Perception of Fourier and non-Fourier motion by larval zebrafish

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A moving grating elicits innate optomotor behavior in zebrafish larvae; they swim in the direction of perceived motion. We took advantage of this behavior, using computer-animated displays, to determine what attributes of motion are extracted by the fish visual system. As in humans, first-order (luminance-defined or Fourier) signals dominated motion perception in fish; edges or other features had little or no effect when presented with these signals. Humans can see complex movements that lack first-order cues, an ability that is usually ascribed to higher-level processing in the visual cortex. Here we show that second-order (non-Fourier) motion displays induced optomotor behavior in zebrafish larvae, which do not have a cortex. We suggest that second-order motion is extracted early in the lower vertebrate visual pathway.

Zebrafish larvae innately begin responding to moving stimuli shortly after hatching. In their optomotor response, which is elicited by large moving stimuli presented from below or the side[1,2], larvae swim in the direction of perceived motion. The distance they travel in a given time indicates the effectiveness of the stimulus. By observing the response of many larvae to computer-animated displays, we could determine which attributes of a moving stimulus the zebrafish visual system detects.

If luminance-defined features drift smoothly or jump in space, they can produce strong sensations of motion. A number of proposed models explain how motion information can be extracted. In a simple model, a point-to-point comparison is made between the luminance pattern and a spatially displaced copy of the pattern that was seen a short time before[3]. The displacement that gives the best fit tells the brain the direction and speed of movement. A more complex strategy is to look at the Fourier motion energy in the visual scene[4]. A number of biologically plausible methods of calculating this motion energy have been proposed[4,5,6].

Although there is evidence that humans can use both feature matching and motion energy to detect movement[7], they may also sense motion when presented with stimuli in which only second-order features such as contrast, texture or flicker are moving[8]. This has been called second-order motion[9] or, because such stimuli contain no overall motion energy, non-Fourier motion[10]. There is much evidence that humans and primates can see second-order motion, but this has not been established for non-mammals[11]. Neurophysiological recordings in monkeys[12] and cats[13], and psychophysical and neurological findings in humans[14] suggest that the visual cortex contains separate processing streams for first-order and second-order motion[15]. These studies imply that an elaborate visual cortex enables humans and some other mammals to perform 'higher-level' motion processing, raising the question of whether an animal without an elaborate cortex can see second-order (non-Fourier) motion.

Here we find that the fish larvae detect moving features of visual stimuli in a way that is qualitatively similar to humans: both first-order and second-order cues drive their behavioral response. Our demonstration of second-order motion detection in fish challenges the idea that higher-level, cortical mechanisms are necessary to explain this capacity of the visual system.

Results

Optomotor responses to Fourier motion

The assay used to measure optomotor responses is similar to the one described previously[2] (Methods). Movies showing drifting gratings evoke strong optomotor responses in almost all fish in a clutch. Fish do not respond to a moving grating with a stripe width narrower than approximately 9°, which is slightly less than the predicted resolution limit of the larval cone mosaic, 6° at this age[1,16]. They respond well to gratings at lower spatial frequencies and at all temporal frequencies tested up to 14 Hz, which is the limit set by the update rate of our monitor.

In the following experiments, responses were normalized to the effect of a designated strong stimulus, a 100% contrast square wave subtending 100° of visual angle per cycle and moving at 1 Hz for 30 seconds (Fig. 2a). The normalized quantity was called the optomotor index (OMI). Relatively long stimulus durations were chosen because they produced clear shifts in the distribution of fish even with very weak stimuli, but long integration times were not necessary to produce the optomotor response. By averaging over many trials, we could detect behavioral responses to stimulus presentations lasting less than one second (Fig. 1a), suggesting that some fish responded almost immediately to the motion presented.

