

Head-bobbing of walking birds

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Abstract Many birds show a rhythmic forward and backward movement of their heads when they walk on the ground. This so-called “head-bobbing” is characterized by a rapid forward movement (thrust phase) which is followed by a phase where the head keeps its position with regard to the environment but moves backward with regard to the body (hold phase). These head movements are synchronized with the leg movements. The functional interpretations of head-bobbing are reviewed. Furthermore, it is discussed why some birds do bob their head and others do not.

Keywords Optokinetic response · Vision · Depth perception · Balance · Head-bobbing species

Introduction

Head-bobbing as observed, e.g. in pigeons and chickens, means a rhythmic forward and backward movement of the head during bipedal walking on the ground. Dunlap and Mowrer (1930) were the first to report that the backward movement is based on illusion: in this phase the head position is kept stable with regard to the environment while the body moves continuously forward (Fig. 1). In this way head movements during walking are characterized by a hold phase and a thrust phase (Fig. 2). The forward and

backward movements of the head are usually synchronized with the movements of the legs, i.e. there is one head cycle per one step or two head bobs during a complete walking cycle.

Smaller birds often do not walk but hop. Since this includes a rapid head (and body) movement and a stop of the head movement, it may be compared to the head-bobbing of walking birds. However, hopping will not be considered in more detail in the present review.

Origin of head-bobbing

It has been shown repeatedly that the hold phase is triggered by vision: a hand-held chicken (Dunlap and Mowrer 1930) or pigeon (Frost 1978) shows head-bobbing when moved forward by the experimenter. Pigeons walking on a treadmill (stable environment) do not bob their heads (Frost 1978). Blindfolded animals never show head-bobbing when walking (Dunlap and Mowrer 1930; Necker et al. 2000 and unpublished own observations). Friedman (1975) confirmed the visual context of head-bobbing and excluded an influence of the movement of the legs (no bobbing when legs walk but visual environment is stable) and of the vestibular system (no bobbing when body moves but visual environment is stable). Frost (1978) noted that there is a slight forward movement of the head during the hold phase (about 3 mm/s compared to about 500–800 mm/s during the thrust phase) which was confirmed later on (Troje and Frost 2000). Such a stimulus is necessary because an absolutely stable eye position cannot generate an error signal for triggering head movements as already noted by Dunlap and Mowrer (1930). Altogether head-bobbing has been compared to the optokinetic response in mammals with a slow motion of the eye when fixing an object (hold phase) and a

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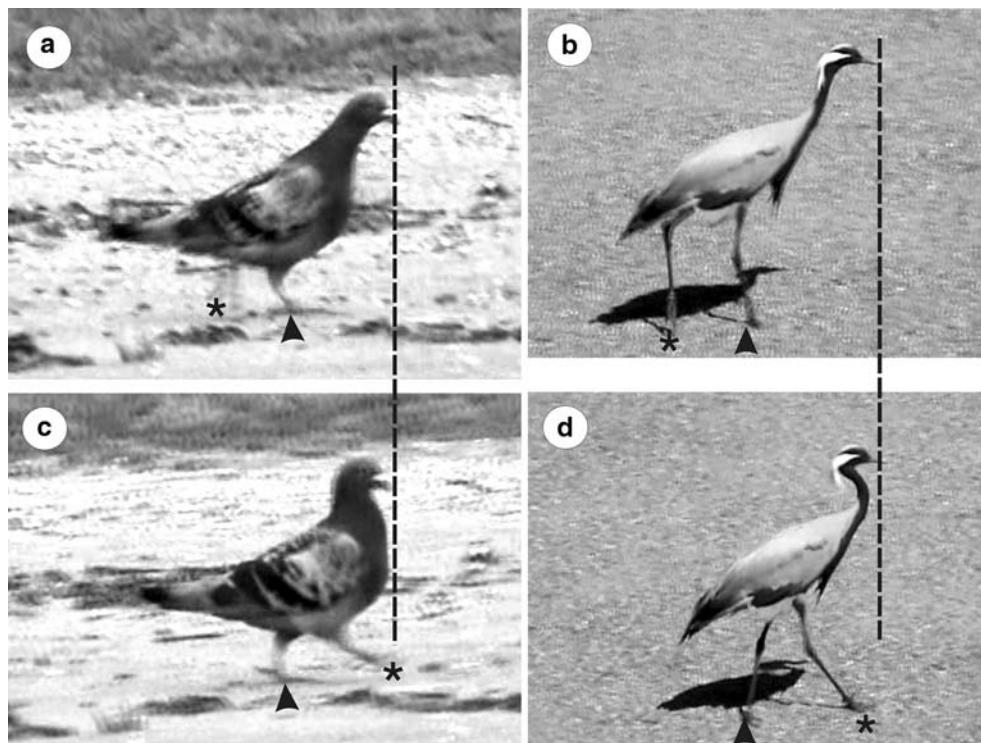


