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Published in:
Journal of Experimental Biology

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1982

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):
Jüch, PJW. (1982). Do the Extraocular Muscles in the Carp Compensate for Eye Displacements Induced by Respiratory Movements? *Journal of Experimental Biology*, 99(AUG), 363-368.

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DO THE EXTRAOCULAR MUSCLES IN THE CARP COMPENSATE FOR EYE DISPLACEMENTS INDUCED BY RESPIRATORY MOVEMENTS?

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(Received 12 February 1982 - Accepted 30 March 1982)

SUMMARY

The eyes in normally respiring carp are induced by elements of the respiratory pumping system to make small displacements in phase with the respiratory cycle. The ocular movements were studied by film analysis during the normal respiratory cycle and the cough. In the course of the movement, the optic axis remains nearly parallel to its starting position. This results in a smaller retinal image shift than would be produced by angular movements.

Electromyography of the extraocular muscles showed that the external rectus and superior oblique muscles contribute to image stabilization during strong respiration, and the external rectus and the superior oblique muscles contribute during the cough.

INTRODUCTION

In fish, three types of spontaneous eye movements, known as saccades, stretches and slow movements can be distinguished (Easter, 1971; Hermann & Constantine, 1971). Saccades are short twitches by which the eye suddenly shifts its angle of gaze. Stretches are short movements during which the eye jerks in the caudo-ventral direction in tenths of seconds. Slow movements are interposed between saccades and appear as small and slow eye drifts.

Compensatory eye movements, necessary to maintain the retinal image stationary in spite of movements of the animal, are described in detail for teleosts by Easter *et al.* (1974*a, b*) and by Traill & Mark (1970) and for dogfish by Harris (1965). Visual input and activation of the vestibular organs are the main stimuli eliciting compensatory eye movements.

Small lateral movements of the eyes in phase with the respiratory cycle can also be distinguished in free-swimming carp. These movements are induced by elements of the respiratory pumping system surrounding the eyes on three sides.

In this paper, electromyography of the extraocular muscles (EOM's) is used to investigate whether induced eye movements are reduced through compensatory contractions of the EOM's.

METHODS

The carp (length 15–25 cm) were fixed to a frame with a clamp on the skull, the body being supported by a plastic trough. Under MS 222 anaesthesia (35 mg/l) the spinal cord was transected to eliminate all movements except for those of the head (e.g. respiration and eye movements). The animals were then placed in the experimental tank without anaesthetic and allowed to recover for 2 h prior to the experiments.

(A) Movement analysis

A polyethylene stalk (2 mm wide, 10 mm long) was fixed on the cornea by suction (Easter, 1972), indicating the angle of gaze. Eye movements were filmed with a 16 mm cine camera (Beaulieu, 64 frames/s) from dorsal and frontal directions with the aid of two mirrors. Analysis of the displacements of tip and base of the eye stalk was performed on a Vanguard motion-analyser. Only eye movements induced by respiration were analysed. The movement of the hyomandibula was used to represent respiration.

(B) Electromyography

For electromyography electrodes were placed before the effect of anaesthesia disappeared. Two wire electrodes (Karma alloy wire, 25 μm in diameter), insulated except for the tip, were separately inserted with the aid of a 30-gauge hypodermic needle in one of the EOM's, while the eye was turned away with forceps. The wire was pulled through the needle and the distal end folded over its tip (Basmajian, 1974). After insertion the hypodermic needle could be withdrawn, while the electrode remained in the muscle. Care was taken not to damage periocular tissues, to prevent leakage of the fluid behind the eye. Such leakage reduces the pressure behind the eye and results in a change in its movement characteristics. Electrode position was checked by electrical stimulation.

A second pair of electrodes (copper wire, 50 μm) was inserted in the levator hyomandibulae to obtain information on respiratory pumping activity. The signals from the electrodes were amplified with Grass-P15 preamplifiers. Movement of the hyomandibula was recorded with a mechano-electrical transducer. Horizontal eye movements were recorded with a mechano-electrical transducer placed against the polyethylene stalk on the eye. All data were recorded on FM tape.

RESULTS

(A) Movement analysis

Displacement and angular rotation of the eye ball were determined from movements of the base and tip of the eye stalk. In all fish, a different pattern was observed during normal respiration than during the cough (e.g. Fig. 1).

During respiration the eye moves in three directions: it moves in and out, up and down, and also forwards and backwards. The backward movement is the largest: more than 1 mm. During normal respiration the vertical movement is nearly circular, the horizontal an ellipse. During the cough, when the hyomandibula performs a

