INVESTIGATIONS INTO THE BIOMECHANICS OF HEAD-BOBBING PIGEONS

by

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Abstract

Walking pigeons display a characteristic behaviour: head-bobbing. Head-bobbing consists of two phases, the hold phase during which the head is kept stable in space, and the thrust phase during which the head is quickly moved forward. But why do pigeons and so many other birds head-bob? Two theories have been developed to answer this question. First, head-bobbing may have a visual function, namely object detection during the hold phase and depth perception during the thrust phase. Second, head-bobbing may have the biomechanical function of increasing the stability.

The present study aimed to gain further insight into why pigeons head-bob. A gait cycle analysis of walking pigeons revealed that the hold phase starts at a specific point in the gait cycle and is not dependent on the walking speed. The point in the gait cycle at which the hold phase starts indicates a potential increase in stability during the single stance phase, as it leads to a longer period of time during which the center of mass is above the base of support. The end of the hold phase, however, is dependent on the walking speed, specifically the step length for a given walking speed. I found that the thrust phase duration is constant for all walking speeds and the distance the head travels during that time is equal to the step length. With increasing walking speed the head moves faster during the thrust phase and the hold phase duration is decreased leading to a higher head-bobbing frequency. With fast enough walking speed the hold phase is eventually eliminated, marking the transition point from walking with head-bobbing to fast walking without head-bobbing. The exact velocity of this transition point was predicted for each individual and was dependent on the maximal step length of each pigeon. All head-bobbing parameters could be described with the step-frequency, the thrust phase duration, and the maximal step length, indicating that head-bobbing behavior is individual for every pigeon and depends on its body size.
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List of Abbreviations

AOS – Accessory Optic System
BoS – Base of Support
CoG – Center of Gravity
CoM – Center of Mass
CoP – Center of Pressure
DAQ – Data Acquisition Device
DTN – Dorsal Terminal Nucleus
EMD – Elementary Motion Detector
Fx – Horizontal Shear Force in Walking Direction
Fy – Horizontal Shear Force perpendicular to Walking Direction
Fz – Vertical Force
GRF – Ground Reaction Force
HS – Heel Strike
LTN – Lateral Terminal Nucleus
MTN – Medial Terminal Nucleus
nBOR – Nucleus of the Basal Optic Root
PCA – Principal Component Analysis
QTM – Qualisys Track Manager
TO – Toe-Off
UACC – Queen’s University Animal Care Committee

For a list of notations used in formulae see Table 3.1.
Chapter 1

Introduction

1.1 Terrestrial Locomotion in Pigeons

Walking pigeons display a distinct behaviour: head-bobbing, whereby the pigeon’s head seems to move back and forth very quickly compared to the body. With respect to the surrounding environment, however, the head is either quickly moved forward or held stable in space. Therefore, the head movement is divided into two distinct and alternating phases, the thrust and the hold phase (Dagg, 1977; Davies and Green, 1988; Dunlap and Mowrer, 1930; Friedman, 1975; Frost, 1978; Troje and Frost, 2000). The head is kept at one point in space during the hold phase and then quickly accelerated and moves forward during the thrust phase (Figure 1.1). The body maintains an almost constant forward velocity. Figure 1.2 shows a series of photographs demonstrating the same effect as shown on the kinematic data plot in Figure 1.1.

The head-bobbing movement and the stepping motion are synchronized (Dagg, 1977; Frost, 1978; Troje and Frost, 2000; Fujita, 2002; Fujita, 2003), with one hold and one thrust phase taking place per step (Fujita 2002, own observations). During one part of the step both feet touch the ground, called the double support or double stance phase and during the remainder of the step only one foot has contact with the ground, denoted as the single support or single stance phase. The hold phase starts shortly after the transition from double to single stance and lasts until some point during the second half of the single stance phase (Fujita, 2002). The following thrust phase is present during the remaining single stance and through the entire double stance phase (Fujita,
As the hold and thrust phase seem to be gait cycle dependent, the different parameters describing head-bobbing behaviour (frequency, hold phase duration, thrust phase duration etc.) are expected to be dependent on walking speed as well. And indeed, the duration of the hold phase with respect to the duration of the step cycle decreases linearly with increasing walking speed (Davies and Green, 1988). The hold phase proportion can be used to classify walking speeds. Natural walking speed of pigeons has been shown to range from 150 mm/s to 750 mm/s, with 750 mm/s defining the transition from walking to running (Davies and Green, 1988). At this point, the hold phase proportion is expected to reduce to 0% of the step cycle which leads to a continuously positive head velocity as no hold phase is present anymore (Davies and Green, 1988). Further evidence for the synchronization of feet and head is an increase in the frequency from 3-8 Hz of both head-bobbing and stepping with increasing walking speed (Fujita, 2004; Troje and Frost, 2000), indicting a constant synchronization over all walking speeds. At speeds faster than 750 mm/s a bobbing motion can still occur, but in the absence of the hold phase. Instead of being stabilized in space the head moves with a smaller but positive speed than during the thrust phase (Frost, 1978; Davies and Green, 1988). As a result, this phase is no longer called ‘hold phase’ but rather flexion phase. The flexion phase occurs during landing flights and during terrestrial locomotion with velocities above the running speed threshold (Frost, 1978; Davies and Green, 1988; Green et al. 1994).

1.2 Function of Head-bobbing

The function of head-bobbing has been an enduring question. Head-bobbing is ubiquitous among bird species, although not universal (Dunlap and Mowrer, 1930; Dagg, 1977; Frost, 1978; Fujita, 2006). One particularly comprehensive study by Jiménez Ortega (2005) found that
approximately 50% of the 322 analyzed species either exhibited constant head-bobbing or head-bobbed in certain situations. There appears to be a phylogenetic basis for head-bobbing. Often all members of a family or order show the same type of locomotion, either head-bobbing or not (Dagg, 1977; Jiménez Ortega, 2005; Necker, 2007). It has been hypothesized that body size and diet can determine whether or not a species head-bobs (Abourachid, 2001; Fujita, 2006; Dagg, 1977). Tall birds tend to head-bob, while small birds do not, and birds that consume seeds and fruit tend to head-bob, while insectivorous species do not. There are two major theories for the function of head-bobbing: the potential visual function of head-bobbing and the potential biomechanical function of head-bobbing. Such theories are not mutually exclusive and together attempt to explain the proposed function of head-bobbing.

1.2.1 Theory I: The Optokinetic Theory of Head-bobbing

The optokinetic theory of head-bobbing is based on the visual function of head-bobbing and is rooted in behavioural observations. Dunlap and Mowrer (1930) described that a hand-held chicken started to head-bob when moved by the experimenter and the same phenomenon has been shown in pigeons (Frost, 1978; personal observations). Such observations were the first evidence of the importance of the visual system on head-bobbing. Friedman (1975) substantially strengthened this theory by demonstrating the effect of visual motion on head-bobbing. Doves (Streptopelia risoria) exhibited head bobbing when exposed to visual motion, but walked without head-bobbing when deprived of visual motion. Doves walked on one spot on a moving ground with the visual surroundings either attached to the moving ground, generating the naturally expected visual motion, or independent of the ground, eliminating the visual motion. In a second study, doves that were passively moved displayed head-bobbing when visual motion occurred,
but suppressed head-bobbing when the visual motion was eliminated by moving the visual environment with the same speed as the dove. The results demonstrate that the effect of the visual motion is independent of the walking motion itself. Therefore, even though head-bobbing generally occurs in synchronization with the feet, it is independent of the foot motion, as head-bobbing and foot movements can occur independently from each other. Furthermore, these results indicate that head-bobbing is not merely an anatomical or mechanical consequence of walking, as the behavioural response to visual motion can abolish head-bobbing but still allow walking.

The influence of visual motion on head-bobbing was demonstrated in a second study conducted by Frost (1978) requiring pigeons (Columbia livia) to walk on a treadmill. It was noted that when the treadmill speed matched the pigeon’s walking speed the pigeon did not display head-bobbing. In this situation the pigeon remained stationary while walking which eliminated the visual motion.

These two studies demonstrated the importance of the visual system on head-bobbing and led to the following visual functions being proposed for each head-bobbing phase.

1.2.1.1 Visual Function: Hold Phase

During the hold phase the visual motion of the environment is minimized, as the pigeons head is stabilized with respect to the environment. This allows an easier detection of moving objects, which generate visual motion themselves (Pratt, 1981; Davies and Green, 1988). In most animals visual stabilization is accomplished by eye movements rather than head-movements, like the eye saccades in humans. Eye movements only stabilize the image in a small fovea, though, and the effect of visual motion in the peripheral regions of the visual field increases the closer the objects
are to the observer. When stabilizing the head to the environment, however, the entire visual field is affected by the reduced visual motion.

Frost (1978) described a small head velocity of approximately 2.5 – 3.6 mm/s during the hold phase, which he defined as slippage, which was confirmed by Troje and Frost (2000). No biological system is perfect, so even if pigeons try to perfectly stabilize the head in space during the hold phase, small errors can be expected (Dunlap and Mowrer, 1930; Frost, 1978; Troje and Frost, 2000).

1.2.1.2 Visual Function: Thrust Phase

During the thrust phase the visual motion is much faster than during the hold phase, due to the greater head velocity. Like most birds, pigeons have eyes placed laterally on the head with a small overlapping visual field and therefore poor stereoscopic vision and stereoscopic depth perception (Wallmann and Leterier, 1993; Marting and Katzir, 1999; Grundlach et al. 1945; Catania, 1964). The thrust phase could be used to derive monocular depth cues from the environment, via motion parallax. Motion parallax uses the differences in the relative velocity between objects in the observer’s retinal image to determine relative depth perception of stationary objects (see Figure 1.3) (Dagg, 1977; Pratt, 1981; Davies and Green, 1988; Rogers and Graham, 1979). The faster a stationary object moves over the retina when the observer displaces the visual organ the closer is the object to the observer. Moving objects induce visual motion themselves and can alter the depth cues gained with motion parallax. If the object moves in the same direction as the observer the object appears further away than it truly is, if the objects moves in the opposite direction of the observer it appears to be closer.
The flexion phase during landing flights and high running speeds supports the function of depth perception during the thrust phase. Even though the hold phase function cannot be accomplished anymore the flexion phase leads to a thrust phase with increased head velocity and therefore increased motion parallax effect (Davies and Green, 1988; Green et al. 1994; Necker, 2007).

1.2.2 Theory II: The Biomechanical Theory of Head-bobbing

The biomechanical theory of head-bobbing began with the observation that birds with more erected walking posture tend not to head-bob (Dagg, 1977). Additional evidence for a biomechanical function of head-bobbing is the dependence between the stride length and head-bobbing (Daanja, 1951). Head-bobbing birds have a reduced step frequency and an increased step length for a given walking speed, than when walking without head-bobbing. This dependency between stride length and head-bobbing was experimentally verified by Fujita (2004, 2006), who observed that naturally behaving grey herons (Ardea cinerea) and black-headed gulls (Larus ridibundus) did not head-bob when taking small steps but did head-bob when walking with larger stride length. Additionally, Fujita (2004) described an increase in stride length in conjunction with a decreased step frequency when birds switched from non-head-bobbing to head-bobbing while maintaining the same walking speed, indicating that the biomechanical effects of head-bobbing change walking behaviour. Fujita (2004) found a non-linear relationship between step length and walking speed in six head-bobbing species, including the pigeon, and a linear relationship between step frequency and walking speed. In a study of the black-headed gull Fujita (2006) verified these results and additionally revealed an increased upright body posture when the
birds switched from head-bobbing to not head-bobbing, supporting previous hypotheses (Dagg, 1977).

This relationship between head movements and step length and frequency suggests a biomechanical function of head-bobbing. Although head-bobbing seems to have a visual function it does not explain why the head movements occur in synchronization with the stepping motion. The visual function could be accomplished during any part of the gait cycle, yet the head and legs are synchronized and there is a measurable effect of head-bobbing on the gait parameters (Fujita, 2004). The biomechanical function of head-bobbing is a shift in the center of mass (CoM) due to both body posture and head-movements, influencing the biomechanics during walking (Dagg, 1977; Fujita, 2002). Indeed, the head-movements have a significant effect on the position of the CoM in the pigeon’s body (Fujita, 2002). During the thrust phase the head and neck, which were estimated to constitute 7.71% of the body weight, shift the CoM forward (Fujita, 2002). During the hold phase the CoM is shifted backwards in conjunction with the decreasing head-body distance. A shift of the CoM by positioning the head has been described in flying birds, which moves the CoM between the wings by the stretching out the neck, lending support to this theory (Burtt et al. 1988; Necker, 2007).

