The Evolution of Gaze Shifting Eye Movements

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Abstract In animals with good eyesight most eye movements consist of saccades, which rapidly shift the direction of the eye's axis, and intervals between the saccades (fixations) in which gaze is kept stationary relative to the surroundings. This stability is needed to prevent motion blur, and it is achieved by reflexes which counter-rotate the eye when the head moves. This saccade-and-fixate strategy arose early in fish evolution, when the original function of saccades was to re-centre the eye as the fish turned. In primates, and other foveate vertebrates, saccades took on the new function of directing the fovea to objects of interest in the surroundings. Among invertebrates the same saccade-and-fixate pattern is seen, especially in insects, crustaceans and cephalopod molluscs.

Keywords Fixation · Invertebrates · Saccade · Stabilising reflexes · Vertebrates

1 Saccades and Fixations: A Universal Pairing

In humans, all other vertebrates, and in invertebrates with good eyesight, there is one pattern of eye movements that is almost universal: the pairing of fast gaze-shifting movements (saccades) with periods of stable gaze (fixations). In humans there are other types of eye movement – pursuit and vergence – but our usual method of

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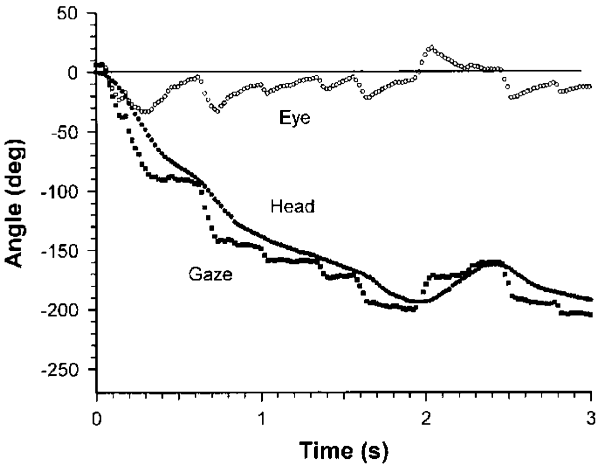

Fig. 1 The author's left eye, looking round a room. The eyes perform saccades and between these compensate for head movements. Gaze (eye + head) moves in a series of discrete fixations, around the direction of the moving head. From Land and Tatler (2009). Note the similarity to Fig. 2

interrogating the surroundings is by using saccades to move our high-resolution foveas around the scene in a series of fixations (Fig. 1).

It seems natural for us to think of saccades, primarily, as movements that shift our direction of acute vision, but this is not how they began. Gordon Walls, in a landmark article, provided an outline of the way that fixations and saccades came about in vertebrates (Walls 1962). As he puts it, the origin of eye movements '. . .lies in the need to keep an image fixed on the retina, not in the need to scan the surroundings'. By the Ordovician period, at least 450 mya, the first fishes already had a reflex in which rotations of the head during swimming evoked compensatory movements of the eyes. This, the vestibulo-ocular reflex (VOR), was brought about by signals from the ampullae or semicircular canals of the vestibular system, and its function was to keep the image still with respect to the surroundings, in spite of movements of the head. At the same time, or slightly later, a second reflex evolved, which took retinal motion signals and fed them back negatively to the eye muscles via the optic tectum. This optokinetic reflex (OKR) also functioned to clamp the image to the surroundings. The need for this double image-stabilising system can be attributed to the fact that vertebrate photoreceptors are slow, cones taking 20 ms or more to respond fully to a change in intensity (Friedburg et al. 2004), so that if the eyes moved passively with the head, the image would be degraded by motion blur. We know from studies on human vision that blurring starts to occur when the image moves across the retina at speeds greater than about 1 degree per second, so compensatory eye movements are essential for clear vision, especially at higher spatial frequencies. These eye movements are continuous, and equal or at least proportional to the disturbance caused by the natural motion of the head, or imposed by an experimenter.