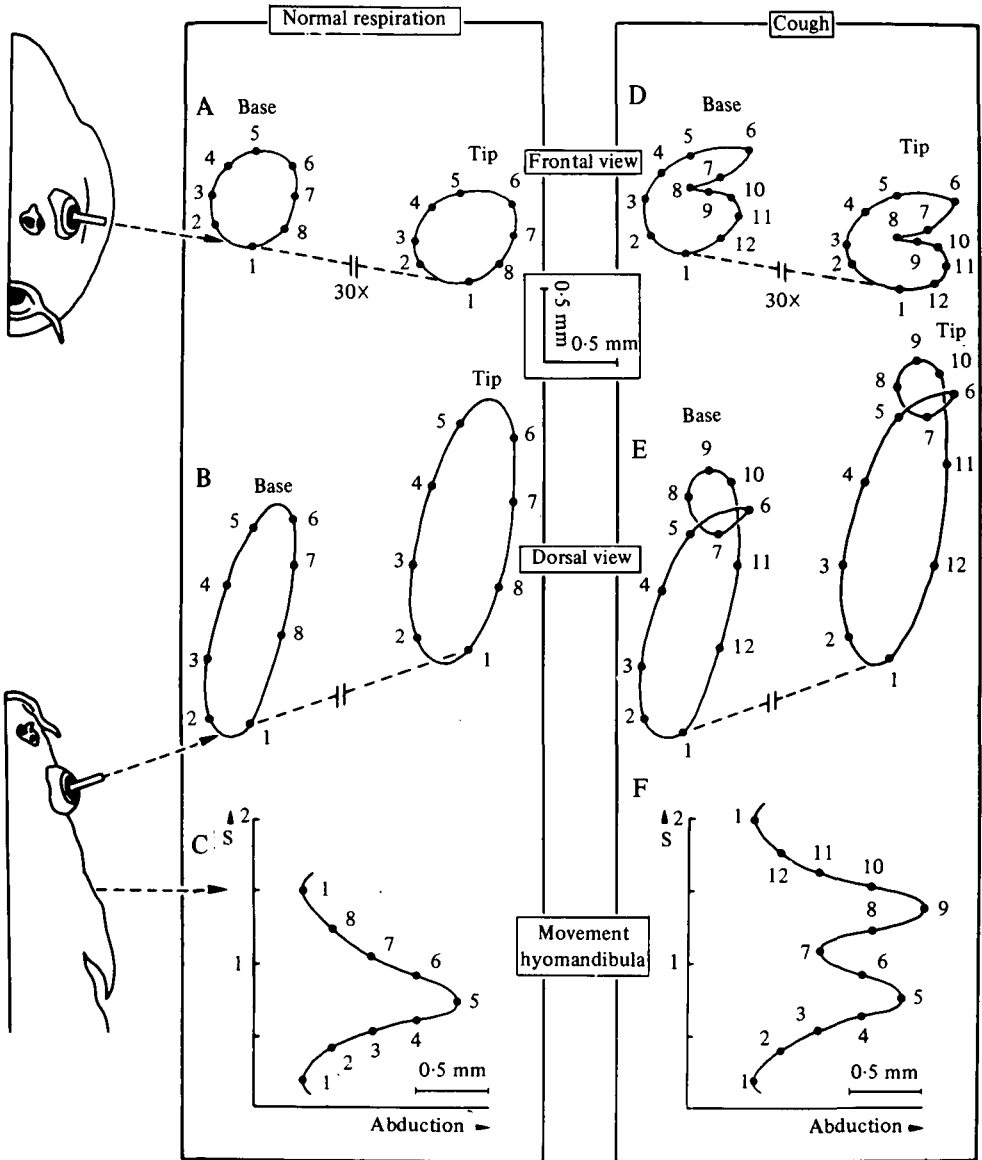


Fig. 1. Showing the head of the carp as seen on the cinematographic records, together with the graphs of the eye stalk and hyomandibular movements during normal respiration (left box) and the cough (right box), averaged over 10 respiratory cycles. In A and D the movements of the tip (right graphs) and base (left graphs) of the eye stalk are projected in the transverse plane, in B and E in the horizontal plane. Note that at the given magnification, these curves should be 30 × further apart. C and F display the movements of the hyomandibula against time. The numbers in the graphs represent corresponding times during the cycle.

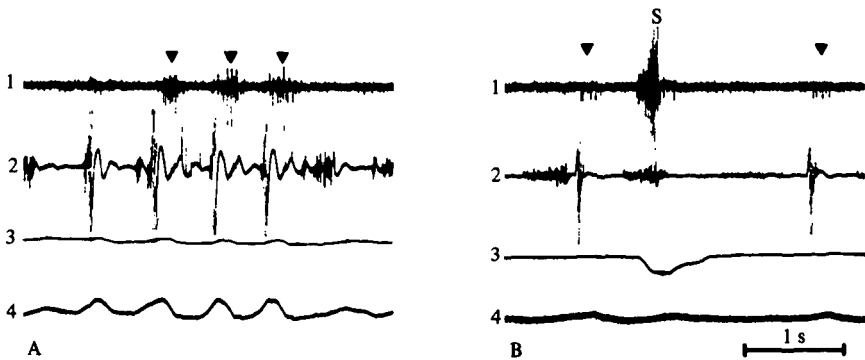


Fig. 2. Electromyograms recorded from the oblique muscles. (A) activity of the superior oblique muscle during strong respiratory movements (arrows). (B) EMG of the inferior oblique muscle recorded during the cough (arrows) and the stretch (S). 1, EMG eye muscle; 2, EMG levator hyomandibulae; 3, horizontal movement transducer, eye (upward = nasal direction); 4, movement transducer, hyomandibula (upward = abduction).

double abduction movement of greater amplitude (Ballintijn, 1969), the eye displacements get more complex. In the vertical plane the circle shows an indentation while in the horizontal plane an extra loop develops, increasing the total amplitude of the movement (Fig. 1).