The synchronization of head-bobbing phases and the stepping motion lead to a synchronization between the CoM position and the stepping motion as well, as the CoM is influenced by the head-movements (Fujita, 2002, 2003). Two key events in the gait of pigeons have been described by Fujita (2002). First, the hold phase starts shortly after the transition from single to double stance (toe-off, TO), and the exact point of initiation is when the CoM enters the area above the supporting foot (see Figure 1.4). This area is called the base of support (BoS), meaning that it is above the area of the ground between all contact points of the body on the
ground. The second event is the termination of the hold phase, which occurs when the CoM leaves the BoS. This means, that the hold phase is maintained for the entire duration of the CoM being above the BoS (Fujita, 2002). This finding is a strong indication that head-bobbing may increase stability during the single stance phase in walking pigeons. During the hold phase the CoM is believed to be above the BoS. Standing humans maintain stability by placing the CoM above the BoS (reviewed in Winter, 1995). Due to the hold phase the CoM velocity is reduced in head-bobbing pigeons compared to the body velocity. Therefore, the CoM is longer above the BoS than in non-head-bobbing pigeons, increasing stability during the single stance phase (Fujita, 2002). Once the CoM leaves the BoS and moves ahead of it the thrust phase is initiated and is maintained until the CoM enters the BoS again. A later study on little egrets (Egretta garzetta) described the same CoM cycle indicating a consistent biomechanical effect of head-bobbing on the position of the CoM within the body (Fujita, 2003).

Nevertheless, pigeons presented with no visual motion are able to walk without head-bobbing and therefore without the effect of head-bobbing on the CoM position (Friedman, 1975; Frost, 1978).

Even though pigeons can walk without head-bobbing, in natural conditions it is always present. The CoM alteration induced by the head movements during head-bobbing may be advantageous. However, intuitively accelerating and decelerating the head would be an additional energetic expense of walking. Yet, head-bobbing persists in many bird species and therefore head-bobbing may not only influence the CoM but also be more energy efficient assuming it behaves like a spring mass system (Troje et al. 2012). A spring mass system would have the ability to store and transfer energy leading to a reduced energetic cost. To verify this hypothesis the ground reaction forces (explained and further elaborated in 1.4) as well as the metabolic rate of pigeons walking with and without head-bobbing would have to be analyzed.
1.3 Gaze Stabilization and Movement Detection

As previously described the visual function of the head-bobbing phases are based on visual motion. The visual stabilization and moving object recognition during the hold phase requires two separate neuronal motion detection systems: one detector for self-induced visual motion and one detector for visual motion induced by moving objects. These two cases of visual motion can be differentiated based on how they affect the visual field. Self-induced motion almost always affects the entire visual field, as the eyes are moving themselves, while object-induced motion is normally restricted to a small area of the visual field (Gibson, 1950, 1979). Despite the different visual motion patterns, both types of visual motion require a fundamental neuronal system capable of detecting motion in the visual field.

1.3.1 Motion Detection.

Motion detection is assumed to be a low level process, as even small movements of stimuli with less amplitude than the distance between two photoreceptors can lead to behavioural (e.g. Hirsh, 1977; Horridge, 1966) and to electrophysiological responses (e.g. Zaagman et al. 1977). With as little as two visually stimulated retinal input channels motion specific optomotor responses in dipterans can be observed (reviewed in Kirschfeld, 1972).

A famous model of visual motion detection was the Reichardt model, which modeled the smallest possible motion detector, the elementary motion detector (EMD). An EMD is a system of two retinal receptive fields, where each can consist of as little as one photoreceptor and connecting ganglion cells between receptive fields, enabling motion detection in a small part of
the visual field. An extended model of the Reichardt model for EMD based motion detection is the energy model introduced by Adelson and Bergen (1985).

To detect motion over wide ranges of the visual field, the information of many EMDs can be compared and processed together. There is evidence that this is the case, as Franceschini et al. (1989) found wide field neurons in flies that integrate the signals of many EMDs distributed over the visual field. In birds there are two different locations of directional motion specific wide field neurons in different streams of the visual pathway, each with slightly different response patterns. The first population of directional motion responding cells in pigeons is located in the optic tectum. These cells respond to visual motion in a relatively small receptive field, but the response is strongly mediated by motion in the broader surrounding of the receptive field. The influencing background field could be as much as 40° of the visual field, with the receptive field only comprising 1° of the visual field (Frost and DiFranco, 1976). Each cell has a direction specific response for the small motion stimulus, but the response can be cancelled-out if the surrounding background is moving in the same direction as the stimulus. A response is maintained if the background moves in a different direction (Frost and DiFranco, 1976; Frost and Nakayama, 1983; Frost et al. 1990; Frost et al. 1988). Therefore, these cells are able detect visual motion of a restricted part of the visual field while filtering out self-induced motion. In other words, these cell populations might be involved in object-induced motion detection. Furthermore, Frost and DiFranco (1976) found cells in the pigeon’s optic tectum that would even reduce their response for stimuli that moved anterior to posterior (i.e. self-induced motion), if the stimulus would be continuous over time. These so called ‘backwards-notch-units’ may be capable of cancelling out the effect of self-induced motion in flight, where self-induced flow is constant and high, and at the same time detect object induced motion while walking (Frost and DiFranco, 1976).
The second population of directional motion specific cells is found in the accessory optic system (AOS) of vertebrates. In birds, the AOS consists of several subcortical structures that are referred to as the nucleus of the basal optic root (nBOR). In mammals the AOS consists of the dorsal terminal nucleus (DTN), the medial terminal nucleus (MTN) and the lateral terminal nucleus (LTN). First evidence of directional motion responsive cells in the AOS, was found in rabbits. Walley (1967) found cells in the rabbit MTN that had receptive fields of 90° visual angle, and later the response of these to direction specific motion of large texture patterns was observed (Simpson et al., 1979; Soodak and Simpson, 1988). Furthermore, Wylie (1988) demonstrated that the corresponding cells in the pigeon nBOR are not affected by the surrounding background. These cells are responsive to slow-moving stimuli over a large area of the visual field, and are therefore ideal to detect self-induced visual motion (Wylie and Frost, 1990a).

To summarize, there is neuronal evidence that pigeons have separate pathways for identifying either self-induced visual motion or object-induced visual motion. Therefore, visual stabilization and moving object recognition during the hold phase could be accomplished by the visual system. It is important to note that the nBOR cells respond to relatively slow stimuli as compared to the cells in the optic tectum. This suggests that self-induced motion might be measured using landmarks further away from the pigeons than close objects, as the visual motion is reduced the further the object is away (see motion parallax (Rogers and Graham, 1979)).

1.3.2 Gaze Stabilization

The underlying neuronal networks for motion detection have been described above. But how well can pigeons stabilize their head to a moving stimulus? Every time an organism focuses with its visual system on a feature in the environment it has to stabilize the photoreceptor with
respect to it in order to get a clear image. The measure of how accurately an organism is capable of stabilizing gaze is the ‘gain’, which is a measure of the speed of the organism divided by the speed of the visual environment. A gain of 0 represents no stabilization and a gain of 1 represents perfect stabilization between the visual system and the visual environment. In a groundbreaking study, Heisenberg and Wolf (1984) experimentally determined the gain of Drosophila flies to rotational large field visual motion movements. Drosophila were immobilized except for their wings and legs and attached to a torque-meter. A visual pattern was presented and initially moved. The flies’ turning responses were measured by the torque-meter and then either fed back into the visual pattern generator to alter the speed of the visual pattern (closed loop condition), or the signal was not used to adjust the visual pattern speed (open loop condition). In the closed loop condition, flies were able to stabilize the visual pattern and fluctuated around perfect stabilization with small high frequent oscillations. During the open loop condition, however, flies deviated more from the optimal stabilization and integrated the error signal above the maximal correction response of the fly. This led to after-effects in the form of correction movements in the moving direction of the visual pattern, even though the pattern was not moving in that direction anymore (Heisenberg and Wolf, 1984; Heisenberg and Wolf, 1988; Wolf and Heisenberg, 1990). Heisenberg and Wolf (1984) therefore concluded that the gain is integrated over time and eventually approaches one.

In pigeons the results of previous studies indicate a gain during the hold phase of one (Friedman, 1975; Frost, 1978) or close to one (Frost, 1978; Troje and Frost; 2000). As described in the fly, in the pigeon there may be two different types of control systems involved in stabilizing the hold phase: a feed-back (closed loop) controller and/or a feed-forward (open loop) controller.
1.3.2.1 Control System Model Underlying Hold Phase Stabilization

By definition, a closed loop controller has to be in the controlled system and measures the systems state to calculate the deviation between the desired and the actual state in order to control for the latter. One example for closed loop control is the vestibule-ocular system in mammals, which is important for stabilizing the visual image on the fovea during head movements. The vestibular system provides feedback about the head movement and the eye automatically moves in the opposite direction in order to remain the visual focus on the same position of the visual environment. Therefore, in the vestibule-ocular system the eyes are stabilized by measuring the perturbation on the head itself with the vestibular system. During the hold phase in walking pigeons the head is the system that is stabilized and two sensory systems can then measure if the head is kept stable or not: the visual system via visual motion, and the vestibular system via linear acceleration (the vestibular system, however, has previously been excluded from involvement in the hold phase (Friedman, 1975; Necker et al., 2000)). Every sensory system has inherent delays and therefore measurements are not of the actual state, but of slightly prior states. Such an error in measurement is likely to lead to an oscillation around the desired state, as found in the closed loop condition by Heisenberg and Wolf (1984).

An open loop controller, on the other hand, measures the perturbation from the outside world acting on the system and automatically corrects for it using a learned input-output relation. Therefore, the open-loop system does respond faster than the closed-loop system, but also integrates errors of the correction response as there is no feedback as to whether the control actions are successful or not. If the correction response for a given perturbation is slightly off the
optimal response the error will integrate over time and linearly increase, as found in the open-loop condition by Heisenberg and Wolf (1984).

In the pigeon, the lumbosacral system, which may function like a vestibular system located in the body, could provide the needed measurements. This extra-vestibular system is located in the spine of the pigeon, close to the hip (Necker et al. 2000; Necker, 2001; Necker, 2006). During the hold phase the body is constantly moving, and therefore pushing the head forward, which is why the body movement can be considered a source of perturbation on the head. The lumbosacral system could measure the body perturbation and be part of an open loop controller (Kroker et al. 2012). A combined control loop integrating the beneficial effects of both control systems is represented in Figure 1.5 (Kroker et al. 2012).

The slippage during the hold phase could be a constant error of the open loop system, as it was described as a linear deviation of the optimal hold phase stabilization of 0 mm/s (Frost, 1978; Troje and Frost, 2000).

1.4 Biomechanics of Bipedal Gait

The previous sections of this chapter mainly focused on the head movement and function in walking pigeons. In order to understand the underlying principles of walking pigeons with head-bobbing, the pigeon gait has to be understood as well. Except when flying, pigeons are bipedal organisms, a form of locomotion that comes with certain biomechanical properties. The human bipedal gait is the most studied bipedal gait in animals and therefore the following presented information will be based on studies on human bipedal gait.
1.4.1 Inverted Pendulum Model

In bipeds walking can be modeled as an inverted pendulum. The gait cycle is divided into two sections, the single stance phase during which only one foot has contact to the ground, and the double stance phase during which both feet have ground contact. During the single stance phase the CoM follows an arc trajectory defined by the supporting limb, which, according to this model, behaves as a rigid structure. During the double stance phase the CoM trajectory is redirected to the next arc trajectory of the next stance leg. Donelan et al. (2002a) found that during the redirection of the CoM trajectory the leading leg performs negative work to shift the CoM from one arc trajectory to the next one, while the trailing leg performs positive work to compensate for the energy loss in order to maintain the present CoM velocity (seen in the Fx shear forces of the two legs). Both types of work require muscle work and therefore are metabolically expensive. As there are no muscles connecting the two legs, and muscles essentially are the structures performing the work, no work transfer between the legs in human gait is assumed (Kuo, 2001; Donelan et al. 2002a). Furthermore, Donelan et al. (2002b) demonstrated that the step-to-step transition (the phase of the CoM redirection) is a major component of the metabolic cost of walking in humans. Interestingly though, humans with passively swinging arms reduced the metabolic cost during walking by 12% compared to humans walking without arm swing, indicating a transfer of energy between the legs via the arms (Collins et al. 2009).

In pigeons Troje et al. (2012) proposed that the head movement during head-bobbing and its synchronization with the gait cycle could enable the work transfer between the two legs. Head-bobbing could therefore reduce the energy cost of the step-to-step transition (Troje et al. 2012). This may explain why pigeons invest energy into moving the head, as the metabolically
expensive negative and positive work would be reduced. Additionally, Fujita’s (2004, 2006) observation of the reduced step frequency in head-bobbing birds could indicate a more cost efficient walk, as the step-to-step transition event would not only be more cost efficient but also happen less often.

1.4.2 Ground Reaction Forces of the Human Bipedal Gait

During each step when the foot is in contact with the ground, the foot applies forces onto the surface representing all the forces in the body during that specific time. The exact opposite force is applied by the ground back into the body – the ground reaction force (GRF). The GRF is three-dimensional and can be measured using ground force plates, which essentially are capable of measuring forces in all three dimensions as a function of time. The measured forces are the vertical force perpendicular to the ground (Fz), the horizontal force in walking direction (Fx) and the horizontal force perpendicular to the walking direction Fy. Fz therefore is the vertical force, whereas Fy and Fx are also referred to as the shear forces (Hennig and Lafortune, 1997). The GRF analyzed in the present study are the vertical force and the shear force in walking direction (Fx).

