in a richly structured and changing environment containing numerous possible targets. It becomes clear, then, that investigating head-eye coordination under natural conditions would be of great fundamental and practical importance. However, examining how the head and eyes coordinate under natural, unrestrained, conditions is difficult to do and few attempts have been made. This thesis presents the results of one such attempt by Herst, Epelboim and Steinman (2001). With the understanding of the importance of examining the coordination of the head and eyes under natural conditions, and noting the lack of prior research, Herst et al. (2001) described the patterns head-eye coordination under natural, unrestrained conditions while performing a natural task.

I begin with a brief historical overview of some of the more notable attempts at understanding how the head and eyes are coordinated. I present a more historical summary in order to show why the results obtained by Herst et al. (2001), and other experiments examining head-eye coordination under more natural conditions, are noteworthy. I then present the results obtained by Herst et al. (2001) and conclude with a discussion of the theoretical implications of my research. Since 2001, when our experiment was published, there have been investigations of the coordination of the head and eyes under natural conditions while the head free was to move. I reinterpret the original results of Herst et al. (2001) given the more recent experimental findings.

## Section 2 Historical Review

Interest in the temporal coordination of head and eye goes back at least as far as 1921 when Dodge wondered whether gaze-shifts, which involve both the head and eyes, are integrated into a single unit of reaction. In other words, do synchronized rotations of head and eyes represent a centrally-programmed orienting response? Contemporary interest in human head-eye coordination began when Bartz (1966) published a report in Science in which he used EOG[1] to record horizontal eye rotations and a helmet-mounted potentiometer[2] to record horizontal head rotations of three participants who were asked to look at 1 of 4, randomly-chosen, Nixie-tube[3] targets. These targets appeared at randomly-chosen locations along the horizontal meridian within a 110º field. Participants were required to report the digit displayed on the Nixie-tube. This requirement was imposed to encourage accurate gaze-shifts. It also had the virtue of making Bartz's task more "natural" than most later experimental tasks. Note that Bartz's participants were asked to shift gaze to accomplish a useful purpose; namely, to find out which randomly-chosen number, 4, 5, 6 or 9, had come up on the Nixie-tube display on a given trial. Shifting gaze to get information is precisely the kind of thing humans do a lot of. Shifting gaze simply to line it up with a LED[4] because it flashed, which is a common task used in studies examining head-eye coordination, is more characteristic of what is likely to happen in an oculomotor laboratory than in the real world.

Bartz's participants were highly-practiced, i.e., their performance was recorded only after they had served in 19 daily practice sessions. Bartz noted that the limited prior work on head-eye coordination done before his own had found that eye movements occur first, followed by head movements. His results confirmed this earlier finding. Bartz (1966) reported that "After a latency period the eyes begin to move toward the stimulus while the head remains stationary" (p. 1644). Note that the eyes of his participants must have led appreciably – EOG recordings have relatively modest bandwidth.

Bizzi, Kalil and Tagliasco (1971)[5] extended Bartz's work to the monkey, using trained and, therefore, predictable, as well as unpredictable, target locations. Bizzi et al. (1971) reported that predictable target locations resulted in patterns of head-eye coordination in which the head moved first, followed 150 ms later by a saccadic eye movement. The potential importance of predictability of the target's location on human head-eye coordination has received relatively little attention in the human head-eye coordination literature (see Corneil, Hing, Bautista, & Munoz, 1999; Corneil & Munoz, 1999, for exceptions) since Bizzi et al. (1971) called attention to its effect in the monkey.

Gresty (1974) examined the head-eye coordination problem as well but shifted the emphasis from temporal coordination of the head and eye because of a proposal made by Mowrer (1932) who claimed that the slow phase displacement of the eye, following the head movement, was due to the VOR[6]. Unlike Bartz (1966), Gresty did not study the effect of predictability on human head-eye coordination. Like Bartz, Gresty recorded the horizontal head and eye movements of eight participants who were highly acquainted with the experimental procedure. EOG was used to measure eye movements, a head-mounted potentiometer to measure head movements, and an array of 13 red LEDs, instead of Nixie-tubes, which meant that his participants shifted gaze for shifting's sake. The other major change in Gresty's protocol was the addition of a condition in which the target was flashed for only 40 ms, extinguished for 1s, and then re-illuminated. The dark interval was designed to reveal the operation of the VOR free from the influence of visible targets. Passive head rotations were also measured. Target location was hard to predict with both the continuously visible and flashed targets. This paper had relatively little to say about temporal coordination of the head and eyes except that, because of the dynamics of the eyes, the eyes move first followed by a head movement only after the eye have reached their peak displacement. The eye tended to lead the head with both the highly practiced participants and with the knowledgeable unpracticed participants, regardless of whether the targets remained visible or disappeared. Moreover, the goal of the task also had little effect. The eye continued to lead the head when either gaze was shifted to acquire information or when gaze was shifted for its own sake.

Bartz's methodology and Gresty's approach continued to be influential. We find Barnes (1979) also using EOG, a head-mounted potentiometer, and LED targets flashed for different intervals (long or short). Barnes did not cite the work of Bizzi et al.'s (1971) with the monkey, and did not include any predictable target locations, but did include both voluntary (active) and passive head rotations. At this point our understanding of human head-eye coordination becomes more complicated. Barnes (1979) reported that the head lead the eye 22% of the time during continuous target presentation and 15% of the time when the target was flashed. The head (averaged over six participants) led the eye by 1 ms [sic] when the target, which was beyond 50º of the initial fixation point, appeared and remained visible. The eye led the head when the target offset was smaller (less than 45°). Overall, Barnes found that the eye led the head, but the head led on an appreciable number of trials, particularly with very eccentric targets.

The nature of human head-eye coordination continued to interest a number of investigators, with emphasis placed on the generation of saccades when the VOR was used to stabilize gaze. Gaze-shifts to unpredictable target locations were studied both during active and passive head rotations. Zangemeister and Stark (1981) found that the eye led the head when both moved in the same direction (see their Fig. 11 for example). Head latency was reduced when the target's location was predictable, but the eye still tended to lead the head. Biguer, Jennerod and Prablanc (1982) examined eye/head/hand coordination in a pointing task. Their experiment was more like a natural human behavior than most described so far because gaze shifted to help guide a pointing hand – a common task in everyday life. Biguer et al. (1982), in examining gaze shift and arm movements, introduced their work by claiming that under normal conditions one moves their eyes first, then their head, and finally point their arm in the proper direction. Otherwise this work was done within the tradition and with the methodology introduced by Bartz, namely, (i) nine red LEDs arranged with 10º spacing about a central target, (ii) EOG was used to record binocular horizontal eye movements and (iii) a helmet-mounted potentiometer was used to record horizontal head rotations. The five participants were instructed to track and point at the target as quickly as possible. When doing this, the eye movement "always" occurred first with the head movement lagging behind (pp. 302-303). The eye led the head in a relatively natural task that required coordination of the hand along with the eyes and head. The eye-first tendency emphasized in all of this research seemed to be a rather robust characteristic of human participants.