Although the fish seemed to follow a motion signal in the movies, it was possible that they were tracking features such as light or dark regions or edges that were being displaced. We did an experiment to show that the optomotor response is truly a response to motion. A motion display was shown of a sine wave grating that

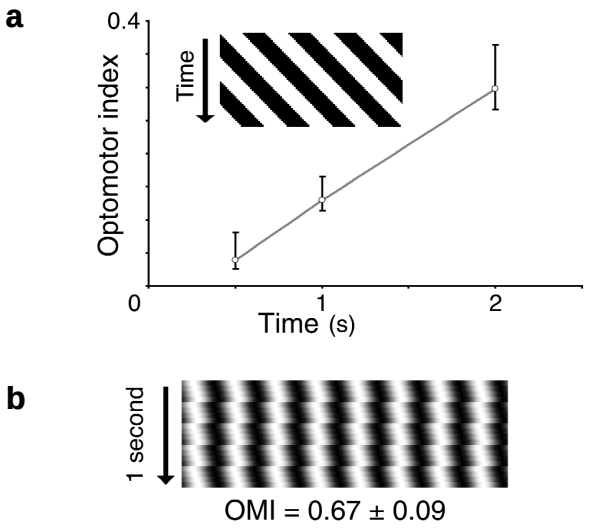


Fig. 1. The optomotor response of zebrafish larvae does not depend on long integration times or feature displacement. (**a**) The optomotor response is elicited by short stimulus presentations. Normalized difference in average position of fish (optomotor index, OMI) after short presentations of a square wave drifting in alternate directions. The stripes of the square wave subtended 60° of visual angle, and the frame update time was 40 ms. Upper error bars, standard deviation between trials; lower bars, 90% confidence intervals ($n > 12$). (**b**) The optomotor response is a response to motion. Space–time plot of a movie in which a drifting sinusoidal grating with 60º visual angle per cycle moving at 0.8 Hz is reset to its original position every 200 ms. The frame update time is 50 ms. The stimulus evokes robust optomotor behavior (OMI ± s.d., 0.67 ± 0.09, $n = 9$).

moved with constant velocity, but was reset every 200 ms to its original position, thus never moving through more than one sixth of its spatial period (Fig. 1b). If the fish were tracking features, we would expect little or no response from them, because there was no net displacement of the bars. However, the fish swam vigorously with the direction of smooth movement (OMI ± s.d; 0.67 ± 0.09), suggesting that they indeed detected motion cues in the display.

In a drifting square-wave grating (Fig. 2a), Fourier motion energy and edges or other features all move in the same direction. To determine which attribute of the motion stimulus is detected by the zebrafish optomotor system, we modified the square wave by subtracting out the spatial fundamental[4] (Fig. 2b). In this 'fluted square wave' movie, the features of the stripes still moved to the left, but the Fourier energy contained in the dominant third spatial harmonic moved to the right. In this case, the fish saw motion to the right. When we then subtracted the third harmonic, the fish saw the leftward moving fifth spatial harmonic (Fig. 2c). The contrast and apparent velocity of the third and fifth harmonic are one third and one fifth of the fundamental, respectively. As expected, the responses to the latter stimuli were only a fraction of the response to a square wave, but they were always consistent with a Fourier mechanism.

We were concerned about spectral artifacts that were caused by the jumpy animation necessary for the fluted square wave effect. However, in all three cases discussed, these artifacts would have net motion energy in the direction opposite to the direction of swimming, and so could only serve to obscure the effect seen. In another study, a cleaner stimulus consisting only of equal-contrast third and fourth harmonics was used[7]. If animated in leftward jumps of one quarter the spatial period, then the third harmonic stepped in quarter-phase to the right, and the fourth harmonic was stationary, whereas the pattern's features stepped to the left (Fig. 2d). The fish followed the third harmonic to the right, indicating that in this and the above cases, Fourier cues were dominant over feature cues.

To further explore what cues induce motion perception in zebrafish, we used another test from human psychophysics[3,17,18]. White stripes jumping leftward on a gray surround (Fig. 2e) elicited an optomotor response to the left. In the 'reversed-phi' movie, the stripes reversed polarity on each consecutive movie frame, alternately appearing white and black (Fig. 2f). The salient features of the display, including edges and objects, still moved to the left, but the highest-amplitude Fourier component moved to the right[4]. In agreement with a motion energy-based model, the fish responded to this stimulus by swimming to the right, in the direction opposite to stripe movement.

