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Analysing Visual Attention In Freely Navigating Birds Using On-Board Video



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Analysing Visual Attention In Freely Navigating Birds Using On-Board Video

Abstract

Avian navigation has been a field of fascination for thousands of years. The importance of visual information in bird homing remains poorly understood, but recent technological advances are allowing exciting new research into the roles of landmarks in orientation and pilotage. Here, pre-existing video data obtained from miniature video cameras on pigeons (*Columba livia*) navigating home over a familiar route are analysed, using head movement behaviour as an indicator of potential visual attention. Using novel methods, behavioural data is extracted from the videos, visualised and assessed. Head nystagmus movements, potentially involved in gaze-stabilisation, are shown for the first time in pigeons turning in flight. Also, the birds show increased rates of head movement during initial phases of flight, potentially indicating a gathering of visual information from the landscape. Similar head movements in one direction are identified outside of turns, and it is suggested that such movement may indicate the birds focussing on particular distant objects. A preference for one eye is cautiously suggested, along with the potential physiological explanations of such a preference. This work is the latest attempt to extract information from these videos, and succeeds in obtaining basic but very interesting and reliable data, while these results hint at the important use of such technologies for the future.

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Introduction

1.1 – Avian navigation: a brief background

For centuries the remarkable ability of birds to navigate over long and short distances has fascinated humans. From the earliest domestication of homing pigeons thousands of years ago to a wealth of research in the last few decades, bird navigation has always been of great interest to man. Any work that aims to advance our understanding of any aspect of bird navigation must do so with an awareness of the historical development of our current knowledge.

In recent decades, widespread research efforts have led to a realisation of the complexity of bird navigation, and an understanding of some of the mechanisms involved. A large portion of the work done on bird navigation systems has been based on the homing pigeon, *Columba livia* (Wiltschko & Wiltschko 2003) and it is this work that is built on in this project.

The concept of avian navigation encompasses a variety of behaviours and mechanisms, from trail following and familiar route-based orientation, to “true” navigation and map formation. A variety of experimental and theoretical techniques have been used to investigate such systems. Early experimental investigations into bird homing involved displacing birds, and revealed the impressive extent to which they could return home, even over open unfamiliar sea (Watson 1908). Subsequent experiments showed the importance of learning in navigation, where applicable, but certain physical barriers prevented much advance in understanding of navigation techniques. Between release and return, there could be little to no recording of the birds’ movements or behaviours, meaning that return rate and speed were initially the only recordable variables (Wiltschko & Wiltschko 1993).

There are a variety of orientation mechanisms employed by birds. For example, egocentric route development, or basic route-reversal allow for effective orientation, while innate directional preferences have implied the genetic component of some young animals’ ability to orient themselves (such as in starlings, Perdeck 1958). A distinction must be made between navigation over long distances, and familiar area route following. True navigation requires two component aspects: a compass to determine the desired direction, and a map to fix the current and future positions of the birds. Early and advancing work suggested two primary compass mechanisms – the sun-compass (Kramer 1950), and a compass mechanism based on the earth’s geomagnetic field (first proposed by Wiltschko 1968).

Numerous acclaimed studies have shown support for the sun-compass, most notably those involving the “clock-shift” effect. In these, birds’ sense of time is manipulated, and their subsequent directional navigation is predictably altered as they misjudge the sun’s azimuthal

position (Schmidt-Koenig 1958; Keeton 1974 and others). The earth's magnetic field is another widely accepted stimulus used by birds in compass establishment. Strong support for this has been shown by the impairment of bird navigation when strong magnets are attached to them, particularly on overcast days, when the sun compass use is restricted (Keeton 1971; Ioale 1984). Magnetic sensitivity was first revealed in Robins in 1972 (Wiltschko & Wiltschko 1972). Furthermore, the genetic component of this magnetic detection has been shown in young birds, which have an innate ability to detect geomagnetic field lines, and this compass mechanism provides a vital foundation for the navigation system (Keeton 1971). In addition to these, star compasses have been suggested, and shown in a classic planetarium experiment by Emlen in 1970.

In addition to the compass, true navigation requires map formation to fix a location. Grid maps have been suggested as being key, in which a minimum of two cues vary in different directions over large scales. The cues that birds could potentially use to establish these maps are numerous, varying from the sun, the geomagnetic field, and large-scale visual gradients. The olfactory map, whereby the bird's location is determined by extrapolating known information about chemical composition of a familiar area, is frequently cited as a dominant map, and its importance has been shown in many experiments (Papi 1976, 1982, 1989; Wallraff 1980, 1981.)

The various aspects and nuances of avian navigation are not fully understood, by any means. Birds show significant redundancy in their navigational systems (Keeton 1969) and use a range of cues to develop their navigation, orientation and homing strategies. The role of visual cues during bird flight is yet another aspect that has been hotly debated, and it is this facet of bird navigation that this project addresses.

1.2 – Bird vision, and the use of visual cues for orientation.

The role that visual cues play, excluding the visual aspect of sun-compass use, is not fully understood. Experiments have revealed that visually impaired pigeons can still home from 15-130km away (Schmidt-Koenig and Schlichte). Particularly in unfamiliar territory, visual landscape information does not seem to be essential to successful navigation. However, in familiar areas, visual activity in birds does appear to aid bird homing abilities. Gagliardo et al. (1999) showed that birds deprived of olfactory and sun-compass cues could still home successfully. One of the most interesting proposals of visual based homing has been the pilotage map, whereby regularly travelled routes are developed according to sequential landmark following. Birds are seen to follow such routes loyally, and this route stereotypy has been thought to potentially indicate visually-driven route learning (Meade et al. 2005; Biro et al. 2004, 2007). Other experiments have shown that pigeons can home faster and more directly when allowed to preview their surroundings before release than can pigeons deprived of such sight (Braithwaite and Guilford 1991, Biro et al. 2002). This may suggest a possible role for visual information

processing in at least the initial stages of flight, although the exact implications and advantages of previewing the landscape are not fully explained.

In some circumstances, it seems clear that birds can and at times do use visual cues in map formation and route development. There is a potential role in familiar area navigation, even if the importance of such cues is less likely in long distance novel area navigation.

Advancing technologies are facilitating entirely novel approaches to this field of study. Miniature GPS trackers, such as those used by Biro et al. in 2002, have allowed for detailed studies of in-flight movement and behaviour of birds. In 2006 Lau et al., revealed that edge-containing land features attract homing pigeons. Using an automated edge-detection procedure they analysed the type of landscape the birds habitually favoured, and deduced that the routes coincided with clear “edges” in the landscape, and that the birds’ “navigational states” were affected. Such discoveries arise from the intelligent use of powerful new technologies, which hold boundless potential for future developments of our understanding. This project seeks to exploit the possibilities of a novel technique for assessing bird in-flight behaviour: video cameras can now be attached unobtrusively to the back of pigeons in order to record the head movement of the birds throughout the flights. The significance of this is that pigeon physiology means that eye movement is generally dictated by head movement, and vice-versa. This lack of dexterity in the eye movements of the birds mean that their head movements can be taken to, in general, indicate where their visual attention must be focussed. Such videos allow, for the first time, the study of “undisturbed behaviour of wild, free-ranging birds” (Rutz et al. 2007). Early studies into pigeon homing were restricted to recording initial trajectories and homing times; this technique allows a much fuller picture of bird in-flight activity to be painted for the first time, and deductions about their decision-making and use of visual landmark stimuli to be made.

Any attempt to use this technology to investigate the visual activity of birds during flight must consider the basic visual system of the birds in question. Pigeons’ visual capacities are great. Compared to the highly visual human, pigeons have superior abilities of luminance discrimination (Hodos et al. 1985) and colour difference identification (Emmerton and Delius 1980). Relative to brain size and head volume, avian eyes are very large (Güntürkün 2000). Evidently, vision plays an important role in bird life. Fundamentally, the birds’ vision can be considered as frontal binocular vision working with monocular lateral vision. Each visual field appears to be represented in different areas of the neuro-visual system and serve different functions (Güntürkün 2000). The exact use of the different visual systems is not completely understood. Undoubtedly, in some circumstances a lateral point of view is adopted, with pigeons being known to orient themselves sideways relative to an object of interest to inspect it. Monocular lateral vision provides higher resolution than that of monocular frontal vision (Güntürkün and Hahmann, 1994). However, the usual binocular frontal vision has been measured, particularly in young pigeons, to have equal acuity to the lateral systems (Hahmann & Güntürkün 1993).

A further aspect of pigeon vision is the lateralization of the visual system. This asymmetry has been shown to be of potential advantage to the birds, and in many cases a preference for a single eye has been shown. It may well be that birds have a preferred eye for certain tasks. For example, there has been shown to be unequal performance of the eyes (Güntürkün et al. 2000). A right- or left-hemisphere dominance for visual information processing is a likely explanation for such imbalances. The physiological aspect of in-flight vision remains a scarcely studied field, and is yet another intriguing aspect of visual attention in birds that could be investigated using on-board video cameras.

1.3 – Aims

In 2009, researchers from Oxford obtained videos by attaching miniature cameras to pigeons' backs, and allowing them to repeatedly fly a familiar route home. The work presented in this project is based on those videos, and is the most recent attempt in an on-going series of work aiming to develop our understanding of the visual behaviour and activities of pigeons during flight. Previous work on these videos has attempted to analyse the movements of the birds (Ozawa 2010), and develop an automated procedure to extract usable, quantitative behavioural data from the videos (Fayet 2010). It has so far proven difficult to obtain simple and functional quantitative data from the videos, due to their length, complexity and quality. My project therefore aims to first develop a simple method whereby data relating to the head and eye movements of the bird can be obtained. This then allows an analysis of the visual attention of the bird as it flies in certain ways and over particular areas of interest in the landscape. For the first time, it is possible to see whether the behaviour of pigeons in flight reflects visual attention to the underlying landscape.

Materials & Methods

2.1 – Video collection and previous work

Six pigeons (*Columba livia*), between 3 and 6 years old and weighing more than 450g, were released a total of 96 times from Weston Woods and allowed to fly the 10.6km distance back to their loft at the Oxford University Field Station (Loft: Whytham, UK, 51°46'58.34" N, 1°19'02.40" W. Release Site: 51°51'17.6" N, 1°12'58.35" W) in 2009. 6 to 15 video flights were recorded for each bird, with each bird flying no more than twice in any one day. Modified FlyCamOne2 cameras (ACME, Germany) attached to the pigeons' backs using a Velcro strip in a way that did not affect neck or wing movements recorded frames at 25Hz. 60 videos were recorded, and 31 (corresponding to 3 birds) were manually transferred into spatial data on Google Earth (Google Inc., USA) by Ozawa during her DPhil. This produced route maps as can be seen in Fig. 2.1. For detailed methods see Ozawa 2010 and Fayet 2010.

