

NOTE

SACCADE-CONTINGENT SPATIAL AND TEMPORAL ERRORS ARE ABSENT FOR SACCADIC HEAD MOVEMENTS

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ABSTRACT

Psychophysical studies extending over a thirty-year period have repeatedly demonstrated that visual stimuli presented close to the onset of a saccadic eye movement are mislocalised both spatially and temporally. When post-saccadic visual references are available, this spatial distortion is best characterised by a compression of visual space toward the target of the saccadic eye movement. An important but unresolved issue, concerns the specificity of saccade-dependent visual mislocalisation phenomena. We investigated this by examining whether saccade-dependent spatial and temporal mislocalisation are observed in an individual (A.I.) who cannot make any form of eye movement (ophthalmoplegia), but compensates when reading or scanning visual scenes by making saccadic head movements. We demonstrate that saccade-dependent spatial and temporal mislocalisation are absent in subject A.I. and suggest that spatiotemporal mislocalisation may be specific to rapid forms of movement, such as ocular saccades, that necessitate predictive re-mapping to maintain space constancy.

Key words: saccades, saccadic head movements, saccadic remapping, parietal cortex

INTRODUCTION

Psychophysical studies have repeatedly demonstrated that visual stimuli presented close to the onset of a saccadic eye movement are mislocalised spatially (Burr et al., 2001; Cai et al., 1997; Dassonville et al., 1992, 1995; Lappe et al., 2000; Matin and Pearce, 1965; Ross et al., 1997; Schlag and Schlag-Rey, 1995) and temporally (Yarrow et al., 2001). For spatial stimuli presented in the dark, this distortion in the perceived position of a visual stimulus is characterised by a displacement of the stimulus in the direction of the eye movement (Cai et al., 1997). However, when postsaccadic visual references are available, the distortion is best characterised by a compression of visual space toward the target of the saccadic eye movement spatially (Burr et al., 2001a; Lappe et al., 2000; Ross et al., 1997; Yarrow et al., 2001).

Saccade-dependent mislocalisation errors are frequently large in magnitude (typically in the order of 10°); can precede the onset of an eye movement by some 50-80 ms; and reach maximum effect around the time of saccade onset.

Saccade-dependent mislocalisation errors have been linked to changes in the receptive field properties of neurones found within the parietal cortex of the monkey (area LIP) that show anticipatory shifts in their receptive fields immediately prior to a saccadic eye movement (Burr et al., 2001b; Ross et al., 1997). Such cells are thought to dynamically and predictively re-map visual space in advance of an eye movement, so that the representation of a visual stimulus is translated

from a coordinate system with the initial fixation point as origin to one with the upcoming fixation point as origin (Batista et al., 1999; Duhamel et al., 1992; Ross et al., 2001).

Saccade-dependent visuospatial mislocalisation is completely abolished, however, if following the execution of a saccadic eye movement, subjects are required to point to the perceived location of a visual stimulus with their eyes closed (Burr et al., 2001a). One interpretation of this finding is that the anticipatory re-mapping that precedes the onset of a saccadic eye movement does not extend beyond movements that are planned and executed within oculocentric coordinates (Husain and Jackson, 2001). This interpretation is consistent with the proposal made elsewhere, that reaching movements executed without vision are planned using an intrinsic (limb-centred) coordinate system while those directed to visually defined targets are planned largely in extrinsic (oculocentric) coordinates (Jackson et al., 2000; Newport et al., 2001). It is of interest to note that cells exhibiting predictive re-mapping properties have, to date, only been reported for neural areas that are known to code visual stimuli in oculocentric coordinates, including the parietal reach region (PRR).

An important but unresolved issue concerns the specificity of saccade-dependent visual mislocalisation phenomena. Do predictive re-mapping processes precede other, non-ocular, forms of movement? Or, is it the case that predictive re-mapping processes are specific to the planning and execution of ocular movements? We investigated this issue directly by examining whether saccade-

dependent visual mislocalisation also accompanies saccadic *head* movements in an individual (A.I.), who presents with a congenital ophthalmoplegia that has resulted in a complete lack of eye movements since birth, but compensates when reading or scanning visual scenes, by making saccadic head movements (Gilchrist et al., 1997).

EXPERIMENT 1 MATERIALS AND METHODS

Case A.I.