Optomotor responses to non-Fourier motion

Our experiments showed that zebrafish use Fourier (first-order) cues to determine the direction of motion, raising the question of

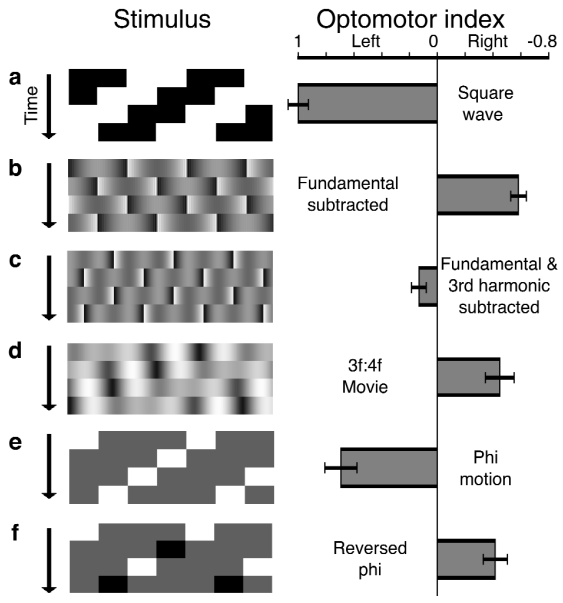


Fig. 2. Psychophysical tests for the detection of Fourier motion by zebrafish. Six different stimuli and the corresponding optomotor responses. The optomotor index (OMI) is a measure for the strength of the stimulus (**Fig. 1**). (**a**) A high-contrast square wave, in which each stripe subtends a visual angle of 60°. (**b**) The same square wave after subtraction of the fundamental Fourier component. (**c**) The same square wave after subtraction of fundamental and third harmonic. (**d**) A stimulus consisting of two superimposed 50% contrast gratings of relative spatial frequencies 3f and 4f. The resulting pattern has a fundamental spatial frequency of f. The 4f grating remains stationary, whereas the 3f steps to the right, causing the contrast modulation, which has frequency f, to move to the left. (**e**) Phi motion. Drifting white bars subtending a visual angle of 33° on a gray background. (**f**) Reversed phi motion. The same stimulus as (**e**), but with every other frame reversed in contrast. Error bars, standard deviation of OMI between individual sets of stimulus presentations ($n = 6$ to 22). All stimuli were presented at four frames per second.