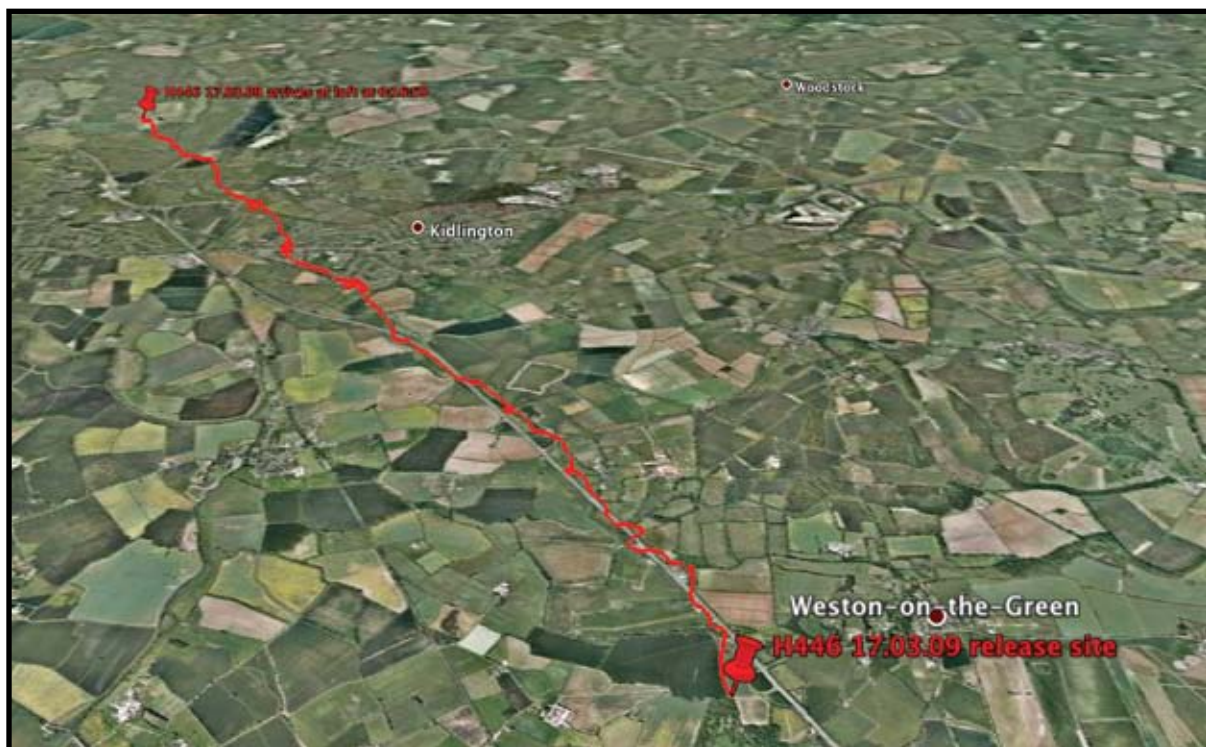


Figure 2.1 – Visualised track in Google Earth, relating to a single video

2.2 – Data extraction

The main challenge presented by the video data is the difficulty in obtaining usable information. The videos undoubtedly hold huge amounts of potential information about the bird behaviour, but converting such information into a form that can be analysed and reviewed practically is not immediately obvious. Previous work (by Annette Fayet in 2010) attempted

to develop an image-processing program to detect and record head movements of the birds automatically. Each video is very lengthy (roughly 20,000-30,000 frames), so an automated procedure was a desirable option. This method struggled to produce a reliable track of the head movements throughout the videos for a number of reasons, although some great strides were made and preliminary results obtained. The technologically demanding nature of such computer program editing meant that it was not feasible for me to continue in this vein, while the nature of the videos, necessarily recorded on low-quality cameras in variable conditions, mean that computer-automated analyses would regardless continue to be difficult. The approach of this work, therefore, was to develop a simple, manual method of obtaining data relating to head movements from the videos.

Rather than recording exact head positions of the bird at every frame, the approach taken was to categorize head movements into three categories – Left, Right and Centre. In each frame of any given video, the position of the bird's head can be categorized as pointing left, forward, or right, depending on the visibility of the eye in the video, as shown in Fig. 2.2.



Figure 2.2 - Screenshots of the video during the three possible head positions according to eye visibility: left, centre and right.

One pilot data extraction was carried out entirely manually – working through a video, frame-by-frame, in Quicktime (Apple Inc., USA), the head position (L, C or R) of the bird in every frame was recorded in Microsoft Excel. Given the large frame count of the videos, this approach was more time and energy demanding than might be hoped. Therefore, a basic program was written in MatLab (Mathworks Inc. USA) (written by Shane Windsor) that allowed easier allocation of a category to each frame. To avoid having to assign a category to every individual frame, head movement was only recorded in frames in which the head position state changed. For example, the frame in which an eye appeared on the video on a certain side, or disappeared having been visible in the previous frame, would be categorised, and no more frames would be marked until an eye reappeared/fell out of view again.

The slow process meant that a small sample size was inevitable. A total of 9 videos were

processed in this way – 7 from one bird (known as H446) and one from each of two other birds (H444 and S040). This produced, for each video, a record of every frame number in which there was a change in head position, and the direction of this head movement.

2.3 – Data Manipulation

9 very large data sets of roughly 2000 points were produced by the above method. While valuable, data this large is hard to analyse and visualise fully. Therefore, with the aim of easier pattern identification in the movements and analysis, the data was simplified. This was done by manipulating the results in a way that reduced the noise caused by frequent minor head movements inevitable in any moving animal. Head movements were re-categorized into those in which the head movement was directly from one side to the other, and those in which head movement was repeatedly out in the same direction from the centre (see fig 2.3). Occasions when the head moved directly from one side to the other were marked by “1”, while head movements repeatedly in the same direction were assigned “0”. As a result, repeated head movements in the same direction are recorded and referred to as “sequences of 0s”. This data is referred to as the “binary data”.

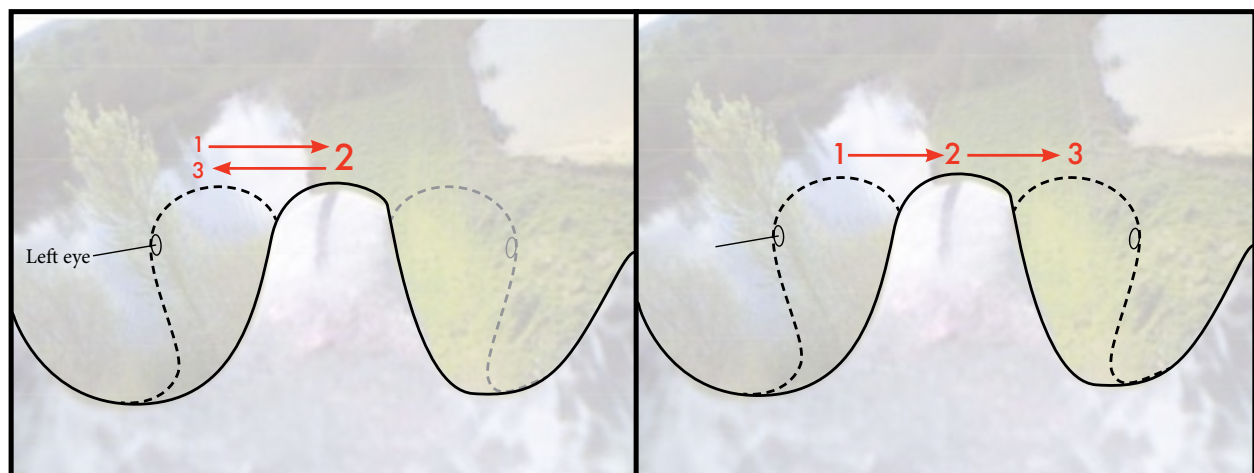


Figure 2.3 - Two types of head movement patterns. Red arrows and numbers indicate head movement sequence.
Left: “0” - head movements are repeatedly out to the same direction.
Right: “1” - head moves from one side to the other.

Consequently, the data exists in two forms – the initial raw data, recording the head movement and position at any given frame, and this binary data, indicating the type of head movements over any period.

2.4 – Development of analysis strategy

The exploratory nature of this work dictates that specific hypotheses and expectations are hard to produce. The overall hypothesis investigated is that *a bird's patterns of head movement (and hence eye movement) during flight will reflect important features of its visual attention to the underlying landscape*. In order to direct my research, I concentrate on a few specific aspects of the flights.

Firstly, unequivocal turns (defined as occasions when the bird's flight crosses its own path, completing a "loop") are concentrated on. It is expected that when turning in flight, birds show nystagmus head movements, moving their heads into turns. This is involved in gaze stabilization and has been seen in many birds, but never explicitly shown in pigeons. Therefore, this initial avenue of study acts as a test of the validity of my method as well as a potential indicator of an interesting in-flight gaze-stabilizing activity.

The next approach is to concentrate on various flight sections likely to be of particular significance. The first measure of head movement activity is the rate of head movements. For example, at the start of the flight, the bird may be attempting to determine its location by visually assessing the landscape. Furthermore, all the birds' flights cross the village of Kidlington for a period of time. This constitutes a stark change in landscape type, and may be associated with a change in visual activity. The end phase of the routes and areas where the birds' route loyalty is strongest (that is, areas over which the birds' routes consistently pass) provide further areas of potential interest.

Finally, identified patterns of head movements can be related to the underlying landscape and route followed. For example, periods of non-random head movement that do not coincide with turns in the route must be indicative of a different sort of behaviour or activity, and these are investigated in relation to the underlying landscape.

These approaches aim to reveal and characterise major patterns of head movement during pigeon flight. By investigating the flights first from a "bottom-up" approach, determining whether or not the bird's head movement is different when flying over specific areas, and then in a data-led manner, identifying patterns in the data before relating these to the landscape, I hope to discover the extent to which the patterns of head movement in a flying bird reflect its visual attention to the landscape.

Results

3.1 – Data visualisation

The detailed and lengthy nature of the data sets mean careful visualisation is required, in order that patterns of head movement can be assessed. Fig 3.1 shows the initial graphs generated. One data point (blue dot) on the graph indicates a change in the head position of the bird, so these graphs reveal the head position at any point along the route.

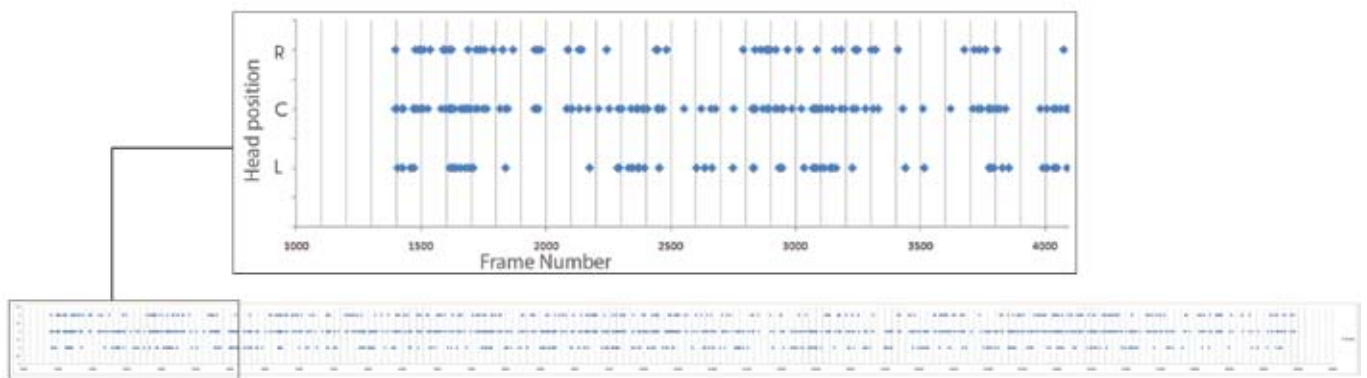


Fig 3.1 – Initial graphs produced from data. Very long & rich graphs, ideal for close analysis of any local areas of each flight.

To visualise better the entire data sets and reveal larger patterns of movement, graphs were produced from the simplified binary data. Fig 3.2 on the following page shows how the visualisations in this section and the appendix relate these graphs to points of interest on the video. These images represent an original and novel way of presenting this sort of video data, and are of significant importance to the analysis. They clearly relate type and patterns of head movement to the videos.

