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RESEARCH ARTICLE

Weakly electric fish distinguish between envelope stimuli arising from different behavioral contexts

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ABSTRACT

Understanding how sensory information is processed by the brain in order to give rise to behavior remains poorly understood in general. Here, we investigated the behavioral responses of the weakly electric fish *Apteronotus albifrons* to stimuli arising from different contexts, by measuring changes in the electric organ discharge (EOD) frequency. Specifically, we focused on envelopes, which can arise either because of movement (i.e. motion envelopes) or because of interactions between the electric fields of three of more fish (i.e. social envelopes). Overall, we found that the animal's EOD frequency effectively tracked the detailed time course of both motion and social envelopes. In general, behavioral sensitivity (i.e. gain) decreased while phase lag increased with increasing envelope and carrier frequency. However, changes in gain and phase lag as a function of changes in carrier frequency were more prominent for motion than for social envelopes in general. Importantly, we compared behavioral responses to motion and social envelopes with similar characteristics. Although behavioral sensitivities were similar, we observed an increased response lag for social envelopes, primarily for low carrier frequencies. Thus, our results imply that the organism can, based on behavioral responses, distinguish envelope stimuli resulting from movement from those that instead result from social interactions. We discuss the implications of our results for neural coding of envelopes and propose that behavioral responses to motion and social envelopes are mediated by different neural circuits in the brain.

KEY WORDS: *Apteronotus albifrons*, Envelope, Perception, Electric organ discharge

INTRODUCTION

Understanding how sensory input gives rise to behavior (a.k.a. the neural code) is often complicated by the fact that natural sensory input displays complex and varying spatiotemporal characteristics. In several sensory modalities, natural stimuli consist of a fast-varying waveform (i.e. first-order) whose amplitude (i.e. second-order or envelope) varies independently and more slowly. These features have been observed in the auditory (Heil, 2003; Lewicki, 2002; Theunissen and Elie, 2014; Zeng et al., 2005), visual (Baker, 1999; Derrington and Cox, 1998), somatosensory (Lundstrom et al., 2010) and electrosensory systems (Fotowat et al., 2013; Metzen and Chacron, 2014; Stamper et al., 2013; Yu et al., 2012). Although it is recognized that these envelopes carry behaviorally relevant information and are critical for perception and behavior [visual processing (Grosof et al., 1993; Mante et al., 2005; Mareschal and Baker, 1998), stereopsis (Langley et al., 1999; Tanaka and Ohzawa, 2006), speech perception (Calhoun and Schreiner, 1998; Gourévitch et al., 2008; Nourski et al., 2009; Smith et al., 2002; Zeng et al., 2005), sound localization (Lohuis and Fuzessery, 2000) and determining whisking amplitude in the somatosensory system (Fee et al., 1997)], the nature of the underlying neural mechanisms remains poorly understood. It is important to note that, because the frequency contents of first- and second-order signals differ in general, nonlinear transformations are necessary to extract the envelope (Joris et al., 2004; Rosenberg and Issa, 2011; Stamper et al., 2013).

Gymnotiform wave-type weakly electric fish have recently gained popularity as model organisms for studying neural processing of envelopes in part because of their well-characterized anatomy and neural circuits (Bell and Maler, 2005; Maler, 2009a,b) and because of stereotyped and easily elicited behavioral responses (Metzen and Chacron, 2014; Stamper et al., 2012). These fish generate a quasi-sinusoidal electric field through the electric organ discharge (EOD) and can detect perturbations of this field caused by objects such as prey, rocks or plants, the conductivity of which is different than that of the surrounding water. When two conspecifics are within close proximity of each other (<1 m), interference between their EODs creates a beat with a frequency equal to the difference between the two EOD frequencies. Recent studies have shown that the amplitude of the beat (i.e. the depth of modulation or envelope) varies strongly as a function of the relative distance and orientation between both fish (Fotowat et al., 2013; Metzen and Chacron, 2014; Yu et al., 2012; see Stamper et al., 2013 for review). Thus, movement observed under natural conditions will create a time-varying 'motion' envelope that is *a priori* independent of the beat itself and carries behaviorally relevant information. Previous studies have shown that several species of weakly electric fish will display 'tracking' behavior when presented with motion envelope stimuli in that the animal's instantaneous EOD frequency will track the detailed time course of the envelope (Martinez et al., 2016; Metzen and Chacron, 2014, 2015). This implies that the information pertaining to the detailed time course of the envelope must be retained in the animal's brain. Previous studies have shown that natural motion envelopes predominantly contain temporal frequencies below 1 Hz (Fotowat et al., 2013; Metzen and Chacron, 2014).

Envelopes in the electrosensory system can also be caused by interference between the EODs of three or more conspecifics located in close proximity to one another. Indeed, interference between the two resulting beats will then create a 'social' envelope whose frequency is given by the beat frequency difference (Stamper et al., 2012) (see Stamper et al., 2013 for review). It is important to understand that social envelopes, unlike motion envelopes, do not require movement. Also, unlike motion envelopes, the frequency content of social envelopes is completely determined from the animals' EOD frequencies. Previous work has found that weakly

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Received 27 January 2018; Accepted 14 June 2018

Journal of Experimental Biology (2018) 221, jeb178244. doi:10.1242/jeb.178244

electric fish display an envelope avoidance response (EAR) when presented with low (<10 Hz)-frequency social envelopes (Stamper et al., 2012). Specifically, the fish will change its EOD frequency in order to increase the temporal frequency of the envelope, thereby moving away from the frequency range of more behaviorally relevant stimuli (e.g. prey). The EAR behavior shares some similarities with the previously characterized jamming avoidance response (JAR) in weakly electric fish (Heiligenberg, 1991). However, it should be noted that the JAR only occurs in the presence of a low (<10 Hz)-frequency beat, whereas the EAR can also occur when two high-frequency beats are presented, provided that their frequency difference is low (Stamper et al., 2012). There is significant overlap between the temporal frequency contents of social and movement envelopes, although the former can contain higher frequencies than the latter (Fotowat et al., 2013). Under natural conditions, both motion and social envelopes will occur concurrently, provided that there are three or more fish present. However, while desirable, evidence as to whether weakly electric fish can distinguish motion from social envelopes is currently lacking. Here, we constructed mimics of movement and social envelope stimuli that were as similar to one another as possible and used these to test whether the weakly electric fish *Apteronotus albifrons* (Linnaeus 1766) could distinguish between envelope types.

MATERIALS AND METHODS

Ethics statement

All experimental procedures were approved by McGill University's animal care committee and were in accordance with guidelines set forth by the Canadian Council on Animal Care.

Animals

Specimens of the weakly electric fish *A. albifrons* (*N*=17) of either sex were purchased from tropical fish suppliers and were