Much of the work described so far was summarized by Fuller (1992) who reviewed publications through 1989 with both head-fixed and head-free humans, as well as with some other mammals. Ten of these papers dealt with free-headed humans. Eight of these used visual stimuli, which make them germane to the present paper. None of these eight experiments, however, can be described as either very natural or even accurate because (i) head rotations were restricted to rotation about the vertical axis, (ii) head rotations might have been affected by friction within the potentiometer (a possibility played down by those who used them), (iii) EOG, a relatively crude method, which is well known to be subject to several artifacts, was used to measure eye rotations, and (iv) the stimulating conditions were most often flashed targets that came on for variable intervals in otherwise dark environments, conditions quite different from those in which human beings perform most of their natural, coordinated, visuomotor acts. Fuller (1992) expressed concern with these problems. He also raised the issue of the relevance of these papers for explaining human head-eye coordination during natural tasks in the real world. Fuller concluded that “The reliability or variability of different strategic patterns is highly dependent on the experimental design, which may become so constrained that the behavior no longer resembles that of the freely moving subject” (p. 111).

## Section 3 Recording with the head free to move

The problem of studying head-eye coordination under relatively realistic, natural conditions had been solved for the rabbit by Collewijn (1977) even before Fuller’s review (1992). Collewijn solved the problem when he introduced the cube-surface field-coil, phase-detecting, magnetic eye/head recording system. Collewijn’s new method made it possible to record both head and eye rotations accurately while rabbits walked freely about in a relatively large field. Under these novel, rather natural, conditions, rabbits, who did not make saccades when their heads were immobilized, showed themselves capable of relatively stable patterns of saccades and head movements. Collewijn (1981) summarized his observations on the head-eye coordination of the freely-moving rabbit as follows: “It must be concluded that ... most gaze changes are achieved by combined eye and head movements. In many of these, head and eye movements are both saccadic and initiated simultaneously” (p. 19).

Steinman and Collewijn (1980) used this rabbit instrumentation to record human gaze-control as the head was actively oscillated about its vertical axis, while distant objects, seen through a window on the 15th floor of the Medical faculty in Rotterdam, were fixated binocularly. They reported several features of human oculomotor performance that could not have been anticipated from more conventional observations made with the head restrained in a visually-impoverished environment usually used in more conventional laboratory experiments.

Fuller (1992) discussed two papers (Collewijn, Steinman, Erkelens, Pizlo & Van der Steen, 1992; Kowler, Pizlo, Zhu, Erkelens, Steinman & Collewijn, 1992) which used Collewijn's recording technique after it had been implemented in a much larger, and more accurate, phase-detecting instrument called the Maryland Revolving Field Monitor (MRFM). This instrument was scaled-up sufficiently to make it more comfortable for research with human participants. Within these papers are descriptions of the control of gaze during both natural and unnatural visuomotor tasks. Once again, it was shown that oculomotor performance under relatively natural conditions is different from performance under the constraints that were ubiquitous before Collewijn's important contributions to recording instrumentation. For example, as described by Collewijn et al. (1992), peak saccadic velocity was found to be higher when the head was entirely free, leading these authors to conclude that when eye movements are recorded while a participants head is held on a bite board (or bolted to a metal frame), the data obtained could reflect inaccurate performance caused by the inhibition of natural gaze-shift commands. Similarly, Kowler et al. (1992) examined natural eye movements during reading and scanning with the head free and found that having the head entirely free to move "revealed a natural tendency to program head and eye movements concurrently in similar spatial and temporal patterns" (p. 426). Recently, Lee (1999), Seo and Lee (2002), and Proudlock et al. (2003) continued, and extended, these observations of free-headed reading and found a strong correlation between eye and head movements when they examined the effects of text familiarity and direction of text (either vertical or horizontal).

We can see that the utility of measuring the eyes and head under more natural conditions, with the head free to move normally, has been recognized. Over the past 15 years a number of studies have been published that that make use of a more natural environment with natural movement. This recent work has shifted the emphasis from a focus on ocular-motor dynamics to the role eye movements play in selecting visual information during complex tasks (Welchman & Harris, 2008). These studies on eye, and sometimes head, movements while performing complex, every-day activities, examine driving through a neighborhood (Land, 1992; Land & Lee, 1994; Land & Tatler, 2001), playing baseball (Land & Furneaux, 1997; Land & McLeod, 2000), making a cup of tea (Land, Mennie, & Rusted, 1999), making a sandwich (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003), washing one's hands (Pelz & Canosa, 2001), and copying a pattern of blocks (Ballard, Hayhoe, & Pelz, 1995; Smeets, Hayhoe and Ballard, 1996; Hayhoe, Bensinger, & Ballard, 1998; Pelz, Hayhoe, & Loeber, 2001). This recent trend began when Land (1992) published a paper in Nature in showing that he could predict human head-eye coordination during driving. This was an interesting contribution, in part, because Land points out that understanding the human being's natural way of coordinating the head and eyes can be observed when the coordination required is done, as Land put it, "unthinkingly." Driving a real car safely on a real street in real traffic benefits from confining attention to the task at hand. It discourages observing, or attempting to modify, one's natural propensity for coordinating the head and eyes. Land performed his study by recording a view of the driver's gaze superimposed on a view of the scene with a head-mounted video camera. Land's rationale was that "If there are 'natural' patterns of oculomotor coordination that emerge in every day situations these should be detectable from the predictable way that the head and eye co-vary" (p. 318). Therefore, the onset of both the eye and the head movements made during every gaze shift would be determined by the sizes of the gaze shifts themselves. Land found that occasionally the head led the eye by up to 150 ms, but strict synchrony (20 ms or less) was the most common pattern of head-eye coordination. Land concluded that while driving, and under circumstances where eye and head movements are generated unthinkingly, the eyes and the head receive the same command at almost the same time by default. And while we can consciously override this mechanism that directs gaze by either making or suppressing head movements, we usually do not.

Smeets, Hayhoe and Ballard (1996) also examined head-eye coordination while participants performed a visuomotor task "unthinkingly." Their task was also natural but quite different. They examined gaze-shifts while participants manipulated objects (toy DUPLO building blocks). These manipulations required participants to make gaze-shifts of about 30º as they reproduction a model. Smeets et al. (1996) introduced their study by pointing out that what we know about human head-eye coordination is based mainly on studies conducted under highly artificial laboratory conditions. And while simple tasks conducted under artificial laboratory conditions are well suited to studying basic mechanisms of neural control, when such experiments are used to study the interaction of such mechanisms the results sometimes tell us more about the experimental constraints than about the control mechanisms we want to study (Steinman, Kowler & Collewijn, 1990). Smeets et al. (1996) studied humans who are performing natural tasks, while focusing their attention on the task instead of on the variables they were interested in studying.