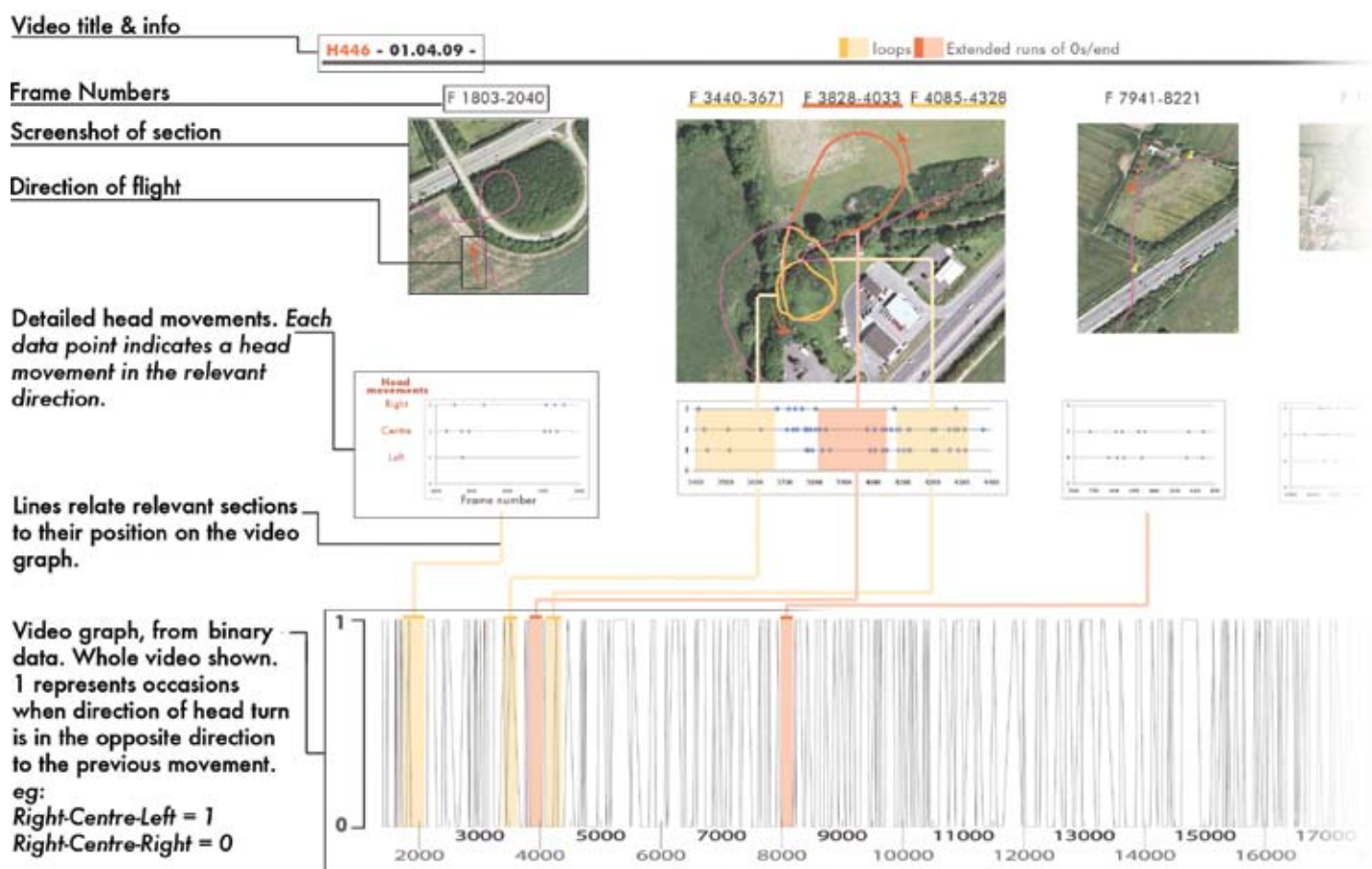


Fig 3.2 – Key to the visualisations featured in the appendix and on page 13.

Note on results & analysis: All statistical tests are carried out on just the H446 sample unless otherwise stated, as the other two flights cannot be considered as part of the same single sample. Patterns and suggestions from the H446 data are, however, considered in the other two flights, although such patterns cannot be statistically investigated in just two other flights.

3.2 – Head movement behaviour while “looping”

“Loops” are unequivocal turns, defined as occasions when the birds turns entirely and crosses its own track (see Fig 3.3). It is expected that head movement in turns will be repeatedly in the direction of the turn, as nystagmus movements. These are expected to show in the binary data as extended sequences of uninterrupted 0s (as 0 indicates movements in the same direction).



Figure 3.3 - An example of a loop in the track

The video **H446: March 17th** contained 7 distinct loops (at least 4 more than every other video). As such, it was used as a model to test for the nystagmus head movements. These loops, and the head movements associated with them, can be seen in Fig 3.5 (page 13). These 7 periods were compared to 7 randomly selected periods (selected using a random number generator to determine the start frame), 352 frames in length (the mean length of the loops). The value compared was the 0:1 ratio in the binary data set. Since 0s represent repeated head movements in one direction and 1s indicated head movements in opposing directions, a high 0:1 ratio shows high levels of head movement in one direction. The 0:1 ratio was found to be significantly higher in the loops than out (paired t-test: $t_6=3.84$, $p=0.0043$). The average rate of head movement was also generally higher in the loops than out, although this difference was not statistically significant (paired $t_5=1.025$, $p=0.2929$), perhaps due to the small sample size. This pattern is found in the H446 videos and is also found in the S040 and H444 videos. Table 3.1 shows the summary data.

Video	0:1 Ratio		Average rate of head movement	
	In loops	Video average	In loops	Video average
H446 - March 17	7.57	2.52	0.08	0.05
All H446 videos average	3.42	1.97	0.07	0.06

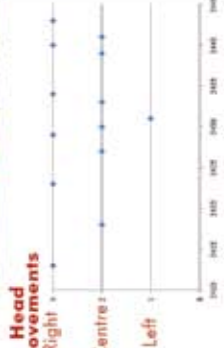
Table 3.1 - 0:1 ratio and average head movements during and across the rest of the videos. Rate of head movement is shown as turns/frame.

Results continue on p.14. Image on next page is Fig 3.5 - loop visualisation for H446 March 17 —————>

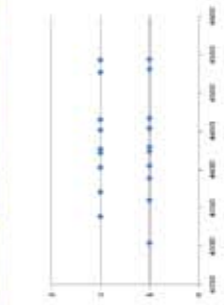
H446 - 17.03.09 - Loops only

loops Extended runs of 0s/end

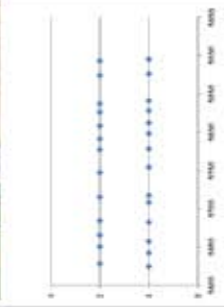
F2412-2554 - Loop



F4302-4554 - Loop

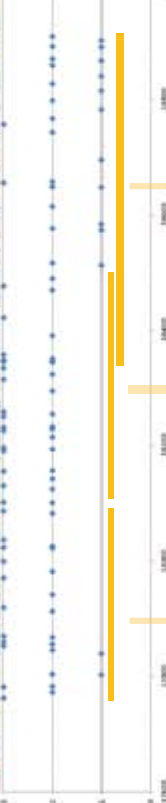


F5622-5895 - Loop

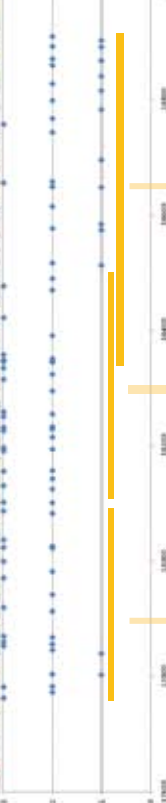


F17734-18083 - Loop
(First of three
successive loops)

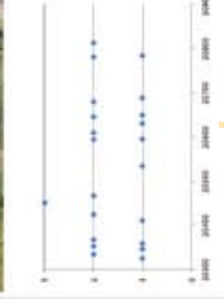
F18118-18511 - Loop
(Second full loop)



F18385-18909 - Loop
(Last of loops)



F20319-20850 - Loop

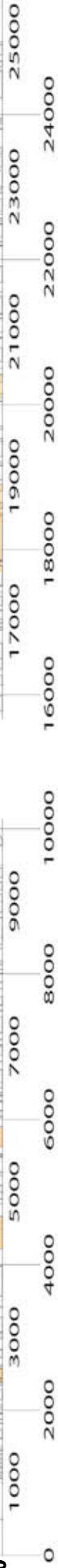


Frame number

1

0

bird sits
between
F9850 &
15750



It is clear from this data that there is significant non-random head movement activity associated with looping. More specifically, there is evidence that head movement is *into* the turns the birds are making. Fig 3.4 shows the loops, and indicates whether the turns are in a left or right direction. For the duration of each loop, the number of times the bird's head moves left has been subtracted from the number of times the head turns right. A positive number indicates more head movement to the right, and negative results show predominant head movement to the left. In the strong majority of cases, the bird moves its head into the turn.

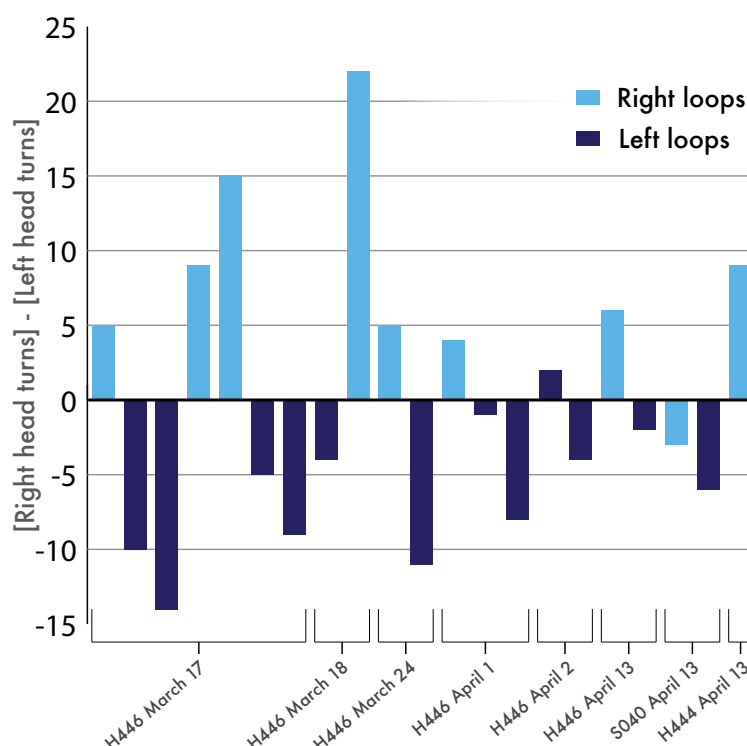


Fig 3.4 - Direction of head movement during right and left turns.

3.3 – Variations in head movement during selected flight sections

Four periods of the flights were identified as areas in which visual activity might potentially be interesting. For this analysis, rate of head movement (in head turns/frame) is generally used as a measure of head movement activity. The raw data from the flights were separated into segments 1000 frames long for easy analysis.

The first period of interest is the initial phase of flight, when the bird may be processing visual information about its surroundings to determine its location (Fig 3.5a).

Similarly, on approaching the loft at the end of the route, the birds are consistently approaching a clear landmark, and always from a similar direction, so at this point there may be head movement to indicate visual focus on the building (Fig 3.5b).

The third period is at a point of “low track variance”. Ozawa’s work on these videos identified areas along the route where the pigeons repeatedly flew over, and areas where the

birds' routes were more varied. At the areas where their loyalty to the route was highest, the birds consistently flew over the exact same point on the landscape. These points were called areas of low track variance. These could potentially be places where the bird is aiming for a visual landmark, and its visual activity might be thought to indicate such targeting. Fig 3.5c shows the comparison of head movements approaching one such area with the average head movements.