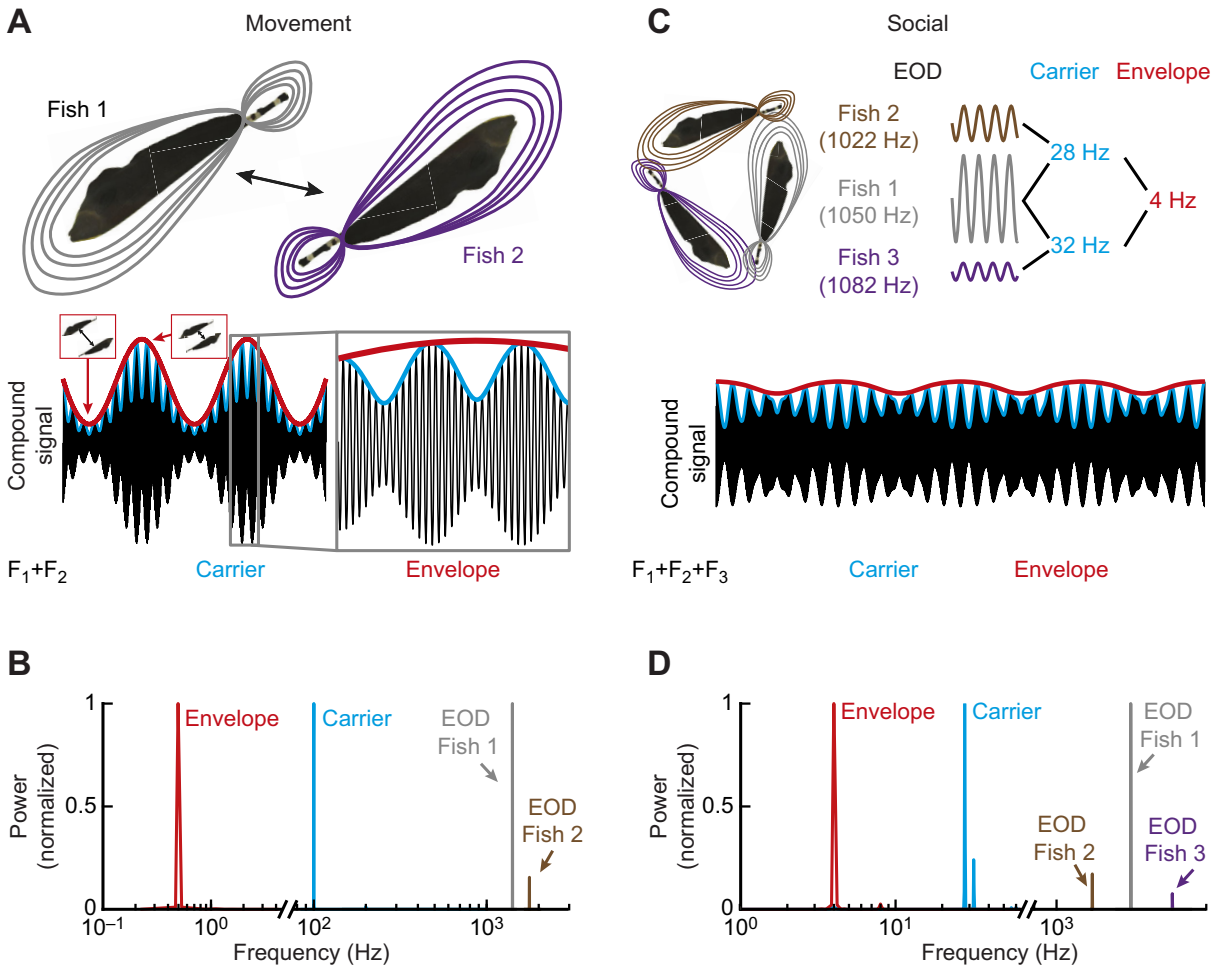

Fig. 1. Comparison of social and movement envelopes. (A) Movement envelopes are generated by the relative locomotion between two fish (top). Electric organ discharge (EOD) waveform from *Apteronotus albifrons* (black) with carrier (cyan) and envelope (red) waveforms (bottom). Note that the envelope corresponds to the depth of modulation of the carrier. The inset (bottom right) shows a snippet of all waveforms on a shorter time scale. (B) Power spectra of the individual EOD signals (fish 1: gray; fish 2: brown), the carrier (cyan) and the envelope (red). (C) Social envelopes are generated by the interaction of the EODs of three weakly electric fish. (top). The three EOD signals (gray: fish 1, 1050 Hz; brown: fish 2, 1022 Hz; purple: fish 3, 1082 Hz) with their individual frequencies and relative intensities (middle). Owing to the differences in the individual EOD frequencies, two prominent carrier frequencies (cyan) arise, that in turn create an envelope (red). The compound signal (black) is the sum of the EOD signals of the three fish (bottom) that has a carrier beat frequency (cyan) and an envelope (red). (D) Power spectra of the individual EOD signals (fish 1: gray; fish 2: brown; fish 3: purple), the carrier (cyan) and the envelope (red). Note that the carrier (cyan) has two frequency peaks (28 Hz and 32 Hz), corresponding to the two beat frequencies arising from the three interacting EOD signals.

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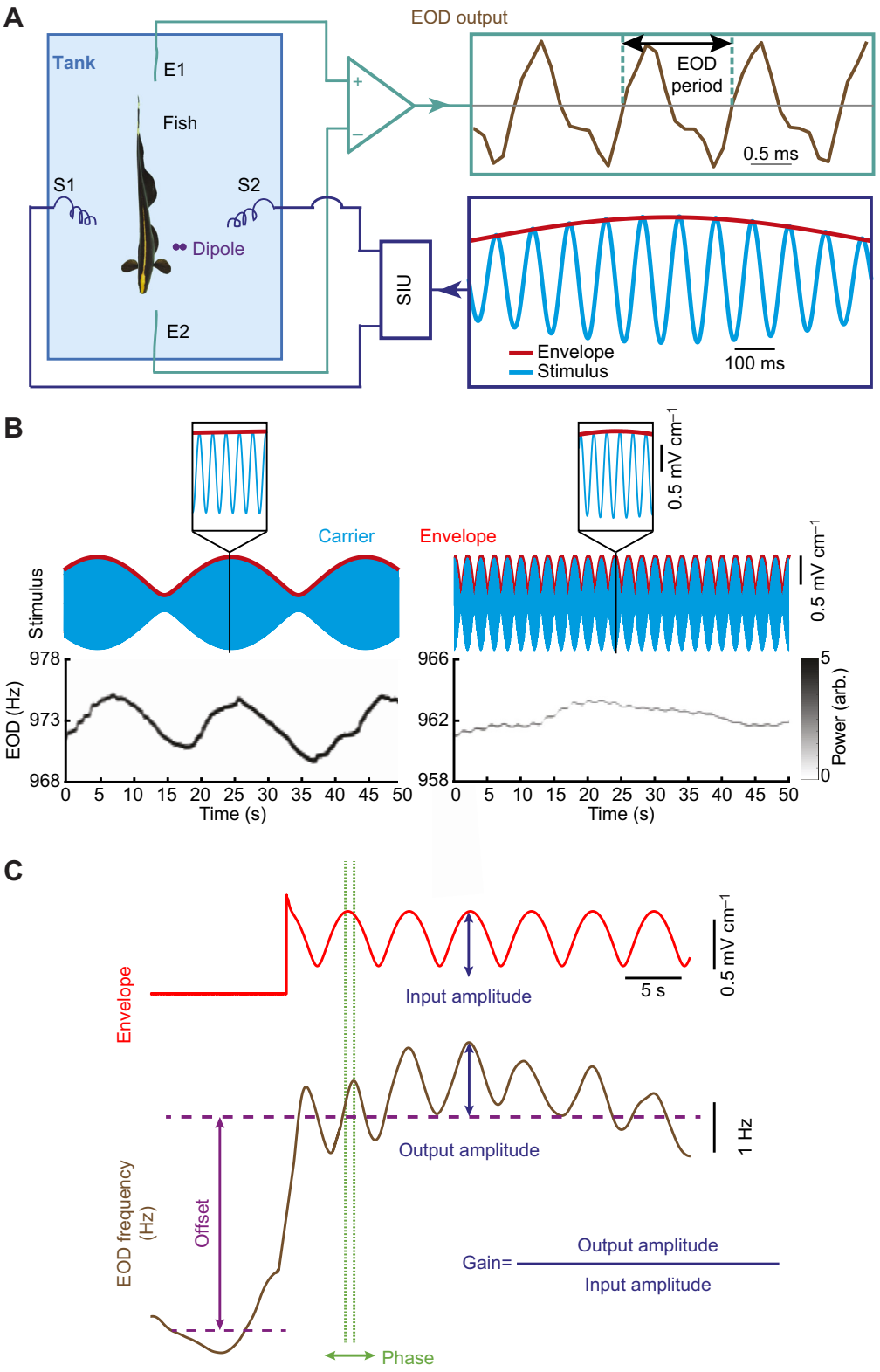

Fig. 2. Methodology and analysis. (A) Schematic of the experimental setup. The fish's electric field is monitored by electrodes located near the head and tail (teal curves E1 and E2). The stimulus is delivered from the stimulus isolation unit (SIU) using a separate pair of electrodes on each side of the fish (dark blue spirals S1 and S2). (B) Top: example stimulus from a social envelope for two different envelope frequencies: 0.05 Hz (left) and 0.5 Hz (right). The carrier (cyan) is the addition of two sinusoidal beat frequencies (11 plus 11.05 Hz on the left and 11 plus 11.5 Hz on the right). The extracted envelopes are shown by the red lines. The insets show magnifications of the stimulus waveforms and their envelopes. Bottom: EOD spectrograms (EOD power spectrum as a function of time) in response to the stimuli shown. (C) Example stimulus of a 0.2 Hz social envelope (top, red) and EOD frequency response (bottom, brown). The parameters used to characterize the fish behavior are indicated. The gain is expressed as ratio between the amplitude of the EOD response and the envelope stimulus amplitude (blue arrows). The phase is the time difference between the peak the envelope stimulus and the peak of the EOD response frequency (green dotted lines), normalized to the stimulus period. The offset (purple arrow and dashed lines) is the mean EOD frequency during stimulation minus the mean baseline frequency before the stimulus start point.

acclimated to laboratory conditions as per published guidelines (Hitschfeld et al., 2009). Fish ranged from 7 to 10 cm in length with EOD frequencies ranging from 712 to 1202 Hz. Prior to the experiment, each animal was immobilized by intramuscular injection of 0.1–0.5 mg tubocurarine chloride hydrate (Sigma-Aldrich, St Louis, MO, USA) and was then respirated via a mouth tube at a flow rate of ∼10 ml min^{-1} throughout. This was done in order to minimize movement within the experimental tank. We note that *A. albifrons* possess a neurogenic electric organ that is unaffected by injection of curare-like drugs. Thus, all experiments were performed with the animal's natural EOD.