Fig. 1 Two phases of one step in the pigeon (left) and in the demoiselle crane (right). **a, b** Stretched head at the end of the thrust phase; **c, d** retracted head at the end of the hold phase. Pictures are aligned to the ground foot (arrowhead) which does not change its position with

regard to the environment. *Vertical dashed line* shows position of the beak. Asterisks indicate the swinging foot. Successive frames from videos taken by a digital camera (Sony DCR-HC23)

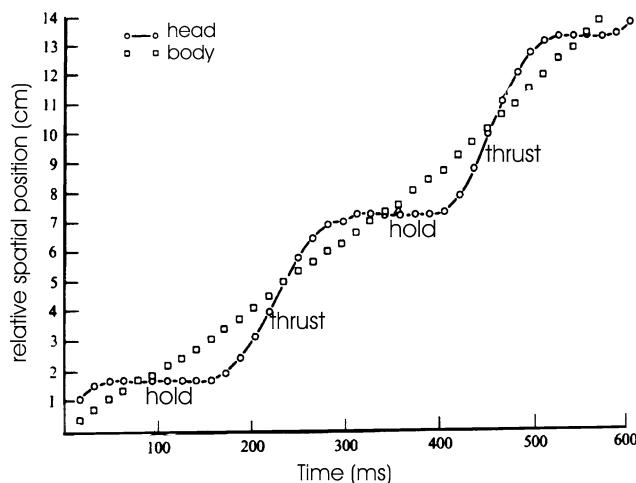


Fig. 2 Relative spatial position of head and body of a pigeon walking with normal speed. Note hold and thrust phases of the head and continuous movement of the body (modified from Frost 1978)

rapid saccadic eye movement to fix a new object (thrust phase). Although head bobbing birds like the pigeon are able to move their eyes (Nye 1969; Gioanni 1988; Wohlschläger et al. 1993) it seems that the long neck favors moving the head rather than the eyes.

As to the neuronal network underlying head-bobbing both optokinetic eye movements and head movements are controlled by the accessory optic system (Frost and Wylie 2000). This system responds to movements of large visual fields as is the case when the body moves forward. The information from displaced ganglion cells of the retina is first processed in two nuclei, the nucleus of the basal optic root (nBOR) and the pretectal nucleus lentiformis mesencephali (LM). These nuclei project either directly or via the inferior olive to the vestibulocerebellum. In the vestibulocerebellum, information from the visual and the vestibular system are integrated, and there is an output to the premotor system of the neck which controls head movements (Arends et al. 1991).

Functional implications for vision

During the hold phase the image of the surrounding world is stabilized for a short while on the retina, which increases the time to recognize and identify objects, especially moving ones. This is comparable to fixing an object during self-motion (slow phase of the optokinetic response).