Smeets et al. (1996) recorded the position and orientation of the head and the hand with a 3-D electromagnetic system. The position of the left eye was recorded with a head-mounted IR camera. The accuracy of their latency measurements was between 16 and 20 ms – as long as they "averaged many trials." Four participants were required to make reproductions of DUPLO building block models. Smeets et al. (1996) found that the movements of the eye, head, and hands followed a highly coordinated pattern, namely that the eye moved first, followed by a head movement, followed then by a hand movement. They go on to state that the specific onset characteristics of the eye and head movements were dependant on the movement of the hand. They go on to conclude that, contrary to Land (1992), even when gaze is shifted unthinkingly, the eyes and head can receive different commands at different times.

In keeping with the theme of examining patterns of coordination while participants behave "unthinkingly," Einhauser et al. (2007) had participants explore very natural environments – a train station, a forest, and an apartment. A completely portable recording device was created which used video cameras mounted to a helmet to record head movements and gaze shifts in four human participants during natural, free-headed movements in the various environments. There was no task to perform – participants were simply instructed to ignore the recording device and make natural movements while exploring the environment.

While Einhauser et al. (2007) were specifically interested in understanding the extent to which head-eye coordination is responsible for gaze stabilization under extremely natural conditions, and not in the timing of head and eye movements, they did conclude that eye and head movements are highly coordinated, and that this pattern of coordination "…held for all subject in all environments" (p. 277).

By 1992, the year in which Land published his driving experiment, the development of the MRFM had progressed to the point where it became possible to study gaze-control very accurately under the conditions that are arguably the most significant for the human's success as a species. Namely, the human's ability to manipulate and fashion objects held in the hands. In other words, to fashion and work with objects well within arms' reach. Measuring gaze accurately under these conditions required measuring translations of the head, as well as head and eye angles, very accurately. The Smeets et al.'s (1996) experiment (described above) clearly falls into this category of significant, natural experiments, at least with respect to the nature of the task. The temporal and spatial resolution was less than what was possible with the MRFM, but it was sufficient to add some useful information to the human head-eye coordination problem. The coordination of the head and eye depended on what the hand was going to do, but does the eye continue to lead the head whenever the hand manipulates nearby objects?

Data that would answer this question had already been collected (1992) and analyzed for other purposes (Epelboim, J., Steinman, R. M., Kowler, E., Edwards, M., Pizlo, Z., Erkelens, C. J. & Collewijn, H., 1995). In these experiments, participants were seated with heads and torsos completely free as they either looked at (LOOK-ONLY) or tapped rods (TAP) in a specified sequence, arranged nearby in 3-D space. The TAP task resembled activities humans are often called upon to do in the real world under natural conditions. It was also rather similar to what Smeets et al. (1996) had asked their four participants to do. No explicit instructions were given as to how the head and eyes should be coordinated in either task. Both tasks encouraged the participants to perform “unthinkingly.” They were required to complete the sequence as fast as they possibly could without making any errors in the order in which the tapped or looked at the sequence of rods.

Herst, Epelboim & Steinman (2001) reported the results of additional analyses of the database that had produced four publications so far, viz., Epelboim et al. (1995); Epelboim, Steinman, Kowler, Edwards, Pizlo, Erkelens and Collewijn (1997); Epelboim (1998), and Malinov, Epelboim, Herst and Steinman (2000)[7]. All dealt with the control of gaze under relatively natural conditions. This earlier research described four findings, (i) visual search, gaze-shift accuracy and the function of gaze-shifts, (ii) gaze-shift dynamics, (iii) gaze and retinal-image-stability, and (iv) the size of binocular saccades, how well saccade size matched in the two eyes, and saccadic vergence. This thesis describes the temporal coordination of the head and eye when these participants tapped a sequence of targets. Head-eye coordination was not analyzed for the conditions in this database in which participants LOOKED-ONLY at targets because all four participants tended to sit very still, keeping head movements to a minimum. There was not sufficient head movement to make an analysis of the temporal coordination of head and eye interesting. The TAP task was quite different. The head and eye made many coordinated movements. We found that the head tended to start moving before the eyes, a result at odds with much of the prior literature on human head-eye coordination, including the only two papers (described just above) that studied human head-eye coordination under rather comparable, relatively natural, conditions.

# Chapter 2: Method

## Section 1 Measuring eye movements while tapping targets

Binocular eye/head movements were measured while participants tapped (TAP) sequences of 3-D targets (colored LEDs) located on a worktable in front of them. The angular separation of targets was random, varying between about 1.5° and 35° of visual angle. The distance from the participants' eyes to the targets varied from about 50 to 90 cm, depending on where the targets were and how much each seated subject moved. All targets were arranged before the beginning of each trial and were stationary and visible throughout. Eyes were closed between trials. Each target configuration was tapped 10 times before a new randomly-generated configuration was presented. See Epelboim et al. (1995) for additional procedural details.

Herst et al. (2001) examined the temporal relations between the onset- and offset-times of head rotations and saccades (relative to the head) which met the following two criteria for a coordinated head-eye movement: (1) the head and eye moved in the same direction, and (2) the horizontal components of both the head and eye were larger than 10º. The criterion used for saccade and head onset and offset was a horizontal velocity = 20% of its peak. This criterion was chosen because Smeets et al. (1996), the prior experiment most closely related to ours (see above), had used “a very conservative threshold to detect the onset of movement ... velocity surpassed 50% of its maximum value.” (p. 436). We also desired a conservative criterion, but were able to set it lower (20%) because our temporal resolution was much better, viz.,

~2, rather than 16 ms. Head and eye movements were considered to begin simultaneously if their onset occurred within ±8 ms of each other, also a conservative value, i.e., 4 times our resolution limit. In all, 2729 “coordinated” head-eye movements met these criteria (N/Subject: ZP = 637, HC = 649, RS = 720, CE = 723). The MRFM data used in these analyses consist of angular positions measured to 1 minarc with successive samples separated by 2.04 ms. Examples of the different kinds of head-eye coordination we observed can be found in Figs, 1-4.

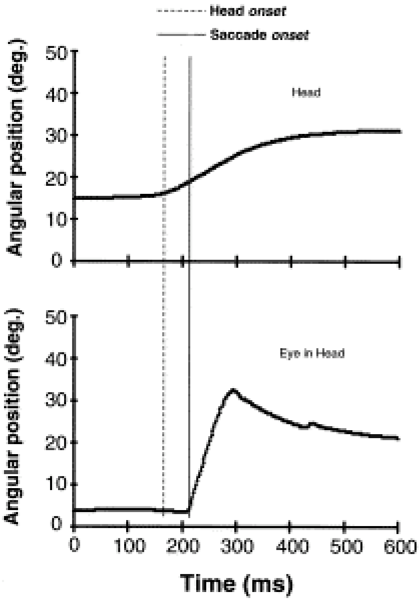
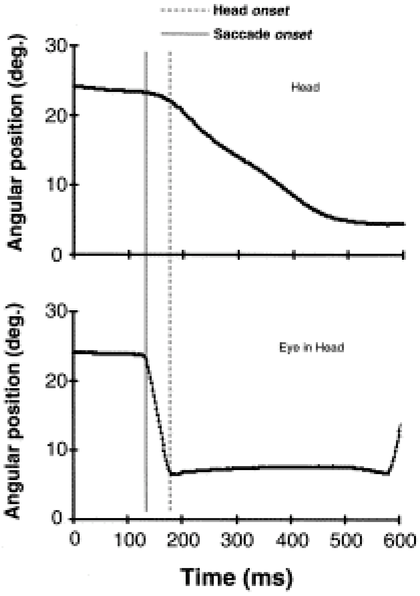
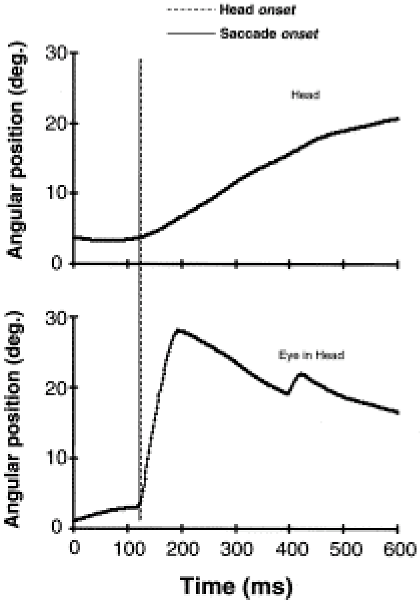