Finally, the majority of the bird route is over fields and roads, so the period when the bird flies over the urbanised village of Kidlington represents a stark change in the landscape type. Therefore, visual activity might be thought to be noticeably different in this area than in the rest of the flight, so this is the fourth area assessed (Fig 3.5d).

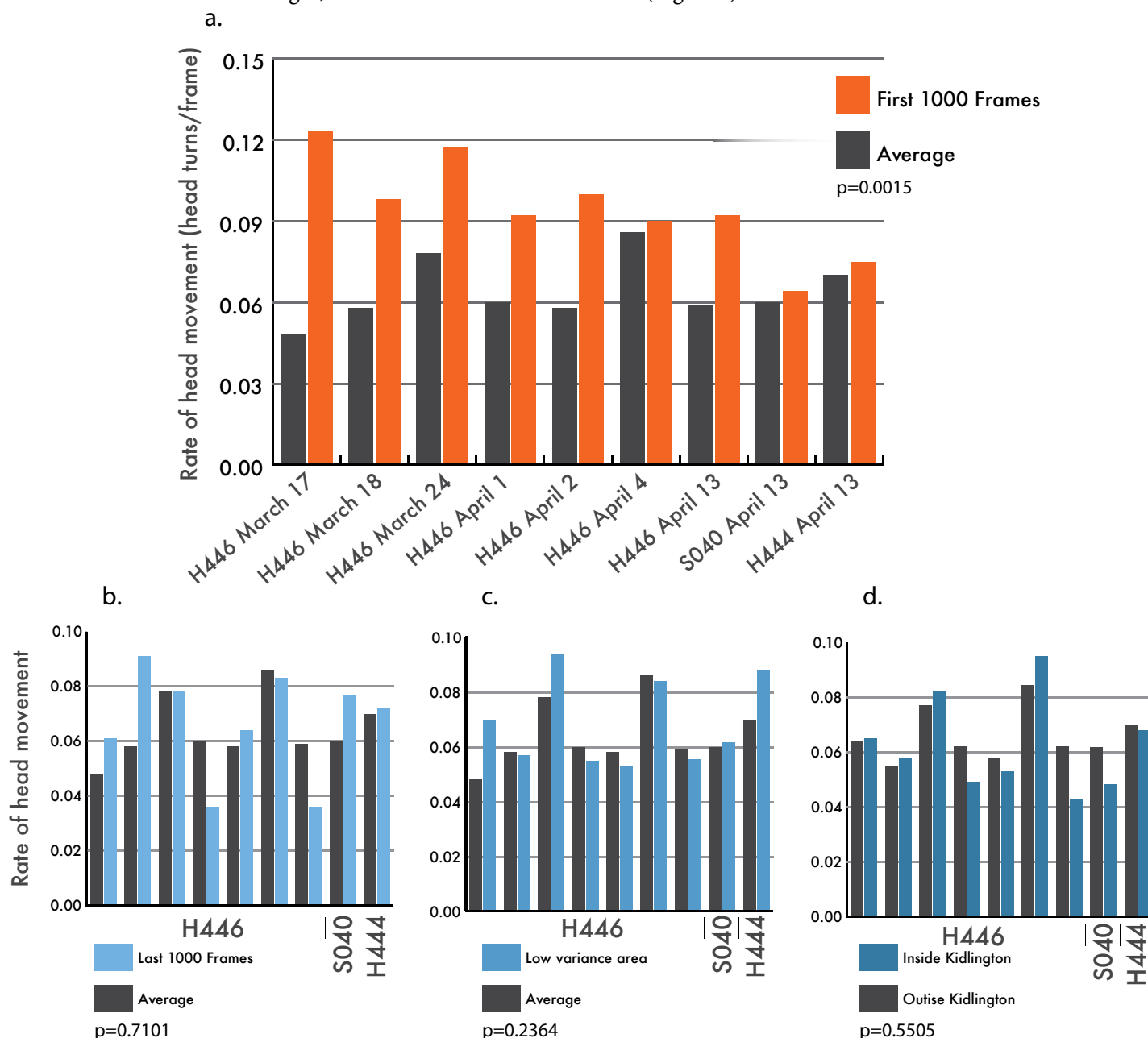


Fig 3.5 (a,b,c,d) – Graphs to show rate of head movement in: a – the first 1000 frames of flight. b – the last 1000 Frames of flight. c – an area of low track variance. d – in Kidlington compared to out of Kidlington. p-values resulting from paired t-tests for the relationships are shown for each graph.

Of the four sections investigated, a significant difference in head movement rates was only found in the first 1000 frames. The rate of head turns in the initial stage of flight is significantly higher than would be expected on average (paired t-test: $t_6=4.81$, $p=0.0015$). All statistical tests have been carried out on only the H446 videos. Consistency between birds cannot be statistically tested due to the small sample size. The other two birds do, however, also show higher rates of head movement during the first 1000 frames of flight.

Each of the other comparisons showed no consistent differences in head turn rate (see p-values from paired t-tests for the comparisons on Fig 3.5). In each of the visualisations in the appendix, the end periods of the videos have been highlighted, and show that no obvious pattern can be seen.

3.4 – Relating patterns of head movement to the landscape

Sequences of 0s indicate repeated non-random head movement in one direction, and are often associated with turning (section 3.2). For each video, the two/three longest sequences of 0s (depending on whether there were two clear longest sequences, or if there were three of equal maximum length) that did not overlap with any loops were identified. Of these 22 sequences, 13 corresponded to clear turns along the tracks (although not full loops. See Fig. 3.6).



Fig 3.6 – Areas of track relating to long sequences of 0s.

Left: in 13 of the 22 sequences, the period in question is a clearly identifiable turn.

Right: in the remaining 9 sequences, the bird follows a relatively straight trajectory.

Of the remaining 9 sequences, all of which were periods of relatively straight flight, 8 represented head movements to the right. The implication is that at times not associated with turning when the bird is repeatedly moving its head out in one direction, it is almost always moving it right. Many such periods are highlighted in the appendix visualisations (see appendix – H446: 13.04.09 for particularly clear illustration).

Although there was no difference in rate of head movement between sections above

Kidlington and those over rural areas, one noticeable pattern was observed: in 7 of the 9 total flights, as the bird enters Kidlington a sequence of 5-12 0s is seen in the binary data set. This pattern is shown in table 3.2. Small sections of the binary data are shown, relating to the time the birds enter Kidlington. In each case these 0s represent repeated movement of the head to the right.

Video	Sequence of 0s & 1s	
H446 March 17	0001010000	0000000010
H446 March 18	1011000000	0011000001
H446 March 24	1010001000	0001011001
H446 April 1	1000110110	0100011100
H446 April 2	1001100101	0010000110
H446 April 4	1100100100	0001011000
H446 April 13	0100000000	0001100000
H444 April 13	1101010000	0111011110
S040 April 13	0100100000	1000110010
Bird enters Kidlington		

Table 3.2 - In 7 of 9 videos (or 5 of the 7 H446 videos), as the bird enters Kidlington it moves its head to the right hand side at least 5 times in succession.

A further finding is that the birds look to their right more than to their left in all but one H446 video, and both other videos. The birds look significantly more to the right than left when all videos are assessed (paired $t_8=2.56$, $p=0.033$), although the statistical significance is less strong when just H446 videos are analysed (paired $t_6=1.75$, $p=0.13$).

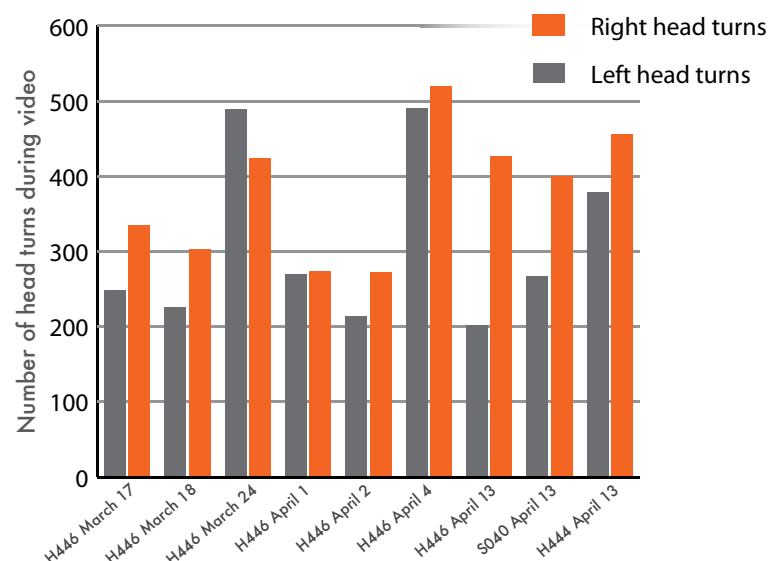


Figure 3.7 Graph to show the number of right and left head turns in each video.

Long sequences of 1s were also related back to the tracks they presented. No consistent patterns were found in this relationship. Sequences of 1s lasting 5 or more data points were far less frequent than sequences of 0s (9.3 times less frequent), and the longest sequences of 1s were 5-7 numbers long, while the longest sequences of 0s were 9-24 data points long. We can conclude that runs of 1 were less frequent and shorter than runs of 0s.

Discussion

Throughout this study I have taken the assumption that head movement is indicative of eye movements, and hence visual attention. It is very possible that head movements could be involved in other sensory perception. For example, there is the possibility of magnetoreceptor capabilities in the beak, while the role of olfaction in navigation is well known. The possible implications of the head movements for visual attention are discussed here, but it should be remembered that such movements do not all necessarily indicate visual activity exclusively.

4.1 – Head movement behaviour during turns.

Head nystagmus in birds has long been observed (Money and Correia 1971). It is rapid movement of the head, often closely associated with concurrent eye nystagmus, followed by slower sweeping movement. Its primary role is in gaze-stabilization, and has been suggested to account for roughly 80% of the pigeon gaze stabilization (Gioanni 1988), while the eye nystagmus reflex is thought to be less active (Haque & Dickman 2004). In 1998 Warrick et al. showed that birds with restricted neck (and hence head) movement failed to bank through a slalom course and navigated it much more slowly than unrestricted birds.

It was predicted that when turning the pigeons would show sharp head nystagmus movements into turns. Due to our understanding of this concept, this strong prediction allowed for this aspect of the analysis to validate my method. The conclusive evidence that the pigeons studied do move their heads repeated into the direction of looping turns suggests that my method has faithfully recorded the head movements of the birds. My research has shown, as clearly as could be hoped given the sample size, that pigeons undoubtedly do move their heads into turns during flight. This work represents the first formal evidence of this gaze-stabilising head nystagmus movement during flight in pigeons. This work does not directly show that this behaviour is involved in gaze-stabilization, and it could be involved in the turning dynamics of flight, although wider knowledge of such head movements suggests at least a partially visual role. Since head nystagmus in pigeons is considered to be a horizon-stabilizing mechanism (Warrick et al. 2002), we can suggest that the behaviour shown here may play an important role in allowing pigeons to make full use of visual landscape cues while navigating.

4.2 – Head movement behaviour at points of interest along a homing route

The results presented here suggest significant head movement during the very initial stages of pigeon flight. A series of experimental “preview” studies have shown that having the opportunity to view the area prior to departure affects homing times (Braithwaite and Guilford 1991, Braithwaite 1993, Braithwaite and Newman 1994, Burt et al 1997, Biro et al. 2002). A common explanation suggested for this result is that visually mediated site recognition occurs at the start of/before the flights over familiar areas. The birds used in this study were transported in an opaque box with small holes. They were then removed and had cameras attached – a process that took a couple of minutes. There was therefore some limited preview time, but this was not free uninterrupted landscape viewing.