Behavioral response and stimulation

The animal's behavioral responses, consisting of changes in the EOD frequency, were recorded via a pair of electrodes placed near the animal's head and tail within the experimental tank and were digitized at 10 kHz using a Power1401 (Cambridge Electronic Design, Cambridge, UK) and stored for offline analysis. The stimuli consisted of amplitude modulations of the animal's own EOD that were generated using standard methodology (Deemyad et al., 2013; Marquez and Chacron, 2018, 2017; Metzen et al., 2015, 2016; Toporikova and Chacron, 2009). Movement envelopes were simulated using either noisy (5–15 or 60–80 Hz) or sinusoidal (11, 31 or 71 Hz) carriers that were amplitude modulated using sinusoidal envelope waveforms with frequencies of 0.05, 0.1, 0.2, 0.5, 0.75 and 1 Hz. For social envelopes, two sinusoidal waveforms were added. The first sinusoidal waveform had a frequency of 11, 32 or 64 Hz whereas the second sinusoidal waveform had a frequency equal to that of the first plus 0.05, 0.1, 0.2, 0.5, 0.75 or 1 Hz. Stimulus contrast was typically 20%, as in previous studies (Martinez et al., 2016; Metzen and Chacron, 2014, 2015), and was matched such as to minimize any difference between motion and social envelopes. It is important to realize that any change in the animal's EOD frequency will not affect either the carrier or the envelope frequency content when stimuli are delivered in this manner. Further, we note that previous studies have shown that the characteristics of the envelope tracking behaviors considered here are not affected by immobilization or by using amplitude modulations instead of natural beats (Martinez et al., 2016; Metzen and Chacron, 2014, 2015). Finally, we note that our social envelope waveforms deviated slightly from sinusoidal, thereby causing the resulting waveform to reach its half-maximum value earlier than the motion envelope. This is simply due to the fact that these were obtained by adding two sinewaves with a large modulation depth. However, it is unlikely that our observed behavioral responses are caused by this difference. This is because, for a given frequency, our social envelope stimuli initially increased at a faster rate than our motion envelope stimuli, thus one would then expect the response to social envelopes to occur with lower latency. We instead observed the opposite.

Analysis

Behavioral responses were analyzed as in previous studies (Martinez et al., 2016; Metzen and Chacron, 2014, 2015, 2017). Briefly, the recorded EOD signal was thresholded in order to obtain the zero-crossings. The inverse of the time difference between consecutive zero-crossings was used as a measure of instantaneous EOD frequency. We next averaged the extracted EOD frequency over the number of envelope cycles present in the stimulus in order to get the response. We further computed the power spectrum of the envelope extracted from the dipole using a Hilbert transform. The gain is defined as the ratio of output to input modulation. The phase lag is defined as the difference between the phases at which the input and output reach their local maxima. Finally, the offset was

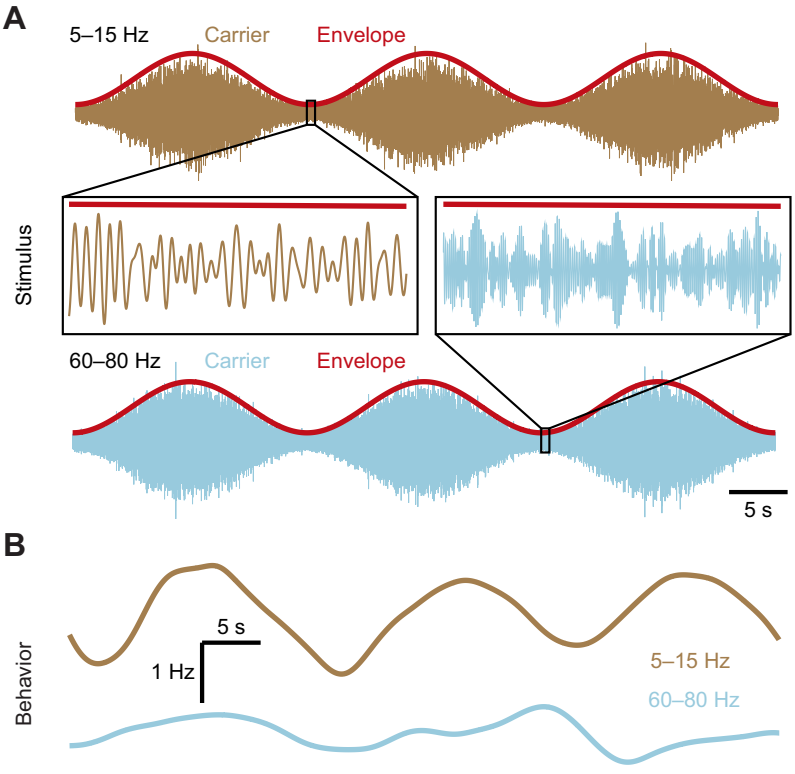

Fig. 3. Example behavioral responses to motion envelope stimuli with noisy carriers. (A) Examples of a 0.05 Hz envelope (red) stimulus with either a 5–15 Hz (top, brown) or a 60–80 Hz (bottom, cyan) noisy carrier. (B) EOD frequency in response to a 0.05 Hz envelope with low (brown) and high (cyan) frequency carrier.

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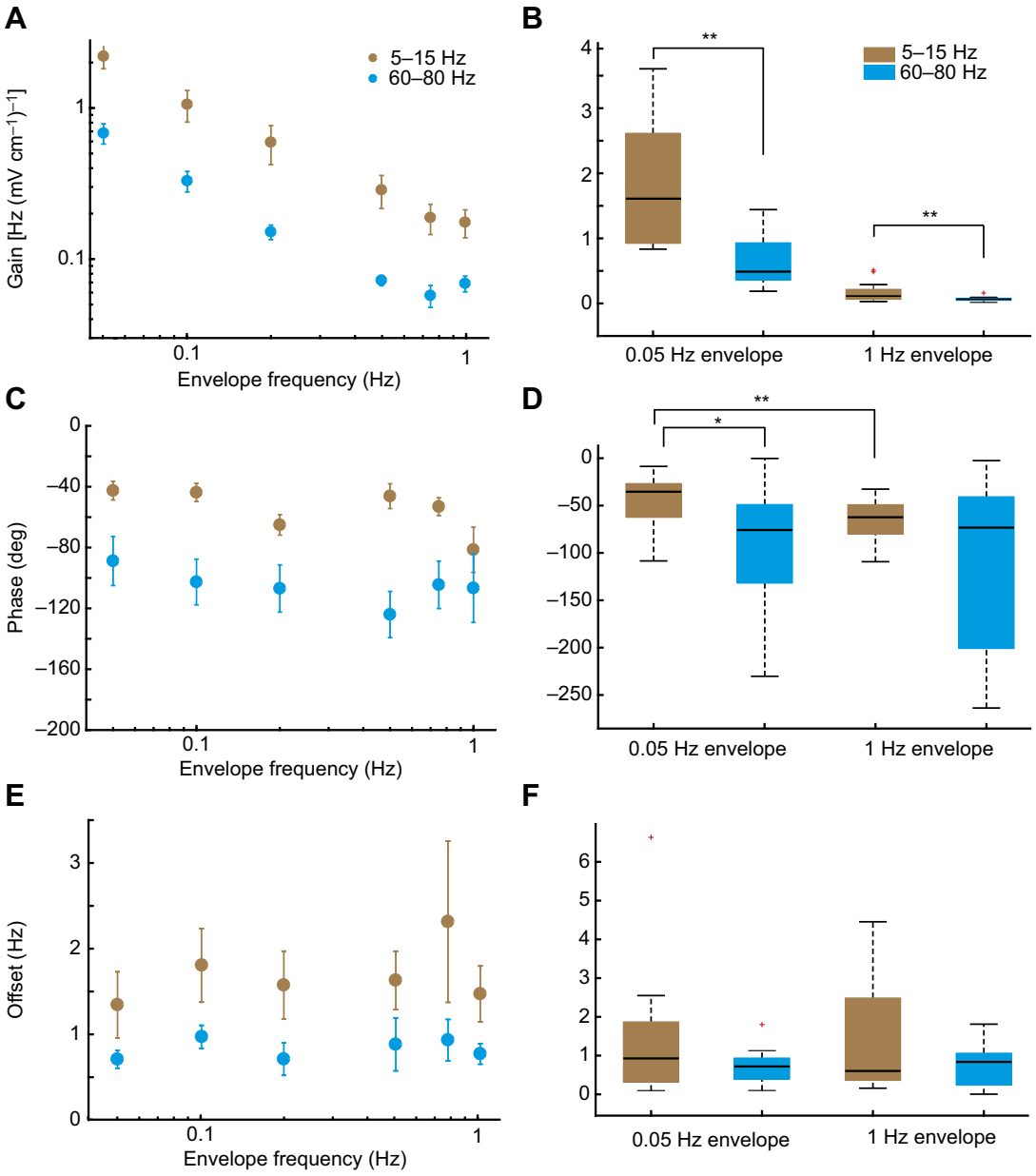