The GRFs have a distinct pattern which is gait cycle dependent (Kirtley, 2006). As shown in Figure 1.6 Fz has a characteristic M-form during the duration of the step cycle, while Fx is S-formed first being negative and then positive (Winter, 1984). The amplitude of the forces are dependent on body weight and body velocity, but the shape of the form is consistent across humans (Henning and Lortune, 1997; Stansfield et al. 2001). To enable comparison between different subjects, the ground forces are often normalized against the body weight and the duration of one step cycle (Winter, 1991).
1.4.2.1 Ground Reaction Forces during the course of one Step in the Human Gait

As already mentioned the vertical force has a characteristic M-shape. Initially, when the foot touches the ground (heel strike event, HS) the vertical force starts to rise and keeps increasing above the resting force, which represents the first peak of the M-shaped curve (see Figure 1.6). Up to the point when the vertical force initially increases above the resting force, the gait cycle is in the double stance phase (loading response). As soon as the force increases above that threshold the single stance phase is initiated. During the course of a step cycle the body keeps moving forward and once the vertical force reached the initial maximum it decreases towards the minimum between the two peaks of the M-shaped curve. As soon as the foot starts to push-off, the vertical force begins to increase again until the maximal push-off force is reached, representing the second maximum (the second M peak). Shortly after this point in the gait cycle the next foot has its initial heel strike event and therefore leads to the double stance phase. During the terminal phase with double stance support the vertical force decreases as the foot reduces the contact area until it eventually falls to zero when the foot lifts off. At this point the next single stance phase starts (Winter, 1991).

The horizontal Fx shear force can be either negative or positive. A negative force indicates breaking leading to a reduced CoM velocity, while a positive force indicates pushing off leading to an increased CoM velocity. The usual pattern of the horizontal Fx shear force is that it reaches a minimum shortly before the first vertical force peak and reaches the maximum shortly after the second horizontal force peak. The temporal zero shear force (intersection with x-axis) is shortly after the vertical force minimum.
1.4.2.2 The Center of Mass Trajectory with Respect to the Base of Support in Human Gait

Fujita (2002) described the dependency of the hold phase on the CoM position in pigeons and when the CoM is above the BoS using estimates, but was not able to measure the actual CoM trajectory. In humans this work has been done and even though foot anatomy and BoS form deviate between the two species, the knowledge of the human BoS will increase the understanding of the biomechanical effects of head-bobbing in walking pigeons, specifically the effect of increased stability.

In humans the CoM has to lie within the BoS in order to have a stable stance (reviewed in Winter, 1995). During walking, the inertia of the upper body mass and the moment in the direction perpendicular to the walking direction would lead to instability if the CoM trajectory entered the BoS (Winter, 1990; Winter 1995). Shiba (1984) showed that the CoM trajectory moves with a sinusoidal trajectory between the two BoS (the two feet) and never enters the BoS but only touches the medial border of each BoS.

Adamczyk and Kuo (2009) showed that the CoM is next to the BoS during the single stance phase based on vertical forces. After the initial peak but before the intermediate minimum, the CoM enters the area next to the BoS and moves ahead of the BoS shortly before the push-off. During the push-off the CoM is ahead of the BoS as the muscles generate energy to move the body above the other leg (Winter, 1991).

1.5 Research Question

Why do pigeons and other birds head-bob? Head-bobbing may have visual and biomechanical advantages, but little work has been done in trying to verify the functions of this behaviour. With this study, we aim to get a better understanding as to why pigeons head-bob. To
do so, the main question was divided into three individual research questions. The first objective of this study is to understand the order of events during head-bobbing. A gait analysis will be conducted to describe the order of events of both head and foot movements during the course of one gait cycle. Gait cycle and head-bobbing behaviour in pigeons has been described previously, with the most accurate studies conducted by Fujita (2002) and Troje and Frost (2000). Both studies used a temporal resolution of 60Hz and a DCR camcorder to acquire the data. Using new motion capture technology, I aim for a temporal resolution 6 times higher and a spatial resolution impossible to reach with the previous technology. The synchronization between head and feet will be determined, and the effect of the CoM on the stability in walking pigeons will be observed. This analysis will use the kinematics of head and body obtained through motion capture technology in combination with ground reaction force data in order to obtain information about the feet’s behaviour.

The results of this analysis will be used as basis to answer the second question: how does walking speed affect the head-bobbing behaviour? The effect of walking speed on both the feet and head movements will be analyzed and a mathematical description for the change of each head-bobbing parameter with walking speed will be developed.

Based on this mathematical description, the third question of this study will be answered: how long can a pigeon maintain head-bobbing with increasing walking speed? Davies and Green (1988) showed that pigeons cannot maintain head-bobbing above a certain walking speed. In this study I will determine for each individual pigeon this point and the key parameters determining the gradual transition from head-bobbing to no head-bobbing will be described.

Another important question with regard to head-bobbing that has previously been answered is: how much energy does head-bobbing require? This question indicates how
important head-bobbing is for pigeons and how much work pigeons have to perform for head-bobbing, or if any additional energy is required compared to walking without head-bobbing. Troje et al. (2012) presented evidence of the effect of head-bobbing on the energy consumption of head-bobbing pigeons, under the assumption that the head behaves like a spring mass system. Their results will be compared to the findings of the previous three questions in order to get a better understanding why pigeons head-bob.

To summarize, the order of events during head-bobbing will be characterized by conducting a gait cycle analysis. The change of the head-bobbing parameters with increasing walking speed will be analyzed. Additionally, the maximal walking speed at which head-bobbing can be maintained will be determined. The results will be discussed with the evidence about energy consumption of head-bobbing presented by Troje et al. (2012).

The gained knowledge will be an asset to future experiments that try to answer why pigeons head-bob. Knowing how to describe and classify head-bobbing, the exact sequence of events during a gait cycle including feet motion, and potential sources and evidences for energy transfer will enable future studies to look at features of head-bobbing that have not yet been described.
Figure 1.1 – Overview of head-bobbing kinematics and highlighted head-bobbing phases.

The head kinematics during the hold phase are in red and in purple during the thrust phase. The back kinematics are represented in green. The single stance phase estimation after Fujita (2002) is represented in grey and the double stance phase is represented in orange.
Figure 1.2 – Picture series of head-bobbing pigeon depicting the thrust and hold phase.

The blues bas is stable in space.

Figure 1.3 – Motion parallax: Objects closer to the observer generate more visual motion on the retina than objects further away.
Figure 1.4 – The position of the center of gravity (CoG) with respect to the BoS and the head-bobbing phases (copied from Fujita, 2002). The BoS is represented by the square drawn over the pigeon. As long as the CoG is outside the BoS the pigeon is in the thrust phase. As soon as the CoG enters the BoS the hold phase is initiated and is maintained for the duration of the CoM being above the BoS.
Figure 1.5 – Control system that may underlie the hold phase control in pigeons (proposed by Kroker et al. 2012). In yellow, open loop controller and in blue, close loop controller.
Figure 1.6 – Ground reaction forces in the human gait. The ground reaction forces are presented as a function of the gait cycle. The top curves represent the horizontal $F_y$ shear forces. The curves in the middle represent the horizontal shear forces in walking direction $F_x$. The bottom curves represent the vertical force. The ground forces of the right foot are plotted as the solid lines whereas the forces induced by the left foot are plotted with the dotted lines.

Abbreviations: IC – Initial Contact, OT – Opposite Toe Off, HR – Heal Rise, OI – Opposite initial Contact, TO – Toe Off, FA – Feet Adjacent, TV – Tibia Vertical. The graph is copied from Whittle (2007), Fig. 2.19, page 81.
Chapter 2

Methods

2.1 Subjects

Six homing pigeons (*Columba livia*) obtained from Limestone City Flyers, an association of racing pigeon breeders around Kingston, Ontario, Canada were used in this study. Three male and three female birds were chosen for the study. The six birds had been maintained in a colony in the Troje Lab aviary at Queen’s University for between 5.5 to 6 years (M = 5.58, SD = 0.38) and were between 6 and 10 years old at the time of the study (M = 6.83, SD = 1.60). The aviary was maintained on a 12 h light-dark cycle with light from 8 am to 8 pm. The humidity was kept around 38% and the room temperature was 21 °C. The experimental birds were food restricted to 90% of their free feeding body weight to motivate behavioural responses for food rewards and were kept in individual metal wire cages in a rack to control food consumption. The birds were weighed once a day around 5 pm and fed afterwards with a limited amount of food specific to each individual bird to maintain body weight. The animal weights ranged between 378 g and 451 g (M = 418.20, SD = 26.98). The pigeons had unlimited access to water. Once a week the animals were released for 20-24 h with no access to food during aviary cleaning. The animal housing as well as all procedures were approved by the Queen’s University Animal Care Committee (UACC) and conducted in compliance with UACC protocol Troje-2011-021-R1-A2.
2.2 Experimental Procedures

Experiments were conducted 5-6 days a week for a period of 5 months. Each bird was tested for 30 minutes per experimental day. Every 4-6 weeks the Velcro systems on the pigeons necessary for the motion capture system were renewed. To attach the passive motion capture markers, Velcro pieces with a radius of around 7 mm were firmly attached to the skin of a pigeon’s head and back with white school glue. The feathers were cut down to a length of approximately 5 mm and the glue was applied and ‘massaged’ onto the skin. One piece of Velcro was attached to the center of the head, while two pieces were attached to the back between the wings with a distance of approximately 35 mm between them. No experiments were conducted during Velcro attachment days to reduce distress.

For the experiment the animals were trained to walk between two feeders with alternating food availability for 3 s. Experiments were conducted from 1pm to 5pm in order to maximize food deprivation before the experiment to at least 20 h. The walking between the two feeders was captured with motion capture technology (2.3.2). The markers were attached immediately before each experiment and removed immediately afterwards (see Figure 2.1). The duration of each bird’s experimental session was between 30 and 35 minutes to ensure the birds were only removed from their cages for a maximum 45 minutes per day.

2.3 Setup

2.3.1 Motion Capture with Ground Reaction Forces Arena

The setup consisted of a 1930 mm by 610 mm aluminum plate, painted in non-reflective black and elevated 800 mm above the ground on a table (see Figure 2.2). The pigeons walked
along the 1930 mm surface of the plate, defined as the walking axis. Embedded into the center of the aluminum plate were two HE6X6 Force Platforms (ATMI) with the orientation of Fz being the vertical ground reaction force, Fx being the horizontal ground reaction force in walking direction, and Fy being the horizontal ground reaction force perpendicular to Fx. The dimensions of each force plate were 152.4 mm by 152.4 mm. Two pneumatic feeders running on 2 bar air pressure were centered on each end of the walking axis. Feeders were located 120 mm from the edge of the aluminum plate and presented food 80 mm above the ground. Two white lights 100 mm to the left and right of the food access were used as visual cues to indicate when the feeder was presenting food. Each feeder was connected to a light barrier positioned 100 mm in-front of the feeder which signaled when the pigeon was in proximity of the feeder. Food was only presented at one feeder at a time and was time limited to 3 s when the animal reached the feeder (see Figure 2.2).

62 mm underneath the aluminum table, two PDG-DWL2500 Ultra Short Throw DLP projectors (Sanyo) were centered on the long side of the aluminum plate. On each long side of the aluminum plate a 2500 mm by 1700 mm projection screen was attached to the ceiling with a distance of 600 mm to the aluminum plate and 220 mm to the projector. On each screen a 2442 mm by 1528 mm image with a resolution of 1280 pixels by 800 pixels was projected with a refresh rate of 120 Hz. The visual pattern presented was a stationary sinusoidal low-contrast bar pattern with a spatial frequency of 10 bars/m.

Both the feeder-light barriers and the visual environment were controlled in Matlab R2007b, version 7.5.0.342 (Mathworks). The feeder-light barrier control was conducted using a USB-1208fs data acquisition device (DAQ) (Measurement Computing).
The motion capture system was mounted 1250 mm above the aluminum plate, with an effective camera lens position at approximately 850 mm above the ground, depending on the camera elevation angle. Further technical details on the motion capture system will be elaborated in Section 2.3.2. Eight motion capture cameras were attached above the aluminum plate and positioned around the aluminum plate edges to capture the entire plate surface.

To prevent birds from flying away, a 1850 mm by 600 mm by 40 mm mist net cage was placed above the aluminum plate and the feeders.

### 2.3.2 Motion Capture system

The motion capture system used was manufactured by Qualisys (Gothenburg, Sweden). The system uses infrared cameras with an infrared LED ring around the lens. When the infrared light is reflected from a surface the reflection is detected by the camera chip. Two cameras filming the same rigid object (and the same reflective markers) will lead to enough information to recalculate the three dimensional structure of the object and its behaviour in space. With as little as three cameras and four markers placed in a structure with no axis of symmetry the system can unambiguously detect rigid structures and track them through space (Ullman, 1979). Seven Oqus300 and one Oqus301 cameras were used to capture the back and head kinematics, and the system ran on the firmware Qualisys Track Manager (QTM) version 2.7 (QTM 2.7 build 783). The capture frequency was set to 360 Hz.