What then happens when a fish makes a turn? If the reflexes are operating as they should, the eyes will become trapped at the limit of their range, and a mechanism is needed to return them to a central point in the orbit. In practice, fish tend to make

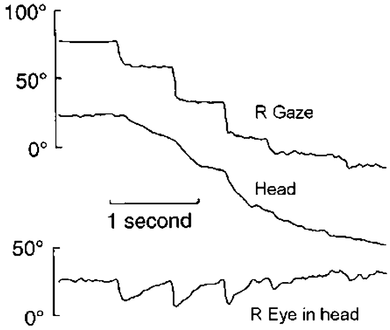

Fig. 2 Records of the eye, head and gaze movements of a goldfish making a turn. The eyes make saccades, but between these their movements are equal and opposite to those of the head. This results in gaze moving in a series of rotationally stable fixations. Goldfish lack a fovea, so the gaze shifts are more a necessary consequence of making a turn than a need to redirect a region of higher resolution. Redrawn from Easter et al. (1974)

these recentring movements early in a turn rather than when the eyes hit a backstop (Fig. 2). These movements need to be fast, since vision will not be possible or desirable during the reset, and this seems to be where the need for saccades originated. To quote Walls again: 'even in the lowest fishes, we see a good reason for saccadic eye movements to be as quick as they notoriously are'. In clinical practice, these reflex movements in humans have become known as 'slow phases' and 'flick backs' or 'fast phases' and together referred to as 'nystagmus'. But they are actually the ancient raw material from which almost all normal movements are derived.

2 Variations in Vertebrates

In some species of most vertebrate classes, this 'saccade and fixate' system has been adapted for a second use, namely, for targeting particular objects in the surroundings for more detailed scrutiny. Where this has evolved, it is always associated with a region of high resolution on the retina, either an area of elevated retinal ganglion cell density, as in a cat, or a smaller distinct fovea, as in a pipefish, chameleon, hawk or primate (Land 2015). These targeting movements do not occur in vertebrates with more uniform retinae, such as goldfish, toads and rabbits: here the appearance of a novel object does not provoke a saccade. The ability to target objects also requires the ability to hold them on a high- resolution area or fovea, and this has led, in humans and other primates, to further oculomotor refinements. These include the ability to fixate and to track moving objects smoothly. Tracking usually means that the reflexes which keep the overall image stationary (VOR and OKN) have to be suspended or modified, so that the eye can move with the target and allow the background to drift (e.g. if you track your moving finger, while observing the background, you can appreciate the destructiveness of motion blur). In primates

Fig. 3 Head, eye and gaze movements of a rabbit tracking the hand of an observer. Unlike primates, the target is tracked with the head, while the eyes make nystagmus-like saccades and compensatory movements, resulting in steplike gaze shifts. Modified from Collewijn (1977)

tracking extends to the third dimension, so that the foveas of the two eyes can converge on a single object independent of its distance. In mammals with lateral eyes, objects are tracked, but with the head rather than the eyes. Figure 3 shows a rabbit tracking the experimenter's hand with head movements. The eyes remain locked to the background, making a series of saccades and compensatory movements, so that gaze follows the head in a series of discrete fixations that do not directly follow the target, as they would in humans.

In humans, a saccade may be attracted to objects that are novel or otherwise 'eye-catching', but more commonly they are made to objects from which information is needed for the execution of a task, for example, to the spoon needed to stir the coffee or the nail that will be hit with a hammer (Land and Tatler 2009). This implies that the saccadic system has swift access to memories of where things are in the surroundings and information about their identities. Even when the eyes are not involved in information collection, they show the same pattern of saccades and fixations, at a rate of about three per second (Fig. 1).

