Using the eye-movement system to control the head

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We tested the hypothesis that A.I., a subject who has total ophthalmoplegia, resulting in a lack of eye movements, used her head to orientate in a qualitatively similar way to eye-based orientating of control subjects. We used four classic eye-movement paradigms and measured A.I.'s head movements while she performed the tasks. These paradigms were (i) the gap paradigm, (ii) the remote-distractor effect, (iii) the anti-saccade paradigm, and (iv) tests of saccadic suppression. In all cases, A.I.'s head saccades were qualitatively similar to previously reported eye-movement data. We conclude that A.I.'s head movements are probably controlled by the same neural mechanisms that control eye movements in unimpaired subjects.

Keywords: active vision; saccades; ophthalmoplegia; human vision

1. INTRODUCTION

Research into the control of saccadic eye movements has made considerable progress in recent years. Many behavioural findings appear to be well explained by known neurophysiological mechanisms, and the area offers a success story for computational neuroscience (Sparks & Groh 1995; Wurtz 1996).

In this article, we report findings from an individual who has total ophthalmoplegia resulting from extraocular muscle fibrosis. Her eyes are unable to move relative to her head. As we have reported briefly elsewhere (Gilchrist *et al.* 1997), she produces saccade-like orientating movements with her head, which allow her to maintain near-normal visual perception in almost all situations. We have investigated the extent to which the programming of these head-orientating movements is similar to normal eye-orientating movements. We used a number of standard experimental paradigms that have elucidated the process of saccadic eye-movement control.

The gap paradigm was first reported by Saslow (1967). The saccade latency, the time between target-onset and the onset of a saccadic eye movement, is surprisingly unaffected by the visual properties of the target. However, visual events at the fixation location before the saccade have a substantial effect on the latency. If the stimuli at fixation disappears shortly before target-onset (leaving a gap), then the saccade latency is up to 100 ms shorter than if the same stimulus at fixation remains visible after the target's appearance (overlap). One plausible account is that it reflects the effect of the 'fixation region' of the superior colliculus, an important stage in the output pathway for saccadic eye movements (Dorris & Munoz 1995). Cells in this region are directly implicated in the triggering process that initiates a saccadic movement (Wurtz 1996).

The remote-distractor effect (RDE) concerns a similar automatic influence on the latency to produce a target-elicited, saccadic eye movement. When a subject makes a saccade to a target, simultaneous appearance of a second visual stimulus at a distant location in the visual field results in an increased latency. The effect was first reported by Lévy-Schoen (1969) and occurs even when the subject knows in advance the location of the target (Walker *et al.* 1995). Recent work (Walker *et al.* 1997) has shown that the effect occurs with distractors at locations throughout the visual field, with the exception of a sector around the target axis. The effect is stronger for distractors close to the fovea, again suggesting that the effect may be a manifestation of the properties of the collicular fixation system.

The anti-saccade paradigm, first devised by Hallett (1978), requires the subject to respond to a visual target with a saccade in exactly the opposite direction. This is a demanding task and normal subjects typically are unable to avoid making occasional erroneous pro-saccades to the target. Correct opposite-direction saccades show increased latencies and amplitude variability. The ability to generate anti-saccades may be severely compromised in certain cases of brain damage, particularly damage to areas of frontal cortex (Guitton *et al.* 1985; Pierrot-Deseilligny *et al.* 1991), suggesting that these structures are required for the task.

Saccadic suppression refers to the drop in visual performance when stimuli are presented at the time of a saccadic eye movement. The maximum drop in visual sensitivity occurs after the saccade (around 20 ms) but begins before the movement is initiated (Latour 1962). The cause of suppression remains unclear, although it appears likely that a number of factors contribute. Suppression is probably partly the result of visual masking of the stimuli. However, it still occurs when the

visual stimulus to be detected is a whole-field brightening (a so-called Ganzfeld), which would not be subject to masking in the same way. It is likely that suppression is also controlled by central neural processes that are initiated by the preparation to make a saccade (see Volkman (1986) for a review).

We tested the orientating performance of the ophthalmologic subject in each of these paradigms. We asked the basic question: will A.I.'s head movements show the same experimental phenomena as the eye movements of controls?