### 2.3.3 Passive Motion Capture Markers

Two marker plates with four individual passive reflective markers each were custom made, one for the head and one for the back. The individual markers were spheres with a
diameter of 6 mm. The head marker plate was based on an isosceles triangle with one side being 30 mm long and the other two sides being 40 mm long. One marker was placed in each corner and one marker was placed between the two corner points on one of the long sides. The body marker plate consisted of two panes aligned in a T-shape, each plane containing 2 markers. The horizontal plane of the T-shape was elevated 37 mm while the vertical plane of the T was elevated 24 mm.

A total of 8 individual markers were used to track the back and the head kinematics. The markers were attached with Velcro to the bird (see Figure 2.1).

2.3.4 Data Acquisition

The force plate data were transmitted from the plates through the 10-pin analog output and was converted into eight BNC analog output channels using a custom made ACS-analog-output-to-8x8BNC converter. The signal was input into the 64 analog channels USB-2533 DAQ by Measurement Computing with specifications for the Qualisys motion capture system. The USB-2533 DAQ was synchronized with the motion capture system and the force plate data were captured with the motion capture frequency specified at 360 Hz. Files were saved in both .qtm and .c3d-format.

2.3.5 High Speed Video Analysis

QTM's high speed video feature was used in conjunction with the Oqus310 to capture high speed videos at a frame rate of 360 Hz. Two Promaster VL-306 LED Studio Lights were used to illuminate the setup with the needed light intensity. The video was saved as an .avi file and was transformed into a .mat file for later analysis in Matlab.
2.4 Data Analysis

The QTM generated files were transformed from .c3d to .mat files and processed in Matlab. A custom made Matlab program pipeline processed the files fully automated. The analog data from the force plates were used to recalculate the three forces, momentums, and the center of pressure (CoP) for each force plate following the AMTI instructions. The force data were low-pass filtered before the analysis using a second order Butterworth low pass filter with a cut-off frequency of 25 Hz. As the data of interest were straight walks, a principal component analysis (PCA) over a time window of 0.55 s was run across the data to determine the start and end points of straight walks. Using PCA it is possible to transform the kinematic data into a coordinate system were the highest variance of the data is on the axis in a new orthogonal axes system, the first principal component. If the pigeons walks straight over the setup almost all of the variance in the kinematic data is in walking direction. When 97.5% of the variance of the data was on the first principal component the data set was defined as a straight walk, with a straight walking being forward locomotion with no change in direction. To determine the variance the eigenvalue of each principal component was determined and divided by the sum of all eigenvalues of all principal components. The smaller the variance of the data in the direction of a principal component, the smaller the eigenvalue. Therefore, straight walking was defined when 97.5% of the sum of the eigenvalues of the principal components was due to the eigenvalue of the first principal component.

The start and end points of the hold and thrust phases were calculated in a three-layered process. First the head and body motion were subtracted to determine primary estimates of hold phase start (maxima) and hold phase end (minima) points. As the two phases are alternating the
hold phase start is the thrust phase end and hold phase end is the thrust phase start (see Figure 2.3). Robust linear fits using a bisquare weighting function with a tuning constant of 4.685 were used to generate the first linear fit for each phase (see Figure 2.4). The intersection points of the phase specific linear fits were used to determine more specific secondary phase index values by calculating the intersection between the angle bisector of the two linear fits and the data (see Figure 2.4). The final index values were calculated by applying a circle around the secondary index values. The radius of the circle was determined to be 27.8 ms for the hold phase start index and 22.2 ms at the thrust phase start index. The intersection between data and circle determined the last index value. All phase dependent as well as gait cycle dependent variables were calculated based on these phase index values.

Walking speeds of all steps were calculated based on the body motion. Unlike the head, the pigeon’s body moves with a constant velocity. Therefore, walking speed was obtained by dividing the body displacement in walking direction by the duration needed to travel the distance. The transition from walking with head-bobbing to walking without head-bobbing (also referred to as the maximal walking speed (Davies and Green, 1988)) was defined as the point at which head-bobbing no longer occurred, as the head velocity during the thrust phase was equal to the body velocity. This was identified by finding the point at which the hold phase did not occur anymore.
Figure 2.1 – Motion capture marker attachment on a pigeon. One set of back markers and one set of head markers is visible with four individual markers on each.
Figure 2.2 – Motion capture setup. The aluminum table is displayed in blue with the embedded ground force plates in black. The feeders are on either side of the experimental arena. The entire arena is captured by eight Qualisys motion capture cameras. On both sides a visual environment can be projected onto a screen by short throw projectors.
Figure 2.3 - Determining the initial head–bobbing phase indices. A: Head kinematics are shown in blue while the linear fit of head-kinematics is shown in green. B: Relative distance of head kinematics and linear fit. Maxima are hold phase starts and minima are thrust phase starts.
Figure 2.4 – Final indices for head-bobbing. The initial index values are used to generate linear fits for each phase (hold and thrust). The intersections of these points are used to calculate further detailed index values. The intersection between the angle bisector of the two linear fits and the data was calculated. For hold phase starts a circle with a radius of 27.8 ms was applied to calculate the final index values. For the thrust phase start starts a circle with a radius of 22.2 ms was applied. The final index values are the intersection of the circle and the data.
Chapter 3

Results

3.1 Gait Cycle Analysis in Walking Pigeons

The 157 gait cycles of six birds were analyzed with the goal of describing the gait cycle of walking pigeons. Assuming symmetry between the legs only one step per gait cycle was analyzed. In order to compare the steps of different birds the data were normalized against the gait cycle duration and are presented in percentages of one gait cycle instead, with the heel strike (HS) defining the start of the gait cycle (0%) and the next HS of the same foot defining the end of the gait cycle (100%). The average gait cycle duration was 519.32 ms (SD = 44.30 ms) with a linear decrease in duration with increased walking speed.

I observed that two thrust and two hold phases occur per gait cycle, starting with a thrust phase. Therefore, one thrust and one hold phase occur per step in the named order (see Figure 3.1). HS was defined as the first positive vertical force after the initial small negative force prior to every step. The toe-off (TO) event was defined as the last positive vertical force before the small negative force after each step. The duration from HS to TO averaged 77.19% of the gait cycle (SD = 4.23%). Between HS and TO two thrust phases and one hold phase occur, though the second thrust phase is part of the second step already as it occurs during the second double stance phase. The first thrust phase starts 3.50% (SD = 2.43%) after initiation of the gait cycle and therefore is during the double stance phase. The first hold phase occurs at 24.57% of the gait cycle (SD = 2.00%) and occurs shortly after the single stance phase is initiated. The second thrust
phase starts at 52.09% of the gait cycle (SD = 2.75%) and therefore occurs at the beginning of the double stance phase. The second hold phase (last phase of the gait cycle) initiates at 73.55% of the gait cycle (SD = 2.69%) and occurs 3.64% after the next single stance phase begins.

Therefore, the hold phase occurs from shortly after the initiation of the single stance phase until shortly after the initiation of the double stance. The thrust phase mainly occurs during the double stance phase.

The first maximum peak of the vertical forces occurs 20.85% into the gait cycle (SD = 2.95%). Therefore, it occurs 6.47% (SD = 2.95%) after the maximum speed of the thrust phase is reached and 4.29% (SD = 2.09%) prior to the first hold phase of the gait cycle. At 35.82% into the gait cycle (SD = 3.78%) the intermediate minimum of the vertical forces occurs. The second maximum peak occurs at 48.91% of the gait cycle (SD = 3.40%). Therefore, on average, the hold phase extends from before the minimum until shortly after the maximum of the vertical forces (16.84% after the minimum, SD = 4.15%). The next step is initiated shortly after the second maximum as the other foot HS event initiates the second double stance phase. Therefore, the second thrust phase is initiated 3.76% into the double stance phase. The second thrust phase is terminated 2.22% after the TO event (SD = 2.36%) and is therefore during the second single stance phase of the gait cycle.

For the horizontal shear forces in walking direction, the initial minimum occurs after 17.2% in the gait cycle (SD = 2.34%). The shear force minimum therefore occurs 2.82% (SD = 1.68%) prior to the initial vertical force maximum and therefore 3.77% after the thrust phase maximum speed is reached (SD = 2.35%). The transition from negative to positive shear forces occurs at 35.13% of the gait cycle (SD = 2.91%). The transition point is shortly after the initiation of the first hold phase which starts 0.55% prior (SD = 2.96%). The maximum shear force is
reached after 54.54% of the gait cycle (SD = 3.51%) and therefore 6.14% (SD = 2.30%) after the second vertical force maxima. The second thrust phase is initiated 2.48% prior to the maximum shear force being reached (SD = 2.77%).

The vertical body displacement exhibited a characteristic movement similar to the arc trajectory of the CoM in the inverted pendulum model. The vertical body movement minimum was reached during the double stance phase at 13.79% after the initiation of the gait cycle (SD = 3.75%). The thrust phase starts 10.81% (SD = 4.05%) prior to the occurrence of the minimum in the vertical body displacement. The first maximum of the arc trajectory is reached after 36.88% (SD = 4.37%) and is 12.45% after the initiation of the hold phase (SD = 3.44%). The second minimum of the gait cycle occurs at 62.40% of the gait cycle (SD = 5.67), therefore lying in the thrust phase in the double stance phase. The second and last vertical body maximum is reached after 84.29% of the gait cycle (SD = 4.56%) and therefore occurs during the hold phase in the single stance phase. The maximal head velocity during the thrust phase is reached 3.80% after the vertical body minimum (SD = 2.39%).

When comparing the gait cycle at different walking speeds it was found that the hold phase is initiated at the same phase of the gait cycle. The thrust phase, however, seems to start earlier within the gait cycle the faster the pigeon walks (see Figure 3.2).

The data presented above indicated dependencies between the step length and step frequency and the walking speed. The analysis was conducted for six pigeons. The presented data in 4.1 indicated that one head-bob occurs per step. Additionally, the head must move an equal distance as the feet per step.
3.2 The Role of Step Length and Step Frequency in Walking Speed

Using the gait cycle relationships described above, the contribution of step length \( l_s \) and step frequency \( f_s \) to walking speed \( v_{ws} \) was analyzed. Walking speed can be described as the fraction of step length and step duration \( d_s \) (equation (1), for notations see Table 3.1). As the inverse of duration is frequency, equation (1) can be rewritten as the product of step length and step frequency (equation (2)).

\[
v_{ws} = \frac{l_s}{d_s} \quad (1)
\]

\[
v_{ws} = l_s \times f_s \quad (2)
\]

Each step contains one thrust and one hold phase (see Section 3.1), which combined represent one head-bob. Therefore, during one step one head-bob occurs and the step frequency can be rewritten as the head-bobbing frequency \( f_{hb} \) (assuming symmetry between the two parameters), which is known from the kinematic data (equation (3)).

\[
v_{ws} = l_s \times f_{hb} \quad (3)
\]

As on average the head has to travel equally far in space per step as the body in order to have the same average speed, the step length can be rewritten as the distance travelled by the head in one thrust \( amp_t \) and one hold phase \( amp_h \) combined (equation (4)).

\[
v_{ws} = (amp_t + amp_h) \times f_{hb} \quad (4)
\]

Shown in Figure 3.3 A is the walking speed dependency of the head-bobbing frequency, which is identical to the step frequency. The data indicate a linear increase of the head-bobbing frequency with increasing walking speed. As shown by the linear fit, which was gained by a robust fit approach, the linear increase in head-bobbing frequency does not start at the origin (walking speed=0 and head-bobbing frequency=0) but rather has an offset value specific for every bird (see Table 3.2, column 2). This would indicate that at zero walking speed (still
standing) the pigeons would still head-bob. The head-bobbing frequency is therefore described as a linear function of the walking speed with a slope $m_f^{hb}$ and a constant additional term $c_f^{hb}$ (see equation (5)).

$$f_{hb} = m_f^{hb} \cdot v_{ws} + c_f^{hb} \quad (5)$$

By definition, the step duration is the inverse of the step frequency and can therefore be described by equation (6) (see Figure 3.3 B).

$$d_s = \frac{1}{m_f^{hb} \cdot v_{ws} + c_f^{hb}} \quad (6)$$

The step length seems to increase non-linearly with increasing walking speed (see Figure 3.3 C). By rearranging equation (3), a non-linear description of the step length is obtained (see equation (7)). As shown in Figure 3.3 C, equation (7) describes the step length increase with walking speed and starts in the origin. Walking speed is the product of step length and step-frequency (equation (2)). Even though at a walking speed of 0 mm/s a head-bobbing frequency would be expected based on equation (5), because the step length starts in the origin, the theoretical walking speed is zero.

$$l_s = \frac{v_{ws}}{m_f^{hb} \cdot v_{ws} + c_f^{hb}} \quad (7)$$

Therefore, walking speed increases are obtained by linearly increasing the step frequency and non-linearly increasing the step length. No data could be collected for walking speeds less than 90 mm/s. The statistical analyses summarized in the Tables 3.4a -3.4c and 3.5a, b indicates that the above mathematical description predict the data significantly for all six birds.
3.3 The Change in Head-Bobbing Behaviour with Different Walking Speeds

In the last section (see Section 3.2) the change of step frequency and step length with walking speed was determined. The change is step length was based on the sum of the hold and thrust phase amplitude. Therefore, either the hold phase or thrust phase amplitude or both are expected to change non-linearly with increasing walking speed. In the following section the changes in head-bobbing behaviour with different walking speeds are described assuming that during each head-bobbing phase the head velocity is constant for the entire phase (the mean head-velocity of either thrust or hold phase for a given walking speed). Head-bobbing, therefore, can be imagined as a staircase-like head movement pattern.