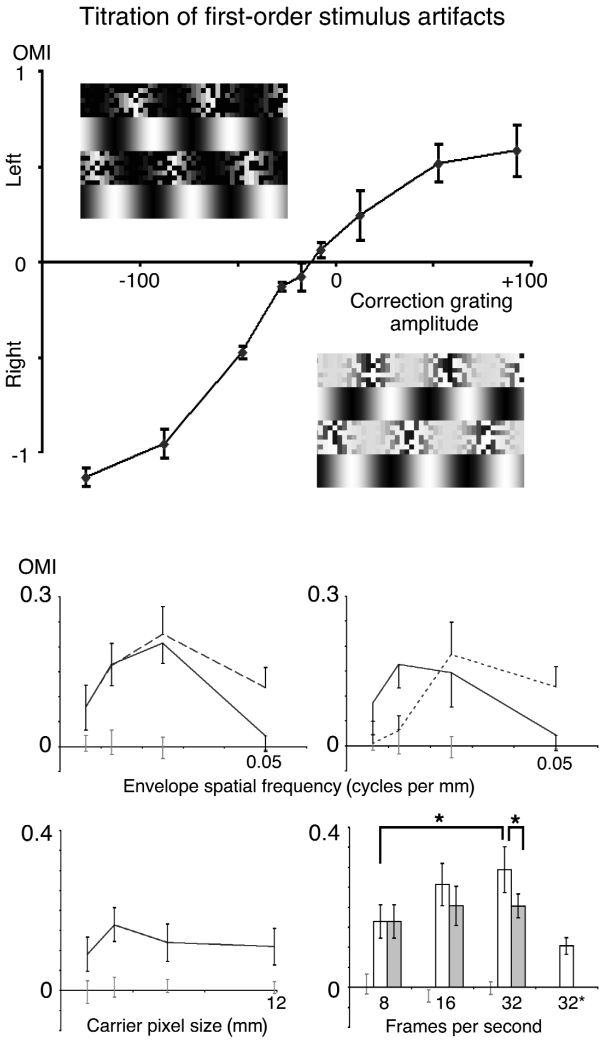


Fig. 3. Contrast-defined second-order motion evokes optomotor behavior in zebrafish. (**a**) Control stimulus used to measure first-order cues in a contrast-modulated random dot array. A 4-frame movie was devised in which the contrast-modulated grating was alternated with a high-contrast sine wave at the spatial frequency of the contrast envelope (75° per cycle). The peak of the sine wave/contrast envelope was shifted one quarter-cycle to the right between each frame. A sinusoidal correction grating of variable amplitude was added to the odd-numbered frames. Insets, two extreme amplitudes of the correction grating, –127.5 (left) and +92.5 (right) look-up table units. OMI is plotted as a function of the added correction. The fish either swam to the right or to the left, and their response could be canceled (that is, OMI = 0) at some intermediate amplitude. The carrier dots subtended a visual angle of 5.5°. Error bars, standard deviation of the OMI between individual stimulus presentations (n = 2 or 3). Each stimulus was presented for 60 seconds at 1 Hz (4 frames per second). (**b**) OMI varies with envelope spatial frequency (black line, downward pointing error bars), when temporal frequency is held constant at 2 Hz, and the frame update time is 125 ms. Carrier pixels subtend 5.5°. The tuning is different than for a 5% contrast luminance grating (dotted line, upward pointing error bars). Error bars, 90% confidence intervals ($n \geq 10$, here and in **c–e**). Confidence intervals for the control movie under the same conditions are shown in dark gray. Both control and test movies are presented for 30 seconds at 8 to 32 frames per second. (**c**) Similar to (**b**), but the velocity is held constant at 55° per second. Note the difference in tuning between the first-order and second-order responses. (**d**) Keeping envelope spatial frequency constant at 87° per cycle and moving the envelope with temporal frequency 2 Hz and a frame update time of 125 ms, we measured the variation of OMI with carrier pixel size (black line). Pixels subtending 2.7–22° (2 to 16 screen pixels) were used. (**e**) Holding velocity and spatial frequency constant as in (**d**), we varied the frame rate and animation smoothness. Ninety percent confidence intervals for the control movie played under the same condition are shown. In some cases, both noise and envelope position were updated every frame (white bars), and in others, noise was updated every frame, but the envelope was only updated eight times per second (gray bars). Four-fold smoother animation of the envelope significantly increased OMI, even if the noise was updated at the faster rate (*one-tailed t-test, $p < 0.01$). At 32 frames per second, the smoothly animated contrast envelope could elicit an optomotor response, even if its position was reset every 187.5 ms, before it had moved through a third of its spatial period (white bar, 32*).

how fish would respond to a motion display that lacks motion energy. One such second-order stimulus[10] has been used widely in primate psychophysics. A dynamic random noise pattern is modulated in contrast by a coarse sine wave that drifts to the right. Such a stimulus is said to be drift-balanced, that is, at any spatial frequency range, one would expect equal numbers of leftward- and rightward-moving components. Before determining whether the fish follow the drifting contrast envelope, we had to confirm that this stimulus was a true second-order display.

One potential problem was that first-order artifacts may be introduced because of non-linear properties of the peripheral visual system or the computer display[19,20]. Such unwanted luminance artifacts would move with the contrast envelope and generate first-order motion. We eliminated this possibility with a motion-nulling technique (Z-L. Lu & G. Sperling, *ARVO Abstr.*, 1047, 1999)[20], that removed first-order signals from the stimulus (Fig. 3a). As a control, movie frames containing contrast-modulated (CM) noise patterns were interleaved with luminance-modulated (LM) gratings of the same spatial frequency (Fig. 3a, insets). Two extreme examples are shown. In the first example (Fig. 3a, left), the low-contrast regions appear very dark, as would be the case for an expansive distortion early in the visual pathway, and these can be joined with the dark stripes in the LM frames to generate a rightward moving pattern. As expected, this stimulus drove fish to the right. In the second example (Fig. 3a, right), the low-contrast regions appear very bright (as for a compressive distortion). Bright bars appeared to step to the left and drove the fish to the left. By adding appropriate sinusoidal gratings to the CM frames, we titrated the fishes' response to zero, demonstrating that any first-order artifacts were canceled out[20]. To create our test movie, we replaced the LM frames of the control movie with (corrected) CM frames. This motion display still evoked optomotor responses (Fig. 3b), which must be induced by second-order cues.