In every video, the rate of head movements during the initial phase of flight was higher than the average for the video, and looking at the appendix images it is very clear that in each video there is a short period immediately after take-off in which the bird moves its head in both directions very rapidly.

There are several potential explanations for this result. Firstly, during this period of the flights vigorous, altitude-gaining flaps can cause large head movements, or disturbances to the camera that cause results to show head movement. During the data collection and extraction I did note that there were occasions when vigorous flapping meant the video image was temporarily indistinguishable, skewed, or seemingly at an unnatural angle. However, these periods tended to last only a few frames in length (typically less than 10), so would be unlikely to cause the effect over the whole 1000 frame period.

The next possibility is that the large amount of loops and turns in the initial phase of flight cause high levels of head movement. We have seen that turns are associated with distinct patterns of head movement, and so the curved initial trajectories of the birds may be the cause of the high recorded head movement rates. Ideally, the tortuosity, or degree of turning, in these phases would be compared to that of the rest of the flight, but given the format of the track data this was not feasible. Video H446 24.03.09 suggests a counter-example to this theory, however. As Fig. 4.1 (p.21) shows, the first 1000 frame period appears to be more direct than the second 1000 frames. However, the rate of head movements in the first and second 1000 frame sections were 0.117 and 0.062 head turns per frame, respectively, indicating that, in this particular video, the high initial rate of head movement may be independent of turning. This is however, the only clear example of this pattern, and the first 1000 frames are still far from straight.



Figure 4.1 - H446, 24th March: The flight of the bird is less dramatically curved in the first 1000 frames (between the release site and the “1000F” marker) than in the second (between the 1000F and 2000F markers).

The curved initial paths of the bird flights undoubtedly plays a role in this result, but there is a final potential explanation. This is that the initial period of any homing flight is spent visually assessing the surrounding landscape, and identifying landmarks. This explanation fits both my data and matches the suggestions of the “preview” experiments. The theory, first proposed by Braithwaite and Guilford (1991), that recognition of visual cues at the start of (or, in their case, before) flight plays an important role in the initial orientation of birds, is well supported by this data.

No conclusive changes in head movement behaviour could be identified on approach to the end of the flight, a point of low “track variance”, or over Kidlington. This does not prove that the bird is not directing visual attention in interesting ways at these junctures, but just that this attention is not manifested as increased rates of head movement.

4.3 – Identified patterns of head movement

Early analysis revealed that one of the most prevalent patterns of head movement was that in which the head repeatedly moves out in one direction from the centre and back again. Much of this activity can and has been explained by its association with turning. However, this pattern of head movement (“sequences of 0s”) exists in the data in areas where the bird does not appear to be significantly changing its direction.

The first important implication of this clearly non-random head movement is that is very likely does indicate some sort of visual attention activity. These movements suggest periods of notable visual activity. What this activity specifically indicates is open to speculation.

The retina of the pigeon can be considered as two areas – the yellow field and the red field. The yellow field is typically associated with the lateral monocular field of view as discussed in the introduction, and furthermore, is emmetropic or hyperopic (Hahmann and Güntürkün

1993, Nye 1973 and others), while the anterior visual field is myopic. This suggests, logically, that the anterior field is used for nearby targets directly in front of the head and beak, such as food is during pecking. The implication, therefore, is that the lateral field of vision is the primary tool for distance vision, such as landmark observation may be supposed to be. Therefore, the aforementioned movement of the head to a position perpendicular to the body could be thought to be the bird orienting its head so that it can obtain a lateral perspective to a distant object directly in front of it. The repeated “flicking” style movement (as opposed to keeping the head pointing sideways constantly) may be required to avoid interfering with the direction of travel.

Perhaps the most notable aspect of the data I collected was the preference that appeared to be shown by the birds for one direction of head movement over the other. In the majority of cases (8 of 9) when the pattern was identified, head movement was to the right, while in 8 of 9 videos the bird looked right more times than it looked left. The hemispheric asymmetry of pigeons has been suggested as a reason for unequal visual performance for certain tasks, particularly because the visual acuity of the right and left eye systems do not appear to be typically significantly different (Güntürkün and Hahmann 1993). Discrimination performance has been generally higher with the right eye than left when tested under monocular conditions (as referred to in Güntürkün and Hahmann 1993), and this has been attributed to a dominance of the left hemisphere for certain visual functions.

My results, with repeated head movement to the right while flying, suggest that the left eye system is preferred, if these movements do indeed indicate occurrences of the bird focussing its vision on a specific visual cue. There is some support for this idea. Some birds have demonstrated higher left-eye scores in spatial orientation. Rashid and Andrew (1988) suggested that the left eye systems are mainly responsible for orientation (in domestic chicks), while the right eye system is more important in smaller-scale visual processes.

It should be considered, however, that these head movements may not indicate an eye preference, but could be caused by the bird focussing on an object that stays in the same position, relative to the bird. For example, the sun is consistently in a similar position, relative to the birds’ general direction of flight, so these movements may be occasions when the bird is focussing on the directional information provided by this, as part of the sun-compass mechanism. Equally, a very large land feature or distant landmark may provide the same role, rather than this behaviour being indicative of pilotage by individual landmark following.

If this head movement does indicate the bird focussing on a specific object, it might be expected that similar patterns of movement could occur at similar times during different flights. However, no such pattern could be identified on approach to a potential landmark spot

(the area of low track variance), which suggests that either it is not only visual cues that draw the birds to that spot, or that this is not the only head or eye movement behaviour that might indicate attention focussing on a particular object. There was, however, a degree of consistency as the birds entered the village of Kidlington. In 7 out of 9 flights the birds moved their head in this way as they made the transition from the main road into Kidlington. The birds did tend to bear right, off the road, into the village, which would mean that it is possible that this result is indicative of this change in direction, rather than any landmark identification. However, there are several flights where the bird has turned off the road before entering the village, and hence is actually travelling straight during the period in question, so this point presents one of the strongest cases of potential landmark identification and visual interpretation.

4.4 – Conclusions

My research was based on a small sample size, meaning that even with the large data sets generated, no absolutes can be drawn. However, there have been several significant findings that can be built upon and developed in future work. I have shown conclusively nystagmus head movements in turning free-flying birds, for the first time. The visual and anecdotal evidence presented in Fig 3.5 and the appendix reveals the consistency with which the birds studied moved while turning, and I am confident that any future studies would corroborate this finding. The high levels of head movement recorded during the initial phase of every flight are very interesting, particularly in their potential support of previous experiments involving birds previewing landscape. The very novel and intriguing suggestion of a preference for one eye over the other, or “handedness” opens a plethora of potential future research avenues, and the unique method of visualisation employed here could be adapted and used valuably in future work.

My method was necessarily very simple. Bird head movements are clearly more complex than can be fully explained with three categories of movement, and eye movement and focus beyond head position itself adds another layer of complexity not approached by this work. The method has, however, provided clear and reliable tracks of general head movements of the bird over a known route. Naturally a larger sample size with more cross-bird comparisons would have been beneficial and interesting. Equally, some investigation into what other effects head movement may have on non-visual sensory perception and flight dynamics would shed further light on these results.

While my results alone do not, perhaps, determine conclusive facts regarding the importance of vision in bird navigation, they do provide various potential future research routes and indicate the power of this type of data. Our understanding the exact role of the

visual system, and the importance of visual landmarks, will remain blurry for some time, but as technological advances continues to be used as they have been here, great strides in our understanding can be made.

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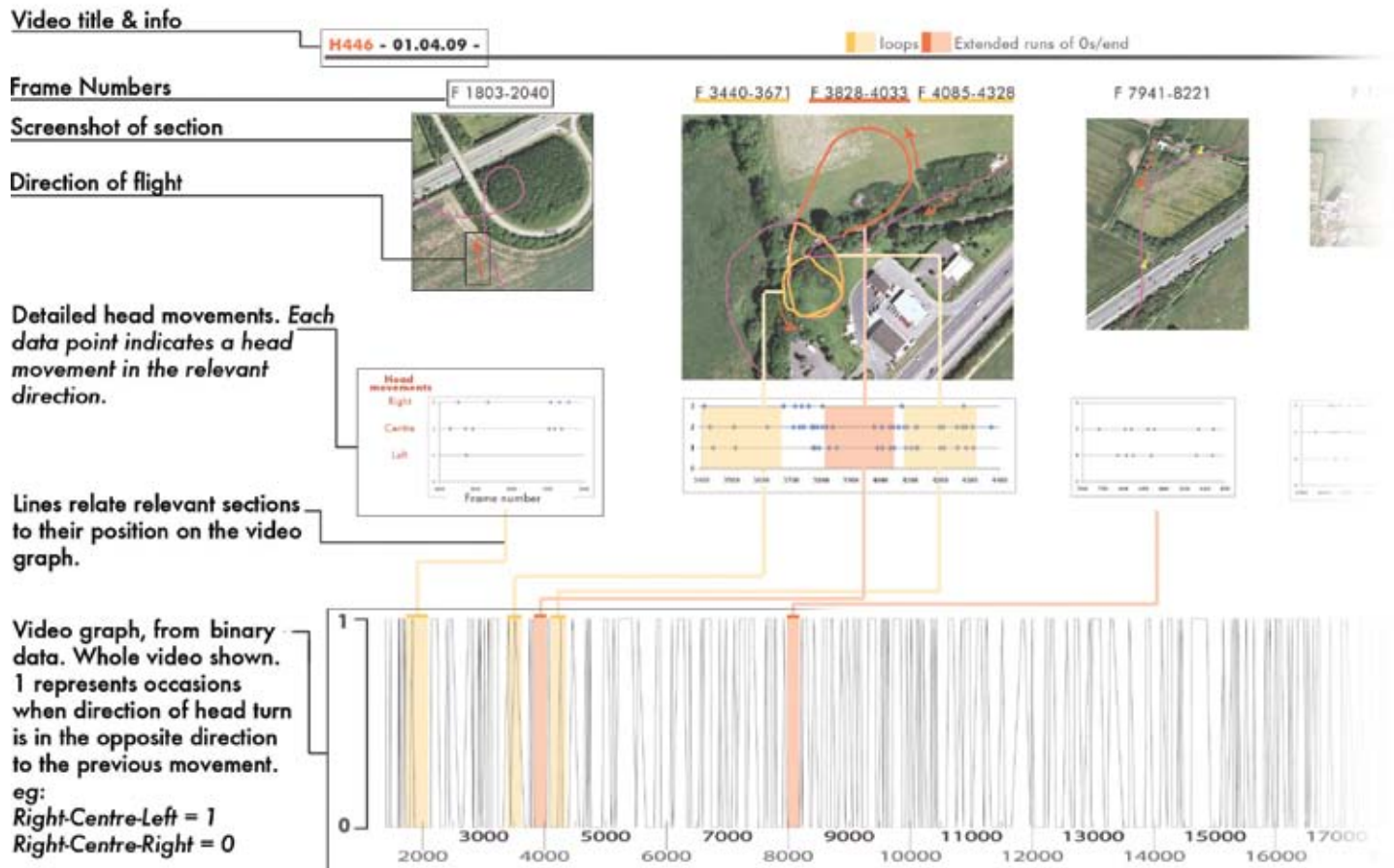
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Appendix

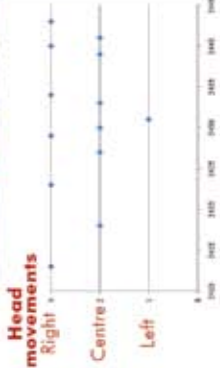
This section contains visualisations of specific sections of each video: loops, selected long sequences of 0s (although not necessarily those analysed in section 4.3) and the final sections of flight.