Subject A.I. is a 25-year-old female right-handed university graduate who is in full-time employment as a personal assistant. Two previous reports have been published describing: A.I.'s inability to make eye movements; the kinematic properties of her saccadic head movements and their similarity to saccadic eye movements (Gilchrist et al., 1997, 1998); and the aetiology and functional characteristics of her ophthalmoplegia (Gilchrist et al., 1998). To summarise, A.I. has a congenital ophthalmoplegia that has been present since birth and results in her having never made eye movements. Medical examination of her extraocular muscles shows that they are thin and fibrotic, consistent with a diagnosis of oculofibrosis syndrome of unknown aetiology. Ultrasonic imaging of the medial, lateral and superior recti has demonstrated that there is no change in the shape or size of these muscles when A.I. attempts to make an eye movement. When tested on several, classic, eye movement paradigms A.I.'s head saccades are qualitatively similar to eye movement data, leading to the conclusion that A.I.'s head movements are likely controlled by the same neural mechanisms that control eye movements (Gilchrist et al., 1998). Further details of A.I.'s condition can be found in Gilchrist et al., 1998

PROCEDURE

To examine saccade-dependent *spatial* mislocalisation in subject A.I. we first modified the task reported in Burr et al. (2001a). Prior testing with neurologically normal subjects had confirmed that this procedure led to clear spatial compression effects for saccadic eye movements. Subject A.I. was required to fixate a black dot, presented 7.5° to the left of midline until it was extinguished, and then make a 15° rightward saccadic head movement so as to foveate a black dot presented 7.5° to the right of midline (Figure 1). Immediately after completing the head saccade, A.I. was required to point, using her outstretched right arm, to the location of a probe stimulus (a large vertical green bar [$2^\circ \times 34^\circ$]) that was presented for a very brief period (10 ms) before, during, or after the saccade. Throughout the

experiment visual feedback of A.I.'s pointing arm was prevented. A.I.'s head movements were monitored throughout using an electromagnetic motion tracking device (see Newport et al., 2001 for details). Her pointing movements were also monitored on each trial using an infra-red optokinetic recording device (see Jackson et al., 2000 for details).

RESULTS

Figure 2A shows the perceived positions, reported by patient A.I. for probe stimuli (bars) which were briefly displayed over the nine target positions within the 50 ms interval immediately preceding head saccade onset. This period has been previously shown to produce maximal perceptual mislocalisation errors (Burr et al., 2001b; Ross et al., 1997). Inspection of this figure clearly indicates that subject A.I. does not exhibit the predicted pattern of spatial mislocalisation errors observed for neurologically normal subjects executing saccadic eye movements (illustrated in Figure 2A by the thick broken curve). This was confirmed by statistical analyses which revealed a significant correlation between the real position of the probe stimuli and their perceived position as indicated by A.I.'s manual pointing movements (Pearson's $R = 0.92$). Furthermore, these data were comparable to those obtained in a control condition in which subject A.I. was required to point to the location of the probe stimuli while maintaining fixation at 7.5° to the left of midline throughout (Figure 2B); which yielded a similar correlation between the real and perceived positions of probe stimuli (Pearson's $R = 0.94$).

As noted above, saccade-dependent visuospatial mislocation errors have been shown repeatedly to be confined to a brief period (> 50 ms) around the time of saccade onset (e.g., Ross et al., 1997). Statistical analyses of subject A.I.'s mean mislocalisation errors as a function of the onset asynchrony between probe stimulus and head saccade onset confirmed that the accuracy of subject A.I.'s localisation of the probe stimulus did *not* vary as a function of SOA. Specifically, her perceptual localisation of probe stimuli was as accurate immediately prior to the onset of a head saccade as for trials where the probe stimulus precedes the onset of the head saccade by 200ms or more.

It should be noted that the latency of head movements has been shown to be significantly longer than that of eye movements. Goossens and Van Opstal report eye latencies of 212 [m40] ms and head latencies of 275 [m37] ms in neurologically healthy adults; a difference of approximately 63 ms. Gilchrist reports that the average latency of subject A.I.'s head saccades (266 ms) across a range of saccade amplitudes (3° , 6° , 9° and 12°) is within the normal range [personal communication]. Furthermore, It could be argued that the spatial re-