In vertebrates with necks, head movements add to eye movements in determining the sizes of saccades. Heads have more inertia than eyes, so the contributions of the head need to be managed so that they do not slow up the gaze shifts. In small saccades (<40°) in primates, eye movement contributes most to the gaze shift, with head movement adding to both the speed and amplitude of the saccade, while gaze-stabilising reflexes are temporarily turned off (Fig. 4a). When the predetermined end-point of the gaze change is reached, VOR is turned on, and the eyes move in the opposite direction, exactly counteracting the ongoing head movement and establishing fixation. For smaller saccades the head contributes about 30% to the gaze change. For larger saccades the eyes reach a 'backstop', and, with VOR still turned off, gaze is carried entirely by the head until the gaze end-point is reached, when VOR is re-established (rectangle, Fig. 4b).

The situation in birds is different. Having light heads and flexible necks, the contribution of head movement to gaze shifts is much higher than in mammals, and it is these head movements that make smaller birds seem so busy and vigilant. In

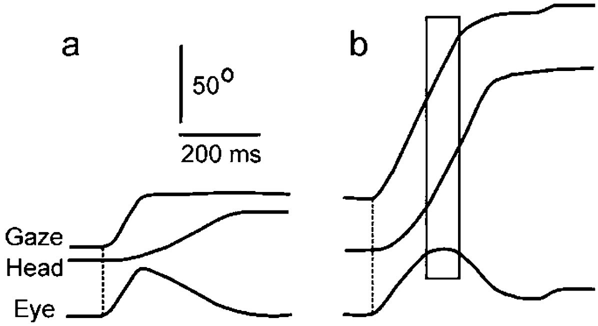

Fig. 4 Eye and head movements during a small (**a**) and large (**b**) combined saccade. Note that in (**b**) VOR remains turned off as the head completes the movement (rectangle) and recommences when the end-point is reached. Redrawn from Guitton (1992)

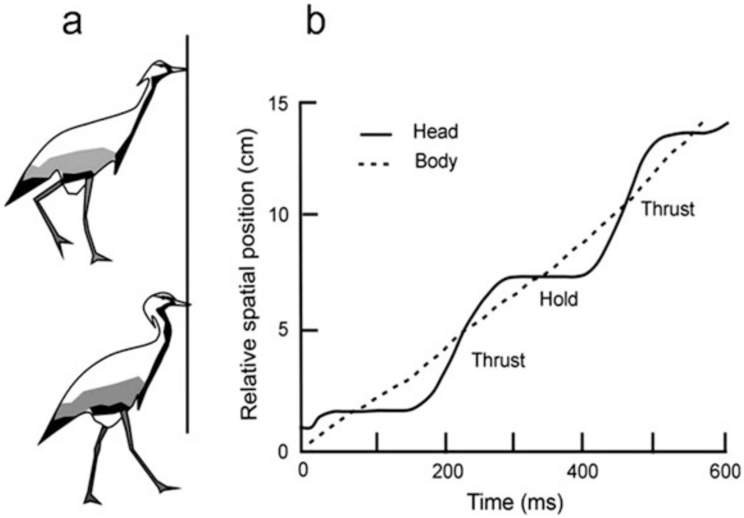

Fig. 5 Translational 'saccades' made by a demoiselle crane (**a**) and a pigeon (**b**). During the 'hold' phases, the head remains still in space (held by an optokinetic mechanism) and then moves forward during the 'thrust' phase. The body motion continues throughout. (**a**) Redrawn from photographs by Necker (2007) and (**b**) records from Frost (1978)

peahens, the head contribution to large gaze shifts (>40°) is almost 90%; although with smaller gaze shifts, this reduces to about 60% (Yorzinski et al. 2015).

Many ground-feeding birds also make what may be called 'translational saccades' while walking. The head moves forward, and then stabilises, as the body continues to walk under the stationary head (Fig. 5). The function of this 'head-bobbing' seems to be similar to that of rotational saccade and fixate behaviour: to allow the view to the side to be held temporarily stationary on the retina while not preventing forward motion.