Fig. 1



Head onset
Saccade onset
Angular position (deg.)
30
20
10
0
Head
Angular position (deg.)
30
20
10
0
Eye in Head
0
100
200
300
400
500
600
Time (ms)

Fig. 2



Head onset
Saccade onset
Angular position (deg.)
30
20
10
0
Head
Angular position (deg.)
30
20
10
0
Eye in Head
0
100
200
300
400
500
600
Time (ms)

Fig. 3

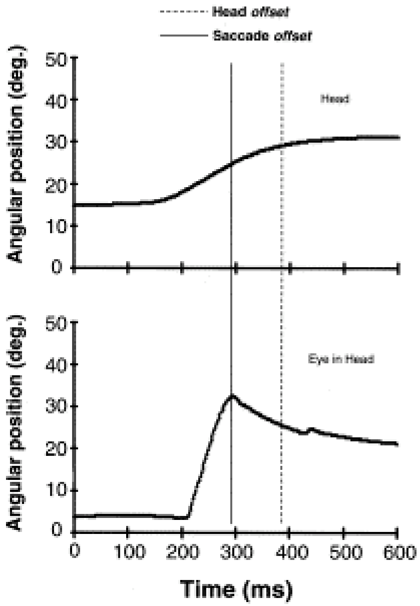

Head *offset*
Saccade *offset*
Angular position (deg.)
50
40
30
20
10
0
Head
Angular position (deg.)
50
40
30
20
10
0
Eye in Head
0
100
200
300
400
500
600
Time (ms)

Fig. 4

# Chapter 3: Results

## Section 1 Overall pattern of head-eye coordination

The overall pattern of head-eye coordination was strikingly similar for all four participants.

## Section 2 Onset of eye and head

For all four participants, the head moved before the eye more often than the eye moved before the head. The head led 48% of the time (range = 46% to 52%). The mean head lead was 22.78 ms (S.D. = 16.85). The head and the eye started moving simultaneously 37% of the time (range = 35% to 40%). The mean when they started simultaneously (± 7 ms) was 5.54 (S.D. = 2.64). The eye led the head only 15% of the time (range = 13% to 18%). The mean eye lead was 33.25 (S.D. = 20.70). The differences among the three groups of proportions of coordinated head-eye movements, summarized in Fig. 5, were all statistically significant ($\chi^2 = 463.2$, df = 2, $P < 0.0001$), which means that we can conclude that the head is most likely to lead, and that the eye is least likely to lead, during coordinated head-eye movements under the natural conditions studied.

Fig. 6A shows the distribution of the three types of coordinated head-eye movements: (i) the eye leading, (ii) eye and head starting simultaneously and (iii) head leading. The data were pooled over the four participants because individual differences were modest. Fig. 6B plots the proportion of the data that fell near (± 20 ms) our temporal resolution limit (~ 2 ms). The head can be seen to be likely to lead the eye even when "simultaneous" is defined as stringently as our instrumentation allowed.

Fig. 7A shows the distribution of gaze-shift sizes for the 3 classes of head-eye relationships (head leads, simultaneous and eye leads). It is shown separately for each subject to illustrate how very similar their performance was with respect to this parameter. Their ages, sizes and builds varied considerably but their performance did not. Apparently, constraints inherent in tapping randomly-configured rods on a 46 cm X 59 cm worktable had a larger influence on performance than the individual differences among the participants' ages and physiognomies. The mean gaze-shift, averaged over all four participants, was 42.6º, S.D. = 15.06.

Fig. 7B shows the distribution of individual subject's gaze-shift directions (leftward or rightward) for the 3 classes of head-eye relationships (head leads, simultaneous and eye leads). All four participants were about equally likely (within ~2%) of making gaze-shifts to the left and to the right, viz., 48.3% went left and 51.7% went right. These leftward and rightward saccades were quite similar in size. The mean left saccade-size, averaged over the four participants, was 42.5º, S.D. = 15.0, and the mean right saccade-size was 42.6º, S.D. = 15.11.

It is clear that performance in the tapping task was not subject to appreciable individual differences. The nature of the task, rather than individual participants' propensities, had the larger influence on the way all four coordinated their head and eyes. On the whole, the head led the eye, or the head and eye started moving simultaneously. The eye was least likely to initiate a gaze-shift during this relatively natural tapping task. Note that gaze-shift-sizes varied over quite a large range, about 68% were between 27º and 57º.

Section 3 Offset of eye and head

The eye of all four participants always stopped moving before the head. On average, the head stopped 136 ms after the eye. The earliest head movement stopped 24 ms after the eye and the latest stopped 487 ms after the eye.

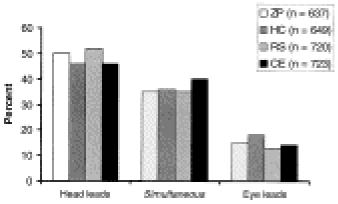


Fig. 5

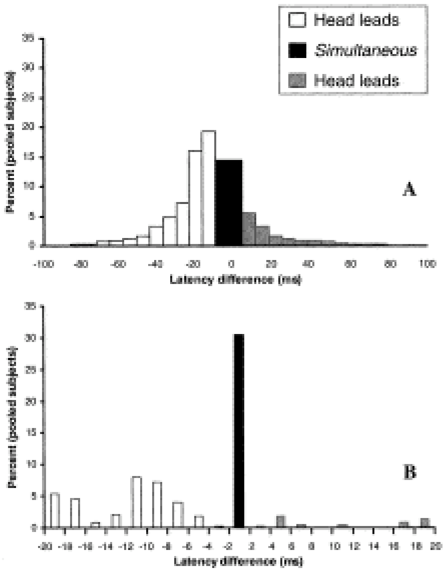


Fig. 6

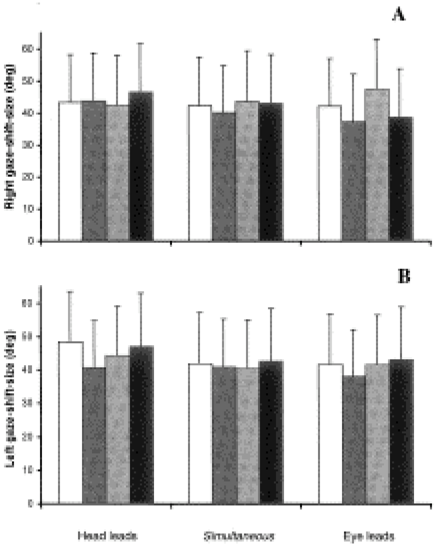
A
Right gaze-shift-size (deg)
0
10
20
30
40
50
60
B
Left gaze-shift-size (deg)
0
10
20
30
40
50
60
Head leads
Simultaneous
Eye leads