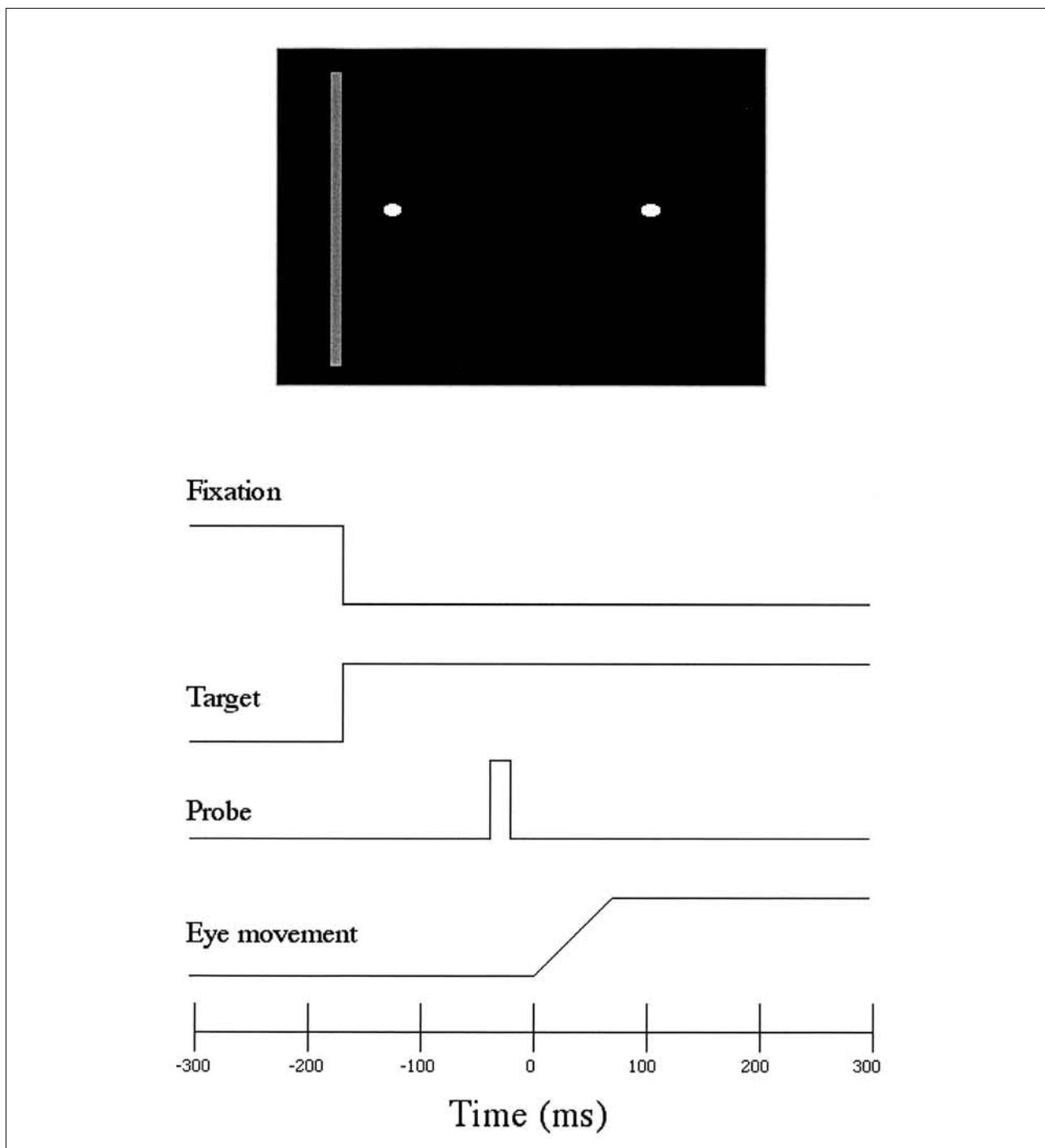


Fig. 1 – Illustration of experimental procedure. Subject A.I. viewed a projection screen from a distance of 1.95 metres through liquid crystal lenses. A.I. was required to fixate a black dot, presented 7.5° to the left of midline until it was extinguished, and then make a 15° rightward saccadic head movement so as to foveate a black dot presented 7.5° to the right of midline. Immediately after completing the head saccade, she was required to point, using her outstretched right arm, to the location of a probe stimulus (a large vertical green bar [$2^\circ \times 34^\circ$]) that was presented for a very brief period (10ms) before, during, or after the saccade. Throughout the experiment vision of A.I.'s pointing arm was occluded by an opaque board. A.I.'s head movements were monitored throughout using an electromagnetic motion tracking device (see Newport et al, 2001 for details). Her pointing movements were also monitored on each trial using an infra-red optokinetic recording.

mapping processes that precede a saccadic eye movement are more properly time-locked to the arrival of the efferent copy of instruction to move the eyes than to the onset of the movement itself. This would indicate that the 50 ms period preceding an eye movement during which spatial mislocalisation might be expected to occur should

be extended by 63 ms for head movements, to take account of the difference in latency between the eyes and the head. We therefore explicitly compared subject A.I.'s localisation for probe stimuli preceding head-saccade onset by 113 ms or less against probe stimuli appearing more than 113 ms before movement onset. Statistical analyses