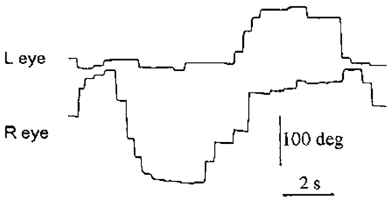

Fig. 6 Asynchronous saccades made by the two eyes of a chameleon, recorded with search coils. Adapted from Ott (2001)

The extent to which the two eyes are yoked during saccades varies considerably across vertebrates. In primates, the eyes are synchronised in timing, and their movements have the same amplitude; in other mammals the eyes are synchronised, but the movement amplitudes are more variable. At the other extreme, chameleon eyes are entirely independent in both the timing and amplitude of saccades (Fig. 6), until the moment preceding a strike, when they both point forwards. Seahorses and pipefish, which, like chameleons, have distinct foveas, have similarly asynchronous saccades. One particularly remarkable fish, the sandlance (*Limnicthyes fasciatus*), differs from all other vertebrates in that, following each saccade, the eye is not held still but drifts back towards a central position (Pettigrew et al. 1999).

3 Saccades and Fixations Outside the Vertebrates

The logic of Walls' argument – that the main function of eye movements is to keep the image still on the retina – should apply equally to those invertebrates that have good eyesight. This means the arthropods, especially crustaceans and insects, and cephalopod molluscs. Figure 7 shows a record of a rock crab, moving in a curvilinear path. Like the goldfish (Fig. 2), the eyes make fast saccadic eye movements with slow movements between them that compensate for body rotations. These slow movements result in periods of stationary gaze. Like vertebrates, crabs have a powerful optokinetic reflex and also the equivalent of a vestibular system that measures body rotation. Clearly, the saccade and fixate strategy is not just an idiosyncrasy of the vertebrate oculomotor system.

Insects too employ saccades and fixations. The situation here is different as the eyes are part of the head, so gaze stability has to be achieved by neck movements to compensate for rotations of the body. Figure 8a shows the head and body of a walking stalk-eyed fly, turning through a right angle. The head makes two saccades, at 120 ms and just before 400 ms, but before and between these movements, the head angle does not change. Flying flies behave rather similarly. In an impressive study, Schilstra and van Hateren (1998) recorded from both the head and thorax of flying blowflies with miniature search coils. Figure 8b shows that both the body and head rotate jerkily, but the head moves faster, and there is compensation for the slower body rotation (head on thorax), resulting in crisp changes of gaze (head).

Hoverflies have such fine control of their body angle during flight that they dispense with neck movements. The result is that 'saccades' appear as rapid changes

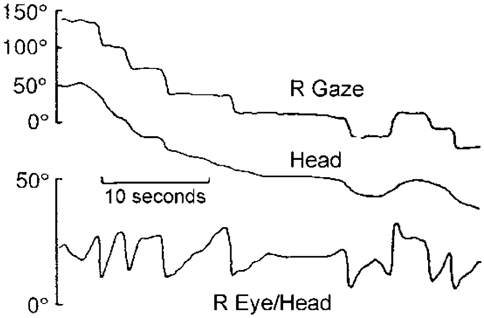

Fig. 7 Gaze, head and eye movements of a rock crab walking on a curved path. As with the goldfish (Fig. 2), the role of eye movements is twofold: to make gaze-shifting saccades and to compensate for movements of the head. Note that the eye/head scale is magnified. Redrawn from Paul et al. (1990)