Fig. 7

# Chapter 4: Discussion

## Section 1 Comparison with other "natural" experiments

The purpose of the investigation by Herst et al. (2001) was to determine (i) whether the eye started moving before the head as had been reported by Smeets et al. (1996) when vision guided a hand that was copying a model, or (ii) whether the head and eye started moving simultaneously as had been reported by Land (1992) while participants were driving. Neither was found. Herst et al. (2001) found that the head was more likely to start moving before the eye when a sequence of rods was tapped. The eyes were least likely to move first. If the head did not lead, the head and eye were more likely to begin moving simultaneously. The finding that the eye was least likely to lead is at odds with most prior work on human head-eye coordination. Furthermore, the coordination of all four participants in the tapping task was similar. Such uniformity was also rare in prior work where considerable inter- and intra-subject variability had been reported (Smeets et al., 1996, see their Fig 5 B; Land, 1992). Individual differences in gaze-shift dynamics in the tapping task were small (see Fig. 4 in Epelboim et al., 1997). The relatively modest inter-subject variability observed in our tapping task suggests that characteristics of this task placed constraints on head-eye coordination that were not imposed by other tasks, i.e., copying models or by driving. In summary, the head-eye coordination of the participants, who served "unthinkingly" in three experiments explicitly designed to be as "natural" as possible, differed quite widely both with respect to the nature and variability of the temporal relationship between the head and eye.

## Section 2 Comparison with less "natural" experiments

A number of rather elaborate studies of head-eye coordination in humans under less natural conditions have been published since Fuller's (1992) review (cited above). The degree to which they shed light on head-eye coordination under more natural conditions is unclear, but highlights of a few will be described here for comparison with the above results.

Ron, Berthoz and Gur (1993) introduced their paper by noting that variability in head-eye coordination onsets have been shown to be dependent on the displacement, predictability and visibility of the target. Ron et al. (1993) used Bartz's (1966) technique, i.e., binocular EOG and a head-mounted potentiometer, to measure the horizontal eye and head rotations of four participants tracking a moving red laser spot. Participants were instructed to follow the stimulus pattern "as quickly and accurately as possible and to remain fixating at the last flash offset until the target reappeared at the initial position" (p. 597). They employed a pair of flashed targets that always went in the same direction, either increasing or decreasing in eccentricity. Ron et al. (1993) predicted that when the head is free to move normally, the head and the eye would be tightly coupled. Furthermore, any change in the saccades, bought on by the change in stimulus characteristics, would result in a change in the patterns of head-eye coordination. Ron et al. (1993) found that head movements preceded eye movements when responding to successive flashes of light in total darkness. They also called attention to the result that when two sequential flashes were presented, some eye and head movements were dissociated with the initial head movement towards the first flash, while the eyes moved to the second flash. This finding was "…contrary to the current belief that tight eye-head coupling is a phenomenon throughout the phylogenetic scale" (p. 609). Ron et al.'s (1993) experiment stands out as probably the only example that reported the head leading the eye consistently, prior to the results of Herst et al. (2001).

Volle and Guitton (1993) used EOG to record binocular horizontal eye movements, but used the amplitude detection, magnetic field method with a sensor coil taped onto the forehead to measure rotations of the head (the head coil was calibrated by having the subject rotate the head while wearing a calibrated, helmet-mounded potentiometer). The targets used were 17 red LEDs separated by 10º within a ±80º field. The main difference between this and prior work was the fact that while Volle and Guitton (1993) studied gaze shifts with the visual axis straight ahead relative to the body (as prior work had done), they also studied gaze shifts with the head offset from the straight ahead position by various angles. They found that for relatively small eccentricities, i.e., 40º or less, eye movements are used to bring the lines of sight close to the target while head movements contribute little to the displacement of gaze. For larger eccentricities, i.e., greater than 50º, head movements contribute increasingly more to the displacement of gaze. Volle and Guitton (1993) conclude that even when the participants were not specifically instructed to move their heads, they exhibited a strong propensity to do so even when head movements were not necessary.

More recently, Goossens and Van Opstal (1997) used the phase-detecting technique introduced by Collewijn (1977) originally developed for the study of freely-moving rabbits, to publish unusually accurate measurements of human head-eye coordination. Goossens and Van Opstal (1997) used both visual and auditory input to define the location of 84 LED targets arranged at spherical polar coordinates with the LED at the origin located “at the straight-ahead position.” Head and eye movements were measured under both aligned and unaligned conditions. In the former, the participant’s head and gaze was directed to the LED in this straight-ahead position. In the unaligned condition, before the trial began the head and eye were aligned to different positions. The participant was required to maintain the direction of the head when shifting gaze to a randomly-selected LED in the array. Participants were explicitly instructed to move their eyes and head towards the targets as fast as possible, but not to move their bodies. The LED targets were beyond the reach (0.85m) of all but the longest human arms.

Goossens and Van Opstal (1997) reported that the eye moves first, followed 50 ms later by a head movement. This was observed in both the aligned and unaligned conditions. So, once again, it seems that the eye tends to lead the head – the most frequently reported result since Bartz began the modern work in 1966.

Corneil and Munoz (1999) and Corneil et al. (1999) also made very accurate measurements by using the magnet field-sensor coil technique to measure head and eye movements. They studied four participants who were able to move around freely while they looked at (or near) LED’s, or towards auditory “noise bursts”, while a second stimulus, of the other modality, was presented either near where the target was presented (their “enhancer” condition) or away from where the target was presented (their “distractor” condition). They selected their four participants that met the criteria for head movers (Fuller, 1992b). The Corneil et al. (1999) report has little direct relevance to the present work because it examined gaze shift dynamics and accuracy when distractions were introduced during gaze shifts. The authors were primarily interested in whether the gaze-shift could be reversed in mid-movement. The research of Corneil and Munoz (1999) is more germane to this thesis because they examined head-onset latency under the conditions described by Corneil et al. (1999). The purpose of this aspect of their experiment was to identify and analyze early head movements (EHMs) that were made before an eye movement – what was referred to as a correct gaze shift (CGS).