2. SUBJECT SUMMARY

A.I. is a right-handed female, aged 21 years, who, at the time of testing, is a university undergraduate reading English. A previous short report of this subject, which focuses on her reading behaviour, can be found in Gilchrist *et al.* (1997). As reported in Gilchrist *et al.* (1997), A.I. shows no optokinetic nystagmus response and the largest eye movements that were recorded in this subject were $\pm 0.5^\circ$; importantly, these drift-like movements did not appear to be linked to the nature of the visual stimulation.

(a) *Subject history*

Reports from A.I.'s medical records reveal a diagnosis of congenital ophthalmoplegia, which appears to have been present since birth; as a result, A.I. has never had any eye movements. In 1978, when she was 12, A.I. had ptosis surgery and a squint operation, which exposed the eye muscles; the surgeon's report records that the extraocular muscles were thin and fibrotic. Neurological examination supported the views that the problem did not originate in the brain stem. This led to a medical diagnosis of congenital oculofibrosis syndrome of unknown aetiology.

Two-dimensional ultrasonic imaging (B-scan) of A.I.'s orbits revealed the following. There was no mass lesion in either orbit. The medial, lateral and superior recti could be distinguished on longitudinal section although not on transverse section, and there was no change to these muscles in either shape or size on attempted eye movement.

Despite having no eye movements, A.I. leads a normal life and experiences few restrictions. However, some tasks have presented problems, particularly those involving fast dynamic scenes; for example, she has so far been unable to learn to drive and she is not active in sports.

(b) *Screening results*

A.I. shows both a normal pupillary light-reflex response and a normal blink reflex in both eyes.

A shortened version of the Ishihara colour test shows A.I. to have normal colour vision. Stereo vision is absent in A.I., and she has some visual suppression (Titmus test). Further testing reveals that A.I. shows very strong suppression in her left eye, probably as a result of a small left-eye divergent squint.

Visual acuity while wearing corrective lenses was tested using the Snellen letter charts (6/12 in left eye, right eye, and binocular).

3. GENERAL METHOD

(a) *Recording of head movement*

Head movements were recorded using the search-coil technique, a method that was developed originally for eye-movement recording (Collewijn *et al.* 1975). To record head movements we fixed the coil to a rigid, lightweight helmet secured on A.I.'s head (cf. Guitton & Volle 1987). We tested the accuracy of the apparatus by recording while A.I. wore the headset and with her head fixed using a bite-bar. The combined residual head tremor with noise from movements of the headset on the head, movement of the bite-bar fixing, and machine noise had a standard deviation of 4.82 arcmin horizontally and 4.36 arcmin vertically.

In all experiments, the analogue signal from both horizontal and vertical dimensions was sampled digitally at 200 Hz. The head-movement records were digitally synchronized with the display onset to allow the relationship between the stimuli-onset times and the head-movement records to be calculated directly. Each block was preceded and succeeded by a calibration procedure in which the subject was asked to fixate in turn on nine points arranged in a three-by-three grid. A semiautomatic procedure was used to analyse the head-movement data. Each record was checked individually and the onset of each rapid head movement was recorded for further analysis. Two features of each movement were extracted: (i) the latency of the movement, that is the time from the onset of the display in the trial to the initiation of the movement, and (ii) the movement size and direction.

(b) *Displays*

For the gap-paradigm experiment and the saccadic-suppression experiment, the displays were generated using purpose-written software for a VSG graphics card (Cambridge Research Ltd, UK) and presented on a high-resolution EIZO 21-inch (1 inch = 2.54 cm) monochrome monitor running at 70 Hz. For the other experiments, stimuli were presented on a Macintosh 21-inch CRT monitor controlled by purpose-written software.