H446 - 17.03.09 - Loops only

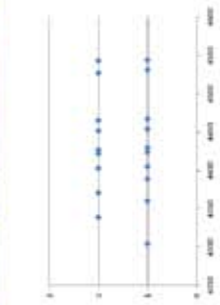
loops Extended runs of 0s/end

F2412-2554 - Loop

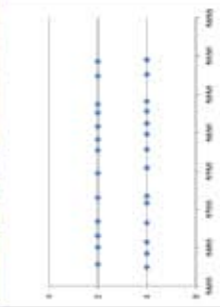


Frame number

F4302-4554 - Loop

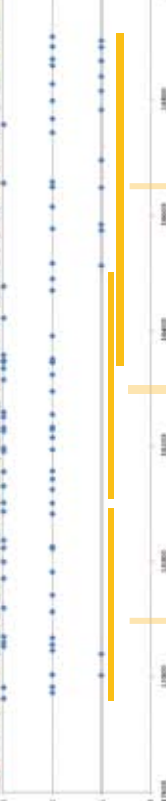


F5622-5895 - Loop

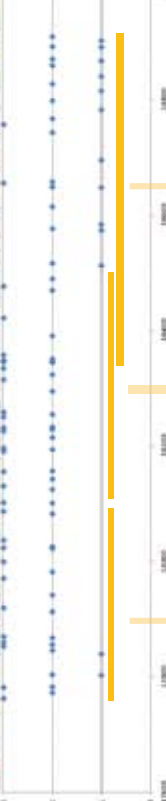


F17734-18083 - Loop
(First of three
successive loops)

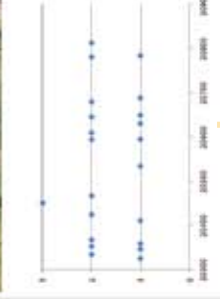
F18118-18511 - Loop
(Second full loop)



F18385-18909 - Loop
(Last of loops)



F20319-20850 - Loop



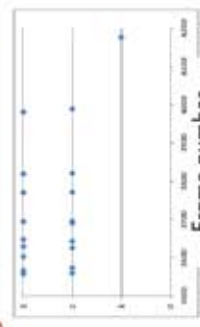
1

0

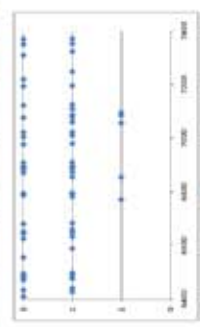
bird sits
between
F9850 &
15750

0

F 3400-4177

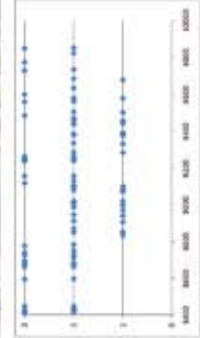


F 6400-7400



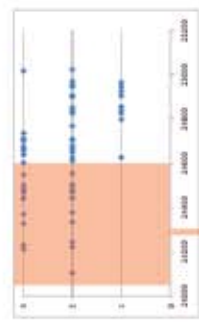
F 8400-9850

(as bird enters Kidlington and approaches seat. Does loop left, but only after ~F8000)



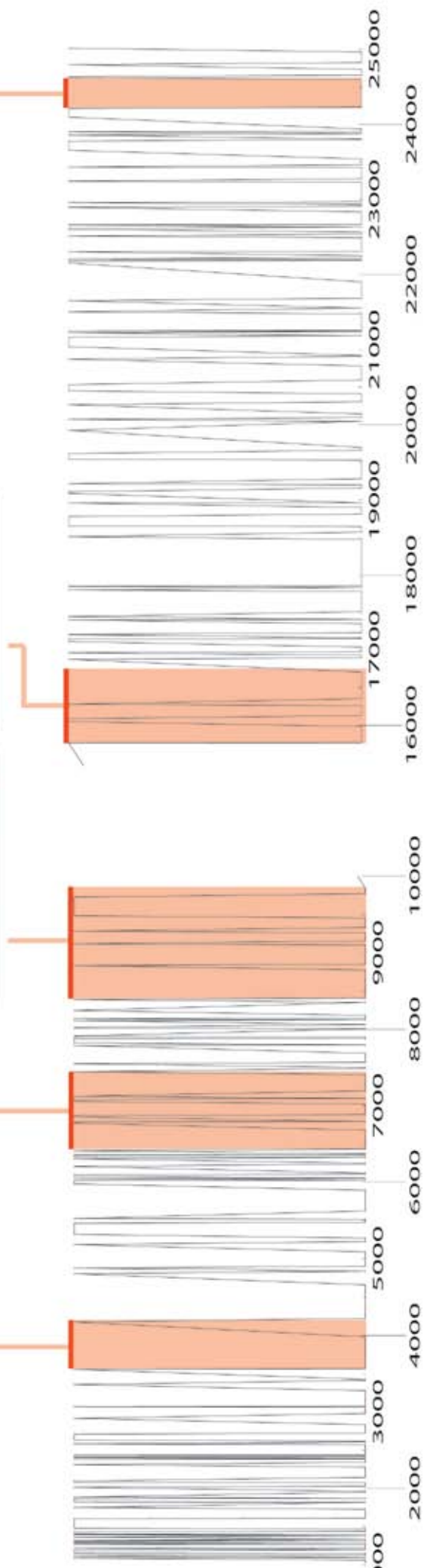
Restart - F 16712

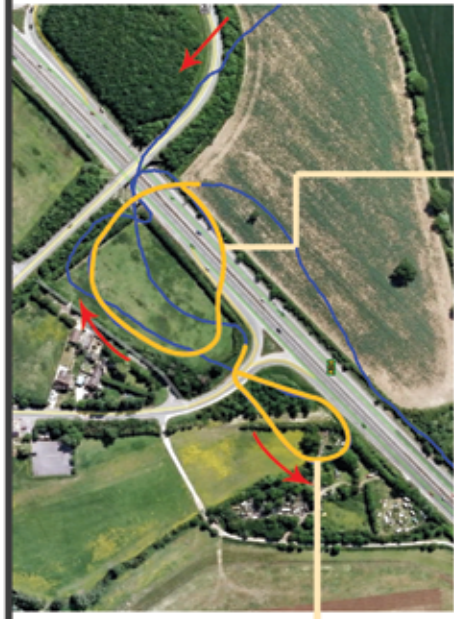
F 24100 - 24600



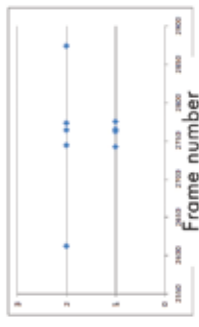
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0

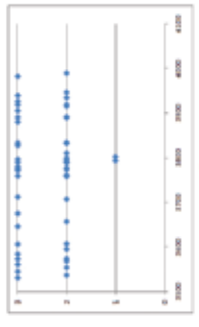




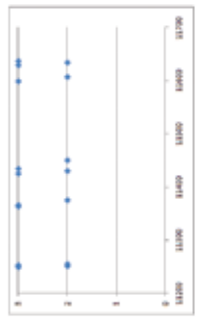
F 2665-2986 - loop



F 3512-4035 - loop

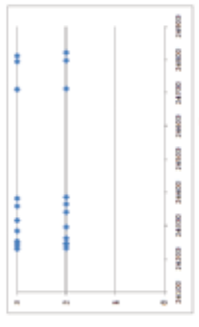


F11249-11628

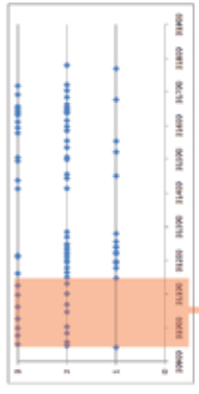


F24229-24821

NB: this is the field that the bird consistently avoids.

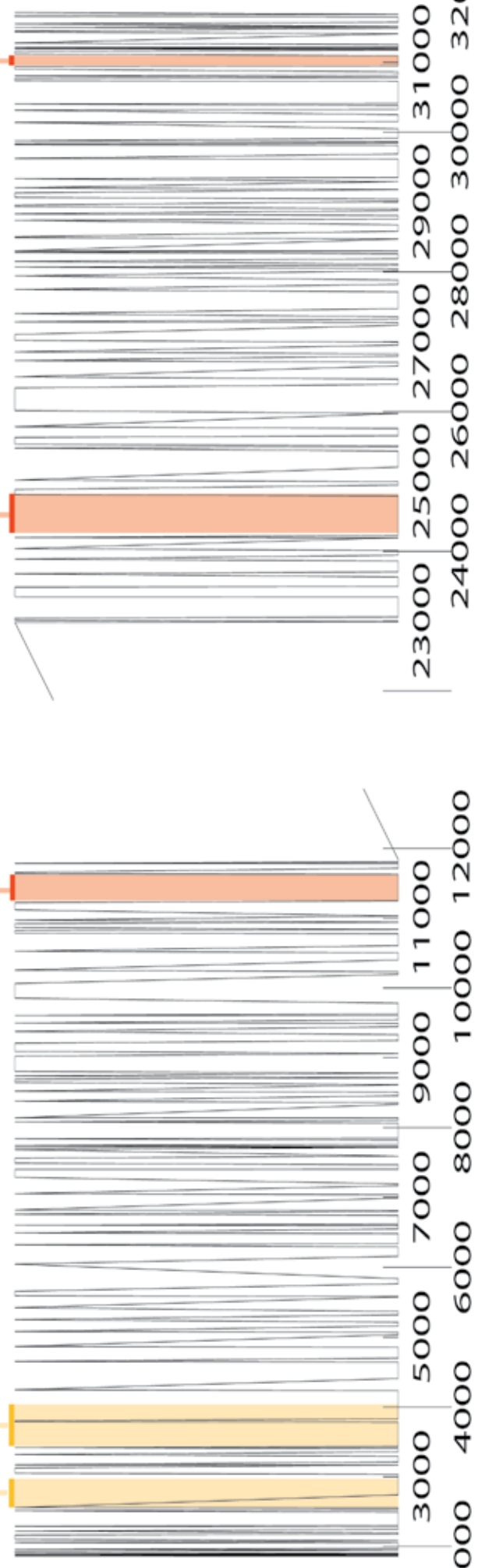


F30940-end

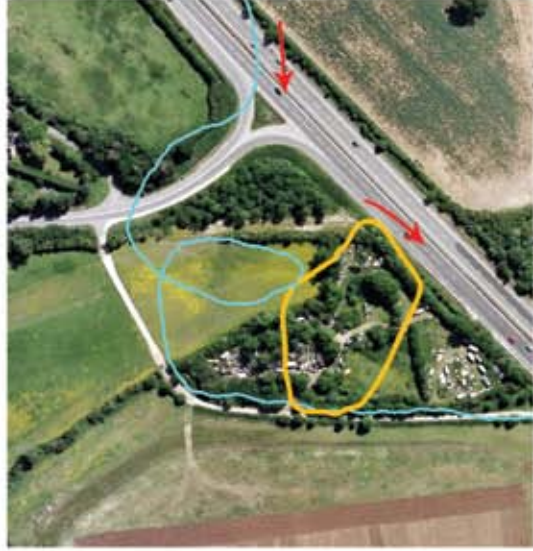


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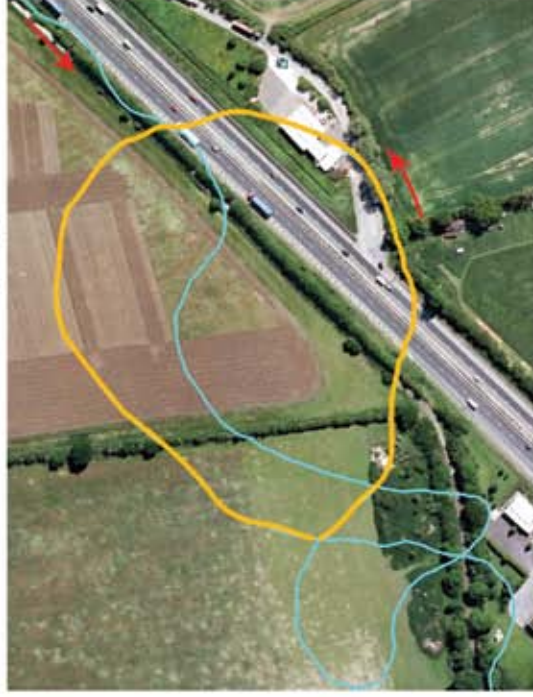
0



