Identification of moving conspecifics in the weakly electric fish *Eigenmannia virescens*

By

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ABSTRACT

Eigenmannia virescens is a gymnotiform weakly electric fish which uses a quasi-sinusoidal electric organ discharge (EOD) to sense their environment. EOD frequency (EODF) is individual-specific. In conspecific interactions, each fish perceives the EODF of the conspecific as a periodic amplitude modulation (AM) of their own discharge. When both fish are stationary, the depth of this AM is constant, but it varies when fish are swimming. We hypothesized that AM variations during swimming act as a noise source that could have no effect on, hinder, or enhance EODF identification. To test this, we quantified the jamming avoidance response (JAR) (a natural behaviour wherein fish are required to accurately determine one another's EODF) in response to stimuli of varying depths of noise. These experiments demonstrated that swimming noise does not impair the ability of *E. virescens* to *identify* conspecific EODF, and actually improves its ability to *detect* the presence of a neighbouring fish.

RÉSUMÉ

Eigenmannia virescens est un poisson faiblement électrique gymnotiforme qui utilise une décharge quasi-sinusoïdale d'organe électrique (EOD) pour détecter son environnement. La fréquence de l'EOD (EODf) est spécifique à l'individu. Dans les interactions conspécifiques, chaque poisson perçoit l'EOD du conspécifique comme une modulation d'amplitude périodique (AM) de sa propre décharge. Quand les deux poissons sont stationnaires, la profondeur de cette AM est constante, mais elle varie quand les poissons nagent. Nous avons formulé l'hypothèse que les variations d'AM pendant le mouvement agissent comme une source de bruit qui pourrait n'avoir aucun effet sur, ni empêcher ou améliorer l'identification de l'EODf. Pour tester cette théorie, nous avons quantifié la réponse d'évitement de brouillage (JAR) (un comportement naturel dans lequel les poissons doivent déterminer avec précision un autre EODf) en réponse à des stimuli de profondeurs de bruit variables. Ces expériences ont permis de démontrer que le bruit de la nage n'altère pas la capacité d'*E. Virescens* à identifier l'EODf conspécifique et, en fait, améliore sa capacité à détecter la présence d'un poisson voisin.

ACKNOWLEDGEMENTS

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LIST OF ABBREVIATIONS

AM – Amplitude modulation

ANOVA – Analysis of Variance

CCF – Cross-correlation function

DF – Difference frequency

EGp – Eminentia granularis pars posterior

ELL – Electrosensory lateral line lobe

EOD – Electric organ discharge

EODF – Electric organ discharge frequency

IQR – Interquartile range

JAR – Jamming avoidance response

NP – Nucleus praeeminentialis

PM – Phase modulation

PPn – Pre-pacemaker nucleus

SD – Standard deviation

SNR – Signal-to-noise ratio

SPPn – Sublemniscal pre-pacemaker nucleus

SR – Stochastic resonance

Stim – Stimulus condition

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1. INTRODUCTION

1.1 Eigenmannia virescens – A Gymnotiform Weakly Electric Fish

Eigenmannia virescens (the Glass Knife Fish) is a gymnotiform wave type weakly electric fish, originating from freshwater habitats of Central and South America (Lovejoy et al., 2010). Using a specialized electric organ, gymnotiforms generate a high frequency electric signal, known as the electric organ discharge (EOD) (Moller, 1995). The EOD results in a weak electric field (in the range of a hundred mV/cm) around the body of the fish, similar to that of an oscillating dipole (Assad et al., 1998; Assad et al., 1999; Kelly et al., 2008). In *E. virescens* and other wave-type electric fish, this electric field is discharged continuously in a quasi-sinusoidal manner and decays roughly with cubed distance (Figure 1.1; Assad et al., 1998; Knudsen 1975; Moller, 1995; Shifman & Lewis, 2018).

Weakly electric fish like *E. virescens* are nocturnal, and tend to live in dark, murky, and cluttered environments, where vision is not a reliable or efficient sense for navigation (Bullock et al., 2005; Zupanc et al., 2001). As such, these fish use their EOD to sense the surrounding environment, secure prey, and interact with conspecifics (Bullock et al., 2005). In this active electrolocation behaviour, tuberous electroreceptors located over the entire body surface detect and encode perturbations or modulations of the fish's own EOD caused by objects or other electric fish in their surroundings (Babineau et al., 2007; MacIver et al., 2001; Caputi & Budelli, 2006). Due to the sensitivity of electroreceptors and the regularity of the high-frequency sinusoidal EOD, gymnotiform wave-type electric fish are able to sample their environments at very high rates, encouraging fast and dynamic swimming motion (Lannoo & Lannoo, 1993; MacIver et al., 2001; Zakon et al., 2002). During conspecific interactions, this

motion results in large EOD modulations over a wide range of time-scales (Yu et al., 2012; Stamper et al., 2013).