Corneil and Munoz (1999) observed that participants occasionally move their head before the gaze shift begins. They grouped these "early head movements" into "correct" or "incorrect" depending on whether the head oriented towards the target or towards the distractor. The group of "correct" early head movements is closet to our situation in which gaze is shifted towards the next target in a tapping sequence. Corneil and Munoz (1999) present some data that can be compared with data of Herst et al. (2001). They report that, over all participants, the average percent of early head movements with a visual target and auditory stimulus in the same location, i.e., an auditory "enhancer", was 33%. The percentages for the four individual participants were 34%, 79%, 19%, and 1%. The 33% overall average tabulated is hardly representative. Herst et al. (2001) found "early head movements", i.e., the head leading the eye, on average, 48% of the time, and the participants' percentages of early head movements ranged from 46 to 52%. The participants described in Herst et al. were much less variable.

Corneil and Munoz (1999) concluded that simply examining the onset times of the head and eyes is insufficient for fully understanding eye-head coordination. The authors proposed that "Future studies will require more complicated experimental protocols, such as employing multiple stimuli to tease apart different facets of orienting commands, and more sophisticated experimental techniques, such as combining extracellular recording of electromyographic neck muscle activity in behaving animals, to further understand the decomposition of orienting signals in to the final movement commands for the eye and head" (Corneil & Munoz, 1999, p. 1419). We agree that more studies are needed to understand the temporal coordination of the human head and eye, but we suspect that simpler and more natural, rather than more complicated, experiments may be a better way to go. This possibility will be emphasized below.

Stahl (1999) also published a rather elaborate, relatively unnatural, but accurate experiment on human head-eye coordination. The rotating magnetic field-sensor coil technique, introduced by Collewijn (1977), was used to recorded head and eye angles. An elaborate stimulus paradigm was designed to elicit quasi-natural patterns of head-eye coordination. A 180º array of LEDs was used to create 76 possible target eccentricities. A complex pattern of target placements were presented throughout each trial, with a set of two to five "peri-test" targets being presented ± 0-2º from an eccentric target whose eccentricity could be somewhere ± 50º of the starting fixation position. Stahl's (1999) intention was to emulate what he believed to be the "natural" human scanning pattern, the kind that might be employed during a "bird-watching hike through a field." Stahl (1999) stated that "We designed our stimulus to parallel the natural pattern of visual search in which large saccades to new objects of interest are followed by series of smaller saccades as the details of the object are inspected" (p. 52). It requires more than a little optimism to believe that the manner in which a human being will track a series of LEDs that appear unpredictably at varying distances from where gaze resides in an otherwise dark, impoverished environment resembles the manner in which a human being will actually search the highly-structured, illuminated world in which a bird-watcher takes a hike to look for birds.

Despite such obvious differences between natural bird-watching and the stimuli provided in this experiment, Stahl (1999) felt that the design of this stimulus paradigm improved upon the traditional laboratory conditions used to examine head-eye coordination by providing a more natural distribution of saccades sizes without having to instruct the participant how to orient the head and body. Ten participants served in this experiment. Intra-participant variability was relatively low, but inter-participant variability was large for unknown reasons. Stahl also reported that head movements occasionally preceded eye movements by up to 20 ms, a result reported first by Barnes (1979) and subsequently noted in a number of relatively unnatural experiments on human head-eye coordination.

Quite recently, Thumser, Oommen, Kofman and Stahl (2008) investigated whether the head movement tendencies observed in free-headed participants under laboratory conditions reflect the head movements made under a more natural environment outside the laboratory. Specifically, Thumser et al. (2008) were interested in whether individual variations in head movements would emerge when you examine the behaviors in across different environments. Eye movements were measured with a helmet-mounted video pupil tracking system that recorded the movements of the pupil reflected off an infra-red reflecting mirror in front of one of the eyes. Head orientations, recorded as yaw angles, were measured using a gyro system that was strapped to the head of the subject. The indoor condition had participants seated in the middle of a semicircular array of LEDs at eye-level and spaced about 1° apart. Participants were instructed to fixate the target as quickly and accurately as possible. The outdoor condition had participants seated on a stool in the center of an open area. The instructions were to look at anything they wanted to for 30 minutes. The authors made a point to not ask the participants to perform a specific task, believing that such specialized tasks account for the lack of variability in head movement tendencies seen between participants in previous studies, namely Land (1992) and Herst et al. (2001).

While Thumser et al. (2008) did not make any mention of the temporal coordination of eye and head movement onsets, they did note that the "Pattern of eye-head coordination recorded outdoors was considerably more complex and varied than indoors" (p. 424). This is not at all surprising considering the unnatural nature of the indoor task – to simply fixate at an array of horizontally situated LEDs arranged in semicircular in front of the participant. Thumser et al. (2008) also demonstrated that we exhibit striking variability in our head movement tendencies. When individuals are free to move about spontaneously and look at anything they like (i.e., they don't have a task to perform), individual differences in eye-head coordination may begin to emerge – a result at odds with those obtained by Herst et al. (2001). While Thumser et al. (2008) did not make any specific mention of the temporal characteristics of head-eye coordination, their results suggest, and they claim, that the tapping task employed by Herst et al. (2001) actually mask individual differences in head-eye coordination rather than reveal the actual characteristics of human head-eye coordination, which is to be highly variability.

In one of the few recent studies to make explicit mention of the temporal onset characteristics of head and eye movements, Chapman and Corneil (2007) examined the similarity of head and eye movement patterns during pro- and anti-gaze shifts. The anti-gaze shift task requires participants to inhibit gaze shifts towards a target once it is present and generate a gaze shift to its diametrically opposite position. Head movements were unrestrained for the 9 human participants who participated in both the pro- and anti-gaze shift trials. Participants were instructed to either make a gaze shift towards a LED (pro-gaze shift task) or make a gaze shift in the opposite direction of a LED (anti-gaze shift task). The eye movements were measured with EOG and head movements were measured with a potentiometer.

Chapman and Corneil (2007) reported that head movements preceding eye movements were rarely seen in either the pro- or anti-gaze shift conditions. This is consistent with almost all the previous literature on head-eye coordination when measuring head movements with a potentiometer, but inconsistent with the results described by Herst et al. (2001).

Oommen, Smith and Stahl (2004) have recently suggested a possible influence on head-eye coordination. They proposed that one coordinates eyes and head in order to maximize efficiency of current, and future, gaze shifts. One’s knowledge or expectations of where visual attention will be directed in the future will influence, or modulate, their pattern of head-eye coordination. While it is completely possible that patterns of head-eye coordination are influenced by past and future gaze-shifts, Oommen et al. (2004) make a point to note that this topic has not yet been formally explored. Not only have future eye movements been suggested as a factor in head-eye coordination, so too have future limb movements. Eye-head coordination, which is influenced from moment-to-moment by the location of the next target, could just as well be influenced by whether or not you will reach for the next target with your hand (Smeets et al., 1996; Hollands et al., 2002). Another possible explanation of head-eye coordination patterns is that different people exhibit differing propensities to move the head (Bard, Fleury & Paillard 1992; Fuller 1992b; Stahl, 1999). A number of investigators (Afanador & Aitsebaono 1982; Bard et al. 1992; Fuller 1992) have described individuals as being "head movers" or "non-head movers", even though there is little evidence demonstrating that there are discrete categories of head movement tendencies. Any tendencies to be a "head mover" or "non-head mover" are most likely the result of the specific task demands rather than some inherent property of the individual's of eye-head coupling mechanisms (Thumser et al., 2008).