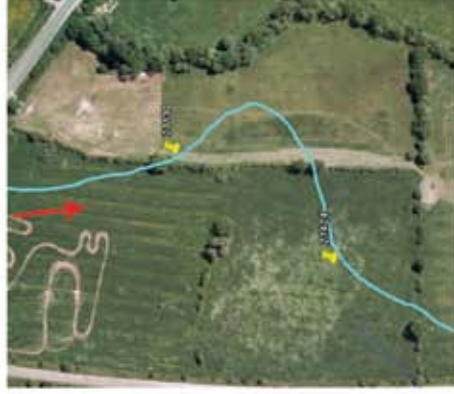
F3689-4024 (loop)



F5487-6243 (loop)



F21134-21424



F24529-end

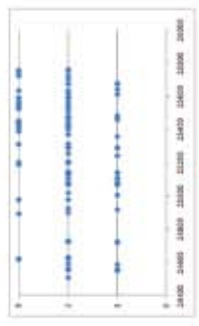
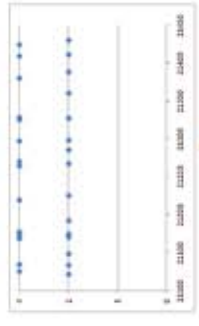
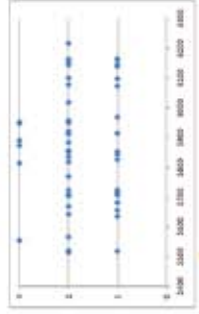
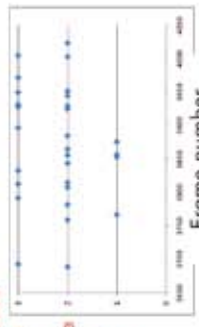


Head movements

Right

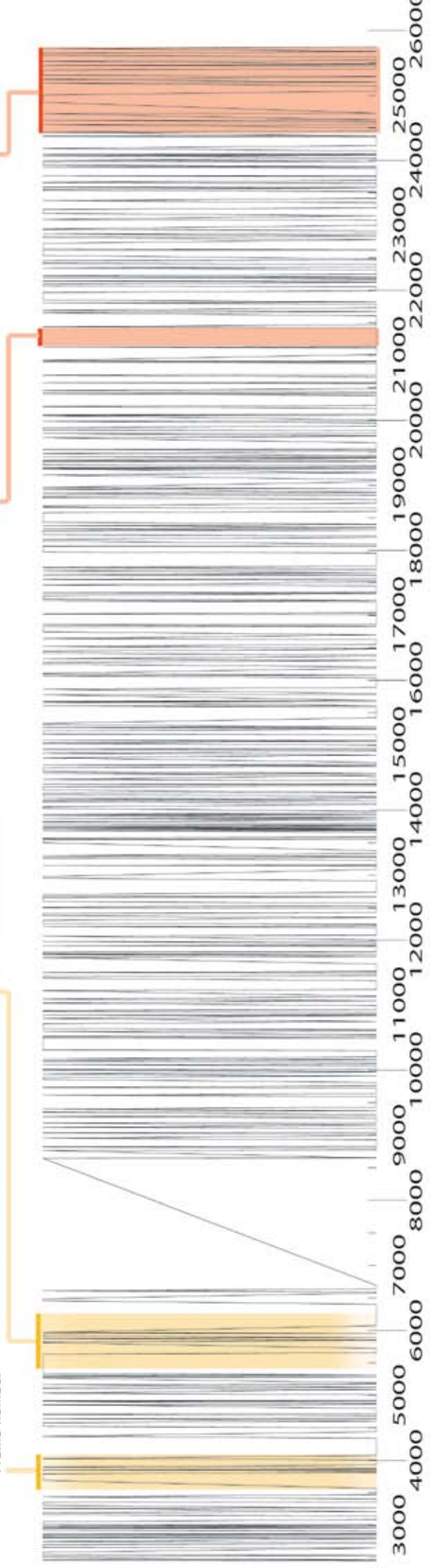
Centre

Left

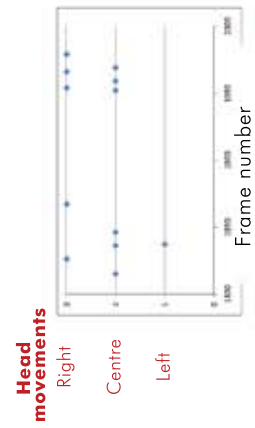


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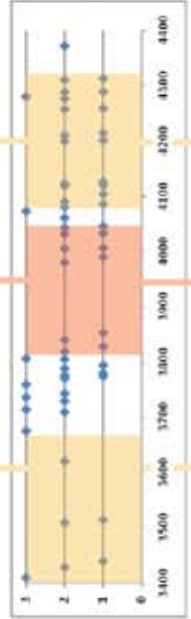
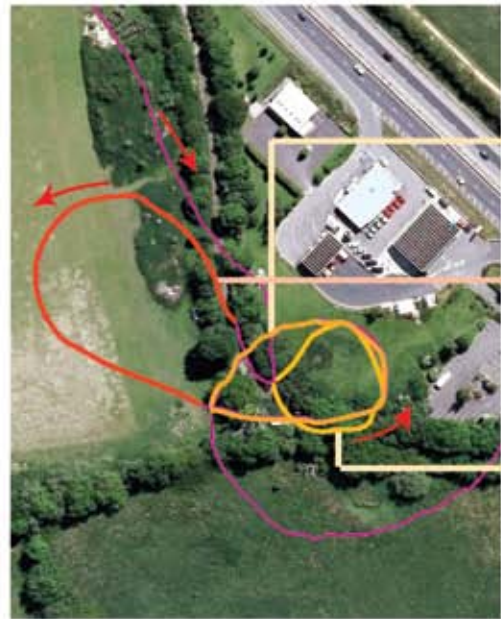
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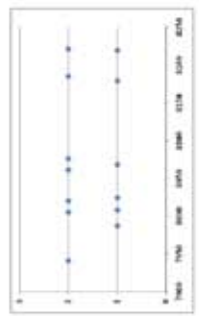
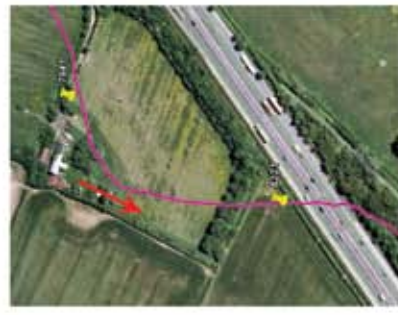
F 1803-2040



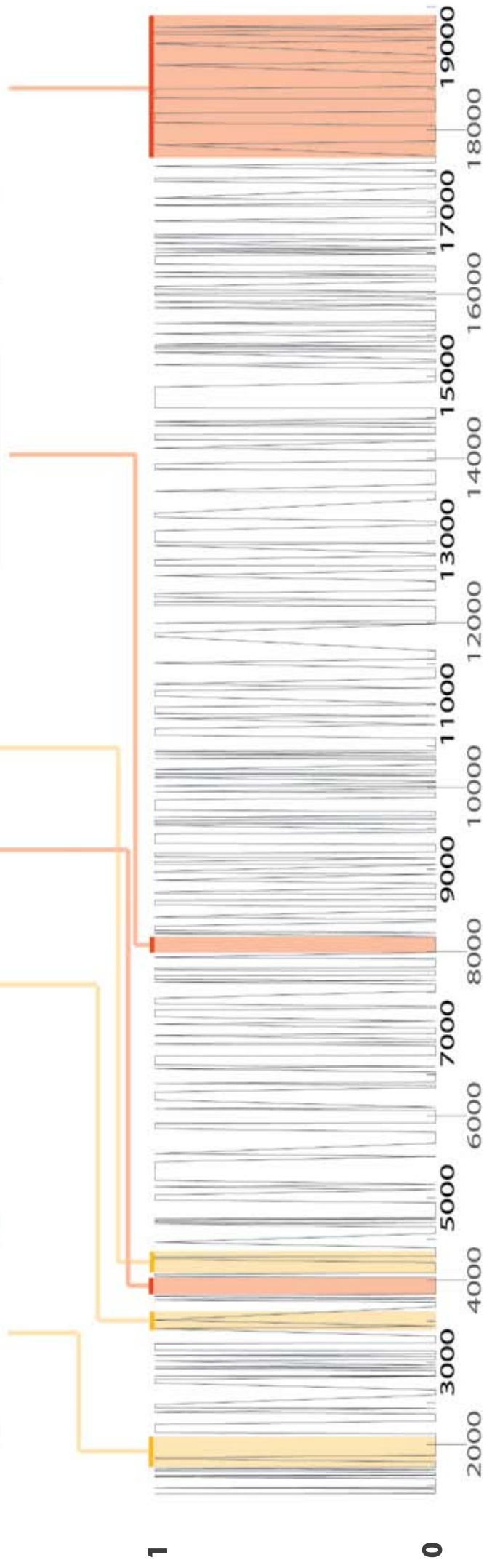
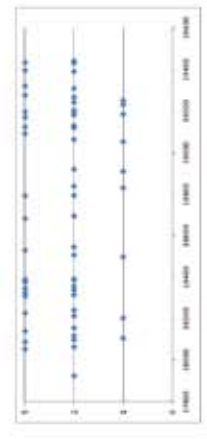
F 3440-3671 F 3828-4033 F 4085-4328



F 7941-8221



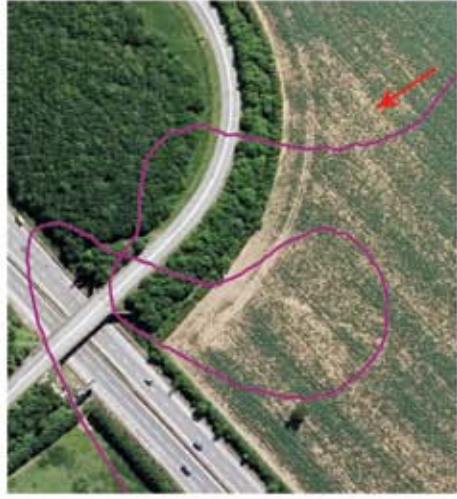
F 17887-end



1

0

F 2289-2750



F 3080-3445



F 6000-6750



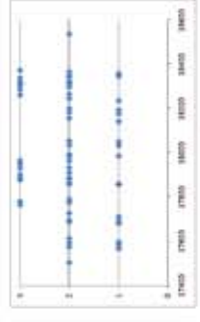
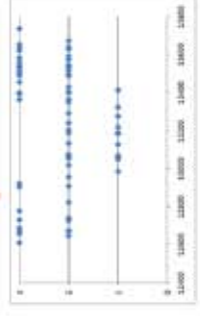
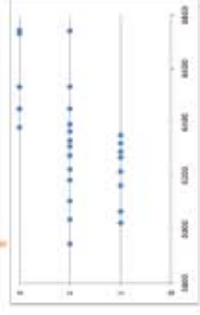
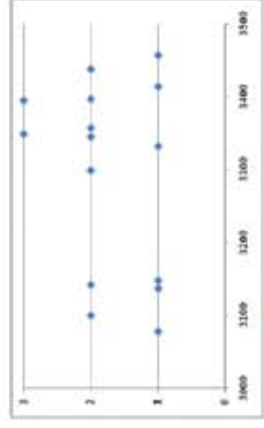
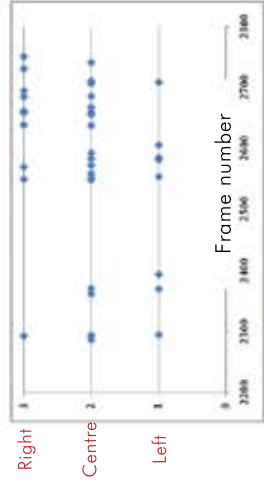
F 17500-end