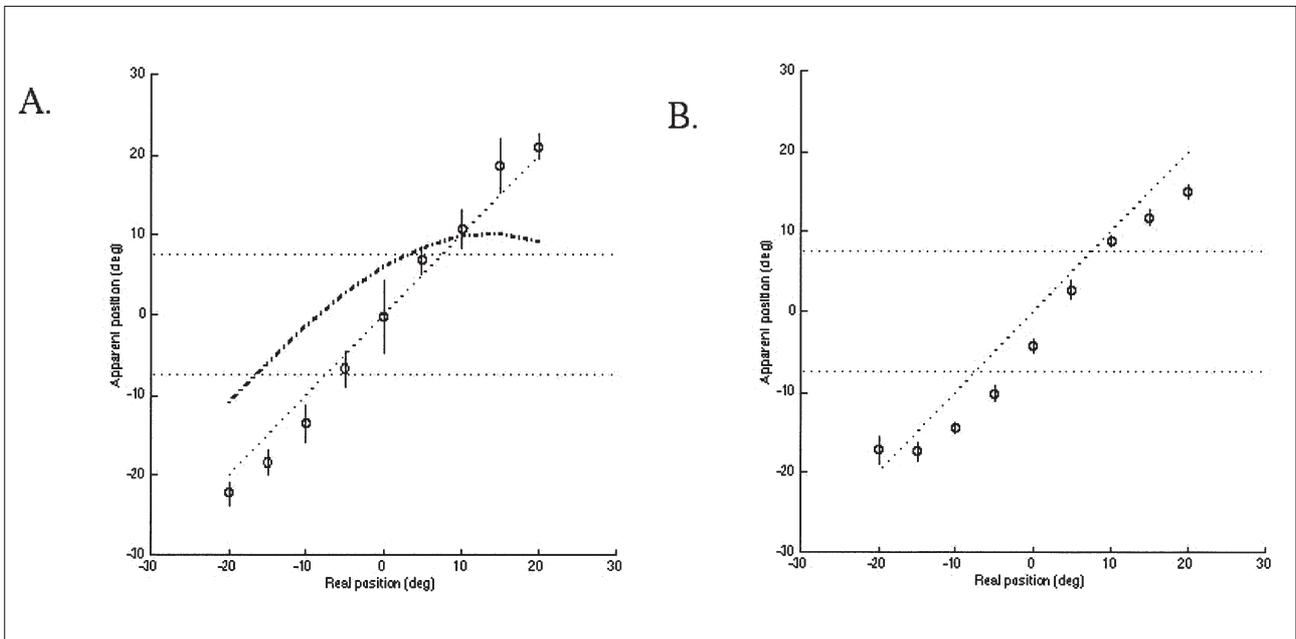


Fig. 2 – A. Manual estimates of the perceived position of the probe (bar) stimulus which was flashed briefly to various positions over a 40° range while subject A.I. made a 15° headsaccade (from -7.5° to +7.5°). Data are reported only for stimuli falling within the 50 ms interval immediately preceding saccades. At this time the head and eyes are stationary, so there is a perfect correspondence between external and retinal coordinates. Error bars represent the standard error of the mean. The thick broken line represents the predicted effect observed in neurologically normal individuals. B. Manual estimates of the perceived position of the probe stimulus obtained from subject A.I. in a control experiment in which she maintained fixation (at -7.5°) throughout the experiment. Error bars represent standard errors.