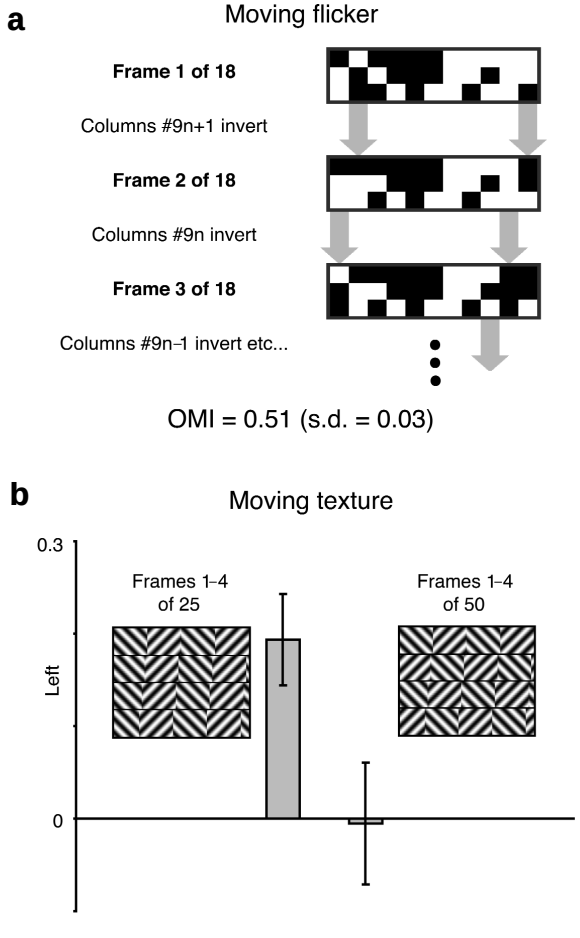
Many models of second-order motion perception involve a full-wave rectification of the luminance pattern, followed by a motion energy calculation[6,10]. This would tend to reduce the spatial resolution of the second-order system, raising the question of whether the hypothetical second-order motion pathway in zebrafish responds to the same range of stimuli as the first-order pathway. The OMI was determined for CM (second-order) and LM (first-order) gratings with different spatial frequencies, while either the temporal frequency (2 Hz; Fig. 3b) or the velocity (55° per s; Fig. 3c) was held constant. The CM grating gave a much lower response than the LM grating at high spatial frequencies,

but a relatively higher response at low spatial frequencies, consistent with the above models. The OMI varied very little with carrier pixel size (Fig. 3d), although it dropped when the pixel size was significantly below the fishes' expected limit of resolution, six degrees[16]. In all experiments and conditions, we ensured that the response to the control movie was zero.

Finally, we tried to enhance the response to the second-order stimulus by animating the CM gratings more smoothly at the higher velocities, although the responses were always weaker than during a high contrast LM movie (Fig. 3e). Increasing the frame update rate introduced an additional variable, flicker rate, which may also increase the response of the fish by making the stimulus more salient. The noise carrier was updated every 125, 62.5 or 31.25 ms, and the CM grating, which always moved with the same mean velocity, was either updated at the same rate (Fig. 3e, white bars) or every 125 ms (gray bars). The higher rates of flicker did not significantly enhance the strength of the motion stimulus *per se*, unless the smoothness of the grating animation also improved. This experiment suggested that spatial contrast is the salient motion cue in this stimulus. It also provided evidence that responses to second-order stimuli are true motion responses, as smoother motion with the same target displacement gave a larger response. To further verify this, we replayed the most smoothly animated movie, but reset it every 187.5 ms, so that the net displacement was zero. The fish still responded (Fig 3e; white bar, right).