Most birds have lateral eyes with a minor binocular overlap, which means poor stereoscopic or depth vision

(Wallmann and Letelier 1993; Martin and Katir 1999). During monocular vision, motion parallax provides depth information. Motion parallax is the apparent relative angular movement of objects at different distances during translatory movements of the eye. It provides unambiguous cues to the relative depth of stationary objects but not of moving objects. Motion parallax increases with the velocity of eye movement. In this way the thrust phase may improve depth information. There is experimental evidence that birds use motion parallax for depth information (van der Willigen et al. 2002; Cavoto and Cook 2006). Pigeons head-bob without a hold phase during landing and when running fast which supports the function of providing depth information (Davies and Green 1988; Green et al. 1994). Cronin et al. (2005) recently confirmed for the whooping crane (*Grus americana*) that with increasing walking speed the hold phase decreased and even disappeared. Davies and Green (1988) suggest that the hold phase serves the recognition of moving objects, and that the thrust phase improves the recognition of stationary food items like grains. The thrust approaches velocities typical of flight: mean flight velocity of pigeons is about 70 km/h (Herzog 1968), whereas thrust velocities may be as high as 30 km/h (calculated from Wohlschläger et al. 1993), i.e. the flight visual neuronal network may be used even while walking (Frost 1978).

It has been reported that during the thrust phase the nictitating membrane (third eyelid of sauropsids) closes (Dunlap and Mowrer 1930), which was not confirmed by a later study (Bangert 1960). There are, however, saccadic eye movements during the thrust phase (Pratt 1982; Wohlschläger et al. 1993). In mammals, vision is suppressed during a saccade. In birds there are more or less regular small tremors of about 25 Hz and of 100 to 500 ms duration (Nye 1969; Pratt 1982) which are thought to serve distribution of blood-borne material (e.g. oxygen), which comes from the pecten, the only structure which contains blood vessels in the avian retina (Pettigrew et al. 1990). Some authors assume that these tremors are saccades (Pratt 1982; Pettigrew et al. 1990). Pratt (1982) found these oscillations mainly during the thrust phase and assumes that vision is blurred during these oscillations, and depth vision should be possible only during rare thrusts without eye oscillations. Gioanni (1988) showed that there are true saccades in addition to the oscillations. In walking pigeons saccades have been found to have a duration of about 23 ms (Wohlschläger et al. 1993) which means that they are shorter than typical thrust phases (100 to 150 ms), i.e. vision should not be impaired during the head thrust. It has recently been shown that pigeons can learn to discriminate patterns during the complete head-bobbing cycle, i.e. both during the hold phase and during the thrust phase (Jiménez Ortega 2005). Pigeons were trained to discriminate two rather large objects (5 cm × 5 cm) presented for 75 ms at

various phases of the head-bobbing cycle while walking at a normal speed. This confirms that there is no saccadic suppression during the thrust phase.

Synchronization of head movements and leg movements

The forward and backward movements of the head are synchronized with the movements of the legs (Bangert 1960; Frost 1978; Troje and Frost 2000; Fujita 2002, 2003). Figure 3 shows an example of a walking pigeon as recorded by Fujita (2002). When both feet contact the ground the center of gravity is caudal to the rostral foot. This foot becomes the supporting foot when the caudal foot starts its swing phase. The thrust is initiated in this phase. This results in a forward shift of the center of gravity so that it is placed above the supporting foot (Fujita 2002). In the course of the step the supporting foot moves backward, which means that the center of gravity moves rostral to this foot. At the same time the head moves backward (relative to the body) which means that the center of gravity is also shifted backwards towards the ground foot. In this way the center of gravity seems to follow the supporting foot which helps to stabilize balance. The same cycle occurs during the stance phase of the other leg, i.e. there are two cycles of head-bobbing during a complete walking cycle. This suggests that one function of head-bobbing is to shift the center of gravity relative to the feet so as to maximize postural stability (Dagg 1977).

Fujita (2002, 2003) studied the contribution of the head to the position of the center of gravity both in the pigeons (Fujita 2002) and in the little egret (Fujita 2003). In both species this contribution is small but significant. A well-known function of the head in shifting the center of gravity can be seen in flying birds which stretch their head to shift the center of gravity towards the wings. Fast running birds