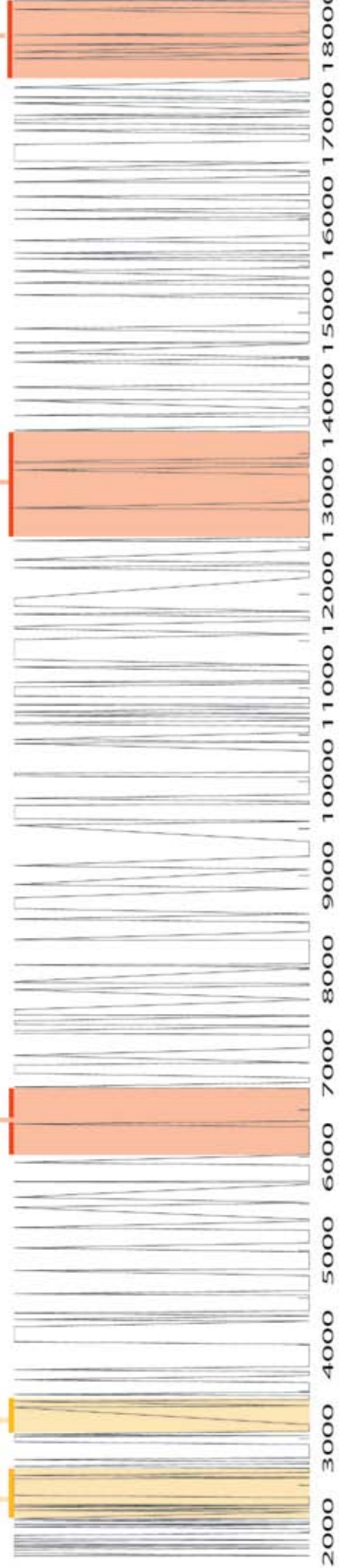
F 12608-13737



Head movements



1
0



H446 - 4.04.09 - Video contains no loops. The two longest runs of consecutive 0s are shown in the first image. The second image shows the final period of flight

loops

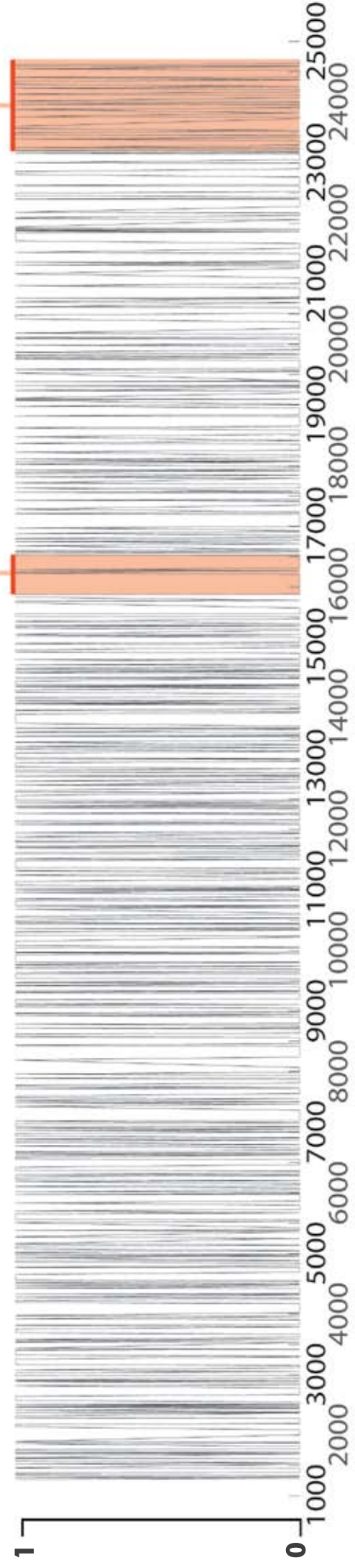
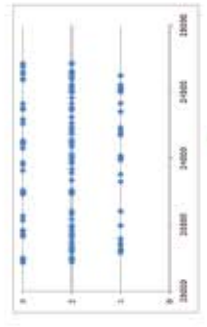
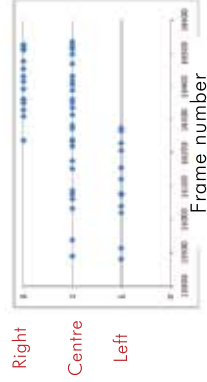
Extended runs of 0s/end

F 15849-16523

F 23206-end



Head movements

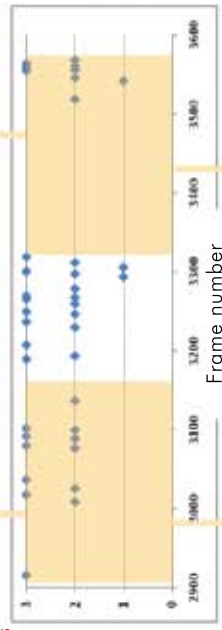


loops Extended runs of 0s / end

F 2920-3155

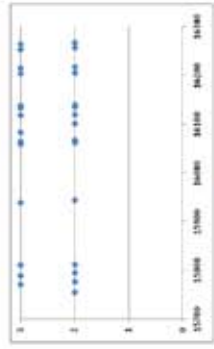


F 3313-3565

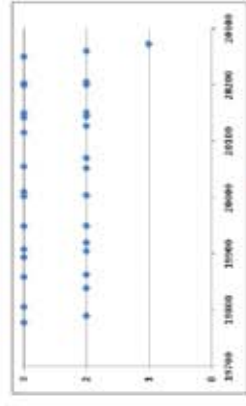


Head movements
Right
Centre
Left

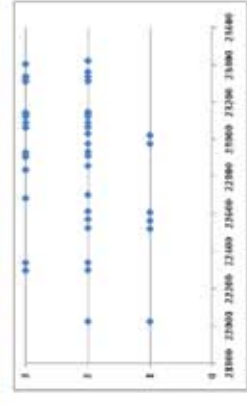
F 15789-16263



F 19806-20272



F 22000-end

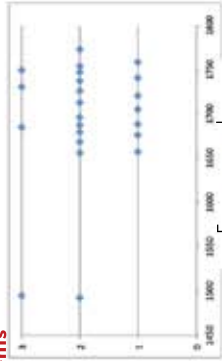


1
0

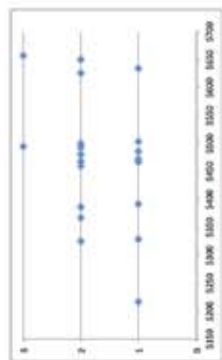


2000 3000 4000 5000 6000 7000 8000 9000 10000 11000 12000 13000 14000 15000 16000 17000 18000 19000 20000 21000 22000 23000 24000

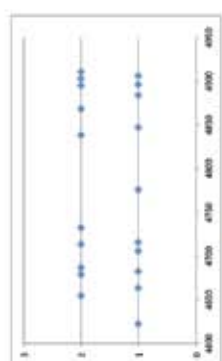
F 1416-1771 - loop



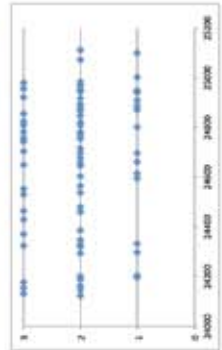
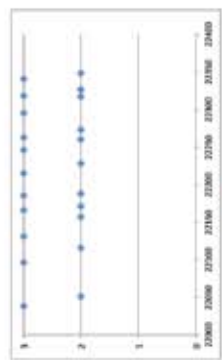
F 5217-5713 - loop



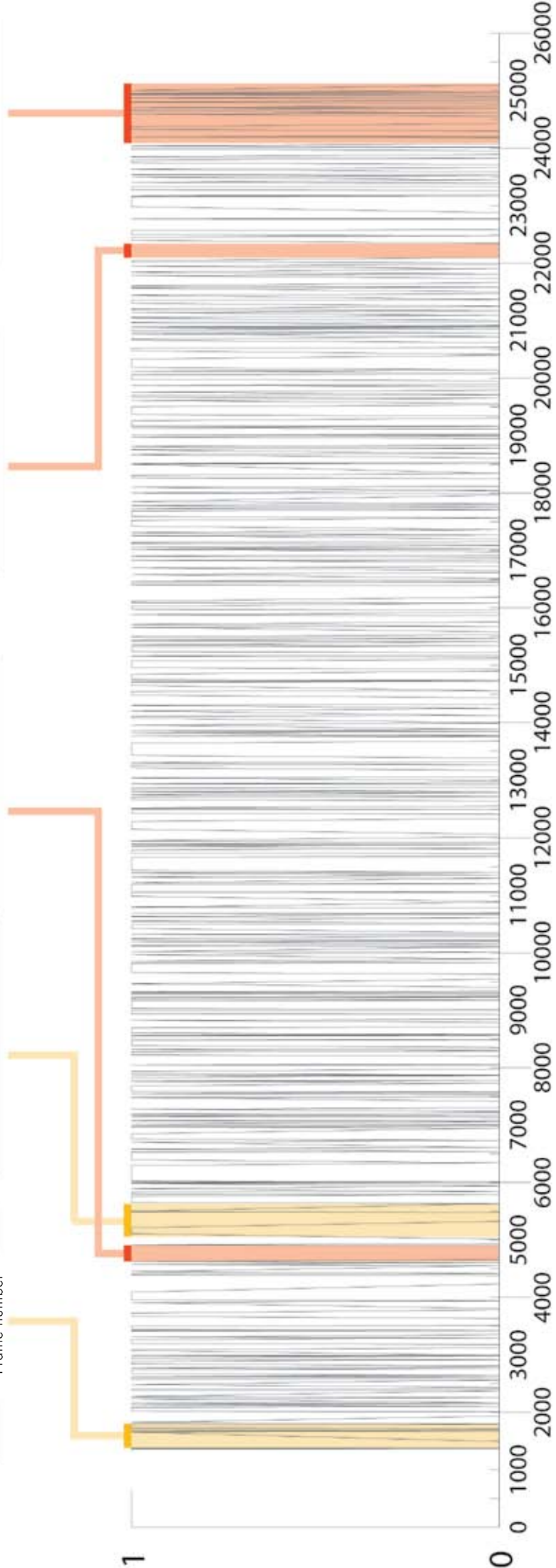
F 4664-4906



F 22097-22341



Frame number



F 1796-2332



F 5014-5206



F 8569-9512



F 21825-end



Head
movements
Right
Centre
Left