It is important to note that generation of the EOD is under the neural control of the pacemaker nucleus, which is the most precise biological oscillator known (Moortgat et al., 1998). As a result of this precise control, each fish has a specific, reliable EOD frequency (EODF) which serves as a marker of their 'identity' (Harvey-Girard et al., 2010; Moortgat et el., 1998; Yu et al 2012). EOD frequency ranges and waveforms differ among species of weakly electric fish, and thus also serve a role in species recognition (Fugère & Krahe, 2010). Within a species, EODF can also be sex-specific. For example, in *A. leptorhynchus*, females discharge at 600-800 Hz and males at 800-1000 Hz (at 26°C) (Zakon et al., 2002). In *E. virescens*, the sexual ranges in frequencies are less precise, but males tend to discharge at lower frequencies than females (Dunlap & Zakon, 1998; Hopkins, 1974). Overall, since EODF is an important marker of species, sex, and individual identity in *E. virescens*, it is important to understand the factors that may affect discrimination of conspecific EODF - such as the large EOD modulations resulting from the characteristic dynamic swimming of these fish - which is the goal of the current study.

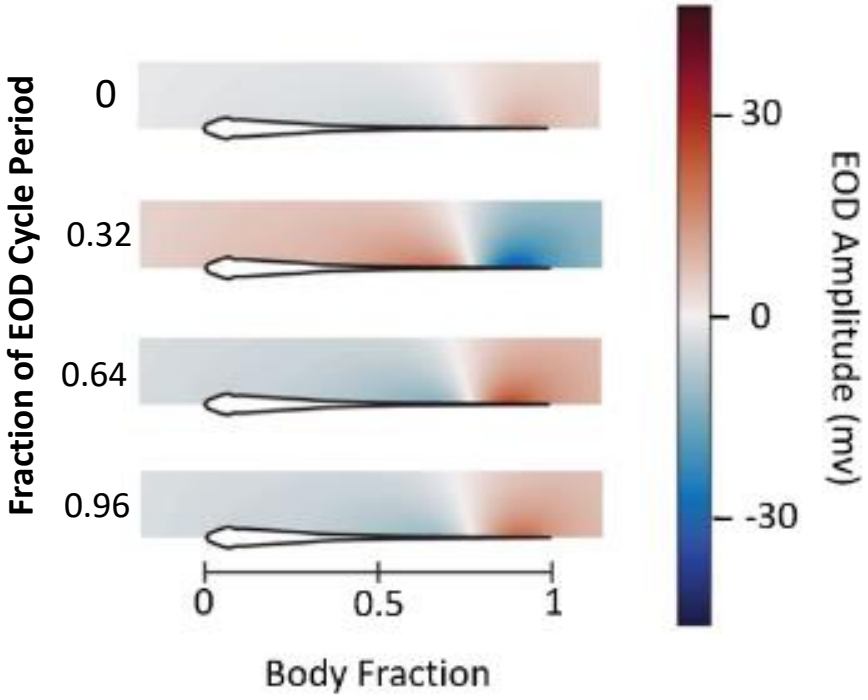

Figure 1.1 Electric field of *Eigenmannia virescens*. Modified from Shifman & Lewis, 2018. Spatio-temporal change in the EOD of *E. virescens*. Panel shows a voltage map for four phases of one EOD cycle, represented as a fraction of the cycle period. Voltage scale (mV) is indicated by the gradient colour bar on the right.