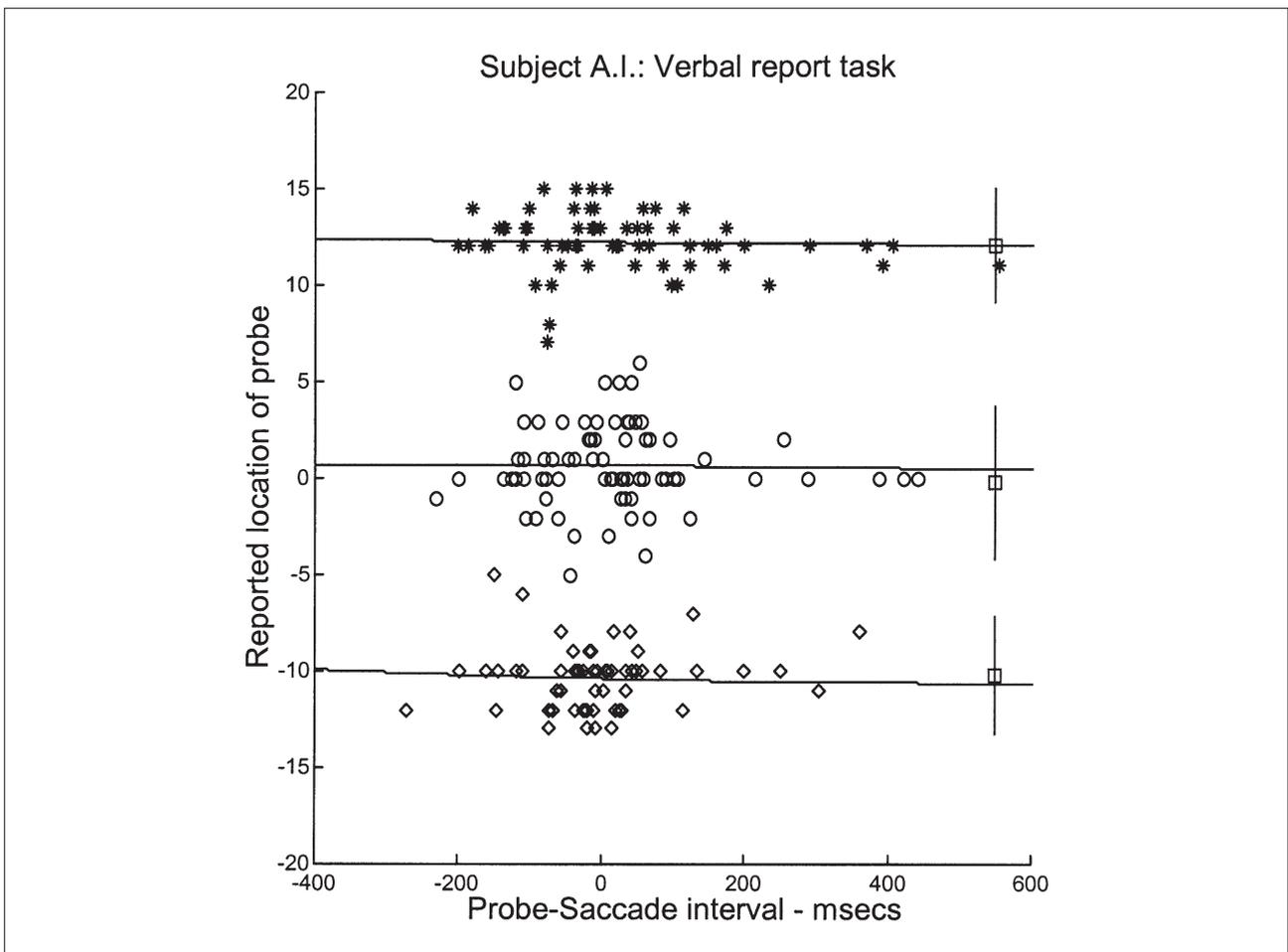


Fig. 3 – Mean spatial mislocalisation error data (measured in degrees) from subject AI and from three individual control subjects (CS 1-3) for probe stimuli presented at (-10°, 0°, and 10°). Early trials (i.e., where probe onset differed from saccade onset by 200 ms or greater) are represented by filled triangles and late trials (i.e., where probe onset occurred within 50ms or less of saccade onset) are represented by open squares. Error bars represent 90% confidence intervals.

confirmed that A.I.'s perceptual localisation was accurate in both cases and that the mean localisation error for these trials did not differ from one another ($p > 0.05$). These analyses confirm that, even when allowing for differences in latency between eye and head movements, subject A.I. does not show any saccade-dependent spatial mislocalisation.

EXPERIMENT 2 MATERIALS AND METHODS

Subject A.I. and ten neurologically healthy adult participants (age range 18-28 years) were recruited to participate in a further experiment. All control subjects were right handed, had normal or corrected-to-normal vision, and gave their informed consent to participate.

To further examine saccade-dependent spatial mislocalisation in subject A.I. we modified the task reported in Ross et al. (1997). Subject A.I. and ten neurologically healthy adult subjects were required to fixate a black circular fixation mark, presented 5° to the left of midline (0°) until it was extinguished and then make a 10° rightward saccadic head movement (A.I.) or eye movement (controls) so as to foveate a second, black, fixation mark presented 5° to the right of midline. Stimuli were presented on a CRT display at a viewing distance of 40 cm. For control subjects only, head movements were prevented using a chinrest. On each trial a probe stimulus was presented randomly at one of three positions, -10° , 0° or 10° . The probe stimulus was a green bar that ran the entire vertical length of the CRT display and was 1° of visual angle wide. Probe stimuli followed the presentation of the second fixation point with a variable SOA between 40-300 ms (SOAs increased by an increment of 5 ms between 100-250 ms and by an interval of 10 ms from 40-100 ms and from 250-300 ms). Probe stimuli were presented for one screen refresh rate (≈ 17 ms) and were followed by the presentation of a horizontal ruler with numbers -15 to 15 displayed immediately above the lower edge of the screen.