4. GAP-PARADIGM EXPERIMENT

(a) *Method*

White targets ($1/2^\circ$ square, 29 cd m^{-2}) on a black background were presented at 6° to the left or right of fixation. Each trial commenced with the central fixation cross (1° extent) being presented after which, at a random interval between 1729 ms and 2729 ms, a target would appear. The central fixation cross itself could be extinguished at nine different intervals between 229 ms before the target appeared and 229 ms after the target appeared; these intervals were 229, 171, 114, 57, 0, -57, -114, -171 and -229 ms. A negative value indicated a gap between the fixation offset and the target-onset, a zero value indicated the simultaneous offset of the fixation point and onset of the target, and positive values indicated an overlap between the fixation offset and the target onset. The timing of the events in each trial was set so that the offset of the fixation point gave only a minimal warning signal for the onset of the target and, in addition, so that the onset of the target could not be predicted on the basis of the time from the start of the trial. The target was presented for 1 s and could appear on the left or right of fixation.

A.I. was simply instructed to fixate a central cross and move her head as quickly and as accurately as possible to the target. She participated in two blocks of 90 trials.

Figure 1. Gap-paradigm experiment. The relationship between the offset of the fixation point and onset of the target, and head-movement latency for A.I. (error bars are s.e.m.).

(b) Results and discussion

Out of a total of 180 trials, two trials were excluded as A.I.'s initial head saccade was in the incorrect direction. Figure 1 shows that the overlap has a systematic effect on the latency of the movement: when a gap is present between the fixation offset and the target onset then latencies are shorter. An ANOVA shows a main effect of overlap on latency ($F_{8,178}=3.5$, $p<0.001$). This effect is illustrated graphically in figure 1. Note that for one response with the longest overlap (229-ms condition), the movement started before the offset of the fixation point (latency = 225 ms).

A.I. shows a normal 'gap effect', that is, the latencies of her head movements are reduced by an introduction of a gap between the onset of a target in the periphery and the offset of the central fixation point. This provides our first example whereby A.I.'s head movements behave in a qualitatively similar way to eye movements in unimpaired subjects.

5. THE REMOTE-DISTRACTOR EFFECT

(a) Method

Targets consisted of small, black-shaded squares (9.3 cd m^{-2}), half a degree in size and presented on a white screen (45 cd m^{-2}). There were three different target positions: single target left of fixation; single target right of fixation; and a double target, one either side of fixation. Each target position had two eccentricities of 4.5° and 9° . All targets were presented on the primary horizontal axis. Each trial consisted of a central fixation square presented for 1 s followed by the target square(s) for 1 s. Each block of 60 trials contained ten targets of each target type: single right, single left or double for both eccentricities.

A.I. was shown an example of the stimuli types followed by one practice session before recording. Data were obtained for two blocks of 60 trials. The task instruction was to look at the target as quickly and accurately as possible. During block 1, A.I.

Figure 2. The remote-distractor effect. The head-movement latencies for A.I. in the remote-distractor experiment. Single targets could be presented either in the instructed direction (I) or in the non-instructed (NI) direction (error bars are s.e.m.).

was instructed to always go right when a double target appeared. During block 2, A.I. was instructed to always go left when a double target appeared.

(b) Results and discussion

Five trials out of a total of 120 were excluded from the statistical analysis. On four occasions, A.I. made a movement in the non-instructed direction on double trials, and on one occasion she made no movement at all. For this experiment, movement amplitude was not examined in detail as we were interested primarily in movement latency. The mean latencies and standard deviations for A.I.'s head movements are presented graphically in figure 2.

To compare the latencies for the double targets and the single targets in the instructed direction, a three-factor ANOVA was done with the following three factors: target type (single or double); target eccentricity (4.5° or 9°); and block (instructed left or right). There was a significant main effect of target type ($F_{1,68}=19$, $p<0.0001$), latencies to double targets were slower than latencies to single targets. There was no significant effect of eccentricity and no significant interaction between target type and target eccentricity. There was a significant main effect of block ($F_{1,68}=10$, $p<0.002$), but no interaction between target eccentricity and block. There was a significant interaction between target type and block ($F_{1,68}=6.3$, $p<0.01$), showing that A.I. produced a larger RDE in the instructed left block. There were no higher-order interactions between the three factors of target type, target eccentricity and block.

A further analysis was done to assess the effect of the instruction on single target latencies. A one-tailed t -test of single target latencies showed that instructing A.I. to go in a specific direction to double targets had an effect on the latencies to single targets for both the first ($t_{17}=3.26$, $p<0.002$) and the second block ($t_{19}=2.82$, $p<0.005$).