1.2 Conspecific EOD Interactions – AMs and Envelopes

When two conspecific gymnotiforms are in close proximity (<1m), their electric fields combine. Each fish involved in the interaction senses the sum of their electric fields, and perceives the EODF (or identity) of the conspecific as a modulation of their own EOD (Bullock et al., 2005; Stamper et al., 2013). During an interaction between two conspecifics, this periodic amplitude modulation (AM) of the perceiving fish's discharge occurs at a rate equal to the difference frequency (DF) between the two fish, called the AM frequency or rate (where DF = neighbor's EOD frequency–own EOD frequency) (Bullock et al., 2005; Stamper et al., 2013; Yu et al., 2012). For instance, if one fish has an EODF of 400 Hz and its neighbour has an EOD of 500 Hz, the AM frequency is equal to the DF of 100 Hz (Figure 1.2 a). By sensing the AM rate, the perceiving fish is able to determine the EOD frequency of a conspecific in an interaction. More specifically, in *E. virescens,* information contained in the EOD has been shown to be important for social cues involved in group formation and discrimination between different conspecific signals (Kramer & Otto, 1988; Kramer, 1999). Furthermore, in another gymnotiform species, *A. leptorhynchus*, it has been demonstrated that fish identify and remember individual conspecifics based on their specific EODF, given by the frequency of the AM (Harvey-Girard et al., 2010).

When both fish in an interaction are stationary, with no relative motion due to swimming, the AM is a periodic oscillation with a constant depth (peak to trough distance) of modulation (Figure 1.2 a) (Walz et al., 2013; Yu et al., 2012). However, when fish are swimming actively, the relative movement between fish will alter the depth of the AM. By changing the depth of the AM in time, varying distances and orientations between two fish create an

envelope of the EOD (Figure 1.2 b,c). This envelope is referred to as 'swimming noise' because the frequencies of these modulations overlap with those required to determine EODF (i.e. the AM) (Yu et al., 2012). When both fish are stationary, the envelope is constant (Figure 1.2 a). As fish approach one another, the depth of the AM increases, and as fish move apart, the depth of the AM decreases, so that the mean of the envelope is reflective of the average distance between the two fish (Figure 1.2 b) (Kelly et al., 2008; Yu et al., 2012). The swimming pattern, which may be extremely dynamic (including bending and turning behaviour), is characterized by the variance of the envelope (Figure 1.2 c) (Yu et al., 2012). In this way, the envelope gives interacting fish information regarding the relative motion and distance of conspecifics through a modulation of the AM, which itself gives information regarding conspecific identity (i.e. EODF).

Accurately identifying conspecifics using information found in AM frequencies may be essential for survival and reproduction in an electrosensory environment. *E. virescens* are often naturally found in groups of up to 30 fish, and are therefore constantly involved in interactions with conspecifics (Oestreich & Zakon, 2005; Stamper et al., 2010; Tan et al., 2005). EODF information given by the frequency of the AM may allow fish to distinguish known and foreign conspecifics (Harvey-Girard et al., 2010; Kramer & Otto, 1988; Kramer, 1999). Furthermore, since the EOD is sexually dimorphic, accurate frequency determination may be essential for mating and reproduction (Fugère & Krahe, 2010; Stamper et al., 2013; Kramer & Otto, 1988). Information regarding movement and orientation, reflected in the envelope, is equally important. Gymnotiforms are highly active swimmers, using rapid back and forth swimming motion to sample their environment (Assad et al., 1999; Bullock et al., 2005; Lannoo & Lannoo,

1993; MacIver et al., 2001). They may also exhibit aggressive territorial behaviours when faced with conspecific intruders, where knowledge of conspecific orientation is essential to avoid injury and triumph in agonistic interactions (Triefenbach & Zakon, 2008; Hopkins, 1974). Since both dynamic swimming patterns and accurate EODF identification (indicating species, sex, and individual identity) are essential for *E. virescens* and other gymnotiforms, it is important to understand how signals regarding both factors interact, and how the conspecific identification abilities of gymnotiform weakly electric fish are affected by swimming noise.