The hold phase amplitude was defined as 0 mm as it could not be measured due to marker attachment problems, but is either 0 mm or close to 0 mm. The thrust phase amplitude is shown in Figure 3.4 A and exhibits a non-linear increase, similar to the step length (Figure 3.3 C). In order to analyze the source of the change in thrust (and hold) phase amplitude with increasing walking speed, the amplitude was broken into the underlying variables.

The amplitude of either of the phases is the distance travelled by the head with a certain speed for the duration of one phase (e.g. thrust phase). Therefore, the phase amplitude can be rewritten as the average head speed during the phase at a given walking speed (thrust phase, \( v_t \); hold phase, \( v_h \)) multiplied by the phase duration (thrust phase, \( d_t \); hold phase, \( d_h \)). The walking speed description of equation (5) can be rewritten as equation (8).

\[
\nu_{ws} = (v_t \cdot d_t + v_h \cdot d_h) \cdot f_{hb}
\]  

During each step one head-bob takes place (see Section 3.1). Therefore, the duration of one step is equal to the duration of the hold phase and the thrust phase combined. The thrust phase duration seems to be constant over different walking speeds (Figure 3.4 B) and is different
for each individual pigeon (Table 3.2). Therefore, the thrust phase duration can be described as the constant offset of the linear fit in Figure 3.4 B (equation (9)).

\[ d_t = m_d^t \cdot v_{ws} + c_d^t \approx c_d^t \]  

(9)

The hold phase duration seems to decrease non-linearly with increasing walking speed (see Figure 3.4 C). The hold duration is the difference of the step duration and the thrust duration (equation (10)) and is obtained by subtracting equation (9) from equation (6). The non-linear model is represented in Figure 3.4 C.

\[ d_h = \frac{1}{m_p^b \cdot v_{ws} + c_p^b} - c_d^t \]  

(10)

So, with increasing walking speed only the hold phase duration is reduced while the thrust phase duration remains the same. This pattern should be visible in the gait cycle analysis conducted in Section 3.1, and indeed, with respect to the gait cycle it was found that the hold phase always starts at the same phase in the gait cycle and is not impacted by the walking speed. The end of the hold phase, however, changes with respect to the gait cycle when walking speed is increased. The faster the pigeon walks, the earlier within the gait cycle the hold phase ends.

Theoretically, the start and end of the hold phase eventually would be at the same phase in the gait cycle, eliminating the hold phase entirely, if the pigeon walks fast enough. This would describe the transition speed from walking with head-bobbing to without head-bobbing and is described in Section 3.4.

The second parameter responsible for the hold and thrust phase amplitude is the head velocity during each phase. The hold phase head velocity is shown in Figure 3.4 D and seems to remain constant over time at 0 mm/s. The hold phase velocity could not be measured unambiguously, though, due to technical difficulties (marker attachment) at walking speeds above 450 mm/s. Therefore, the hold phase velocity defined as 0 mm/s. Therefore, the hold phase
amplitude has to be defined as zero as well. This leads to the new walking speed description shown in equation (11) that is only dependent on the thrust phase data and the head-bobbing frequency.

\[ v_{ws} = amp_t \times f_{hb} = (v_t \times d_t) \times f_{hb} \]  

(11)

The change in thrust phase head velocity can then be described as shown in equation (12) by rearranging equation (11) and the linear description is shown in Figure 3.4 E. The thrust phase amplitude is obtained by multiplying thrust velocity and thrust duration, leading to equation (13).

It can be seen from equations (13) and (7) that the thrust phase amplitude and the step length are identical when the hold phase velocity is zero. The head moves exclusively in the thrust phase during which the head has to move the exact same distance that the body moves during the step. The thrust phase duration is not as long as the duration of a step and therefore the thrust phase velocity must be faster than the body velocity during each step. It is interesting to note that the only parameters needed to describe the thrust phase characteristics are the thrust phase duration and the description of the head-bobbing frequency (equation (12) and (13)).

\[ v_t = \frac{v_{ws}}{c_d(t)(m_f^{hb}v_{ws} + c_f^{hb})} \]  

(12)

\[ amp_t = \frac{v_{ws}}{m_f^{hb}v_{ws} + c_f^{hb}} \]  

(13)

Therefore, with increasing walking speed the hold phase is reduced in duration while the thrust phase remains the same in its duration. This is accomplished by always starting the hold phase at the same point during the gait cycle but ending it earlier the faster the pigeon walks, reducing the hold phase proportion and increasing the thrust phase proportion of each step. Additionally, the head velocity during the thrust phase is increased with increasing walking speed. With the increased head-velocity in addition to the higher proportion of thrust phase during each step the head reaches the same average velocity as the body. The statistical analyses
summarized in the Tables 3.4a -3.4c and 3.5a, b indicates that the mathematical descriptions introduced in the above section predict the data significantly for all six pigeons.

3.4 The Transition from Walking with Head-bobbing to Walking without Head-bobbing in Pigeons

As indicated by the gait cycle data, the hold phase is reduced in duration with increasing walking speed until it eventually is eliminated, abolishing the head-bobbing behaviour (see Section 3.1). At this point the head velocity equals the body velocity at all times. This walking speed was defined by Davies and Green (1988) as the transition from walking to running in pigeons. Davies and Green (1988) used the hold phase proportion of pigeons walking with different walking speeds to calculate the walking speed at which pigeons transition from head-bobbing to no head-bobbing. The hold phase proportion \( p_h \) is the fraction of hold phase duration divided by the duration of one head-bob (hold and thrust phase) and is described by equation (14). The same applies for the thrust phase proportion \( p_t \), leading to equation (15). For both proportions it is important to define that the thrust phase duration can neither be smaller than 0 s nor longer than the duration of one step (equation (16)), as this are the boundaries of head-bobbing.

\[
p_h = 1 - c_d \times (m_f h_b \times v_{ws} + c_f h_b) \tag{14}
\]

\[
p_t = c_d \times (m_f h_b \times v_{ws} + c_f h_b) \tag{15}
\]

\[
0 \leq c_d \leq d_s \tag{16}
\]

Schroedinger’s hold phase proportion is plotted in Figure 3.5. It can be seen that it decreases linearly with increasing walking speed as previously shown by Davies and Green (1988). The change in hold phase duration is only dependent on the thrust phase duration and the
change in head-bobbing frequency with walking speed (equation (14)). As the thrust and hold phase proportion add to one, the thrust phase proportion increases linearly in the same manner that the hold phase proportion decreases and is therefore not plotted in Figure 3.5. The maximal walking speed can be calculated by finding the point when the hold phase proportion is zero, as it was first described by Davies and Green (1988). Using the hold phase proportion equation (14) the maximal walking speed $v_{\text{max}}^{\text{WS}}$ can be calculated by equation (17). The maximal walking speed can be predicted by knowing the thrust phase duration and the change in head-bobbing frequency with walking speed and is different for every bird (see Table 3.2).

$$v_{\text{max}}^{\text{WS}} = \frac{1-c_{d}^{t}+c_{h}^{b}}{m_{f}^{h}+c_{d}^{b}}$$  \hspace{1cm} (17)

The maximal head-bobbing frequency $f_{\text{max}}^{\text{hb}}$ of a pigeon is described by the inverse of the thrust phase duration (equation (18), exchanging the walking speed with the maximal walking speed in equation (5) will result in equation (12)). The maximal head-bobbing frequency averaged 7.64 Hz (SD = 0.95 Hz) and was higher in birds with higher maximal walking speeds.

$$f_{\text{max}}^{\text{hb}} = \frac{1}{c_{d}^{b}}$$  \hspace{1cm} (18)

The maximal step length for each pigeon can be calculated by following equation (19). The maximal thrust phase amplitude is, based on the assumption that the hold phase head velocity is zero, the exact same as the maximal step length. The maximal step length, therefore, is the inverse of the slope of the linear fit of the head-bobbing frequency as it increases with walking speed.

$$\lim_{v_{\text{WS}} \to \infty} (l_{s}) = \lim_{v_{\text{WS}} \to \infty} (\text{amp}_{t}) = \lim_{v_{\text{WS}} \to \infty} \left( \frac{v_{\text{WS}}}{m_{f}^{h}+v_{\text{WS}}+c_{d}^{b}} \right) = \frac{1}{m_{f}^{h}}$$  \hspace{1cm} (19)

The maximal step length is not reached at the transition speed but at higher walking speeds. At the transition speed from head-bobbing to no head-bobbing only 76.18 % of the
maximal step length is reached (SD = 2.53 %). It is important to note that beginning at the transition speed, head-bobbing does not occur anymore, as the hold phase is eliminated when the head velocity during the thrust phase is equal to the body velocity. Therefore, increases in the step length at speeds beyond that transition point are not reflected in the thrust phase amplitude, even though it is described by the same mathematical formulation. There are two reasons for this; first, at walking speed (speeds lower than the transition to running) the thrust phase amplitude is described by the step length rather than the other way around, and second, as no head-bobbing occurs at speeds higher than the transition speed the mathematical descriptions can no longer be applied on the head.

Therefore, the same is true for the head-bobbing and step frequency. Without head-bobbing, no head-bobbing frequency can be defined, but the step frequency can still be measured. It is unknown if in pigeons the step frequency continues to increase linearly or changes its behaviour with respect to the walking speed after the transition speed. But as the pigeon can move faster than the transition speed it can be assumed that both step length and step frequency do increase after this point in some manner. Therefore, only 76.18% of the maximal step length is reached at the transition speed. The statistical analyses summarized in the Tables 3.4a -3.4c indicates that the model predicts the hold phase proportion significantly in all studied individuals.

3.5 Slippage during the Hold Phase

When calculating the walking speed using equation (11) and comparing it against the measured values based on the body position, a small systematic difference (an underestimate in Schroedinger’s case) was found (see Figure 3.6). But where could the systematic error in the calculated walking speed come from?
The walking speed was calculated based on the head movements under the assumption that the head velocity during the hold phase was 0 mm/s. Therefore, under this assumption the entire head movement is covered by the thrust phase, but if the hold phase has a head velocity it contributes to the overall head movement as well. However, the systematic deviation of the calculated walking speed from the measured one indicates that the thrust phase does not describe all head-movements but that the hold phase contributes in a non-random manner to the head movement as well. Two different sources for head movements during the hold phase have previously been described.

Both Friedman (1975) and Frost (1978) described a visual gain \( g_{\text{vis}}^h \) of one during the hold phase. This means that if visual motion is applied to the environment \( (v_e) \), the head of the pigeon will stabilize to the moving environment during the hold phase, effectively moving with the same speed. Additionally, a small slippage during the hold phase (denoted as \( \psi \)) was described by Frost (1978) and Troje and Frost (2000). Therefore, the head velocity during the hold phase can be described by adding the effects of visual gain and slippage together (see equation (20)). No walking speed dependency of the slippage has been described yet, therefore the slippage can either be a constant head velocity independent of the walking speed or a function of the walking speed.

\[
v_h = v_e \cdot g_{\text{vis}}^h + \psi
\]  

(20)

By doing the same mathematical modifications as described above, the new walking speed dependencies for the thrust phase velocity, the hold phase duration, and thrust phase duration can be calculated, incorporating the contribution of the hold phase to the overall head movement (equation (21), (22) and (23), respectively).
\begin{align*}
v_t &= \frac{v_{ws} - (v_e \cdot g_{vs}^h + \psi)}{c_d^t \cdot (m_f^h \cdot v_{ws} + c_f^h)} + (v_e \cdot g_{vs}^h + \psi) = \frac{1}{c_d^t \cdot \left(m_f^h \cdot \frac{c_f^h}{v_{ws}} + c_f^h\right)} - (v_e \cdot g_{vs}^h + \psi) \cdot \left(\frac{1}{c_d^t \cdot (m_f^h \cdot v_{ws} + c_f^h)} - 1\right) \tag{21} \\
amp_h &= (v_e \cdot g_{vs}^h + \psi) \cdot \left(\frac{1}{m_f^h \cdot v_{ws} + c_f^h} - c_d^t\right) \tag{22} \\
amp_t &= \frac{v_{ws} - (v_e \cdot g_{vs}^h + \psi)}{m_f^h \cdot v_{ws} + c_f^h} + (v_e \cdot g_{vs}^h + \psi) \cdot c_d^t \tag{23}
\end{align*}

In this experiment the birds were not exposed to visual flow. Even if the visual gain during the hold phase equals one, no head velocity would be introduced by the visual motion dependent part of the hold phase head velocity (see equation (20)). Therefore, the thrust phase amplitude can be described as in equation (24), with only the slippage contributing to the head movement during the hold phase.

\[ \amp_t = \frac{v_{ws} - \psi}{m_f^b \cdot v_{ws} + c_f^b} + \psi \cdot c_d^t \tag{24} \]

As already described, the walking speed was calculated based on equation (11) and only considered the thrust phase amplitude as described in equation (13) and the head-bobbing frequency. If, however, slippage occurs the measured data of the thrust phase amplitude are effectively described by equation (24) and the resulting walking speed is calculated by a thrust phase amplitude that is not equal to the step length anymore. Therefore, the resulting walking speed is always a little bit different from the walking speed measured based on the body motion.