Fig. 4. Quantification of behavioral responses to motion envelope stimuli with noisy carriers. (A) Gain as a function of envelope frequency for motion envelopes with 5–15 Hz (brown) and 60–80 Hz (blue) noisy carriers. Across all envelope frequencies the gain values for envelopes with a 5–15 Hz noisy carrier are higher than gain values for envelopes with a 60–80 Hz noisy carrier. (B) Gain values are significantly higher for envelopes with a 5–15 Hz noisy carrier than for envelopes with a 60–80 Hz noisy carrier. (0.05 Hz envelope: $P<0.001$; 1 Hz: $P=0.004$). (C) Phase as a function of envelope frequency for motion envelopes with 5–15 Hz (brown) and 60–80 Hz (blue) noisy carriers. (D) Phase values for 0.05 Hz envelopes are significantly higher for envelopes with a 5–15 Hz noisy carrier than for envelopes with a 60–80 Hz noisy carrier ($P=0.031$). However, phase values are not different across different carrier frequencies for 1 Hz envelopes ($P=0.743$). Phase values for envelopes with a 5–15 Hz noisy carrier are significantly higher for 0.05 Hz envelopes than for 1 Hz envelopes ($P=0.004$). However, phase values do not differ across envelope frequencies for envelopes with a 60–80 Hz noisy carrier ($P=0.822$). (E) Offset as a function of envelope frequency for motion envelopes with 5–15 Hz (brown) and 60–80 Hz noisy carriers (blue). (F) Boxplots showing that there are no differences between offset values for any envelope frequency or for different carriers (0.05 Hz envelope, 5–15 Hz compared with 60–80 Hz noisy carrier: $P=0.398$; 1 Hz envelope, 5–15 Hz compared with 60–80 Hz noisy carrier: $P=0.262$) and there are no differences between envelope frequencies for a given carrier (5–15 Hz noisy carrier, 0.05 Hz compared with 1 Hz envelope: $P=0.361$; 60–80 Hz noisy carrier, 0.05 Hz compared with 1 Hz envelope: $P=0.642$). P-values for main effects of carrier frequency across all envelope frequencies were calculated with Friedman's tests and comparisons between different carrier frequencies at individual envelope frequencies were calculated using Kruskal–Wallis tests.

determined by computing the mean EOD frequency during the last envelope cycle minus the baseline value just before stimulus onset.

Statistics

All quantities are reported as means±s.e.m. for all plots as a function of envelope frequencies throughout. Box plots are median values and 25th to 75th percentiles, and the whiskers show minimum and maximum, excluding outliers (indicated by red crosses) throughout. As values failed to pass the Lilliefors test for normal distribution, we concluded the gain, phase and offset values were not normally distributed and therefore used non-parametric tests. Significance was assessed either using a Friedman's test when testing for main

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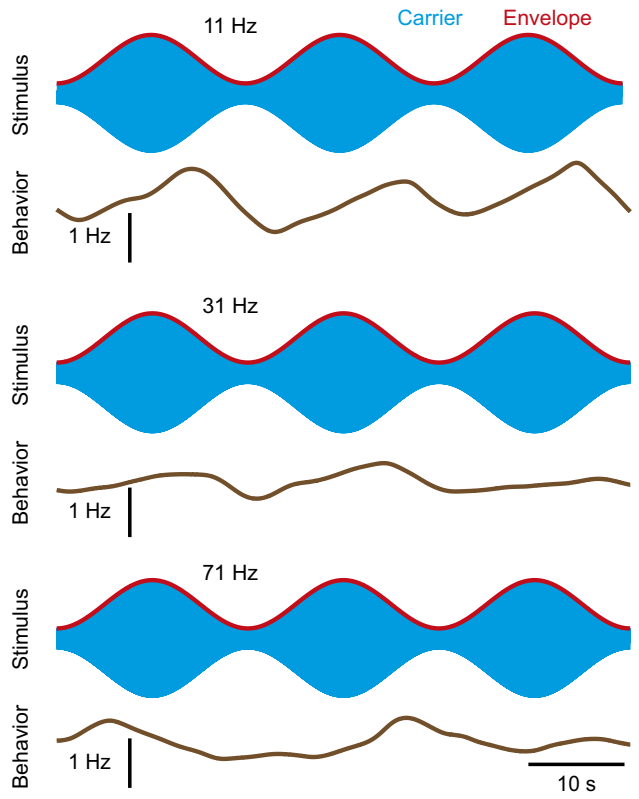

Fig. 5. Example behavioral responses to motion envelope stimuli with sinusoidal carriers. Examples of 0.05 Hz envelope stimuli (red) with sinusoidal beat carriers (blue) for low (11 Hz, top), intermediate (31 Hz, middle) and high (71 Hz, bottom) carrier frequencies. Example EOD frequency responses to each stimulus (brown) are also shown.

effects when changing carrier frequency across all envelope frequencies, or a Kruskal–Wallis test when comparing different conditions (e.g. carrier frequencies, or motion versus social).

RESULTS

We measured the behavioral responses of N=17 *A. albifrons* specimens to envelope stimuli mimicking those due to motion or due to social contexts. We also considered both noisy and sinusoidal carriers, and we varied the carrier frequency content (see Materials and Methods). Fig. 1 summarizes the different behavioral contexts that give rise to both motion and social envelopes. Specifically, motion envelopes consist of changes in the beat depth of modulation that occur when two conspecifics move with respect to one another (Fig. 1A,B). In contrast, social envelopes occur because of the interference between the EODs of three or more conspecifics (Fig. 1C,D). The experimental setup is shown in Fig. 2A.

Although previous studies have shown that *A. albifrons* display envelope tracking behaviors that are similar to those displayed by *A. leptorhynchus* when stimulated with motion envelopes (Martinez et al., 2016; Metzen and Chacron, 2014, 2015), how these fish respond to social envelopes has not yet been investigated. We therefore presented the animals with social envelopes (see Materials and Methods). We found that, as with motion envelopes, the animal's EOD frequency tracked the detailed time course of social envelopes (Fig. 2B). Specifically, the modulations in EOD frequency decreased with increasing envelope frequency (Fig. 2B, compare left and right panels). We used linear systems identification techniques to characterize the relationship between the input envelope and the output behavioral response. These consist of computing: (1) the gain, which is the ratio of output modulation to input modulation; (2) the phase, which is the difference between the times at which the input and output reach their local maxima normalized to the stimulus cycle; and (3) the offset, which is the difference between the mean response and the baseline (i.e. in the absence of stimulation) value. All three quantities are shown in Fig. 2C.

Responses to motion envelopes with noisy carriers

In order to provide a comparison between behavioral responses to motion and social envelopes, we first established how the specimens included in our dataset responded to motion envelopes using noisy carriers (Fig. 3A). These noisy carriers mimic the small fluctuations in EOD frequency that typically occur during natural conditions and have been used recently to characterize both behavioral and neural response to envelopes in *A. leptorhynchus* (Huang and Chacron, 2016; Huang et al., 2016; Metzen and Chacron, 2015; Metzen et al., 2015; Zhang and Chacron, 2016) and in *A. albifrons* (Martinez et al., 2016). We used both low (5–15 Hz, Fig. 3A, top) and high (60–80 Hz, Fig. 3A, bottom) frequency ranges that mimic motion envelopes that would occur when two conspecifics with small and large differences between their EOD frequencies are located close to one another, respectively. EOD frequency responses to the same motion envelope waveform (0.05 Hz sinewave) were strongly dependent on the carrier frequency content (Fig. 3B). Indeed, EOD frequency modulations were strongest for the low frequency carrier (Fig. 3B, compare brown and cyan curves).

Quantification of behavioral responses using linear identification techniques revealed that the gain decreased as a function of increasing envelope frequency (Fig. 4A). Gain values for 5–15 Hz carriers were significantly higher than those for 60–80 Hz carriers (Fig. 4B). Overall, behavioral responses lagged behind the envelope stimulus, as reflected by negative phase values that decreased slightly with increasing envelope frequency (Fig. 4C). Phase lags were significantly greater in magnitude for the high frequency carrier (Fig. 4D). Overall, offset values were relatively independent of envelope frequency (Fig. 4E) and were slightly higher for low frequency carriers, although not significantly so (Fig. 4F).