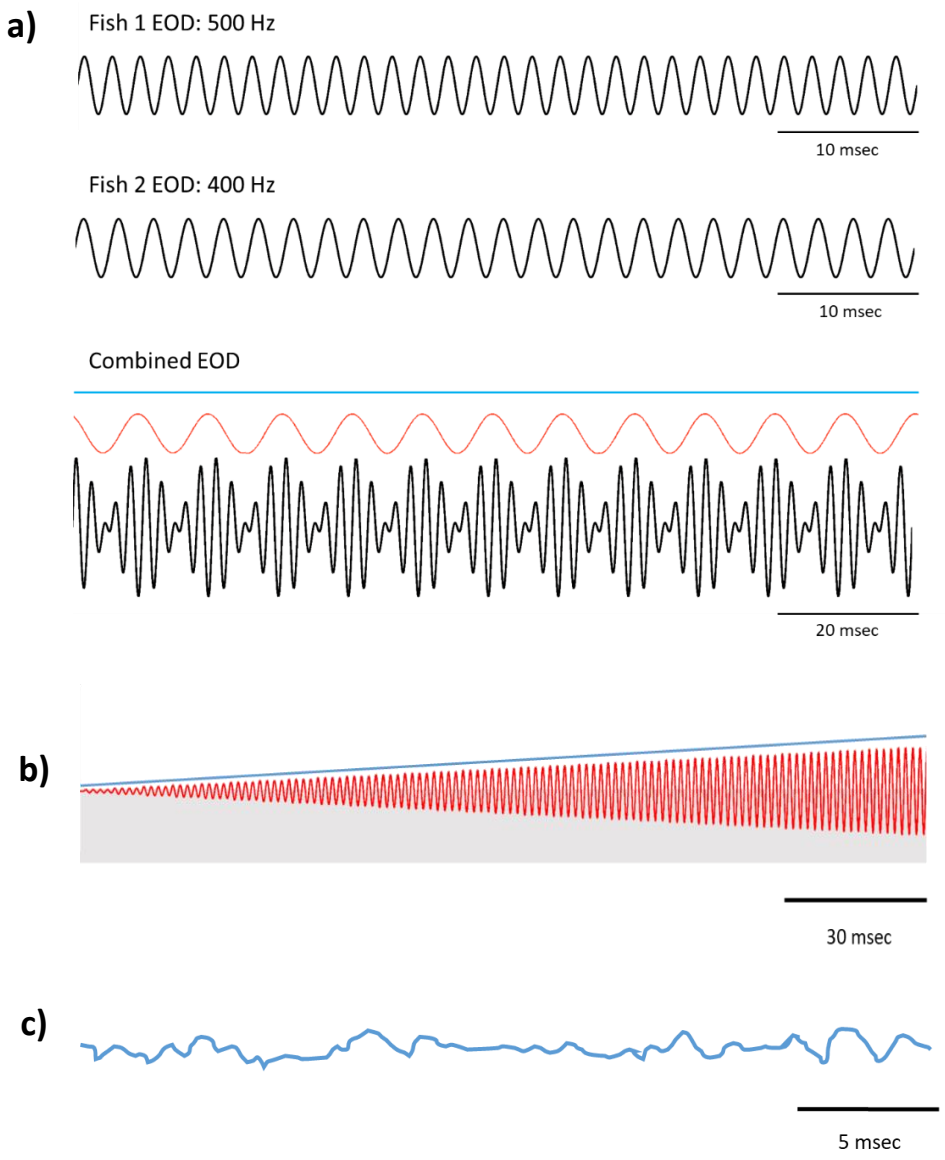

Figure 1.2 Amplitude modulations (AM, red) and envelopes (blue) of the electric organ discharge (EOD, black) during conspecific interactions. (A) Schematic EOD for two fish, one discharging at 400Hz and the other at 500Hz (top). When two fish are stationary in close proximity, these signals are combined to create a regular AM and static envelope (bottom). (B) When a conspecific moves directly towards a receiving fish, the depth of the AM and the slope of the envelope increase. (C) When both fish are swimming actively (varying in distance and orientation relative to one-another), the envelope becomes irregular.

1.3 The Jamming Avoidance Response (JAR)

1.3.1 Defining the JAR

Wave-type weakly electric fish like *E. virescens* are a convenient model for behaviourally examining the effects of movement noise on conspecific identification, since they exhibit documented behaviours that require accurate conspecific EODF recognition. The jamming avoidance response (JAR) is perhaps the most extensively studied of these behaviours (Heiligenberg, 1991; Bullock et al., 2005). When two weakly electric fish with similar EODFs (DF <15 Hz) are in close proximity, the electrosensory abilities of both fish are compromised (Bastian et al., 1987a, b; Heiligenberg 1973). This 'jamming' occurs as electric signals with a small difference frequency (DF) and objects in the environment both produce similar low frequency amplitude modulations of the receiving fish's discharge. In such a case, amplitude modulation information about the surrounding landscape and about the EODF of a close-frequency neighbour become indistinguishable to a receiving fish, impairing its electrosensory abilities (Heiligenberg, 1991, 1973; Bullock et al., 2005). To preserve electrosensory capabilities, some weakly electric fish will shift their frequencies out of the 'jamming' range, in a 'jamming avoidance response' (JAR) (Heiligenberg, 1991; Watanabe & Takeda, 1963). In *E. virescens*, the higher frequency fish will raise its frequency, while the lower frequency fish will tend to reduce its EODF (Heiligenberg, 1991). Fish will shift their EODFs until the DF reaches approximately 5 - 10 Hz (depending on the proximity of the fish), so that the AM frequency caused by EODF interference is pushed beyond the rate of modulations caused by objects in the environment, and electrosensory abilities are restored (Bullock et al., 2005; Heiligenberg, 1991).