Subjects were required to indicate verbally where, relative to the ruler, the probe stimulus had been presented. Horizontal eye movements (EOG) were recorded throughout and saccade onsets, relative to probe onsets, were calculated off line for each trial.

RESULTS

For each subject mean spatial mislocalisation error scores (measured in degrees) were computed separately for each probe location (-10° , 0° , 10°). Separate means were also calculated for trials where the probe onset was 200 ms or greater from the onset of the saccade ('Early' trials) compared to trials in which the probe onset was within 50 ms

of the saccade onset ('Late' trials). Figure 3 presents mean spatial mislocalisation error data from three control subjects and from subject AI. Inspection of this figure confirms that for individual control subjects, spatial mislocalisation errors were small (i.e., zero was within 90% confidence intervals) for early trials (solid triangles), but increased substantially on late trials (open squares). Furthermore, the direction of the spatial mislocalisation errors was clearly observed to be dependent upon the location of the visual probe relative to the target of the saccade. That is, we confirmed previous reports (e.g., Ross et al., 1997) that mislocalisation errors are characterised by a *compression* of visual space toward the target of the saccadic eye movement.

In contrast to the data obtained from controls, subject AI's data is more variable than controls, and does not appear to show either a time-dependent increase in the magnitude of her spatial mislocalisation errors, or any evidence of a compression of visual space toward the target of the saccadic eye movement. First, AI's mean mislocalisation errors on early trials (i.e., a probe-saccade interval of 50 ms or less) were not significantly different from those observed on late trials (i.e., a probe-saccade interval of 50 ms or less.