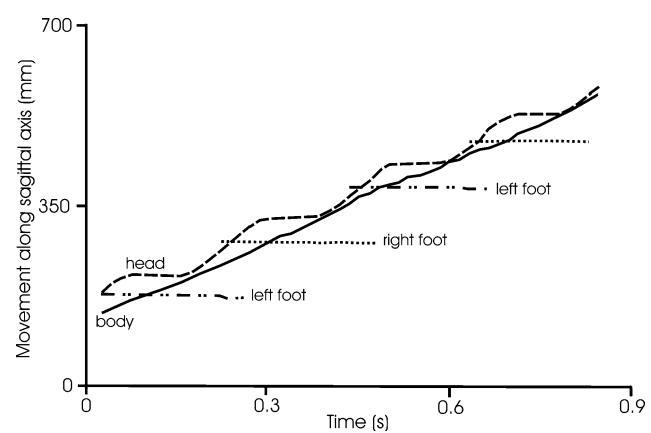


Fig. 3 Head, body and feet movements (stance phase only) in a walking pigeon (modified from Fujita 2002)

usually stretch their neck continuously, which results in a similar forward shift of the center of gravity which supports the forward movement of the body. On the other hand, pigeons walking on a treadmill (Frost 1978) and blind-folded pigeons (Necker et al. 2000) which do not bob their heads are able to keep balance when walking. All these findings show that head-bobbing can help adjust balance during locomotion but the contribution seems to be small, and keeping balance can be achieved without head-bobbing.

Bangert (1960) studied the development of head-bobbing in chickens and found out that both head-bobbing and the synchronization of head and leg movements appear within 24 h after hatching. The cycle frequency decreases with increasing age and size. Chicks which spent 14 days in a dark room after hatching showed the same synchronization of head and leg movements as normal chicks of the same age. Restriction of leg movements for 90 h after hatching did not impair head-leg synchronization. These experiments show that the synchronized movements are organized by an endogenous (innate) mechanism. There is not only a synchronization of head and leg movements but also a dependence of the extent of the head thrust and stride length. Chicks with restricted locomotor experience or an experimental decrease of stride length by hobbling for 12 days after hatching showed both smaller stride lengths and smaller head movements (Muir and Chu 2002; Muir and Gowri 2005). There even seems to be some correlation between stride length and head-bobbing under normal conditions. Species with a short stride length (relative to the height of the hip) like pintails or black-headed gulls show no head-bobbing as compared to e.g. pigeons and herons with longer stride lengths and distinct head-bobbing (Fujita 2004). Furthermore, in one and the same species, the black-headed gull, head-bobbing depends on the stride length, which varies with behavior: while foraging in the mud the stride length increases and they bob their heads (Fujita 2006).

The hopping or jumping of birds is composed of two phases (Daanje 1951). In the first phase the legs are folded and the head is retracted. In the second phase both head and legs are stretched and the bird jumps into the air. Before landing the head is retracted. Daanje (1951) argues that when walking each step is a hop. In this way walking would be alternative hopping with both legs, with the head giving mechanical assistance in the same way as in each hop.

Species dependency of head-bobbing

Not all birds that walk on the ground show head-bobbing. Well-known examples of non-bobbing birds are waterfowls

like ducks, geese and swans (Fig. 4a, b). These species have relatively short and wide-set legs, which is advantageous while swimming but results in waddling when walking on the ground. This raises the question why some species bob their head and others do not. It seems that there is no simple answer to this question; and Dagg (1977), after having listed quite a number of bobbing and non-bobbing species, notes that it is a puzzle why some birds do it and others do not.

Although head-bobbing has been studied mainly in pigeons and chicken, several authors mention this behavior in other species (Dunlap and Mowrer 1930; Daanje 1951; Dagg 1977; Whiteside 1967; Frost 1978; Fujita and Kawakami 2003; Fujita 2006). The most complete study is by Jiménez Ortega (2005); it includes 322 species. It seems that there is some phylogenetic constraint (Dagg 1977; Jiménez Ortega 2005): usually all members of the same family or even order show the same behavior (bobbing or not). Bobbing orders and non-bobbing orders are listed in Table 1. The order of Charadriiformes includes shore birds, some of which bob (e.g. turnstone, black-winged stilt) and others which do not (e.g. silver gull, terns) or only occasionally (e.g. black-headed gull, oystercatcher). Species of the large order of Passeriformes (includes songbirds) generally show hopping and/or head-bobbing (small birds usually hop; larger birds like magpies both hop and bob their heads).