Responses to motion envelopes with sinusoidal carriers

We next characterized behavioral responses to motion envelopes with sinusoidal carriers that more closely mimic natural conditions. Overall, the magnitude of behavioral responses to a given envelope frequency decreased with increasing carrier frequency (Fig. 5). Quantification of responses revealed trends that were similar to those observed for noisy carriers (see previous section). Overall, gain decreased with increasing envelope frequency (Fig. 6A). Moreover, gain values were significantly lower for increasing carrier frequency (Fig. 6B). Phase lags decreased slightly as a function of increasing envelope frequency (Fig. 6C) and were significantly greater in magnitude for greater carrier frequencies (Fig. 6D). Offset values were largely independent of both envelope and carrier frequency (Fig. 6E,F).

Responses to social envelopes with sinusoidal carriers

We next investigated behavioral responses to social envelopes. As mentioned above, it is important to note that the structure of social envelopes differs fundamentally from that of motion envelopes. Indeed, whereas the former consist of amplitude modulations of a carrier owing to movement, social envelopes instead result from the

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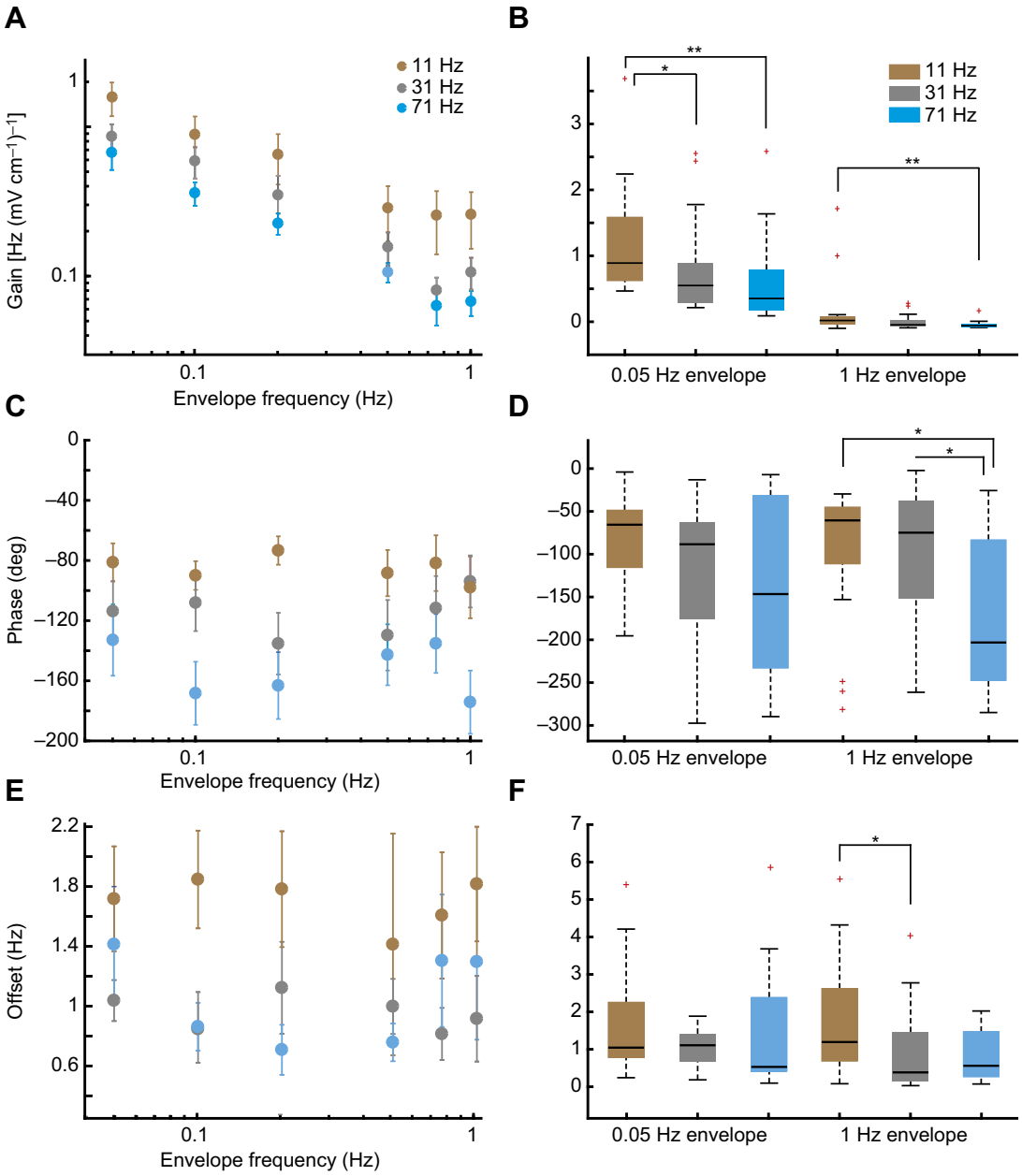

Fig. 6. Quantification of behavioral responses to envelope stimuli with sinusoidal beat frequency carriers. (A) Gain as a function of envelope frequency for motion envelopes with 11 Hz (brown), 31 Hz (gray) and 71 Hz (blue) sinusoidal carriers. (B) Gain values for 0.05 Hz (left bars) and 1 Hz (right bars) envelopes for 11 Hz (brown), 31 Hz (gray) and 71 Hz (blue) carrier frequencies. For a 0.05 Hz envelope, gain values are significantly higher with a low (11 Hz) carrier compared with intermediate (31 Hz) or high (71 Hz) carriers (low vs intermediate: P=0.0211; low vs high: P=0.002). For a 1 Hz envelope, gain values are significantly higher for the low (11 Hz) carrier compared with the high (71 Hz) carrier (P=0.006) but not for the intermediate (31 Hz) carrier (P=0.130). (C) Phase as a function of envelope frequency for motion envelopes with low (11 Hz, brown), intermediate (31 Hz, gray) and high (71 Hz, blue) sinusoidal carriers. Phase values for all envelopes frequencies are significantly decreasing with increasing carrier frequency (P<0.001). However, phase values are constant across envelope frequencies for all of the carrier frequencies (P=0.377). (D) Phase values for 0.05 Hz envelopes are not different across carrier frequencies (11 Hz vs 31 Hz P=0.160; 11 Hz vs 71 Hz P=0.971). For the 1 Hz envelope, phase values are significantly lower for the high carrier compared with the low (11 Hz, P=0.02) or intermediate (31 Hz, P=0.013) carriers. (E) Offset as a function of envelope frequency for low (11 Hz, brown), intermediate (31 Hz, gray) and high (71 Hz, blue) carrier frequencies. Offset values across all envelope frequencies are higher for low carriers than for intermediate or high carriers (low vs intermediate: P=0.006; low vs high: P=0.001). (F) For 0.05 Hz envelopes there is no difference in offset values as an effect of carrier frequency (low vs intermediate carrier: P=0.249; low vs high carrier: P=0.173; high vs intermediate carrier: P=0.691). Offset values are in general lower for the high carrier frequency compared with the intermediate carrier for the 1 Hz envelope (P=0.028), but not for the 11 Hz compared with the 71 Hz carrier (P=0.065). P-values for main effects of carrier frequency across all envelope frequencies were calculated with Friedman's tests and comparisons between carrier frequencies at individual envelope frequencies were calculated using Kruskal–Wallis tests.

interference between two (or more) beats. We thus delivered two sinusoidal beat stimuli and varied their frequency difference to generate social envelopes (see Materials and Methods). Our results show that *A. albifrons* actively track social envelopes with different carriers (Fig. 7). Quantification of the behavioral responses using linear systems identification techniques showed that behavioral gain