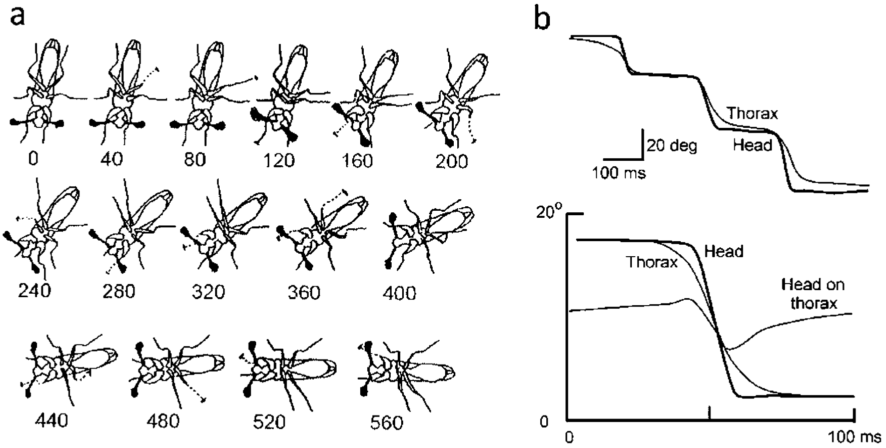

Fig. 8 (**a**) Stalk-eyed fly walking through a right angle on a glass plate. It makes two saccades (at 120 and 380 ms), with fixations in between (redrawn from an unpublished film by W Wickler and U Seibt). (**b**) Three saccadic turns made by a flying blowfly (top) showing the steplike rotations of the head in space and slower movements of the body. Below is a detail of a single saccade, showing the counterrotation of the head on the thorax. Both adapted from Schilstra and van Hateren (1998)

in orientation of the whole body, with ‘fixations’ between them in which translational flight continues but body angle is held constant (Collett and Land 1975). Interestingly, males have a frontal region of higher resolution, not present in females, and they use this to track the females while remaining out of sight by keeping at a distance of 10 cm. Males, in other words, behave like primates; females behave more like goldfish. Praying mantids also track their prey, with their heads. Against textured backgrounds, the tracking is saccadic, but against plain backgrounds, it is smooth, presumably because the optokinetic signal is too weak to prevent head rotation (Rossel 1980).

Outside the arthropods, the only other major group of animals with mobile eyes are the cephalopod molluscs (*octopus*, cuttlefish and squid). They show the same kind of nystagmus as vertebrates when placed in a rotating striped drum (Hanlon and Messenger 1996), and in the cuttlefish *Sepia*, saccade and fixation movements occur during spontaneous swimming (Collewijn 1970). These compensate for yaw and roll. *Octopus* has seven eye muscles, but cuttlefish and squid have an additional six or seven. These extra muscles are involved in the convergent eye movements which provide binocular vision prior to prey capture, movements that are absent in *octopus* (Budelmann 2009).

There are a few invertebrates that break all Walls' rules by making slow scanning eye movements during which they take in information. Jumping spiders scan images with slow torsional movements and faster side-to-side movements whose functions are to determine identity: specifically, whether a newly detected object is a conspecific or potential prey. Mantis shrimps (Stomatopoda) use scanning movements to extract information about colour and polarisation. Heteropod sea snails scan the water beneath them to detect plankton to feed on. In all these cases, the retinas (or relevant parts of the retina) are one-dimensional strips a few receptors wide, and the scanning movements are sufficiently slow that they do not interfere significantly with resolution (Land and Nilsson 2012).

4 Conclusions

Walls (1962) argued that vertebrate eye movements originated in the need to avoid motion blur by maintaining a stationary image and that this was achieved via vestibulo-ocular and optokinetic fixation reflexes, which evolved in the earliest fishes. Saccades evolved initially as movements to recentre eye direction when an animal turned. This saccade and fixate strategy is found in animals with good eyesight in all major phyla. In man, and other foveate vertebrates, this pattern of eye movements became adapted for a second function: the targeting of particular objects by the fovea, to obtain the benefits of improved resolution.

In primates two other types of eye movement supplement this targeting role. Smooth pursuit allows a moving object to be kept in central vision, but this inevitably means that the background is allowed to blur, with VOR and OKN temporarily suspended. Primates, and some other animals with forward facing eyes, use vergence to direct both foveas to targets at different distances, incidentally allowing stereoscopic range finding.

Head movements augment eye movements in many vertebrates and in birds almost replace them. In insects, with immovable eyes, neck movements, and sometimes whole-body movements, perform saccades and stabilise fixations. Cephalopods have a range of eye movements remarkably similar to those of fish, including vergence movements in cuttlefish and squid when they are about to strike prey.

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