Waterfowl with palmate feet seem to be non-bobbing species independent of the order they belong to (e.g. ducks, flamingos, cormorants, pelicans, gulls). One exception is the black-headed gull which shows head-bobbing during foraging in the mud but not when walking on the ground or when swimming. Non-bobbing species generally do not bob either when walking on land or when swimming. There are water-dwelling species like coots and common moorhens which bob their heads both when walking on the ground and when swimming (Fig. 4 c, d). These species have feet specialized for swimming but no palmate feet.

Whiteside (1967) claims that the position of the eyes and the structure of the retina play an important role when it comes to the question whether birds do bob their head or not. Birds whose eyes are forward-looking (raptors, caprimulgiforms like nightjar; see Iwaniuk and Wylie 2006) do not show head-bobbing because the angular velocity of the passing scene is low for objects ahead (Whiteside 1967). In birds with laterally looking eyes the angular velocity of the passing scene is high, and many of these birds show head-bobbing. However, retinal specializations also seem to play an important role. Most birds have a central retinal area with an increased number of photoreceptors (with or without a distinct fovea), and these birds bob their heads or hop (e.g. pigeons, crows, blackbirds, and chaffinch). Birds with a horizontal retinal band of high photoreceptor density,

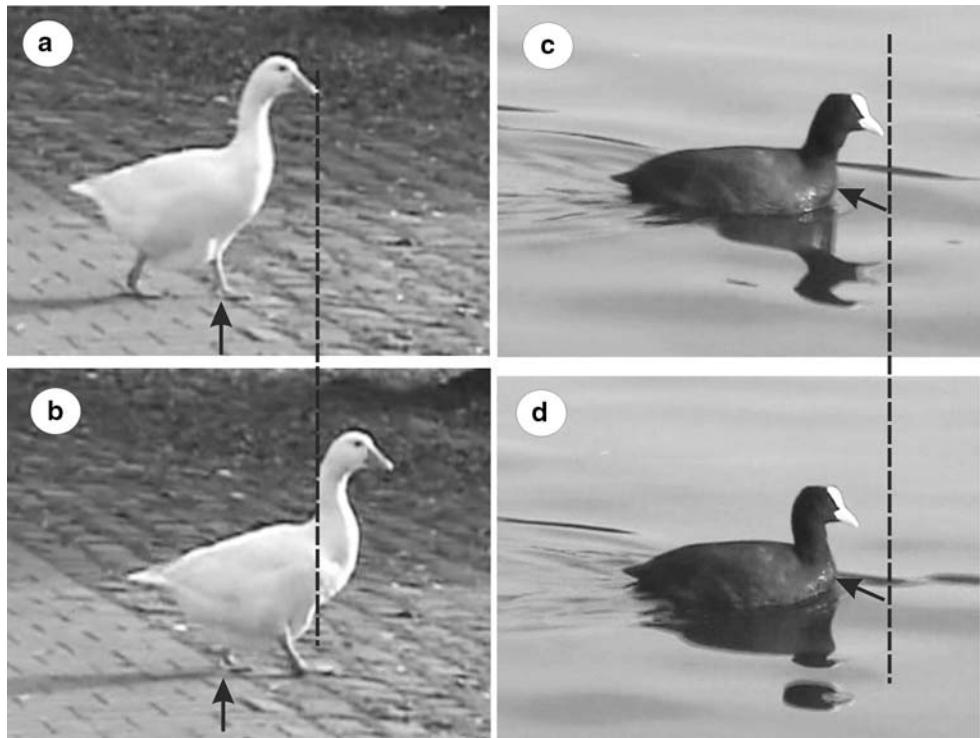


Fig. 4 **a, b** One step in a non-bobbing goose, aligned at the ground foot (arrows). Dashed vertical line reveals forward movement of both head and body. **c, d** Head-bobbing of a swimming coot, aligned at the

breast as indicated by arrows. Dashed line indicates different positions of the head (stretched in **c**, retracted in **d**). Successive frames from videos taken by a digital video camera (Sony DCR-HC23)

Table 1 Orders of birds with head-bobbing, non-bobbing, and mixed behavior (head-bobbing and non-bobbing species)