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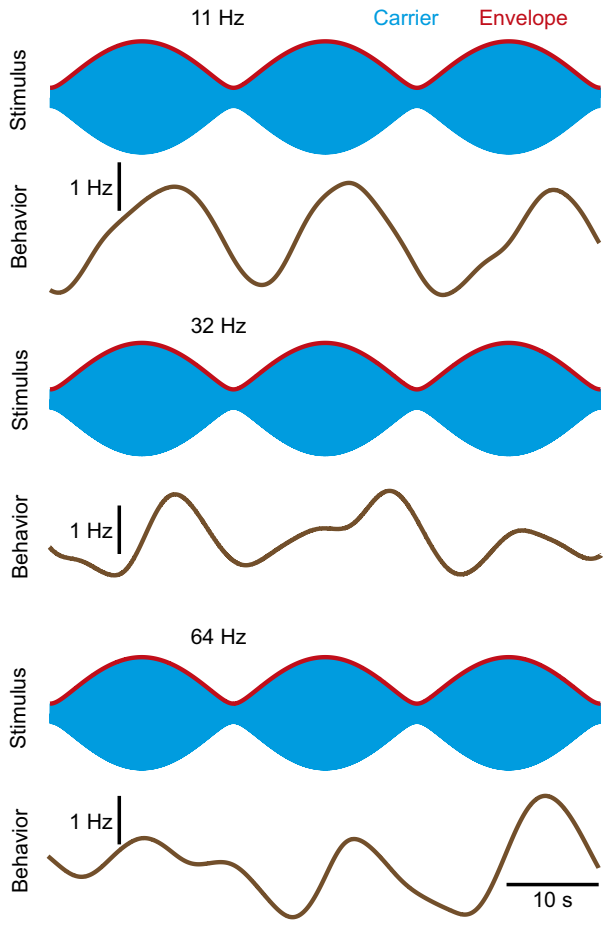

Fig. 7. Example behavioral responses to social envelope stimuli. Examples of 0.05 Hz envelope stimuli (red) with carriers with low (11 plus 11.05 Hz, top), intermediate (32 plus 32.05 Hz, middle) and high (64 plus 64.05 Hz, bottom) 'base' beat frequencies. Example EOD responses to the same envelope stimuli are shown below each stimulus in brown.

decreased as a function of increasing envelope frequency (Fig. 8A). However, in contrast to results obtained for motion envelopes, there were no significant decreases in gain when increasing the carrier frequency content (Fig. 8B). Behavioral responses lagged the envelope stimulus, as reflected by negative phase values (Fig. 8C) that were independent of envelope frequency and, furthermore, were not significantly affected by the carrier frequency content (Fig. 8D). Offset values were also largely independent of both envelope and carrier frequency content (Fig. 8E,F). Thus, our results provide the first characterization of behavioral responses of *A. albifrons* to social envelopes.

Comparison of behavioral responses to motion and social envelopes

We next compared behavioral responses to motion and social envelopes. Fig. 9 shows example sinusoidal 0.05 Hz motion (top) and social (bottom) envelopes. Overall, the animal's EOD frequency tracked the detailed time course of both stimuli (Fig. 9, compare brown curves). There was, however, a marked difference in that the behavioral responses of the two envelope types had different phase lags to the envelope stimuli occurring in either the motion or social conditions (compare dashed lines in Fig. 9). Specifically, the responses to the social envelope showed much greater lagging than those to the motion envelope (Fig. 9, vertical dashed lines and horizontal black arrows). Comparing quantifications of behavioral responses across our dataset confirmed this trend. Indeed, behavioral gains to motion and social envelopes with similar carrier frequencies were roughly equal to one another (Fig. 10A–C). However, qualitatively different results were obtained when looking at the phase of responses, as there was a greater lag observed for social envelopes for low (Fig. 10D) but not high (Fig. 10E) frequency carriers. Indeed, phase lags to social envelopes with low frequency carriers were significantly larger in magnitude than those obtained for similar motion envelopes (Fig. 10F). When looking at offset values, we found no significant differences between motion and social envelopes either for low (Fig. 10G) or high (Fig. 10H) frequencies carriers (Fig. 10I). Thus, our results show that *A. albifrons* have similar tracking responses to motion and social envelopes. However, we consistently observed a greater phase lag for behavioral responses to social envelopes than to motion envelopes across a wide range of envelope frequencies if the carrier frequency was low. This result shows that the animal can distinguish between both envelope types, which has important implications for understanding how these are processed by the brain, as is discussed below.

DISCUSSION

Species differences in behavioral responses to envelopes

Apteronotid species can be found in groups of three or four in the wild (Stamper et al., 2010), indicating that they will experience both motion and social envelopes. Thus, the stimuli presented here are of ethological relevance. However, it should be noted that different species of electric fish use different stimulus features to generate behavioral responses. For example, the neural circuits that mediate the jamming avoidance response in *Eigenmannia* and in *Apteronotus* are fundamentally different from one another (see (Metzner, 1999; Rose, 2004) for review). Thus, it is likely that the mechanisms by which envelopes are processed will differ amongst species. Specifically, whereas *Eigenmannia* spp. use both amplitude and phase information of social envelopes to generate the EAR (Stamper et al., 2012), species such as *A. albifrons* and *A. leptorhynchus* most likely rely primarily, if not exclusively, on amplitude modulations to generate tracking responses (Metzen and Chacron, 2014). As such, further studies should focus on comparing responses to movement and social envelopes of *Apteronotid* species with those of *Eigenmannia* species.

Comparing motion and social envelopes

To our knowledge, this study is the first that explicitly compares behavioral responses to social and movement envelopes. Although we have attempted to minimize differences between motion and social envelopes (e.g. by matching their intensities and temporal frequency content), it should be noted that it is impossible to make a social envelope equivalent to a motion envelope owing to the above-mentioned fundamental differences in their structures. Indeed, whereas motion envelopes consist of amplitude modulations of a beat carrier, social envelopes instead result from interference between two or more beats, which gives rise to amplitude as well as phase modulations. The fact that the observed behavioral responses of *A. albifrons* to motion and social envelopes were largely similar in terms of both gain and offset suggests that the organism primarily uses the amplitude modulation component of social envelopes. However, a contribution of the phase modulation component cannot be fully excluded because we observed significant differences in phase lag

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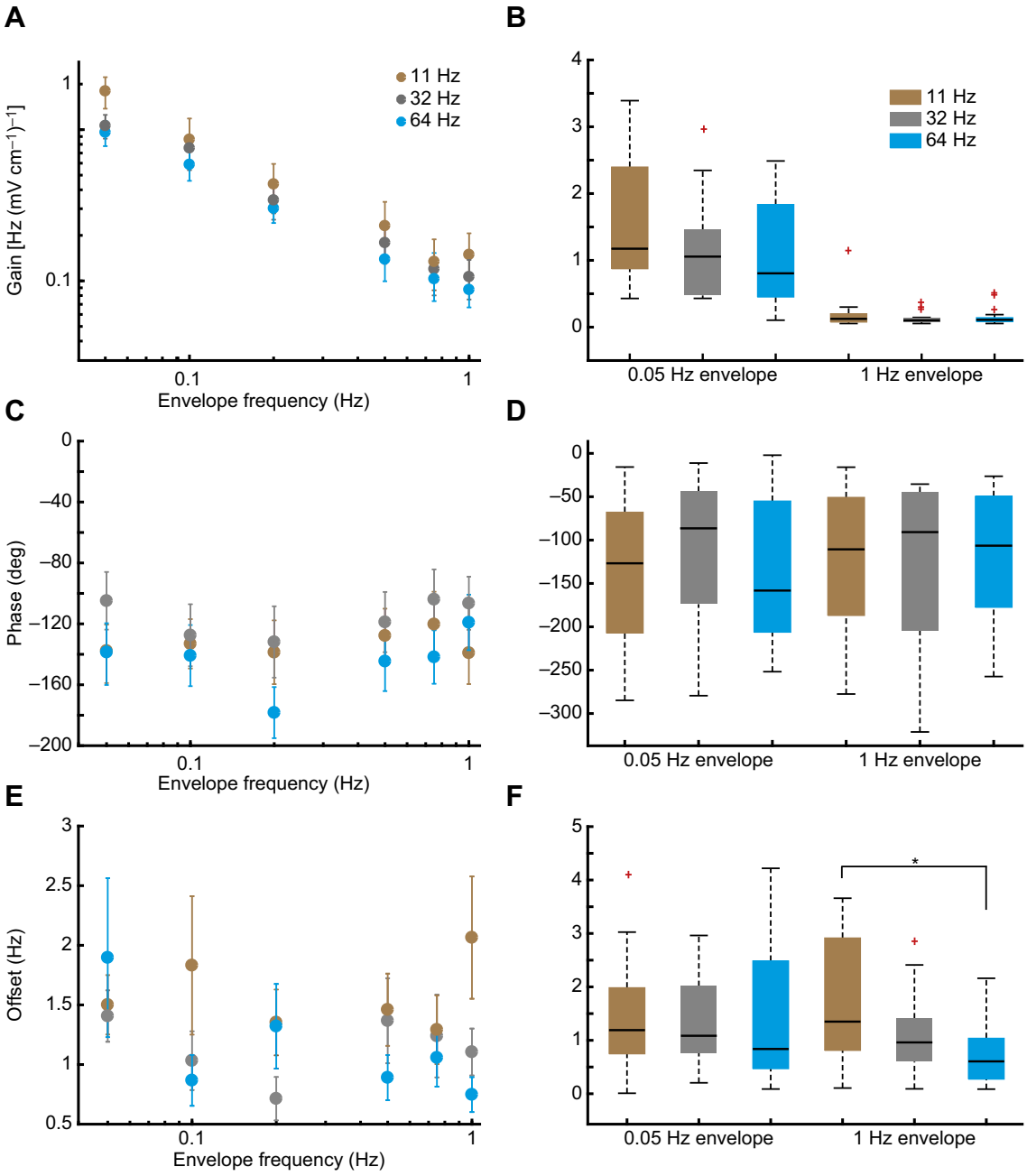