While much is known about age-related changes in the human oculomotor system (see Davidson & Knox, 2002, for a review), what remains unknown is the effect of aging on head movements, let alone the effect it has on the coordination of the head and eyes. Proudlock, Shekhar and Gottlob (2004) investigated age differences in patterns of head-eye coordination and presented aging as a possible explanation for different patterns of head-eye coordination they had noticed in their participants. Their interest in age as a factor influencing eye-head coordination began with an unpublished observation made one year earlier (Proudlock, Shekhar & Gottlob, 2003). While investigating head movements while reading, Proudlock et al. (2004) noted larger saccadic head movement propensities in their more elderly participants.

Proudlock et al. (2004) investigated age-related changes in head-eye coordination under free-headed conditions while participants performed relatively unnatural tasks (tracking a moving dot project onto a screen 1.2m in front of them while seated; tracking a moving dot with smooth pursuit movements; and either looking at, or looking away from, dots flashed on the screen – making either pro- or anti-saccades). While the head was free to move, the tasks the participants were asked to perform did not elicit large head movements. In fact, in order to analyze the data, the head gain values were transformed to $\log_{10}$ (head gain x 100) in order to get something approximating a normal distribution. The data from 53 participants were divided into three groups for statistical analysis: 20-40 year-olds, 41-60 year-olds, and 60+ years. An infrared video pupil tracker was used to record eye and head positions.

Consistent with the findings of Herst et al. (2001), Proudlock et al. (2004) found a high degree of uniformity of head movement tendencies across different tasks. Inconsistent, though, with Herst et al. (2001), Proudlock et al. (2004) found that, for elderly participants, eye movements visibly preceded head movements. These results are not surprising given the unnatural nature of the task the participants were being asked to perform. What is interesting are the patterns of head movements made by the older adults in their study. Proudlock et al. (2004) found that older adults made more, larger, and faster head movements when compared to the young or middle-age participants. It was also noted by Proudlock et al. (2004) that the older adults made "exaggerated" head movements far more often than the young or middle-age participants.

There are a number of possible reasons for these age-related differences in head movement tendencies. Leigh and Zee (1999) have noted a number of cortical and subcortical structures which are involved in coordinated eye-head movements, including the frontal eye fields, posterior parietal cortex, caudate nucleus and substantia nigra, cerebellum, superior colliculus, and the reticular formation, among others. Additionally, several investigations have described age-related morphological changes in the frontal and temporal cortex (Adams, 1987; Bartzokis et al., 2001; Jernigan et al., 2001). A specific indicator of frontal cortical decline are high anti-saccade error rates which were reported by Proudlock (2004) and others (Butler et al., 1999; Klein et al., 2000). Cortical decline in these areas may be the cause of the exaggerated head movements seen in the older participants (Stahl, 1999). The cerebellum and basal ganglia also experience neuronal loss (Huang, Brown & Huang, 1999; Hikosaka & Wurtz, 1983).

Stahl (1999) reported that this cortical and subcortical neural loss associated with aging may be an underlying cause of larger, faster, and more exaggerated head movements seen in older adults. In particular, the cortical decline of the dorsolateral prefrontal cortex and areas of the frontal eye fields which play a role in coordinated head-eye movements. Proudlock et al. theorize that age-related declines in frontal cortical areas may account for the differences in patterns of head coordination between the older and younger adults. Proudlock et al. (2004) make a point to note "The effect of age-related changes of these different neural structures upon the control of head movements is poorly understood" (p. 1377).

Another possible explanation for the larger, exaggerated head movements of the older participants, and the resulting patterns of head-eye coordination, both described by Proudlock et al. (2004), involves the reduction in range of eye movements as a function of age. Clark and Isenberg (2001) have described a decrease in range of sustained horizontal and vertical eye movements of about 0.8% per year between the ages of 20 to 80. The result is an overall reduction of approximately 30% for an average 75-year-old. And while Proudlock et al. (2004) make a point to note that this alone probably cannot account for the dramatic changes in head movements, Pozzo et al. (2001) have suggested that the purpose of head movements and head-eye coordination is to "construct a stable frame of reference" from which we organize and initiate future movements and provide a way to align the head with the next center of visual attention. If older adults experience reduced eye movement range, it would reduce their ability to reference from the frame the head movements provided for them, resulting in the need to make more and larger head movements to provide more frames from which to refer.

One problem with this is, as Proudlock et al. (2004) have noted, the eye movements of the participants in head-eye coordination experiments did not generally approach the range limits of either the older or younger adult. This is because of the task. If the stimuli are placed directly in front of the subject, or close to the fixation point, then no change in the frame of reference would be required. This means that no age differences would be seen, nor would we see patterns of head-eye coordination with the head leading. This frame of reference hypothesis may explain why the oldest participant described by Herst et al. (2001) (RMS) made coordinated head-eye movements with the head usually leading the eye. It would not, however explain why the other three, younger participants also made head-leading patterns of coordinated

## Section 3 Conclusion

There have been two classes of experimental approaches to the study of the temporal coordination of the human head and eyes. The majority of these experiments fall into the first class, which were done under highly unnatural conditions with participants required to shift gaze to suddenly illuminated or flashed targets that appeared in unpredictable locations in otherwise dark environments with the head restricted, more or less, to motions about its vertical axis. Until relatively recently, many of these experiments used a rather crude method (binocular EOG) for recording eye movements as well. In most conditions, in most of these experiments, the eye was found to start moving before the head. A tendency for the head to lead the eye occasionally when the appearance of a target was predictable was also noted. Large subject-to-subject variability, and even within subject variability, has been notable in this work, a fact that has been taken as a tribute to the flexibility of the human beings' motor control systems. It could also suggest something quite different. Namely, the use of experimental designs poorly-suited for examining how these control systems evolved to perform reliably and efficiently. Over the last 35 years we have acquired much information about how individuals perform in a variety of analytical experiments that require movement of both the head and eyes. We are still very far, though, from understanding the general principles underlying the way in which the head and eyes cooperate in the performance of natural tasks. During the last two decades we have seen experiments that fall into a second category which make use of more natural conditions. Instrumentation that evolved from Collewijn's (1977) study of the freely-moving rabbit has made it possible to measure head-eye coordination accurately with few restrictions, but there have been few studies to date that have exploited these opportunities by requiring participants to perform real tasks under truly natural conditions. If successful completion of these tasks requires concentration, if they are performed "unthinkingly", and if they fall within the realm of significant human activities, like crafting tools, or performing surgery, it will become possible to observe the way head, eyes and hands actually are meant to work together reliably and efficiently.