A.I.'s head-movement latencies show a very similar qualitative pattern to eye-movement latencies of control subjects for this type of task (Walker *et al.* 1995). First, she showed with her head movements the characteristic longer latencies when presented with simultaneous bilateral targets. Second, she showed an attentional effect reflected in the slowing of the response to the single item in the non-instructed direction (see Walker *et al.* 1995).

6. ANTI-SACCADES

(a) Method

Targets consisted of a small, black-shaded square on a white background (45 cd m^{-2}), half a degree in size, presented to the left or right of fixation, at two different eccentricities: 4.5° and 9° . All targets were presented on the primary horizontal axis. The sequence of presentation was as follows: central fixation square for 1 s, followed by the target square for 1 s. Each block of 100 trials contained 25 targets of each target type: single right or single left for both eccentricities.

A.I. was shown an example of the stimuli types followed by one practise session before recording. A.I. participated in two blocks of 100 trials. During block 1, the task was to look at the target as quickly and accurately as possible (pro-saccade). During block 2, A.I. was instructed to look at the opposite direction to which the target appeared (anti-saccade).

(b) Results and discussion

Both latencies and landing position were analysed. Movements were classified as errors when they were directed away from the target in the pro-saccade condition, and towards the target in the anti-saccade condition. In the pro-saccade condition, A.I. showed direction errors of 1%. In the anti-saccade condition, A.I. showed errors of 21%. There were no clear left/right differences in the error rate for anti-saccades (13/50 right, 8/50 left), or for near versus far targets (11/50 for targets at 4.5° and 10/50 for targets at 9°).

The head-movement latencies are shown in figure 3. An ANOVA was performed on these latencies with the following three factors: condition (pro-saccade or anti-saccade); target eccentricity (4.5° or 9°); and target position (left or right). There was a significant main effect of condition ($F_{1,171}=57.6$, $p<0.0001$), reflecting the fact that latencies were longer in the anti-saccade task (393 ms) than in the pro-saccade task (287 ms). There was also a significant main effect of target position ($F_{1,171}=4.1$, $p<0.05$); overall, latencies were longer to the left than to the right of fixation. There was, however, no significant interaction between condition and target position and no other significant main effects or interactions were found.

The mean landing position of A.I.'s head movements during the normal and anti-saccade task was sensitive to the target location and, in most conditions, showed a consistent pattern of overshoot to near targets and undershoot to far targets. This finding has been reported before in studies of eye-movement landing position. When subjects are presented with successive targets at two locations they tend to make saccades towards the centre of these target locations—this is known as the 'range effect' (see Kapoula 1985). This modulation also appears to apply to head saccades, which go to a location where there is no target, i.e. in the anti-task.

Figure 3. Anti-saccades. The head-movement latencies for A.I. for the pro-saccade and anti-saccade experiment (error bars are s.e.m.).

A.I. shows a comparable error rate in the anti-saccade task to control subjects (Guitton *et al.* 1985). A.I.'s head-movement latencies also show a similar pattern to eye-movement latencies of control subjects, including the predicted slowing of latencies when the task demands a movement in the opposite direction to the presented target.

7. SACCADIC SUPPRESSION

(a) Method

In a pre-test, A.I. was instructed to fixate a central fixation point and detect the occurrence of a flash (duration 14 ms), against a grey background (4.1 cd m^{-2}). The full screen flash ($40^\circ \times 29^\circ$ in size) occurred randomly on five out of six trials. The brightness of the flash was varied using a linear staircase procedure. At a flash brightness of 5.9 cd m^{-2} , performance was at 79% (26/33 correct). This flash brightness was used for the subsequent experiment.

A.I. was instructed to move her head to fixate a white target ($1/2^\circ$ square) presented on the grey background. The target could appear to the left or right of fixation at 10° eccentricity. Having orientated to the target, A.I. was then instructed to judge whether a flash had occurred in the trial interval (a short beep from the computer served as a reminder to make this response). The flash occurred on five out of six trials, at an interval from 128 ms to 429 ms after the onset of the target. A.I. participated in six blocks of 90 trials over two testing sessions.