The numbered circles in the graphs indicate positions measured at the same time during the cycle. The angular position of the eye stalk (the direction of gaze) can be determined by interconnecting corresponding numbers from the tip- and base-curve (as shown for the circles 1). While the linear movement of the eye is appreciable, a rotational movement is virtually absent and the angle of gaze remains nearly the same (maximal rotation less than 1°).

(B) *Electromyography of the EOM's*

During the stretch the superior oblique muscle becomes active. A slight tonic contraction is recorded when the eye turns away (the temporal phase of the stretch), followed by markedly increased activity in the nasal phase. During normal respiration and the cough the muscle is not contracting, but during the adduction phase of strong respirations it becomes intensely active (Fig. 2A).

The inferior oblique muscle contracts slightly during every cough but no activity can be recorded during normal respirations (Fig. 2B). During the temporal phase of the stretch strong EMG's are observed in this muscle. EMG's in the superior rectus muscle can only be recorded during the nasal phase of the stretch, while the inferior muscle contracts in the temporal phase. Both muscles remain inactive during normal and strong respiration and during the cough.

Saccades in rostral directions are accompanied by contractions of the internal rectus muscle. EMG's also appear during the temporal phase of the stretch. Respiration related contractions of the internal rectus muscle were never observed. Contractions of the external rectus muscle, however, appeared to be present in the abductions of

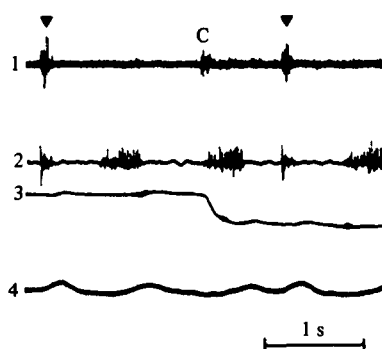


Fig. 3. EMG recording of the external rectus muscle during the cough (arrows) and caudal saccade (c); traces 1-4 as in Fig. 2.

Table 1. *Combined results of electromyography.*

+, activity recorded; -, no activity recorded. During normal respiration no activity was recorded in any of the EOM'S.

	Saccade		Stretch		Strong respiration		
	Rostral	Caudal	Nasal	Temporal	Abduc- tion	Adduc- tion	Cough
Obliquus superior	-	-	+	-	-	+	-
Obliquus inferior	-	-	-	+	-	-	+
Rectus superior	-	-	+	-	-	-	-
Rectus inferior	-	-	-	+	-	-	-
Rectus internus	+	-	-	+	-	-	-
Rectus externus	-	+	-	+	+	-	+

strong ventilations and always accompanied a cough (Fig. 3). The caudal saccades and the temporal phase of the stretch are always attended by external rectus muscle activity. No activity could be elicited in any of the six extraocular muscles as a result of artificial movements of the eye-ball. The results of electromyography are combined in Table 1.

DISCUSSION

The results show that the eye of the carp makes only very small rotations in spite of the large linear movements during respiration. During ordinary quiet respiratory movements no evidence for contractions of any of the six eye muscles could be found. Hence the conclusion must be drawn that the mechanical arrangements in the orbits are such that normal respiration movements cause linear displacements of the eye, and the absence of marked rotation is not due to compensatory EOM contractions.

With high-intensity respiration when the amplitude of all movements is considerably increased, the superior oblique and external rectus muscles are activated during respiratory contraction and expansion respectively. Moreover, the external rectus muscle contracts during the cough in the abduction phase of the intermediate expansion, together with the inferior oblique muscle. As the intermediate expansion is more vigorous than a normal respiration and the movement pattern is different (Ballintijn,

1969), the eye position will be influenced more strongly. It can be concluded, therefore, that during strong respirations and the cough these three muscles do exert an additional stabilizing influence.

The linear displacements which are apparent during normal respiration and remain during strong respiration and the cough will cause minor retinal image shifts. These are corrected centrally according to Ballintijn, Luiten & Jüch, (1979). The compensatory eye-muscle contractions are not elicited by proprioceptive feedback from ocular mechanoreceptors because stimuli changing the eyeball position failed to activate the muscles. It seems therefore possible that the respiratory rhythm generator itself provides correcting input and research is currently performed to test this hypothesis.

Hester (1968) proposed that stretch movements are apparently associated with the respiratory cleaning motion. The present experiments also showed that a stretch occurs during the first normal respiratory cycle after a cough in more than 90% of all records. Its function is still unknown and remains subject of further investigation.

This study was supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for the Advancement of Pure Research (ZWO). The author thanks Dr C. M. Ballintijn and Dr P. G. M. Luiten for their helpful advice and criticism and Mrs J. Poelstra-Hiddinga for her secretarial aid.

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