Head-bobbing	Non-bobbing	Mixed
Columbiformes (pigeons, doves)	Anseriformes (ducks, geese, swans)	Charadriiformes (see text for species)
Galliformes (chickens, pheasants, quails)	Phoenicopteriformes (flamingos)	
Gruiformes (cranes, rails)	Pelicaniformes (pelicans, cormorants)	
Ciconiiformes (herons, egrets, storks, ibis)	Sphenisciformes (penguins)	
	Falconiformes (hawks, eagles, vultures)	
	Strigiformes (owls)	
	Psittaciformes (parrots, budgerigars)	

Examples of well-known species in brackets

which are specialized to see all horizon to detect predators usually do not bob their heads (e.g. gulls, flamingos, terns). However, black-headed gulls do bob when feeding in the mud (Daanje 1951; Fujita 2006). If this band contains a distinct fovea again bobbing occurs (e.g. turnstone, oystercatcher, coot). Pelicans have very movable eyes and therefore do not bob (Whiteside 1967). Despite reports of the retinal specializations of a variety of bird species (Rochon-Duvigneaud 1943; Walls 1963) there is a need for detailed correlative studies which include functional aspects of retinal specializations to prove the hypotheses put forward by Whiteside (1967). Furthermore, other mech-

anisms (kind of locomotion, feeding behavior) may also be important in addition to eye position and retinal structure.

There is general agreement that foraging on the ground is indicative of head-bobbing (Dagg 1977; Fujita and Kawakami 2003; Fujita 2004, 2006). However, ducks and geese feed on land without head-bobbing. The stride length of steps seems to be an important factor as has been pointed out already by Daanje (1951) and supported experimentally by Fujita (2004, 2006). Herons do not bob when taking small steps, and the same is true for black-headed gulls (Daanje 1951; Fujita 2006) and for birds which have short legs and take small steps (swallows, terns, ducks). These

correlations may have to do with the dependence of head excursions on stride length as discussed above (Fujita 2004, 2006; Muir and Gowri 2005). From a bio-mechanical point of view short stride lengths mean that the center of gravity shows fewer deviations from the position of the ground contacting foot while walking, i.e. there is less need for balance support from the head.

Conclusions

Although there are now quite a number of observations available, there is still no unequivocal interpretation of the function of head-bobbing and why some birds bob their head and others do not. Head-bobbing seems to be an innate mechanism in birds coupled with the locomotion of the hindlimbs (Bangert 1960). It develops independent of external stimuli but is under visual control (Friedman 1975; Frost 1978). It seems that relative stride length plays an important role because head excursions depend on this parameter and birds which take small steps do not bob. This speaks in favor of a bio-mechanical component to stabilize balance which is more necessary with long strides. Birds are bipedal animals with a horizontal orientation of the body and a center of gravity rostral to the insertion of the hindlimbs which requires an efficient control of balance when walking on the ground (Necker 2006). Aside from stride length the role of retinal specialization cannot be excluded. The correlation of a horizontal retinal band with non-bobbing behavior (Whiteside 1967) fits many species walking on the ground.

The hold phase and the thrust phase have been suggested to play different roles as far as vision is concerned. The hold phase is thought to help in identifying objects, whereas the thrust phase may improve monocular depth perception. However, these functional interpretations have not yet been tested experimentally in walking birds. There is only evidence that birds can see well during all phases of the head-bobbing cycle (Jiménez Ortega 2005). Long-necked birds often show thrust and hold phases without making a step when foraging on the ground (Fujita and Kawakami 2003; own observations in ostrich, peacock, grey heron, and cranes). In species like coots which bob their heads while swimming there is no need for a stabilization of balance. These birds peck for food on the surface of the water, and head-bobbing may improve recognition of small food items. These examples suggest a visual function of the bobbing behavior.

Altogether it seems that the visual aspect of head-bobbing is the primary function. Head-bobbing may help in improving object detection when foraging on the ground. The coordination of head-bobbing and leg movements is not necessary for keeping balance but may help in stabiliz-

ing position during walking. For those birds that practice head-bobbing, both functions seem to be useful adaptations to cope with walking on the ground.

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