Saccade-contingent spatial and temporal visual mislocalisation is abolished for saccadic head movements

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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 spatially [1-8] and temporally [9]. 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 [5]. However, when post-saccadic visual references are available, the distortion is best characterised by a compression of visual space toward the target of the saccadic eye movement [6-9]. 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 50-80ms; and reach maximum effect around the time of saccade onset. An important but unresolved issue, however, concerns the specificity of saccade-dependent visual mislocalisation phenomena. Specifically, do predictive re-mapping processes precede other, non-ocular, forms of movement? We investigated this by examining whether saccade-dependent spatial and temporal mislocalisation are observed in a rare individual, (subject A.I.), who presents with a complete ophthalmoplegia and cannot make any form of eye movement, but who compensates when reading or scanning visual scenes by making saccadic head movements [10]. We demonstrate that both saccade-dependent spatial mislocalisation and saccade-dependent temporal mislocalisation are completely abolished 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.
Results and Discussion

Psychophysical studies have repeatedly demonstrated that visual stimuli presented close to the onset of a saccadic eye movement are mislocalised spatially [1-8] and temporally [9]. When post-saccadic visual references are available, this distortion is best characterised by a compression of visual space toward the target of the saccadic eye movement [6-9]. 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 [6,8]. 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 [11-13].

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 [8]. 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 [15]. This interpretation is consistent with the proposal made elsewhere [16,17], 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. 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, subject 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 [10].

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 [10,14]; and the aetiology and functional characteristics of her ophthalmoplegia [14]. 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 [14]. Further details of A.I.’s condition can be found in ref. [14].

To examine saccade-dependent spatial mislocalisation in subject A.I. we modified the task reported in ref. [8] and prior testing with neurologically normal subjects 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° x 34°]) that was
presented for a very brief period (10ms) 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 ref. [16] for details). Her pointing movements were also monitored on each trial
using an infra-red optokinetic recording device (see ref. [17] for details).

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 [6,8]
to produce maximal perceptual mislocalisation errors. 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 (≈ 50ms) around the time of saccade onset
[e.g., 6,8]. 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. Goosens 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 63ms. Gilchrist reports that the average latency of subject A.I.’s head saccades (266ms) 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-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 50ms period preceding an eye movement during which spatial mislocalisation might be expected to occur should be extended by 63ms 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 113ms or less against probe stimuli appearing more that 113ms before movement onset. Statistical analyses 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.

Recently a temporal illusion of 'chronostasis' – a perceived slowing of real time – has also been shown to accompany saccadic eye movements [9]. 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 A.I., we modified the task reported in ref. [9]. Subject A.I. 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 1000ms each (Figure 3A). 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. A control condition was also carried out in which the digital counter stimuli were presented at fixation, and subject A.I. 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 1000s by ≈ 50ms plus the duration of the saccadic eye movement [9]. This effect was completely absent in subject A.I. (it should be noted that the chronostasis effect is observed in individual subjects [K. Yarrow, personal communication]).

Figure 3 about here

Figure 3B shows the results of this experiment. Open bars represent means, for each condition, for trials which A.I. judged to be subjectively ‘shorter’ than 1000ms. Solid bars represent trials in each condition that were judged to be subjectively ‘longer’ than 1000ms. For the experimental condition, in which A.I. made a saccadic head movement to foveate the digital counter, the median ‘subjective second’ was 1000ms. In the control condition subject A.I.’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).

Together these findings indicate that saccade-dependent visuospatial and temporal mislocalisation biases are abolished in subject A.I. 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 [11]. Electrophysiological studies in the monkey demonstrate that cells in area LIP -- which can be thought of as the posterior eye field [12] -- show anticipatory shifts in their receptive fields immediately prior to a saccadic eye movement [11]. 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 [11-13]. Such motor prediction mechanisms are important for overcoming delays due to neural transduction and the central processing of sensory signals [18], 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 [19]. 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\(^{-1}\) [10].

In summary, subject A.I. provides a rare opportunity to investigate saccadic head movements in the absence of ocular movements. We have demonstrated that saccade-dependent 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 visuo-temporal 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.

**Acknowledgements**

We are grateful to A.I. for her cooperation and to Drs Iain Gilchrist and Patrick Haggard for helpful discussions regarding these data. The studies reported here were supported by funding from the Wellcome Trust.
References


Figure Captions

Figure 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° x 34°]) 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 ref. [16] for details). Her pointing movements were also monitored on each trial using an infra-red optokinetic recording device (see ref. [17] for details).

Figure 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° head-saccade (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.
Figure 3:

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 1000ms 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.
Fixation

Target

Probe

Eye movement

Time (ms)