The deviation between measured walking speed and walking speed predicted by the model can be illustrated by plotting them with relation to the same linear fit (Figure 3.6). Calculating the linear fit of the calculated walking speed data and setting it equal to equation (11)
using equation (24) for the thrust phase amplitude leads to a theoretical slippage described in equation (25). The equation for the slippage can be simplified, as the slope of the calculated walking speed is close to one, leading to a difference of close to zero (first part of numerator in equation (25)). The parameters to describe the slippage for all six birds are shown in Table 3.2. It is important to note that equation (25) for the slippage is only true if the calculated walking speed can be described as a linear fit, non-linear regressions will lead to different descriptions of the slippage.

\[
\psi = \left( v_{ws} \cdot \frac{m_{wa}^{calc} - 1}{m_{wa}^{calc}} + c_{wa}^{calc} \right) \approx \frac{c_{wa}^{calc}}{c_{wa}^{calc} \left( m_{f}^{hb} \cdot v_{ws} + c_{f}^{hb} \right) - 1}
\]

(25)

The slippage prediction cannot be verified until more precise hold phase head velocity data can be obtained. The statistical analyses summarized in the Tables 4.4a - 4.4c indicates that the calculated walking speed based on an hold phase with perfect stabilization is almost identical to the measured walking speed data and is therefore deviating by a small degree from the measured data.

3.6 Intra-species Comparison of Head-bobbing Parameters

The previous data were analyzed on an individual basis for each bird, as the results obtained in the analysis described above are bird-specific. The results of all birds are compared in the following section to gain more knowledge about the origin of the individual differences.

The data are summarized in Table 3.2. The average head-bobbing frequency increase with increasing walking speed was 0.0046 1/mm (SD = 0.00082 1/mm) and the initial head bobbing frequency was determined to be 1.82 Hz (SD = 0.33 Hz). The head-bobbing frequency increased faster with increasing walking speed when the initial head-bobbing frequency (offset of the hold phase) was smaller. The thrust phase duration averaged at 132.8 ms (SD = 18.1 ms). The
higher the initial head-bobbing frequency was, the higher the thrust phase duration was. This in turn means that the hold phase proportion was smaller. The transition speed from walking with head-bobbing to walking without head-bobbing was 1315.3 mm/s (SD = 351.4 mm/s). The higher the maximal step length (inverse of head-bobbing frequency slope) the higher the transition speed. The parameter determining the slippage, the calculated walking speed offset, averaged -1.5569 mm/s (SD = 4.4206 mm/s) and did not seem to be affected by the head-bobbing frequency but rather an individual parameter of each bird.
Figure 3.1 – Gait cycle with kinematical and biomechanical data. In each graph the hold phase start is indicated by the green dotted line, the hold phase end is indicated by the dashed red line, the maximal thrust phase velocity is indicated by the blue line, the HS is indicated by the purple dash-dotted line and the TO is indicated by the black dash-dotted line. The grey areas represent the single stance phase while the yellow areas indicate the double stance. The presented data are from the pigeon Schroedinger. A: head-kinematics. B: horizontal shear forces in walking direction. In purple is data from force plate #1, in black is data from force plate #2. C: vertical ground reaction forces. In purple is data from force plate #1, in black is data from force plate #2. D: vertical body displacement.
Figure 3.2 – Start of hold and thrust phases in the gait cycle over walking speeds. In blue the hold phase start in the gait cycle with respect to the start of the step. The hold phase start does not change with walking speed; $y=0.0029x + 22.8506$, $r^2 = 0.0069$, N=286, p=0.1624. The thrust phase start is earlier during the gait cycle with increasing walking speed; $y=-0.0107x + 7.2564$, $r^2 = 0.0869$, N=290, p<0.0001. The sample size was 292 and data points deviating by 5.000 standard deviations or more were treated as outliers and excluded from the analysis. The presented data are combined from all six pigeons.
Figure 3.3 – Change in step parameters with walking speed. The presented data are from Schroedinger. A: Step frequency (identical with the head-bobbing frequency). In magenta is the robust linear fit of the data (see equation (5)). B: Step duration with the mathematical prediction in green (see equation (6)). C. Step length, with the mathematical prediction in green (see equation (7)).
Figure 3.4 – Change of head-bobbing parameters with walking speed. The presented data are based on the results from the pigeon Schroedinger. A: Thrust phase amplitude, with the mathematical prediction in green (see equation (13)). B: Thrust phase duration with robust linear fit in magenta (see equation (9)). C: Hold phase duration, with the mathematical prediction in green (see equation (10)). D: Hold phase velocity with robust linear fit of first half of the data in magenta. All data points at walking speeds higher than 450 mm/s were considered compromised by the marker attachment and therefore were not used in any analyses. E. Thrust phase velocity, with the mathematical prediction in green (see equation (12)).
Figure 3.5 – Proportion of the hold phase with walking speed. The hold phase proportion over walking speed is plotted in blue, with the mathematical prediction in green (equation (14)). The presented data are from the pigeon Schroedinger.
Figure 3.6 – Walking speed measurement and mathematical prediction comparison. In blue is the walking speed based on the mathematical description of head-bobbing assuming no hold phase velocity (perfect stabilization, thrust amplitude * head-bobbing frequency, see equation (11)). In green is the mathematical description of the walking speed (not using data values but theoretical calculations). This description fits the measured walking speed. The data points underestimate the linear fit of the walking speed. The presented data are based the results of the pigeon Schroedinger.
### Table 3.1 – List of notations used in formulae

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
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<tbody>
<tr>
<td>( c )</td>
<td>Offset of a linear fit</td>
</tr>
<tr>
<td>( m )</td>
<td>Slope of a linear fit</td>
</tr>
<tr>
<td>( \kappa )</td>
<td>Modeled maximal thrust phase speed (maximum capacity)</td>
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<td>( \lambda )</td>
<td>Modeled growth rate of thrust phase speed.</td>
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<table>
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<tr>
<th>Variables</th>
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<td>Velocity</td>
</tr>
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<td>( l )</td>
<td>Length (distance)</td>
</tr>
<tr>
<td>( f )</td>
<td>Frequency</td>
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<tr>
<td>( \text{amp} )</td>
<td>Amplitude of either of the head-bobbing phases (distance of the head traveled)</td>
</tr>
<tr>
<td>( d )</td>
<td>Duration (time)</td>
</tr>
<tr>
<td>( g )</td>
<td>Gain (how precise the response of the animal fit the stimulus)</td>
</tr>
<tr>
<td>( \psi )</td>
<td>Slippage during the hold phase</td>
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<tr>
<td>( p )</td>
<td>Proportion</td>
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<td>Step</td>
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<tr>
<td>( t )</td>
<td>Thrust phase</td>
</tr>
<tr>
<td>( h )</td>
<td>Hold phase</td>
</tr>
<tr>
<td>( \text{vs} )</td>
<td>Visual system</td>
</tr>
<tr>
<td>( \text{hb} )</td>
<td>Head-bob</td>
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<tr>
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<td>Frequency</td>
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<tr>
<td>( d )</td>
<td>Duration (time)</td>
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<tr>
<td>( e )</td>
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<tr>
<td></td>
<td>$m_f^{hb}$ [1/mm]</td>
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<td>------------------</td>
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<td>Schroedinger</td>
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</tr>
<tr>
<td>Heisenberg</td>
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</tr>
<tr>
<td>Franz</td>
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</tr>
<tr>
<td>Maria</td>
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</tr>
<tr>
<td>Ducky</td>
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</tr>
<tr>
<td>Emma</td>
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<tr>
<td><strong>Mean</strong></td>
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<tr>
<td><strong>SD</strong></td>
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</tr>
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</table>

Table 3.2 – Head-bobbing parameters for all six pigeons

hb Head-bob

calc Calculated based on measured data

t Thrust phase

h Hold phase

model Modeled based on measured data

ws Walking speed
Table 3.3 – Physiological parameters of all six pigeons.

<table>
<thead>
<tr>
<th></th>
<th>Body weight [g]</th>
<th>Shoulder width [mm]</th>
<th>Neck length [mm]</th>
<th>Foot length [mm]</th>
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<td>Franz</td>
<td>378</td>
<td>106</td>
<td>62</td>
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<td>Maria</td>
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<td>5.61</td>
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Table 3.4a – Linear regression statistics of the pigeons: Schroedinger and Maria

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<td>inter.</td>
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<td>calc. walking speed</td>
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</tbody>
</table>

The presented statistics were based on 2073 individual gait cycles by Schroedinger and 36 gait cycles by Maria. Data points deviating by 5 standard deviations or more were considered outliers and were excluded. In three occasions (Calc. walking speed, thrust velocity, and thrust amplitude) the data of each gait cycle was not analyzed but rather the mean values of one entire arena crossing was analyzed containing several gait cycles.
Table 3.4b - Linear regression statistics of the pigeons: Heisenberg and Franz

<table>
<thead>
<tr>
<th>Walking speed as a predictor of:</th>
<th>Heisenberg</th>
<th></th>
<th></th>
<th></th>
<th>Franz</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>slope</td>
<td>inter.</td>
<td>r²</td>
<td>N</td>
<td>p</td>
<td>slope</td>
<td>inter.</td>
<td>r²</td>
<td>N</td>
</tr>
<tr>
<td>Hold phase prop.</td>
<td>-0.0005</td>
<td>0.7320</td>
<td>0.680</td>
<td>619</td>
<td>&lt;0.001</td>
<td>-0.001</td>
<td>0.732</td>
<td>0.641</td>
</tr>
<tr>
<td>Hold phase speed</td>
<td>0.003</td>
<td>0.538</td>
<td>0.003</td>
<td>619</td>
<td>0.179</td>
<td>0.013</td>
<td>-4.523</td>
<td>0.019</td>
</tr>
<tr>
<td>Head-bobbing freq.</td>
<td>0.0042</td>
<td>1.9551</td>
<td>0.681</td>
<td>619</td>
<td>&lt;0.001</td>
<td>0.0047</td>
<td>1.8871</td>
<td>0.641</td>
</tr>
<tr>
<td>Thrust duration</td>
<td>&lt;0.0001</td>
<td>0.1267</td>
<td>0.001</td>
<td>619</td>
<td>0.358</td>
<td>&lt;0.0001</td>
<td>0.1191</td>
<td>0.005</td>
</tr>
<tr>
<td>calc. walking speed</td>
<td>1.042</td>
<td>2.581</td>
<td>0.984</td>
<td>183</td>
<td>&lt;0.001</td>
<td>1.043</td>
<td>-1.864</td>
<td>0.973</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Math. description as a predictor of:</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>slope</td>
<td>inter.</td>
<td>r²</td>
<td>N</td>
<td>p</td>
<td>slope</td>
<td>inter.</td>
<td>r²</td>
<td>N</td>
</tr>
<tr>
<td>Thrust velocity</td>
<td>1.077</td>
<td>-72.956</td>
<td>0.876</td>
<td>183</td>
<td>&lt;0.001</td>
<td>0.994</td>
<td>-54.638</td>
<td>0.802</td>
</tr>
<tr>
<td>Hold phase dur.</td>
<td>0.842</td>
<td>0.026</td>
<td>0.768</td>
<td>619</td>
<td>&lt;0.001</td>
<td>0.829</td>
<td>0.022</td>
<td>0.695</td>
</tr>
<tr>
<td>Thrust amplitude</td>
<td>0.984</td>
<td>-4.101</td>
<td>0.898</td>
<td>183</td>
<td>&lt;0.001</td>
<td>1.013</td>
<td>-5.134</td>
<td>0.825</td>
</tr>
<tr>
<td>Step length</td>
<td>1.085</td>
<td>-9.518</td>
<td>0.889</td>
<td>619</td>
<td>&lt;0.001</td>
<td>1.079</td>
<td>-7.945</td>
<td>0.842</td>
</tr>
<tr>
<td>Step duration</td>
<td>0.828</td>
<td>0.024</td>
<td>0.660</td>
<td>619</td>
<td>&lt;0.001</td>
<td>0.802</td>
<td>0.055</td>
<td>0.593</td>
</tr>
<tr>
<td>Hold phase prop.</td>
<td>0.773</td>
<td>0.089</td>
<td>0.680</td>
<td>619</td>
<td>&lt;0.001</td>
<td>0.942</td>
<td>0.016</td>
<td>0.641</td>
</tr>
</tbody>
</table>