Experimentally, this JAR process can be induced by presenting an artificial EODF stimulus (through electrodes) with a small DF to a receiving fish (Figure 1.3).

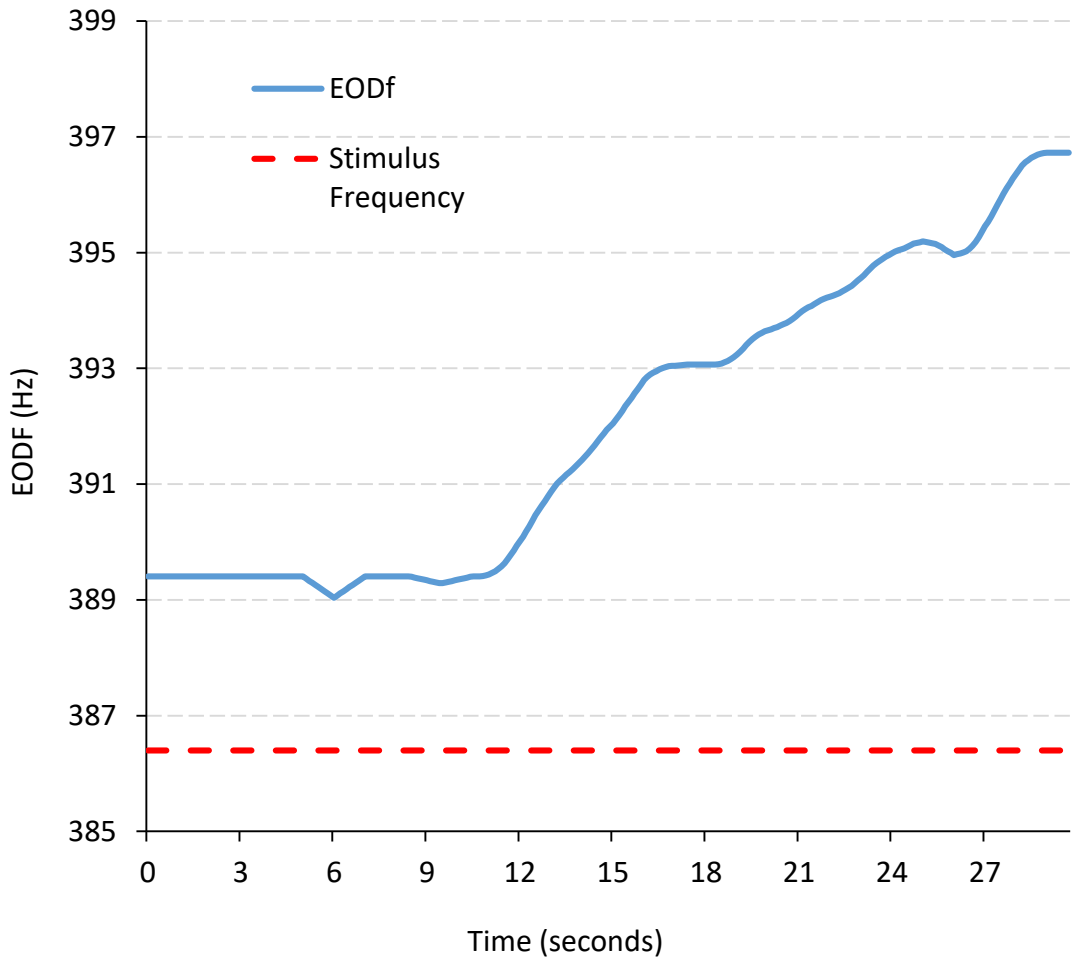

Figure 1.3 The jamming avoidance response (JAR) of *E. virescens* in reaction to an artificial stimulus frequency (DF = -3 Hz). EODF trace is an actual recording of the JAR in response to an un-clamped experimental jamming stimulus.