We already know something about experimental conditions that impose a natural limit on the likelihood of a human being's head participating in a gaze-shift. Recall that head-eye coordination was not analyzed in the LOOK-ONLY experiments described by Epelboim et al. (1995). It was not analyzed because all four participants sat very still, keeping their head movements to a minimum. One could say that they almost froze their heads in space. These participants had not been instructed to hold the head still, but all four adopted this strategy when asked to look as accurately as possible at the same kind of target sequences they were required to tap. Epelboim et al. (1995) noted that the participants in the look-only condition described the task as being more difficult than when asked to tap the targets. When comparing the TAP vs. the LOOK-ONLY tasks, Epelboim et al. (1995) described it as follows: "All four reported that tapping the targets was relatively easy and fun, whereas sitting and looking at the targets in sequence seemed very unnatural, pointless, and required more effort" (p. 3408). Note that 3 of our 4 participants (HC, CE & RS) were highly experienced eye movement participants. They had been fixating and tracking stationary and moving targets for as many as 42 years before they participated in the TAP and LOOK-ONLY experiments. Almost all of their prior experimental participation had been unnatural. Their eye movements had been recorded with the head immobilized on a biting board or chin rest. Once the head is supported artificially there is no need (and apparently no likelihood) of discovering how important it is to hold one's head as still as possible when required to fixate accurately. Note also that the fourth subject (ZP), who had participated in fewer prior eye movement experiments, adopted the same strategy as the very experienced eye movement participants for coordinating his head and eye. He kept his head quite still. It is also important to note that there was very little within or between subject variability when these participants looked accurately at a sequence of targets. All four seemed to know, and acted on the fact, that keeping the head immobile would make it easier to perform this task. In other words, there seemed to be a natural propensity for doing this just as there was a natural propensity for leading with a head movement when they shifted gaze to guide their tapping of similar target sequences. Studying other natural tasks, which might allow coordinated movements of the head and eyes, might be the best way to discover additional propensities for coordinating head and eyes. Knowing what these natural human propensities are might eventually allow us to understand the principles underlying the selection of specific behaviors.

We conclude by claiming that since natural experiments can now actually be done, it is time to do them, rather than to continue to simulate quasi-natural conditions based on information obtained under highly restricted, unnatural conditions. Looking at LEDs arranged in front of you while sitting is not a natural condition that elicits natural behaviors. As Thumser et al. (2008) have noted, this type of task may actually mask natural patterns of behaviors rather than discovering them. Judging by the widespread success of human beings in performing a variety of difficult, visually-guided motor tasks, one should be able to observe a relatively reliable, universal repertoire of coordinated head-eye behaviors, rather than continuing to observe the plethora of factors that may elicit individual differences that permeate much of the existing literature on human head-eye coordination.

# Appendices

1. Electrooculography (EOG) is a method for recording position and movements of the eye by measuring difference in the electrical potential between the front and back of the eyeball. Electrodes are placed around the eye (or eyes), either above and below or to the left and right, which record the corneal-retinal potential. The eye can be thought of as a battery or dipole, and when the eye moves the potential at the electrode becomes more or less negative depending on the direction of the movement. EOG can be used to measure eye movements up to ±70º with accuracy of ±2.0º (Stern, Ray & Quigley, 2001).

2. A potentiometer is a device for measuring rotations of the head. The participant generally wears a helmet attached to the potentiometer, which is then fixed on the vertical earth-stationary axis. A potentiometer is a simple electro-mechanical transducer that converts rotary or linear motion of the head into a change of resistance. This change can be measured and recorded to then determine how far the head has rotated in either direction.

3. The nixie tube was a way to present a different numerical stimulus in the same position at different times. It is basically a cold-cathode tube with 10 separate cathodes, each in the shape of a different number. The cathodes are insulated from one another and are stacked one behind the other. When a sufficient potential is applied (approximately 180 volts) between the selected cathode and plate, the gas

surrounding the selected cathode is ionized and the result is a glowing orange-red number. Nixie tube displays have long since been replaced by light-emitting diode (LED) and liquid crystal (LCD) displays.

4. Light emitting diode, or LED, are commonly-used stimuli in eye-movement research. The LED is a diode that will emit photons, or light, that can then be used as targets. They require much less energy and have a longer life than nixie-tube displays.

5. Following up on Bartz (1966), Bizzi, Kalil & Tagliasco (1971) inaugurated a series of head-eye coordination studies with monkeys. More recently, Freedman & Sparks (1997) published a relatively "natural" study of the head-eye coordination of two rhesus monkeys, whose heads were not restrained. They reported:

> "RELATIVE TIMING OF EYE AND HEAD MOVEMENTS. In all [our italics] instances, changes in the direction of the line of sight were initiated by an eye movement; head movements that occurred before gaze shift onset did not alter gaze position. As a result, eye movement onset and gaze shift onset were identical. During the delayed gaze shift task, gaze latency (Fig 3A) was relatively independent of movement amplitude ... In contrast, the time from gaze onset to head movement onset decreased as a function of gaze amplitude (Fig. 3B) until, for gaze shifts larger than ~40º, movements of the eyes and head began nearly synchronously" (p. 2332).

The Freedman & Sparks (1997) study, and other monkey studies, were not discussed in the body of this paper because we are unwilling to assume that the monkey's oculomotor performance, as studied to date, puts the monkey nearby on the continuum that includes human performance. Specifically, we are unwilling to assume that the "natural" head-eye coordination of a monkey is likely to be observed when it is restrained in a primate chair, and after it has received fixation training with its head bolted to the chair. A long-standing skepticism about treating a monkey's oculomotor performance as "natural," when observed under such conditions, was confirmed by one of the Herst et al. authors (RMS) in collaborations with A.A. Skavenski. Between 1985 and 1989 the "natural" oculomotor performance of several Old and New World monkeys were recorded, who had been gentled, but never restrained or trained to "fixate," before they came to College Park to have their eye movements recorded with the MRFM. All showed a natural preference for using saccades and saccade-like head movements, rather than smooth eye or head movements, to maintain gaze on stationary objects and to track moving objects (bits of banana moved back and forth in front of them). These naive monkeys also showed the well known inclination to "downbeat nystagmus" – the fixating eye drifting up, causing a periodic pattern of downward saccades. On purely behavioral grounds, an unrestrained cat behaves more like an adult human when it comes to head-eye coordination, than an unrestrained, untrained monkey even when allowance is made for the fact that the cat has a smaller available range of coordinated motion. Knowing this, we decided to avoid the common practice of discussing human and monkey head-eye coordination as though they represented the performance of very similar creatures. In our view, this remains to be established (see Steinman, Haddad, Skavenski, & Wyman, 1973; Skavenski, Robinson, Steinman, & Timberlake, 1975, for a description of the training required to encourage a restrained monkey to fixate somewhat like a human being).

6. The vestibular ocular reflex (VOR) is a reflexive eye movement that counters the movement of the head in order to maintain a stabilized image on the retina.

7. See Epelboim et.al. (1995) for a description of the MRFM, the kind of data it generates, and the design of the TAP and LOOK-ONLY experiments.

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