The presented statistics were based on 620 individual gait cycles by Heisenberg and 374 gait cycles by Franz. Data points deviating by 5 standard deviations or more were considered outliers and were excluded. In three occasions (Calc. walking speed, thrust velocity, and thrust amplitude) the data of each gait cycle was not analyzed but rather the mean values of one entire arena crossing was analyzed containing several gait cycles.
Table 3.4c – Linear regression statistics of the pigeons: Emma and Ducky

<table>
<thead>
<tr>
<th>Walking speed as a predictor of:</th>
<th>Emma</th>
<th></th>
<th></th>
<th>Ducky</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hold phase prop.</td>
<td>slope</td>
<td>inter.</td>
<td>r²</td>
<td>N</td>
<td>p</td>
<td>slope</td>
</tr>
<tr>
<td>Emma</td>
<td>-0.001</td>
<td>0.777</td>
<td>0.800</td>
<td>156</td>
<td>&lt;0.001</td>
<td>-0.0002</td>
</tr>
<tr>
<td>Ducky</td>
<td>0.014</td>
<td>-0.606</td>
<td>0.050</td>
<td>156</td>
<td>0.005</td>
<td>-0.010</td>
</tr>
<tr>
<td>Hold phase speed</td>
<td>0.0055</td>
<td>1.3694</td>
<td>0.845</td>
<td>156</td>
<td>&lt;0.001</td>
<td>0.0034</td>
</tr>
<tr>
<td>Head-bobbing freq.</td>
<td>&lt;0.0001</td>
<td>0.1470</td>
<td>0.036</td>
<td>156</td>
<td>0.017</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Thrust duration</td>
<td>1.029</td>
<td>9.974</td>
<td>0.995</td>
<td>34</td>
<td>&lt;0.001</td>
<td>0.965</td>
</tr>
<tr>
<td>calc. walking speed</td>
<td>1.133</td>
<td>-13.830</td>
<td>0.868</td>
<td>156</td>
<td>&lt;0.001</td>
<td>1.125</td>
</tr>
<tr>
<td>Math. description as a predictor of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thrust velocity</td>
<td>0.817</td>
<td>0.044</td>
<td>0.853</td>
<td>156</td>
<td>&lt;0.001</td>
<td>1.133</td>
</tr>
<tr>
<td>Hold phase dur.</td>
<td>1.066</td>
<td>-12.840</td>
<td>0.935</td>
<td>34</td>
<td>&lt;0.001</td>
<td>1.125</td>
</tr>
<tr>
<td>Thrust amplitude</td>
<td>1.303</td>
<td>-392.652</td>
<td>0.918</td>
<td>34</td>
<td>&lt;0.001</td>
<td>1.027</td>
</tr>
<tr>
<td>Step length</td>
<td>1.066</td>
<td>-12.840</td>
<td>0.935</td>
<td>34</td>
<td>&lt;0.001</td>
<td>1.125</td>
</tr>
<tr>
<td>Step duration</td>
<td>-0.847</td>
<td>0.047</td>
<td>0.801</td>
<td>156</td>
<td>&lt;0.001</td>
<td>0.619</td>
</tr>
<tr>
<td>Hold phase prop.</td>
<td>0.711</td>
<td>0.021</td>
<td>0.800</td>
<td>156</td>
<td>&lt;0.001</td>
<td>0.932</td>
</tr>
</tbody>
</table>

The presented statistics were based on 157 individual gait cycles by Emma and 466 gait cycles by Ducky. Data points deviating by 5 standard deviations or more were considered outliers and were excluded. In three occasions (Calc. walking speed, thrust velocity, and thrust amplitude) the data of each gait cycle was not analyzed but rather the mean values of one entire arena crossing was analyzed containing several gait cycles.
Table 3.5a – Nonparametric Spearman correlations for: Schroedinger, Maria, and Heisenberg

<table>
<thead>
<tr>
<th>Walking speed as a predictor of:</th>
<th>Schroedinger</th>
<th>Maria</th>
<th>Heisenberg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Step duration</td>
<td>ρ &lt;0.001</td>
<td>2072</td>
<td>ρ &lt;0.001</td>
</tr>
<tr>
<td>Step length</td>
<td>0.924</td>
<td>2073</td>
<td>0.849</td>
</tr>
<tr>
<td>Thrust amplitude</td>
<td>0.927</td>
<td>514</td>
<td>0.915</td>
</tr>
<tr>
<td>Hold phase duration</td>
<td>-0.899</td>
<td>2073</td>
<td>0.884</td>
</tr>
<tr>
<td>Thrust phase velocity</td>
<td>0.914</td>
<td>514</td>
<td>0.976</td>
</tr>
</tbody>
</table>

Table 3.5b – Nonparametric Spearman correlations for: Franz, Emma, and Ducky

<table>
<thead>
<tr>
<th>Walking speed as a predictor of:</th>
<th>Franz</th>
<th>Emma</th>
<th>Ducky</th>
</tr>
</thead>
<tbody>
<tr>
<td>Step duration</td>
<td>ρ &lt;0.001</td>
<td>374</td>
<td>ρ &lt;0.001</td>
</tr>
<tr>
<td>Step length</td>
<td>0.912</td>
<td>374</td>
<td>0.932</td>
</tr>
<tr>
<td>Thrust amplitude</td>
<td>0.922</td>
<td>100</td>
<td>0.927</td>
</tr>
<tr>
<td>Hold phase duration</td>
<td>-0.856</td>
<td>374</td>
<td>-0.924</td>
</tr>
<tr>
<td>Thrust phase velocity</td>
<td>0.871</td>
<td>100</td>
<td>0.901</td>
</tr>
</tbody>
</table>
Chapter 4

Discussion

4.1 Gait Cycle Analysis

The present study examined the sequence of head and feet related events during the gait cycle of walking pigeons displaying head-bobbing behaviour. Ground reaction forces were used to obtain information about feet in parallel with motion capture technology to obtain kinematical data from the head and body.

The average gait cycle time was 519.32 ms with a strong decrease with increasing walking speed. During each step 77.19% of the gait cycle was stance phase per foot and the remaining gait cycle was swing phase. This is considerably longer than in humans, where the stance phase accounts for about 60% of the gait cycle and can be even smaller in proportion with increasing walking speed (Murray, 1967). In pigeons, however, the proportion of the gait cycle occupied by the stance phase of each foot does not change with walking speed.

Each gait cycle contains two thrust and two hold phases, starting with a thrust phase. Therefore, each step starts with a thrust phase followed by a hold phase. The first thrust phase starts on average 3.50% of the gait cycle after the foot touches the ground (HS). As the HS event initiates the double stance phase, the thrust phase starts shortly after both feet touch the ground. The thrust phase lasts for the remaining double stance phase and ends 3.64% of the gait cycle into the single stance phase. At this point 24.57% of the gait cycle has been reached and the first maximum of the vertical forces as well as the minimum of the horizontal shear forces have been
passed. Therefore, the hold phase is present from shortly after the initiation of the single stance phase until shortly after the initiation of the double stance phase. This finding differs slightly from Fujita’s (2002), who described that the hold phase ended during the single stance phase. Considering that the hold phase ends earlier in the gait cycle when the pigeons walks faster, the gait cycle described by Fujita (2002) may be true for higher walking speeds, but the gait cycle presented in this study is based on the average over all walking speeds.

It is known for humans that shortly after the first vertical maximum force the CoM trajectory enters the area next to the BoS (Adamczyk and Kuo, 2009; Winter, 1991). The hold phase starts 4.49% after the initial vertical force maximum and therefore begins around that time. This observation is relevant to the hypothesis that head-bobbing increases stability in walking pigeons (Dagg, 1977; Fujita, 2002). In standing humans the CoM must remain above the BoS to maintain stability (reviewed in Winter, 1995). In walking humans the CoM trajectory does not enter the BoS but remains next to it until shortly before the push-off (second vertical force maximum). In pigeons, however, the BoS is much wider with respect to the shoulder width and much longer with respect to the step length than in humans. Each foot covers at least 35% of the shoulder width (see Table 3.3) and during walking the feet are usually not placed exactly centered underneath the pigeon’s body, but slightly off center (personal observations). Therefore, the CoM is likely to enter the area above the BoS, which would increase the stability during the single stance phase. Interestingly, the hold phase occurs when the CoM is expected to be above the BoS (Fujita, 2002). As the hold phase reduced the CoM velocity the CoM remains longer above the BoS which could lead to an increase in stability during the single stance phase compared to pigeons walking without head-bobbing.
The length of the BoS relative to the step length strengthens this hypothesis. In pigeons, the length of the foot (BoS during single stance) is only exceeded by the step length at walking speeds higher than 450 mm/s. At walking speeds lower than that, the step length is less than the BoS length itself (see Figure 3.3 C, Table 3.3). Relatively, the BoS is considerably longer than in humans when compared to the step length which explains why the stance duration in pigeons is longer and why the single stance phase occurs later in the pigeon’s gait cycle and is shorter as in humans. Additionally, the longer BoS indicates that the CoM can remain longer above the BoS increasing the stability of walking pigeons.

The presented data thus reinforces the idea that the hold phase increases stability due to an increase in the time during which the CoM is above the BoS (Dagg, 1977; Fujita, 2002).

4.2 The Role of Step Length and Step Frequency in Walking Speed

Walking speed can be described mathematically by step length and step frequency (equation (2)). But how does each of the two variables contribute to walking speed changes? The data presented in Section 3.2 (and Figure 3.3) suggest that the step frequency increases linearly with increasing walking speed while the step length increases non-linearly. The linear increase in frequency does not start at the origin but rather has an offset value (y intercept), meaning that a step frequency would be expected even at zero walking speed. This cannot be true unless the pigeon would step on the spot when not moving forward, which they do not. It is important to note that no data could be collected at walking speeds lower than 90 mm/s, implying that pigeons do not walk slower than a threshold walking speed. In this case, the linear increase in frequency may only be biologically valid for speeds higher than 90 mm/sec. At speed lower than that no stepping motion is possible, but at speeds higher than that walking is occurs and the step
frequency increases linearly. In humans, two different descriptions for the change in step frequency with walking speed were found, a linear description like described above for the pigeon and a non-linear one (Cavagna and Franzetti, 1985; Grieve and Gear, 1966). The type of description was dependent on the individual (human), even though all tested pigeons displayed a linear increase in step frequency.

As seen in Figure 3.3 C, step duration decreases in a non-linear manner with increasing walking speed, as the step duration is the inverse of the step frequency. The inverse of a linear function automatically leads to a non-linear function. The step length, however, increases in a non-linear manner as well. This may be counterintuitive at first, but appears to hold true in pigeons. The non-linear increase of step length with increasing walking speed starts at the origin. Therefore, even though a value is described for the step frequency at zero walking speed, after multiplying step frequency and step length the theoretical walking speed starts at zero, as expected. In humans, the increase in step length with increasing walking speed is described by a non-linear function as well (Collins and Kuo, 2011), as it is described above for pigeons. However, in humans the step length has been described by a power function while in pigeons the step length is described by a rational function. Therefore, in humans the step length would theoretically keep increasing while in pigeons a maximal step length would eventually be reached. In fact the maximal step length in pigeons is the inverse of the slope of the linear increase of the step frequency. Biologically, of course an organism cannot increase the step length infinitely, as eventually the physiological (and biomechanical) boundaries of the body structure would be reached.

The argument can also be used to justify why the step frequency in pigeons is described by a linear function rather than by a non-linear function. The non-linear function used to describe
the changes in step frequency with walking speed in humans was based on a power function as well (Cavagna and Franzetti, 1985; Grieve and Gear, 1966). If the power function is applied to pigeons, it leads to the function shown in equation (26) with $\alpha$ and $\beta$ being constant terms that have to be determined by fitting the function to the data. The resulting step length description is shown in equation (27) and it would always keep increasing according to this formula. As this is unreasonable based on physiological constraints, the linear description of the step frequency change with walking speed is preferred, where the maximal step length is defined as the inverse of the linear increase in the step frequency.

$$f_s = \beta * v_{ws}^\alpha \quad (26)$$

$$l_s = \frac{v_{ws}^{1-\alpha}}{\beta} \quad (27)$$

4.3 The Change in Head-Bobbing Behaviour with Different Walking Speeds and the Transition Speed to Walking without Head-bobbing

The changes in head-bobbing parameters with walking speed were described based on the previously established step length and step frequency descriptions. The head velocity during the hold phase was defined as zero. This means that all head movements occur during the thrust phase and have to be identical to the body movements during each step. Therefore, the thrust phase amplitude is identical to the step length which can be seen in the mathematical description of the two variables, as they are identical. The same is true for the head-bobbing frequency which is identical to the step frequency, as during each step one head-bobbing cycle occurs. This finding indicates that the step movement determines the head-bobbing behaviour, which is expected considering the synchronization between them. The thrust phase duration remains constant for all walking speeds and does not seem to be dependent on the stepping motion. Rather, it seems to be
related to the transition point from walking to running. The shorter the thrust phase duration the higher the transition speed from walking with head-bobbing to walking without (see Table 3.2). The transition speed is defined as the point at which the head velocity during the thrust phase is equal to the body velocity, effectively eliminating head-bobbing. This definition is the same as the previous definition by Davies and Green (1988) defining the transition from walking to running as the point at which the hold phase proportion is zero, effectively eliminating head-bobbing. The hold phase proportion decreases linearly with walking speed and is dependent on the head-bobbing frequency, the thrust phase duration, and the maximal step length (equation (14)). This finding is different from the data presented by Davies and Green (1988). These researchers measured the hold phase proportion of six pigeons and combined the values, while I found that the hold phase proportion and the resulting transition speed is bird specific and depends on both the thrust phase duration and the head-bobbing frequency increase, and as the head-bobbing frequency is dependent on the maximal step length so is the transition speed. The reduction of hold phase during each step with increasing walking speed can also be seen in the gait cycle data presented in Section 3.1. The hold phase starts at the same point of the gait cycle but ends earlier the faster the pigeon walks.