1.3.2 Elements of stimulus required for JAR

For the jamming avoidance response to occur, each fish in an interaction must very accurately identify the EODF of its neighbour, since the direction of the JAR is determined by the sign of the DF between the two fish (where DF is the neighboring fish's EODF – the subject fish's EODF) (Kawasaki et al., 1988). This requires the fish to analyze the interference resulting from the combination of EODs, described by both amplitude modulation (AM) and phase modulation (PM) of the combined signal (Carlson & Kawasaki, 2007; Kawasaki et al., 1988; Stamper et al., 2013). Electroreceptors at different locations on the body surface will receive varying phase and amplitude information, depending on the orientation of the two electric fields (Carlson & Kawasaki, 2007). As in figure 1.4 (a), some electroreceptors may be more "contaminated" by the adjacent EOD (the area marked by A) than others (the area marked by B). To determine the sign of the difference frequency, the fish must combine information about AM and phase differences between locations on the body, such as points A and B (Carlson & Kawasaki, 2007). When the difference frequency between the two fish is less than 0, the site with the greatest contamination (A) will experience an increase in the depth of the AM and a leading phase *or* a decrease in the depth of the AM and a lagging phase, relative to the site with less contamination (B). When the difference frequency is greater than 0, the opposite scenario results – site A will experience either a decrease in the depth of the AM and a leading phase *or* an increase in the depth of the AM and a lagging phase (Figure 1.4 b; Carlson & Kawasaki, 2007; Stamper et al., 2013). This can be succinctly described by Lissajous plots (Figure 1.4 c); to determine the sign of the DF and thus the direction to change its EODF, the fish must determine

the direction of rotation of these amplitude-phase plots (Heiligenberg, 1991; Carlson & Kawasaki, 2007; Shifman & Lewis, 2018).