To determine whether contrast-modulated motion was the only type of second-order motion that the fish could see, we showed two other second-order stimuli, to which the fish gave a consistent response (Fig. 4). The first stimulus, which was drift-balanced, consisted of a static array of black and white pixels (Fig. 4a). Between movie frames, the black pixels of every ninth column turned white, and white pixels turned black. In consecutive frames, these flicker-defined stripes drifted column-by-column to the left, causing humans to perceive a moving illusory column. Strikingly, the fish also followed the flickering column to the left (OMI ± s.d., 0.51 ± 0.03), in the strongest of all the second-order responses observed. A simple brightness non-linearity, or even full-wave rectification, were not enough to explain this response.

We then presented a movie of drifting columns defined by oblique sinusoidal gratings, oriented alternately at +45° and –45° (Fig. 4b, left). The adjacent gratings created an illusory contour, which humans could clearly see. The phase of the grating was randomized in each column between every frame to eliminate first-order cues. The fish swam in the same direction as the columns were drifting (Fig. 4b, left), but it was unclear from this experiment whether the fish were following the regions of similar orientation, the illusory contours between the columns, or the discontinuities, which consisted of local regions of high spatial frequency. When the orientation in each column was switched between frames, the response was eliminated (Fig. 4b, right). This suggests that the fish were not simply following the local components of high spatial frequency or the illusory contours, but were sensitive to the orientations on either side of the break. These experiments demonstrated again that fish larvae are able to respond to motion in the absence of Fourier signals.



Discussion

We used a series of psychophysical tests to dissect the properties of motion processing in larval zebrafish, and showed that these properties are similar to those of primates. We were interested in which attributes of a moving stimulus are detected by the optomotor pathway of this species, and whether fundamental differences in visual processing exist between teleost fish and higher mammals. The fluted square wave (Fig. 2b) and reversed-phi (Fig. 2f) tests show that zebrafish motion detection relies on Fourier motion-energy (if available) to determine direction of a moving stimulus. Edges or other features have a minor role, if any, if their displacement is pitted against that of the Fourier signal.

We show that the fishes' behavior was a response to motion information in the stimuli, not merely to the displacement of a

Fig. 4. Flicker-defined and orientation-defined second-order motion evokes optomotor behavior in zebrafish. (**a**) A second-order motion stimulus, consisting of a random dot pattern in which a region of flicker moves to the left. Columns of dots spaced at intervals of nine dot-widths reversed in contrast between each frame, and the array of columns that were reversing shifted one dot-width to the left. The dots subtended a visual angle of 5.5°. (**b**) Two stimuli were presented to the larvae, each for 60 seconds. The first movie (left) consisted of vertical columns subtending a visual angle of 62°. The columns contained sinusoidal gratings with a spatial frequency of 27° per cycle, oriented at 45° to the column boundaries. The grating in each column was orthogonal to that in neighboring columns. Its phase was randomized between each frame. The column boundaries shifted to the left, and the movie repeated every 25 frames. The second movie (right) was created by taking two repeats of the first movie and flipping every even frame vertically. The OMI for the fish was calculated as in Fig. 1, and error bars show the standard deviation for individual sets of stimulus presentations (n = 16 and 7, respectively).

visual target. The fish responded strongly to a movie in which motion, but not displacement of features, gives a directional cue (Fig. 1b). The fish never swam rigidly in phase with a moving grating, and indeed followed gratings that moved at up to 1100° per s, many times faster than they swim. They responded preferentially to motion energy when it was placed in competition with feature displacement (Fig. 2). Our demonstration of second-order motion detection is difficult to reconcile with a model in which the fish merely track a jumping target.

After having shown that zebrafish larvae extract Fourier-motion energy if available, we wanted to determine whether we could find indications of primate-like 'higher-level' motion processing, of which the neural substrate is assumed to be in the visual cortex. We found optomotor responses to three types of second-order motion displays, which lack Fourier cues. The fish larvae saw a contrast envelope that moved across a random array of twinkling dots (Fig. 3), a sweeping column of random black-and-white dots that reversed the dots' luminance (Fig. 4a), or a moving grating whose borders were defined by obliquely oriented stripes (Fig. 4b). We eliminated any luminance artifacts created by the monitor or by early non-linearity in the fish visual system.