(See also Figure 4A). Second whereas control subjects, both individually and as a group, clearly show evidence of a compression of visual space toward the target of the saccadic eye movement, subject AI reports probes as being *further away* from the target of the saccadic eye movement than they actually were. These effects were confirmed statistically. A repeated-measures ANOVA carried out on the data from the control group revealed a significant main effect of probe location [$F(2, 18) = 21.1$, $p < 0.0001$] and a probe location by probe-saccade interval interaction effect [$F(2, 18) = 17.8$, $p < 0.0002$].

This effect is illustrated in Figure 4B which shows mean mislocalisation errors for early (probe-saccade interval of 200 ms or greater) and late (probe-saccade interval of 50 ms or less) trials at each probe location, for subject AI compared to the control group.

EXPERIMENT 3 MATERIALS AND METHODS

Recently a temporal illusion of 'chronostasis' – a perceived slowing of real time – has been shown to accompany saccadic eye movements (Yarrow et al., 2001). It is suggested that this effect occurs as a result of the visual percept being 'stretched' backwards in time to include the initiation and execution of the eye movement. To examine saccade-dependent *temporal* mislocalisation in subject AI, we modified the task reported in Yarrow et al. (2001).

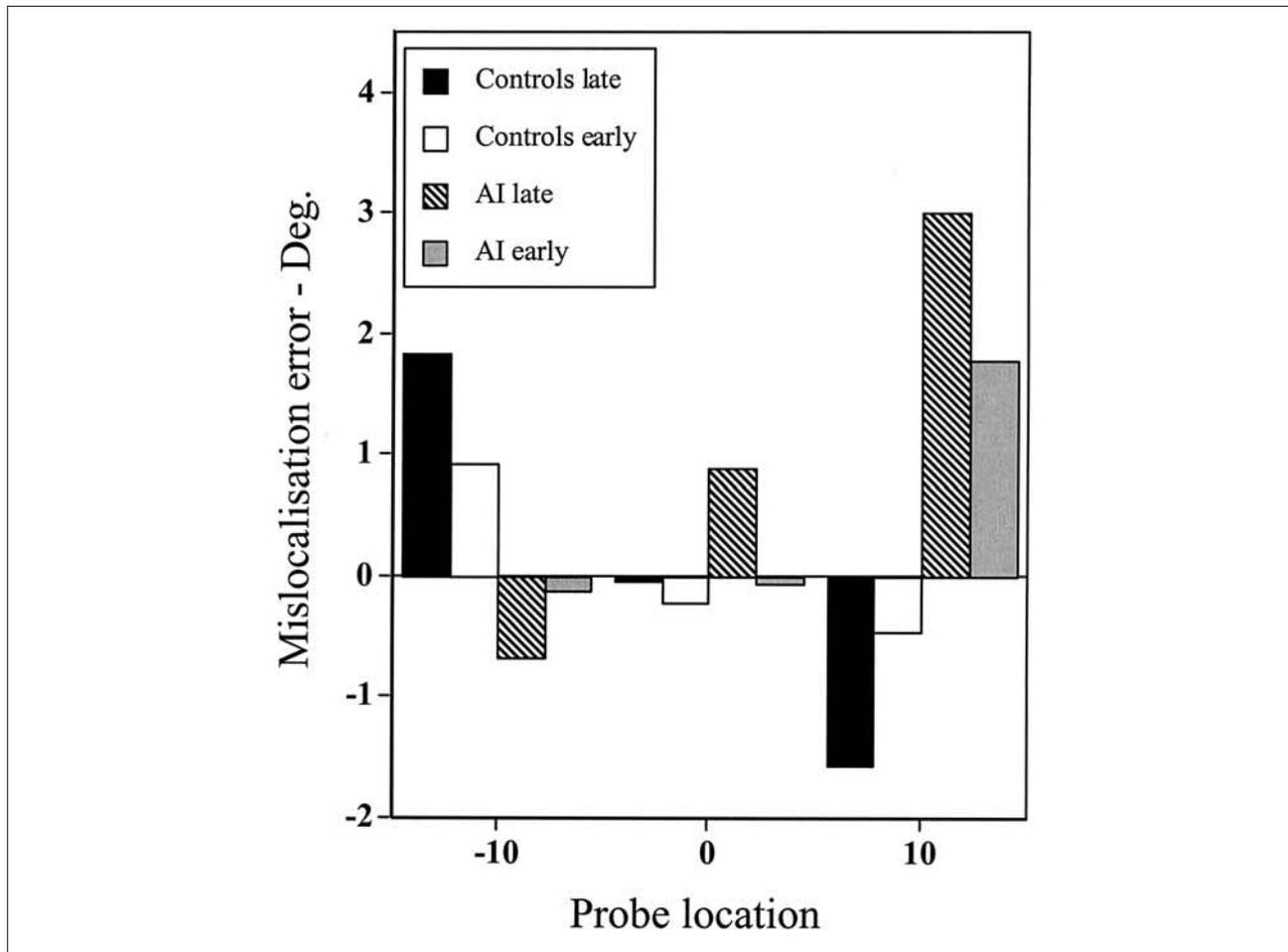


Fig. 4 – A. Subject AI's reported location of individual visual probe stimuli presented at -10° (diamond), 0° (circles), and 10° (star) as a function of probe–saccade interval. Mean estimates of probe location from a no movement control condition are represented by the open squares. Error bars represent 90% confidence intervals. B. Mean mislocalisation error (degrees) for the group of control subjects ($N = 10$) and subject AI. Mean mislocalisation errors are presented separately for early (where probe onset differed from saccade onset by 200 ms or greater) and late trials (where probe onset occurred within 50ms or less of saccade onset) at each probe location (-10° , 0° , and 10°).

Subject AI was required to initially foveate a fixation-cross presented to one side of the visual workspace and to then initiate each trial by depressing a key on a button box.

She then made a voluntary head saccade of 22° to a digital counter '0' on the other of the visual workspace and her head movement triggered a change in the digit from '0' to '1' which then remained present for between 400 to 1600 ms; subsequent digits (2-4) were then presented for 1000 ms each (Figure 5A). Subject AI was then required to indicate whether the duration that she saw the digit '1' was longer or shorter than for the subsequent digits. A control condition was also carried out in which the digital counter stimuli were presented at fixation, and subject AI maintained a fixed head position throughout the experiment. In neurologically normal subjects, executing a saccadic eye movement to foveate the digital counter results in an illusion of 'chronostasis' in which the subjectively-defined second (i.e., the perceived duration of the digit '1') is shorter than 1000 ms by > 50 ms plus the duration of the saccadic eye movement (Yarrow et al., 2001). This effect was

completely absent in subject AI (it should be noted that the chronostasis effect is observed in individual subjects [K. Yarrow, unpublished thesis]).

Figure 5B shows the results of this experiment. Open bars represent means, for each condition, for trials which A.I. judged to be subjectively 'shorter' than 1000 ms. Solid bars represent trials in each condition that were judged to be subjectively 'longer' than 1000 ms. For the experimental condition, in which AI made a saccadic head movement to foveate the digital counter, the median 'subjective second' was 1000 ms. In the control condition subject AI's median subjective second was 980ms. This difference was not statistically significant ($P > 0.05$). Statistical analyses also confirmed that the medians for subjective 'short' trials, and for subjective 'long' trials did not differ between experimental conditions ($P > 0.05$).

DISCUSSION

Taken together, these findings indicate that saccade-dependent visuospatial and temporal