The transition speed is not the maximal velocity the pigeon can reach via terrestrial locomotion but rather is the velocity at which the maximal head-bobbing frequency is reached. At this point the constant thrust duration equals the step duration. The maximal step length is not reached at the transition speed, but can increase further. This is necessary in order to further increase the over ground velocity of the pigeon when walking at speed higher than the transition speed, as at least one of either step length or step frequency must be able to increase. The
behaviour of the step frequency change at speeds higher than the transition speed is unknown and I can make no predictions.

Davies and Green (1988) refer to the transition speed as the transition from walking to running in pigeons. In humans walking and running are two different types of terrestrial locomotion that do not gradually transition into each other. Each type of locomotion is the more energy efficient type for a range of over-ground velocities; walking is the more energy efficient locomotion at speeds lower than the transition speed while running is more energy efficient at speeds higher than the transition (Margaria, 1976). The transition speed, however, is not dependent on the energy consumption itself, but most likely depends on muscle fatigue in the lower leg and therefore humans can actively change the transition point from walking to running (MacLeod et al. 2006). In humans walking and running are two distinct motor patterns. Walking humans can be described by the inverted pendulum model with the CoM moving on an arc trajectory around the stiff leg. At every point in time one foot is on the ground and the vertical ground force of each foot has a distinct M-shape. When running, only one foot touches the ground at a time and between each step is no ground contact. Each leg is no longer stiff, but behaves like a spring transferring kinetic and gravitational energy from the heel strike to the push-off by temporarily storing it as elastic energy in the muscles and tendons (Cappellini et al. 2006). The CoM does not follow arc trajectories anymore but follows a sine wave trajectory, with the maxima occurring during the time of no ground contact and the minima occurring during ground contact. The vertical ground reaction force is no longer M-shaped but consists only of one solitary peak.

In pigeons, the transition from walking with head-bobbing to walking without head-bobbin does not seem to be a switch between two locomotion forms but rather seem to be a
gradual change from one type to the other. The hold phase duration gradually decreases until head-bobbing is eventually eliminated completely. This is a significant difference compared to the transition from walking to running in humans. Additionally, it seems that in pigeons the transition speed is pre-determined by thrust phase duration and leg length (due to maximal step length), while in humans the transition speed can voluntarily be altered. To verify this hypothesis, kinematic data for pigeons transitioning from walking with head-bibbing to walking without head-bobbing are necessary. This data would also reveal the behaviour of the feet during fast walking without head-bobbing. In running humans only one foot touches the ground at a time. Because in pigeons the transition from head-bobbing to no head-bobbing occurs gradually, this transition point should not be referred to as transition from walking to running but rather from walking with head-bobbing to walking without head-bobbing. The stance phase of a gait cycle is not altered at different walking speeds (see Section 3.1) and as the transition seems to be gradual it appears that even at speeds higher than the transition speed the single and double stance may still be present. However, without data the movement of the feet of fast walking or running pigeons is just speculative.

It is not clear from the present data set whether metabolic reasons or the visual function of head-bobbing determine the gradual transition in pigeons. It would be interesting to see the metabolic costs of different walking and running speeds in pigeons, as this could help clarify the cause of the gradual transition from head-bobbing to no head-bobbing in pigeons. However, the gradual transition also indicates that either the visual function of the head bobbing or the biomechanical function of head bobbing are the driving force for the gradual transition rather than the metabolic cost. The head-bobbing phases determine at which walking speed the transition occurs. Purely metabolically determined transition speeds could very well be variable rather than
limited to a certain transition point, as the physiological constraints of head bobbing would not impact this transition. Therefore, head bobbing likely has a constraining effect on both the transition point and the gradual transition due to either the visual importance or the biomechanical function as it is maintained as long as possible.

4.4 Slippage during the Hold Phase

In the previously described findings in Section 3.3, the hold phase velocity was defined as zero and all the head movements occurred during the thrust phase. When calculating the walking speed using thrust phase duration and amplitude measurements based on equation (11) and comparing the results against the measured walking speed based on the body movement, a systematic deviation was found. This deviation could be due to measurement errors or rounding mistakes. However, for each bird the calculated walking speed deviates by a consistent amount and direction (under or overestimation) from the measured one but neither amount nor direction are consistent within the 6 tested animals. This indicates that these sources of error can be ruled out. The other reason for a systematic error in calculated walking speed values could be that the hold phase does contribute to the head movements, though only for a small amount. Previous research identified two sources of head velocity during the hold phase. The visual gain is believed to be almost one and visual motion should induce head movements during the hold phase (Friedman, 1975, Frost, 1978). Additionally, a small head velocity during the hold phase, referred to as ‘slippage’, has been described by Frost (1978) and Troje and Frost (2000).

The sum of the thrust phase amplitude and the hold phase amplitude must equal the step length in order to ensure that the head moves equally as far as the body. Therefore, when following equation (11) only the thrust phase amplitude is taken into account, which does not
reflect the entire head movements. No visual motion was applied to the birds in this study, so the only source for head-movements during the hold phase would be slippage. The results indicate that the head moves during the hold phase and that each bird has a different slippage which is independent of gender, body weight, or head-bobbing parameters. No biological system is perfect, and therefore perfect visual stabilization during the hold phase (a head velocity equal to zero) would likely not be possible. Head stabilization during the hold phase can be achieved by either a closed loop controller leading to oscillatory errors, or an open loop controller leading to linear errors due to error integration. The slippage is individual for every bird and does not seem to be oscillatory (based on equation (25)). Therefore, the slippage may be based on a calibration error in the input-output relation of the open loop controller underlying the head control during the hold phase. To verify this assumption the head velocity during the hold phase would have to be measured precisely. If the slippage is based on the open loop controller’s input-output relations, it could be changed within each bird when recalibrating it. Generating a new visual environment in which the pigeon has to walk could lead to a recalibration which could be measured when the pigeon walks in the original conditions again.

### 4.5 Head-bobbing as a Compromise between Visual and Biomechanical Function

The above analysis indicates an effect of head-bobbing on the biomechanics of pigeons by shifting the CoM and increasing stability during the single stance phase. An additional hypothesis on an effect of head-bobbing on the biomechanics of pigeons was introduced by Troje et al. (2012). To answer the question how much energy head-bobbing costs, Troje et al. (2012) analyzed the potential effect of head-bobbing on the performed work (measure that indicates how much metabolic energy is used) during walking. They showed that head-bobbing could have the
additional function of transferring negative work (breaking energy) to positive work (push-off energy) or the other way around, assuming that the head behaves like a spring mass model with respect to the body. This could effectively reduce the performed work in walking pigeons that head-bob, and would indicate that walking with head-bobbing is the energetically more efficient form of terrestrial locomotion. The highest rate of energy transfer would be reached when the head would be swinging sinusoidally with respect to the body, but this would lead to a ‘hold phase’ with slightly negative head velocity, impairing the visual stabilization during the hold phase (see Figure 4.1). Instead, it seems that head-bobbing fulfills both the visual and the biomechanical function. Perfect visual stabilization would lead to a saw-tooth like behaviour of the head while perfect energy transfer would lead to a sinusoidal head movement (if the head actually behaves like a spring mass model). As seen in Figure 4.1 the head movements in pigeons seem to be a compromise between the two, indicating a compromise between perfect visual stabilization and highest energy transfer efficiency.

Additional evidence for the transfer of work during walking can be found in humans. Passive arm swinging during walking can reduce the metabolic cost of walking by 12% (Collins et al. 2009). Considering that the step-to-step transition is the most energetically expensive part of walking (Kuo, 2001), the ability to transfer energy between the legs with head-bobbing could significantly reduce the metabolic cost.
Figure 4.1 – Natural and optimal head-bobbing: presented in blues is the head kinematics of a head-bobbing pigeon. Displayed in green is the head kinematics of an optimally swinging head with maximized potential for energy transfer. The grey areas represent the thrust phase while the red areas are representing the hold phase.
Chapter 5

Conclusions

The current study investigated several aspects of head-bobbing in pigeons. The primary aim was to find the answer to the question why pigeons and so many other bird species head-bob. This main question was divided into three individual questions of interest. The first question was what happens during head-bobbing? I conducted a gait cycle analysis to determine the order of events in a head-bobbing pigeon. The analysis verified the synchronization between head and feet, with one head-bob per step. The hold phase occurs mainly during the single stance phase and starts at the same phase within the gait cycle for all walking speeds. The start of the hold phase is around the phase in the gait cycle when the CoM enters the BoS, increasing stability during the single stance phase. The thrust phase (occurring mainly during the double stance phase), however, starts earlier within the gait cycle with increasing walking speed, indicating that it is independent of the CoM position within the body. Additionally, this indicates that the hold phase will eventually be eliminated at high walking speeds.

These results lead to the second question. How do head-bobbing parameters change with walking speed? The gait cycle analysis indicated a change of hold and thrust phase parameters with walking speed. In order to answer this question it is important to understand how walking speed changes in the first place. Pigeons increase walking speed by linearly increasing the step frequency and non-linearly increasing the step length. As one head bob occurs per step, the head-bobbing frequency is equal to the step frequency, again demonstrating the synchronization between head and feet. I found that the thrust phase duration is constant for all walking speeds. As the head-bobbing frequency increases with walking speed, the hold phase duration must be
decreasing. This indicates that with increasing walking speed the head moves faster during the thrust phase and more head-bobs occur. It also indicates that the hold phase will eventually be eliminated, leading to no head behaviour above a certain threshold walking speed.

This leads to the third question, how long can a pigeon maintain head-bobbing with increasing walking speed? The reduction in hold phase duration indicates that this transition point from walking with head-bobbing to fast walking without head-bobbing is bird specific and depends on step (or head-bobbing) frequency, thrust phase duration and maximal step length. Therefore, the transition speed, as well the head-bobbing behaviour in itself, are bird specific and depend on the body size of the individual pigeon, as the maximal step length can be seen as an indirect measure of body size. The transition speed seems to be pre-determined rather than voluntary. The visual function of head-bobbing, and especially the visual stabilization during the hold phase is maintained as long as possible for a given walking speed, indicating the importance of the visual stabilization to the pigeon.

Another important question to understand head-bobbing is: how much energy does head-bobbing cost? Knowing how many resources pigeons have to invest into head-bobbing is essential to evaluate how important head-bobbing is to pigeons. Troje et al. (2012) indicated that under the assumption that the head behaves like a spring mass model with respect to the body, head-bobbing would have the potential to transfer energy from one leg to the other in walking pigeons, reducing both positive and negative work. This would indicate that walking with head-bobbing could be the more energy efficient form of locomotion. In order to have the highest rate of energy transfer the head would have to move in a sinusoidal manner with respect to the body which would compromise the visual stabilization during the hold phase. Head-bobbing should therefore be seen as a compromise between visual and biomechanical function.
To summarize, head-bobbing has two primary functions. The present study found evidence for increased stability during walking when due to the hold phase. Head-bobbing is a compromise between the visual function of image stabilization during the hold phase and motion increase depth perception during the thrust phase, and the increase in stability as well as the possibility being more energy efficient. The ideal head-movement for perfect image stabilization would be similar to a saw-tooth function while the ideal head-movements for maximal energy transfer would be sinusoidal with respect to the body. Therefore, it seems that the head movements during head-bobbing are a compromise between both optimal behaviours.

To verify this hypothesis of decreased metabolic cost due to head-bobbing and energy transfer between head and body three important key experiments should be conducted. First, the kinematics and ground reaction forces of non-head-bobbing pigeons have to be measured, in order to calculate the performed work. These results could be compared to the work performed by head-bobbing pigeons indicating which form of locomotion is more energy efficient. To accomplish this, a visual environment has to be developed that eliminates all visual flow for the pigeons, as this should also eliminate head-bobbing (Friedman, 1975; Frost 1978). Second, head-bobbing pigeons have to be motion captured with additional feet tracking. This way the BoS can be measured as well and whether or not the CoM enters the BoS can also be determined. The hypothesis of increased stability during the single stance phase due to head-bobbing can then be verified. The third experiment would need to measure the metabolic cost of head-bobbing and non-head-bobbing pigeons.
References