The zebrafish visual system is equipped with neuronal mechanisms to process higher-order motion. The behavior of the fish in response to our artificial, computer-animated movies was always qualitatively consistent with the human interpretation of the motion signal. Are the mechanisms of motion processing conserved between vertebrates at the circuit level? If so, the site of processing may also be conserved. Many second-order features such as variations in spatial and temporal contrast can modulate the responses of retinal cells[21]. Although it is often assumed that the retina encodes luminance information linearly, there is a second-order output from the retina[22], which could provide an input to the classical 'first-order' motion detection system, without the need for further processing. This is still consistent with the models in which second-order motion is extracted from a rectified first-order signal[6,10], but places the site of this processing outside the cortex, perhaps within the retina. Our results, together with the demonstration of illusory contour perception in a bird[23], suggest that complex processing of visual scenes is not restricted to primates and other mammals, but may instead be an ability of all vertebrates. Further research with other methods is needed to map the motion pathway in the zebrafish brain.

The ability to extract all available motion cues is a crucial asset for the animals to survive in their natural environment. The optomotor response, used in this study as a behavioral indicator of motion perception, has an important function: it helps animals maintain their location in a fast-flowing stream and prevents them from being carried downstream, or from being sucked into the mouth of predators. The vestibular and lateral line systems of fish cannot detect movement at a constant velocity, and a muddy riverbed or moving vegetation may not present a clear first-order cue to motion. Reflective particles, such as sand grains in the river bed, may present a twinkling second-order stimulus, as they are stirred up by flowing water and fish are swept above them. We suggest that the psychophysical displays used here, although highly abstracted, represent real and behaviorally significant features of the animal's visual world[24].

Our results may relate to ongoing attempts to study the genetic underpinnings of zebrafish visual functions[2,25,26]. Our assay allows us to look at the behavior of hundreds of fish simultaneously, and thus might be used as an assay in systematic genetic screens for visual-system mutations, similar to the successful screens for embryonic mutations in this species[27,28].

Methods

Movies were shown on a computer monitor (832 × 624 pixels, 75 Hz, 256 gray levels) using a Macintosh G3 computer. The non-linearity of the monitor output was measured with a photometer, and corrected using a look-up table. Movies were programmed using the macro language of NIH Image, Version 1.6. For each experiment, 100 to 200 larvae (7 days old) were placed into 5 shallow, 230-mm-long acrylic tanks. The fish could swim back and forth in the tanks, 10–20 mm above the screen. A Kodak DC290 digital camera (Eastman Kodak) was used to record the distribution of fish, and could send an image to the computer every 25 seconds. The results were analyzed offline using the 'analyze particles' function of NIH Image, following background subtraction. This function finds all objects in a given size range in a thresholded image and returns their coordinates. After each test stimulus, the fish were driven back to the center of the tank by a strong optomotor stimulus (a converging sine wave, subtending 118° per cycle, played at 2 Hz). Each stimulus was presented for 30 seconds, except in the illusory contour movies, which were played for 60 seconds because it took longer for a clear response to accumulate (Fig. 4b).

Visual angles were calculated for a fish 15 mm from the monitor screen. The proximity of the fish to the screen meant that the retinal image of distant portions of gratings would subtend fewer degrees per cycle than the portion viewed from directly above. However, we observed that the fish do not respond to motion occurring outside about 20° from the vertical. Within this 40° response range, the period of a sine wave does not vary by more than 4%.

The optomotor index (OMI) was calculated as follows. The mean displacement of the fish from the center was averaged for two stimulus presentations, one forward and one backward. Each backward–forward cycle was repeated 4 to 29 times. The response strength (in cm traveled) was then normalized to response to a drifting square wave (Fig. 1a), which is assumed to be a strong stimulus. A positive OMI value indicates that the movie causes the fish to swim to the left. A negative OMI value indicates a response to the right. The movies can be obtained from the authors.

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