(b) Results and discussion

Of the 540 trials, 37 trials (7%) were excluded owing to multiple movements occurring in a single trial (normally a movement back to the fixation point within the trial time). On catch trials, when no flash occurred, responses were 91% correct (51/56). The response on the remaining 447 trials were coded with respect to the onset of the movement and divided on this basis into 16 bins,

Figure 4. Saccadic suppression. The relationship between the proportion of flashes detected (y axis) and the onset of the head movements (x axis). The saccade commences at time 0. Each data point represented 27 or 28 responses (error bars are s.e.m.).

each containing 28 responses (with one bin of 27). The relationship between the onset of the head movement and the proportion of flashes detected is plotted in figure 4.

The figure clearly shows that detection performance is impaired for flashes that occurred around the onset of the head movement, with a tendency for the visual suppression to be greatest in the period before the onset of the movement. Quantitative curve fitting suggests that the maximum suppression occurs about 19.5 ms before the onset of the movement. The model fitted was an inverted normal distribution which had an s.d. of 100 ms and a mean of -19.5 ms. The background response rate was also set as a free parameter and had a value of 0.965. The average deviation from the model was 0.062, and the data did not differ significantly from the model ($\chi^2_{15}=4.35$).

Like the eye movements of control subjects, A.I. shows visual suppression that is temporally linked to her head movements. Although the suppression was qualitatively similar to eye-saccade suppression, it differed in that the peak of the suppression occurred before the onset of the movement. One explanation for this difference is that in unimpaired control subjects, visual suppression may be initiated by the onset of a neural gaze signal. As A.I. makes such shifts solely with her head, the change in peak suppression may simply reflect the longer contraction time of the neck muscles and the inertial properties of the head when compared to the eyes (Bizzi *et al.* 1971). Indeed, in the monkey, Bizzi *et al.* (1971) estimate this mechanical lag to be about 40 ms, which is consistent with these data.

8. GENERAL DISCUSSION

We have presented results in which we investigated the nature of the head movements of an ophthalmoplegic subject A.I. We used four classic experimental paradigms that are typically used to investigate saccadic eye movements. In all four experiments, we showed that A.I.'s

head movements were subject to the same experimental pattern of data found in studies of eye movements. However, two notes of caution are needed. First, A.I.'s head movements are, not surprisingly, slower than eye movements. For example, a typical 7° eye saccade would have a peak velocity of around 400 deg s^{-1} , whereas A.I.'s head movements have peak velocities of typically around 50 deg s^{-1} . Even given this large difference in peak velocity and its associated lengthening of movement times, A.I. appears to demonstrate consistently saccadic orientating behaviours that characterize eye movements, both in simple tasks as reported here, and in complex tasks such as reading and picture scanning as reported in Gilchrist *et al.* (1997). As a second note of caution, the similarity of A.I.'s head movements to the eye movements of control subjects is striking; however, it is an empirical issue whether A.I.'s head movements are like eye movements on all tasks. To date, we have found no such task that reveals a striking dissimilarity.

At its most radical, such a result suggests that saccades, and the experimental phenomena associated with them, are not peculiar to eye movements, but are instead a more general function of 'active vision'. Active vision is a phrase used by Ballard and collaborators in the robot-vision community (e.g. Rao & Ballard 1995) to stress a shift in emphasis towards a view that a saccadic orientating system is in many ways essential to vision, rather than relatively incidental (as the cursory treatment of eye movements in many textbooks of vision would suggest).

Research on the neurophysiology of gaze shifts (a combined movement of the head and eyes) suggests one possible mechanism for the transfer of saccadic orientating from the eye to the head. Freedman & Sparks (1997) recorded from the deeper layers of the superior colliculus to investigate whether single neurons were separately encoding eye- and head-movement signal or encoding a single gaze signal. The results strongly supported the idea that these neurons were encoding a single gaze signal. Given that even at the level of the colliculus the eye- and head-movement information is encoded as a single signal, it appears possible that these same neurons could allow the transfer of saccadic orientating completely to the head.

What remains surprising is that A.I.'s head movements are so similar to the eye movements of control subjects. This single case study case provides striking evidence to support a conception of visual behaviour in which saccades are central.

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