Fig. 8. Quantification of behavioral responses to social envelope stimuli. (A) Gain as a function of envelope frequency for social envelopes with 11 Hz (brown), 32 Hz (gray) and 64 Hz (blue) 'base' beat frequencies. Across all envelope frequencies, the gain values do not differ as an effect of carrier frequency (P=0.244). (B) Gain values for 0.05 and 1 Hz envelopes for 11 Hz (brown), 32 Hz (gray) and 64 Hz (blue) 'base' beat frequencies. Gain values are not significantly different for envelopes with 11 Hz carriers compared with envelopes with 32 or 64 Hz carriers (0.05 Hz envelope on an 11 vs 32 Hz carrier, P=0.245; 11 Hz envelope on an 11 vs 32 Hz carrier, P=0.699; 0.05 Hz envelope on an 11 vs 64 Hz carrier, P=0.109; 1 Hz envelope on a 64 Hz carrier, P=0.480). (C) Phase as a function of envelope frequency for social envelopes with 11 Hz (brown), 32 Hz (grey) and 64 Hz (blue) 'base' beat frequencies. Phase values across all envelope frequencies do not differ as an effect of carrier frequency (P=0.345). (D) Phase values for 0.05 or 1 Hz envelopes are not different between carrier frequencies (0.05 vs 1 Hz envelope for 11 Hz, P=0.480; 32 Hz, P=0.694; 64 Hz, P=0.438). (E) Offset as a function of envelope frequency for motion envelopes with 11 Hz (brown), 32 Hz (grey) and 64 Hz (blue) beat frequencies. (F) For 0.05 Hz envelopes there is no difference in offset values as an effect of carrier frequency (11 Hz vs 32 Hz P=0.835; 11 Hz vs 64 Hz P=0.524, 32 Hz vs 64 Hz P=0.485). For a 1 Hz envelope frequency, however, offset values of the high frequency carrier (64 Hz) are lower than for low (11 Hz) or intermediate (32 Hz) carrier frequencies (low vs intermediate, P=0.168; low vs high, P=0.011; high vs intermediate, P=0.168). P-values for main effects of carrier frequency across all envelope frequencies were calculated with Friedman's tests and comparisons between carrier frequencies at individual envelope frequencies were calculated using Kruskal–Wallis tests.

between motion and social envelopes for low carrier frequencies. We note that the lack of a significant difference obtained for higher carrier frequencies could be due to the fact that slightly higher frequencies (71 Hz) were used for motion envelopes relative to those used for social envelopes (64 Hz). It is thus possible that differences in phase lag between motion and social envelopes will be seen for a wider range of carrier frequencies. Further studies are needed to confirm this prediction. Nevertheless, these differences

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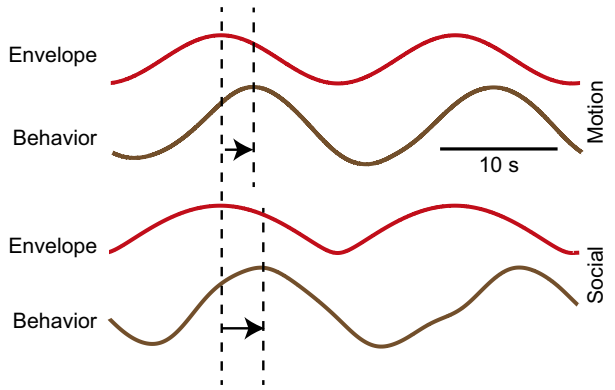

Fig. 9. Comparing behavioral responses to motion and social envelopes. Top: 0.05 Hz motion envelope waveform (red) and EOD frequency response (brown). Note that the behavioral response lags the stimulus (dashed vertical lines). Bottom: same, but for an example 0.05 Hz social envelope. Note the increased response lag.

indicate that the animal can distinguish between motion and social envelopes, which is desirable owing not only to their different structures, but most importantly to the fact that they carry different information, as the former contain behaviorally relevant information whereas the latter can interfere with other stimuli (e.g. prey).

It is important to note that under natural conditions, groups of three of more fish will experience a combination of movement and social envelopes that will have different spatial profiles (Stamper et al., 2013). Importantly, changes in EOD frequency in response to movement envelopes will alter the frequency content of social envelopes and vice versa. The natural situation is thus highly complex and further studies are needed to understand how both envelope classes are processed under these conditions. Moreover, we note that our experiments were designed to minimize differences between movement and social envelopes. In particular, our movement envelope stimuli were not caused by actual movement between two fish, but rather simulated movement by modulating the amplitude of the carrier. It is likely that differences in the spatial profiles of stimulation on the animal's skin that result from movement and social envelopes are used by the animal for better discrimination between both classes under more natural conditions. Further studies are needed to test this hypothesis.

Neural processing of motion and social envelopes

Recent studies have extensively investigated how electrosensory neurons respond to both social (McGillivray et al., 2012; Middleton et al., 2006; Savard et al., 2011) and movement envelopes (Huang and Chacron, 2016; Huang et al., 2016; Martinez et al., 2016; Metzen and Chacron, 2015; Metzen et al., 2015; Zhang and Chacron, 2016). Although most of these studies were conducted in the species *A. leptorhynchus*, it is important to note that *A. leptorhynchus* and *A. albifrons* display very similar brain anatomy (Maler, 1979; Maler et al., 1981, 1991). Further, comparative studies have revealed that electrosensory lateral line lobe (ELL) pyramidal cells have identical tuning properties in response to movement envelopes in *A. leptorhynchus* and *A. albifrons* (Huang et al., 2016; Martinez et al., 2016). This most likely underlies the fact that both species display identical behavioral responses to movement envelopes (Martinez et al., 2016; Metzen and Chacron, 2014, 2015). Specifically, ELL pyramidal cells in both species display high-pass tuning curves that effectively oppose the natural statistics of movement envelopes such as to optimize information transmission (Huang et al., 2016; Martinez et al., 2016). These results strongly suggest that envelope processing strategies will be very similar if not identical in both species. Thus, in the following, we will assume that results obtained in *A. leptorhynchus* will be applicable to *A. albifrons* and vice versa.

Both peripheral (Metzen and Chacron, 2015; Metzen et al., 2015; Savard et al., 2011) and central electrosensory neurons (Huang and Chacron, 2016, 2017; Huang et al., 2016; Martinez et al., 2016; McGillivray et al., 2012; Middleton et al., 2006; Sproule et al., 2015; Vonderschen and Chacron, 2011; Zhang and Chacron, 2016) can respond to both social and motion envelopes. Importantly, the responses of midbrain electrosensory neurons located two synapses away from the periphery can be very selective to envelopes (McGillivray et al., 2012), suggesting that there is a neural circuitry that is devoted to their processing. These neural responses most likely underlie some of the behavioral responses observed here. However, they cannot fully explain them. This is because central electrosensory neural responses tend to lead (Huang and Chacron, 2016; Huang et al., 2016; Martinez et al., 2016) whereas the behavioral responses reported here instead lag the envelope stimulus. Thus, further processing of envelopes by higher-order brain areas determines the behavioral responses. The fact that behavioral but not central electrosensory neural responses to motion envelopes habituate to repeated stimulus presentations supports this hypothesis (Metzen and Chacron, 2014). Unfortunately, how higher-order electrosensory areas process envelope stimuli has not been investigated to date. Nevertheless, it is unlikely that the behavioral phase lags are due to axonal transmission delays. This is because these correspond to large time delays in general. For example, for a 0.05 Hz envelope, a phase lag of 80 deg corresponds to a time delay greater than 4 s, which cannot be explained by axonal transmission delays to higher electrosensory brain areas. Thus, the behavioral phase lags are likely due to filtering in the form of integration by neurons in higher-order electrosensory brain areas. If so, then this would require that neurons in higher-order electrosensory brain areas display large integration time constants in order to explain the large observed behavioral phase lags. We note that this is plausible given that neurons with large (i.e. >1 s) integration time constants have been reported in other systems (Cannon and Robinson, 1987; Prescott and De Koninck, 2005).