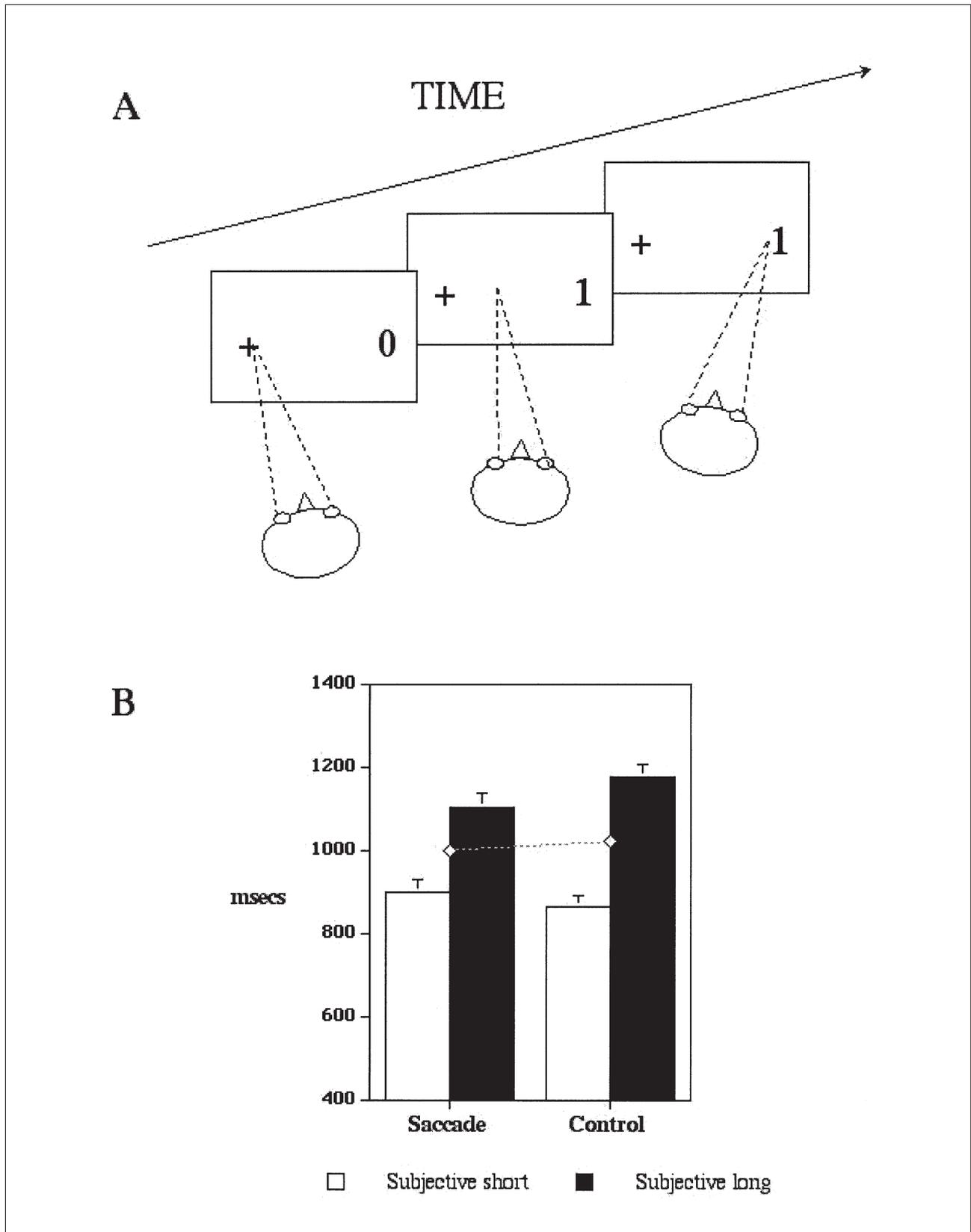


Fig. 5 – A. Illustration of experimental procedure. Subject A.I. viewed a projection screen from a distance of 1.95 metres. She was required to initially foveate a fixation-cross presented to one side of the visual workspace and to then initiate each trial by depressing a key on a button box. She then made a voluntary head saccade of 22° to a digital counter '0' on the other of the visual workspace and her head movement triggered a change in the digit from '0' to '1' which then remained present for between 400 to 1600 ms; subsequent digits (2-4) were then presented for 1000 ms each. Subject A.I. was then required to indicate whether the duration that she saw the digit '1' was longer or shorter than for the subsequent digits. B. Median times (ms) for trials judged by patient A.I. to be subjectively 'short' or subjectively 'long' in an experimental condition where she made a saccadic head movement to foveate the digital clock compared to a control condition where the clock was presented at fixation. The median 'subjective second' for each condition is illustrated by the diamond joined by the broken line. The difference between medians in each condition for subjectively 'short' trials, subjectively 'long' trials, and for the 'subjective second' were not statistically significant.

mislocalisation biases are absent in subject AI for stimuli presented immediately prior to the onset of a saccadic head movement. These data provide strong evidence that the visuospatial compression effects observed immediately prior to saccadic eye movements may be specific to movements planned in oculocentric co-ordinates and may not generalise to other movement systems.

Why should saccade-related spatiotemporal mislocalisation be specific to ocular movements? As noted above, saccade-dependent compression of visual space has been linked to changes in the receptive field properties of neurones within the posterior parietal cortex that precede saccadic eye movements (Duhamel et al., 1992).

Electrophysiological studies in the monkey demonstrate that cells in area LIP – which can be thought of as the posterior eye field (Batista et al., 1999) – show anticipatory shifts in their receptive fields immediately prior to a saccadic eye movement (Duhamel et al., 1992). These changes may serve to predictively re-map visual space in advance of an eye movement, so that the representation of a visual stimulus is translated from a coordinate system with the initial fixation point as origin to one with the upcoming fixation point as origin (Ross et al., 2001). Such motor prediction mechanisms are important for overcoming delays due to neural transduction and the central processing of sensory signals (Wolpert and Ghahramani, 2000), but may be essential for the accurate control of rapid forms of movement such as ocular saccades. By contrast, slower movements may depend less on motor prediction and more on sensory feedback.

Consistent with this proposal, the coding of eye position is provided primarily by efferent oculomotor signals, whereas the coding of head position is largely signalled by sensory (vestibular and proprioceptive) afferents (Desmerget et al., 1998). It should be noted that the velocity of A.I.'s head saccades is substantially lower than the velocity of a typical saccadic eye movement. Thus, a saccadic eye movement of 7° has a peak velocity of approximately 400 deg S-1. In contrast, a saccadic head movement executed by subject A.I. has a velocity of around 50 deg S-1 (Gilchrist et al., 1997).

In summary, subject AI provides a rare opportunity to investigate saccadic head movements in the absence of ocular movements. We have demonstrated that saccadedependent visuospatial and temporal mislocalisation is abolished in an individual who cannot make eye movements but who compensates by making saccadic head movements.

We suggest that the specificity of visuotemporal mislocalisation biases to saccadic eye movements

is most likely a consequence of the rapid nature of ocular movements, and the use of motor prediction mechanisms to re-map visual space in advance of an eye movement in order to maintain space constancy.

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