How do neural circuits in the electrosensory brain give rise to the observed differences in phase lag between social and movement envelopes? As mentioned above, these differences are likely due to differences in filtering. Thus, it is conceivable that different neuron types underlie the observed phase lag differences between behavioral responses to motion and social envelopes. If so, then this would correspond to parallel processing (i.e. different neural circuits would process motion and social envelopes in higher-order brain areas), which is commonly seen across sensory modalities [auditory (Gelfand, 2004; Oertel, 1999; Takahashi et al., 1984), visual (Livingstone and Hubel, 1987; Marr, 1982; Merigan and Maunsell, 1993), electrosensory (Bell and Maler, 2005; Carr and Maler, 1986; Kawasaki, 2005)]. Alternatively, it is possible that the extra phase modulation information present in social envelopes changes the filtering properties of higher-order neurons, thereby giving rise to the observed differences in behavior. Further studies are needed to understand how higher-order brain areas process motion and social envelopes.

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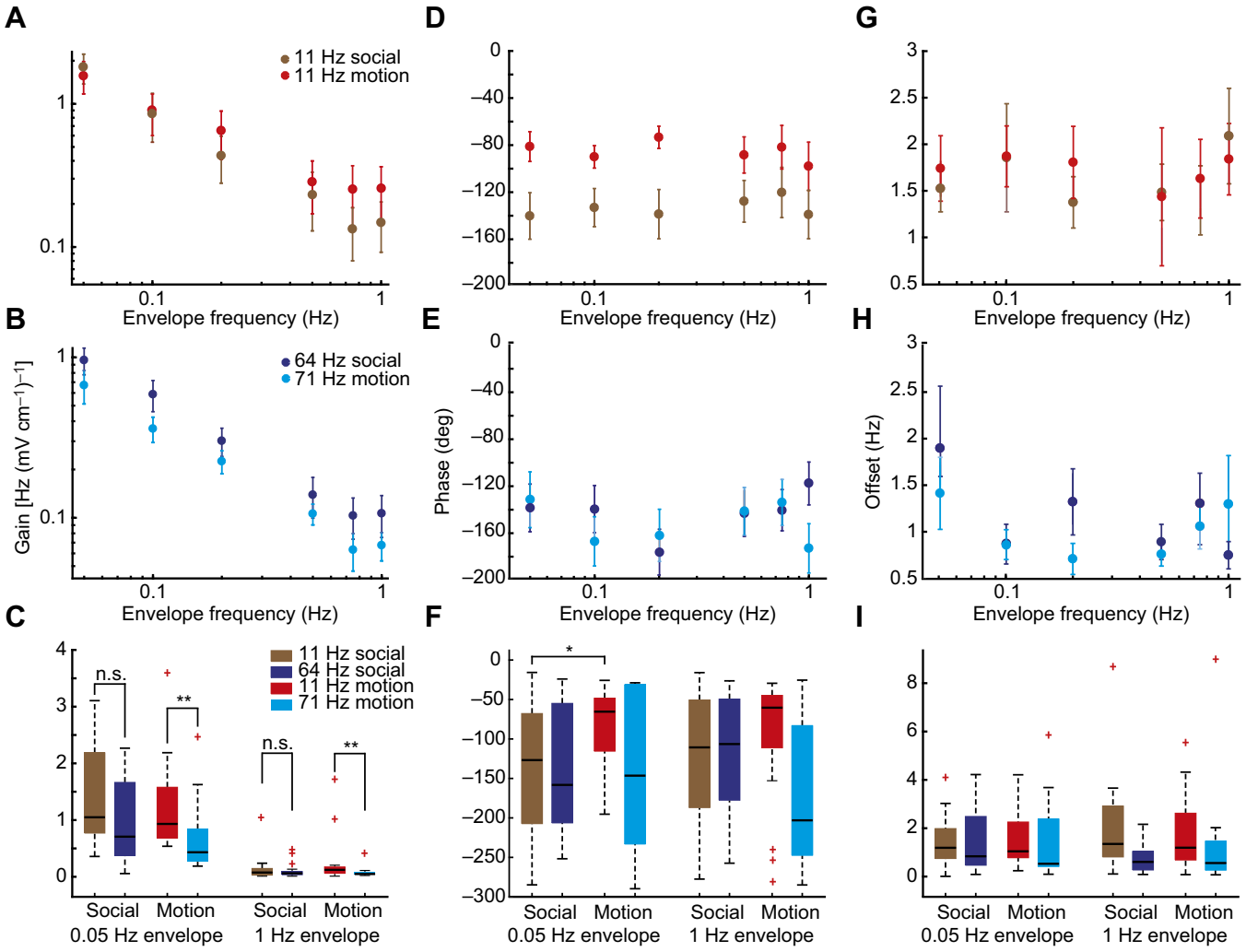

Fig. 10. Comparison of behavioral responses between motion and social envelope types. (A) Gain as a function of envelope frequency comparing motion (red, 11 Hz beat) and social envelopes (brown, 11 Hz 'base' beat frequency) with low frequency carriers. For low frequency carriers, gain values for social envelopes are in general lower than for motion envelopes (P=0.0429). (B) Gain as a function of envelope frequency comparing motion (light blue, 71 Hz beat) and social envelopes (dark blue, 64 Hz 'base' beat frequency) with high frequency carriers. There is no main effect of envelope type on gain values for envelopes with high frequency carriers (P=0.0788). (C) Population-average gain values for 0.05 Hz (left bars) and 1 Hz (right bars) envelopes for social (brown and dark blue) and motion envelopes (red and light blue) with low and high frequency carriers. For motion envelopes, gain values are significantly lower for a high carrier frequency than for a low carrier frequency (0.05 Hz envelope frequency, P=0.002; 1 Hz envelope frequency, P=0.006). There is no difference in gain between high and low carrier frequencies for social envelopes (0.05 Hz envelope frequency, P=0.109; 1 Hz envelope frequency, P=0.480). (D) Phase as a function of envelope frequency comparing motion (red, 11 Hz beat) and social (brown, 11 Hz 'base' beat frequency) envelopes with low frequency carriers. Phase values for social envelopes are lower than for motion envelopes (P=0.0227) across all envelope frequencies. (E) Phase as a function of envelope frequency comparing motion (light blue, 71 Hz beat) and social (dark blue, 64 Hz 'base' beat frequency) envelopes with high frequency carriers. There is no main effect on phase values for envelope types with high frequency carriers (P=0.2007). (F) Phase values for 0.05 Hz (left bars) and 1 Hz (right bars) envelopes for social and motion envelopes with low (brown and red) and high (dark and light blue) carrier frequencies are shown. Phase values for motion envelopes are significantly lower for social envelopes than for motion envelopes with low carrier frequencies (0.05 Hz) (P=0.0241), but not for high envelope frequencies (1 Hz) (P=0.3614). Phase values for motion envelopes do not differ from phase values for social envelopes with high carrier frequencies (0.05 Hz envelope frequency, P=0.8288; 1 Hz envelope frequency, P=0.0609). (G) Offset as a function of envelope frequency comparing motion and social envelopes with low frequency carriers. There is no difference in offset across envelope frequency for low frequency carriers (P=0.8550). (H) Offset as a function of envelope frequency comparing motion and social envelope with high frequency carriers. There is no difference in offset across envelope frequency for high frequency carriers (P=0.3833). (I) There are no differences in offset between motion and social envelopes with low carrier frequencies (0.05 Hz envelope frequency, P=0.9313; 1 Hz envelope frequency, P=0.7696) or for high carrier frequencies (0.05 Hz envelope frequency, P=0.5018; 1 Hz envelope frequency, P=0.7176). Comparisons of envelope types across all envelope frequencies were done with Friedman's test. Comparisons between envelope types or carrier frequencies at different envelope frequencies were performed using Kruskal–Wallis tests.

Conclusions

Our results provide for the first time a quantitative comparison of behavioral responses to both motion and social envelopes of *A. albifrons*. Overall, while both gave rise to deviations in EOD frequency with similar magnitudes and offsets, there were significant differences in phase, which indicates that these fish can distinguish between envelope stimuli arising from two different behavioral contexts.

Competing interests

The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.J.C.; Methodology: R.A.T., M.G.M.; Validation: R.A.T., M.G.M., M.J.C.; Formal analysis: R.A.T., M.G.M.; Investigation: R.A.T., M.G.M.; Resources: M.J.C.; Data curation: M.G.M.; Writing - original draft: M.G.M., M.J.C.; Writing - review & editing: R.A.T., M.G.M., M.J.C.; Visualization: R.A.T., M.G.M.; Supervision: M.G.M., M.J.C.; Project administration: M.J.C.; Funding acquisition: M.J.C.

Funding
This research was supported by the Fonds de Recherche du Québec - Nature et Technologies and the Canadian Institutes of Health Research (M.J.C.).

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