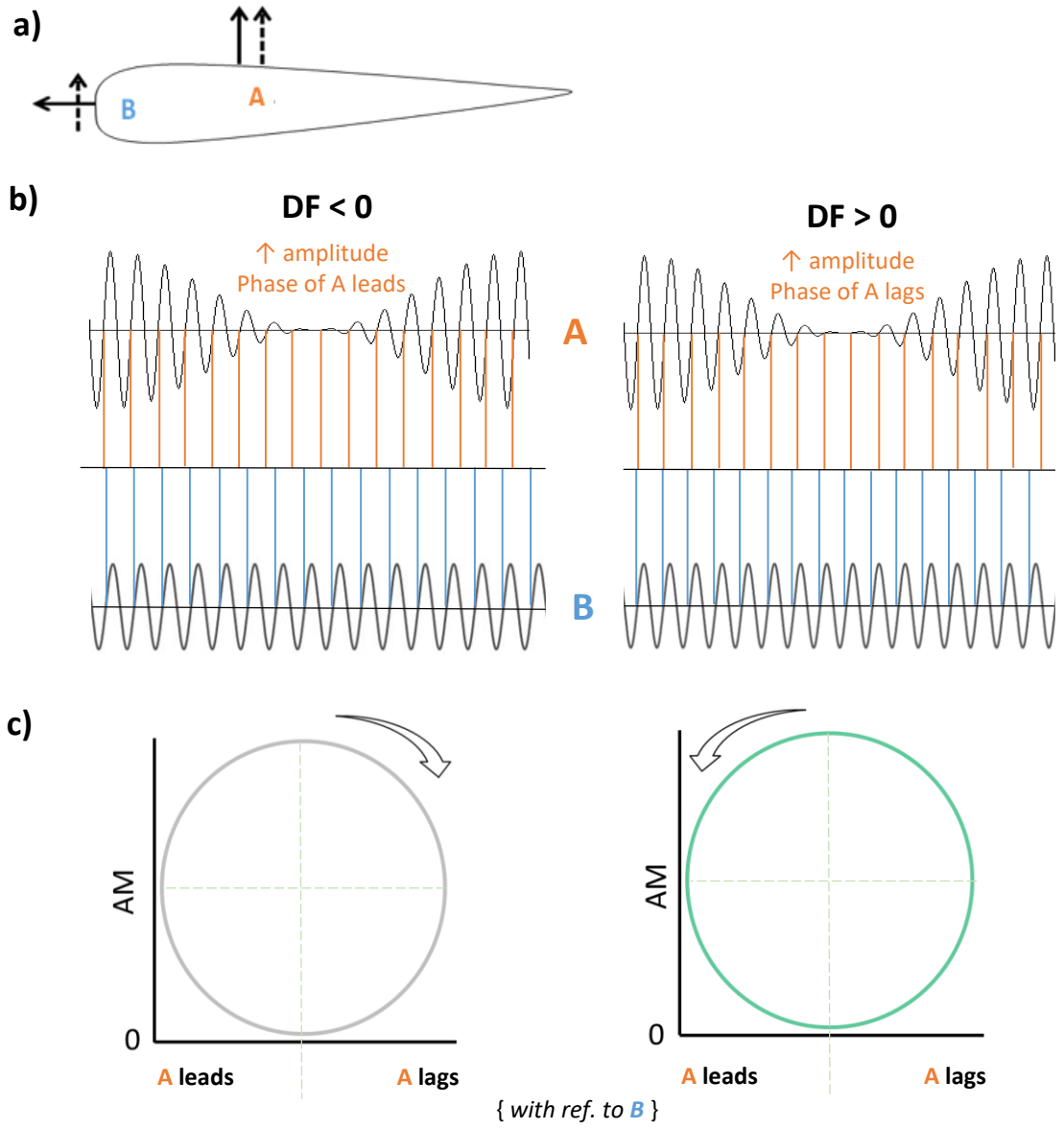

Figure 1.4 Elements of the stimulus required to invoke a jamming avoidance response (JAR). (a) Schematic of *E. virescens*, showing the reception of a conspecific signal at two sites on the body surface (A = high interference, B = lower interference). Solid arrows indicate the direction of current flow of the receiving fish (pictured), dashed arrows indicate the direction of current flow from the neighboring fish. (b) Phase and amplitude differences between sites A and B at a given point in time. Waves represent the signal perceived by the receiving fish (combined EOD). (c) Lissajous plots describing the determination of the sign of the DF. A positive DF is represented in green, a negative DF is represented in gray. Modified from Shifman & Lewis (2018) and Carlson & Kawasaki (2007).

1.3.3 Neural circuitry of the JAR (Figure 1.5)

In *E. virescens*, variations in phase and amplitude used to determine the difference frequency are encoded by two types of tuberous electroreceptors: P-unit electroreceptors and T-unit electroreceptors (Carlson & Kawasaki, 2007). Both electroreceptor types have primary afferents that extend to the electrosensory lateral line lobe (ELL) of the brain. T-unit afferents innervate spherical cells, whose firing is phase locked to the zero crossings of the peripheral signal. By comparing the spherical cell firing from different sites on the body surface (such as A and B in Figure 1.4 a), a higher brain region (the torus) discerns if the phase is leading or lagging at one site versus another (Hagedorn et al., 1992; Metzner 1999; Rose, 2004). On the other hand, P-unit afferents innervate pyramidal cells. E-type pyramidal cells are excited by P-unit afferent firing, thus are driven by a rise in peripheral amplitude. P-unit afferents also act on I-type pyramidal cells, inhibiting their firing. I-type pyramidal cells are therefore driven by a drop in peripheral amplitude (Hagedorn et al., 1992; Metzner 1999; Rose, 2004). In this manner, the P-unit electroreceptors act as amplitude coders, while the T-unit electroreceptors act as phase coders. Both pyramidal and spherical cell information is combined in the region of the torus, where sign selective neurons increase firing for one direction of DF and decrease firing for the other (Metzner, 1999; Rose et al., 1988). These sign selective neurons project to the nucleus electrosensorius (nE) of the diencephalon, which controls the firing of the pre-pacemaker nucleus (PPn). The PPn baseline firing rate is raised by information indicating a negative difference frequency from the nE, and is lowered by information indicating a positive difference frequency. The PPn in turn innervates the pacemaker nucleus, which projects to the electric organ to either raise or lower the fish's own frequency depending on the computed DF

(Hagedorn et al., 1992; Rose, 2004). In this way, amplitude information from P-Units and phase information from T-Units across the body surface allow the difference frequency between the two fish to be determined, and cause the appropriate jamming avoidance response to occur.

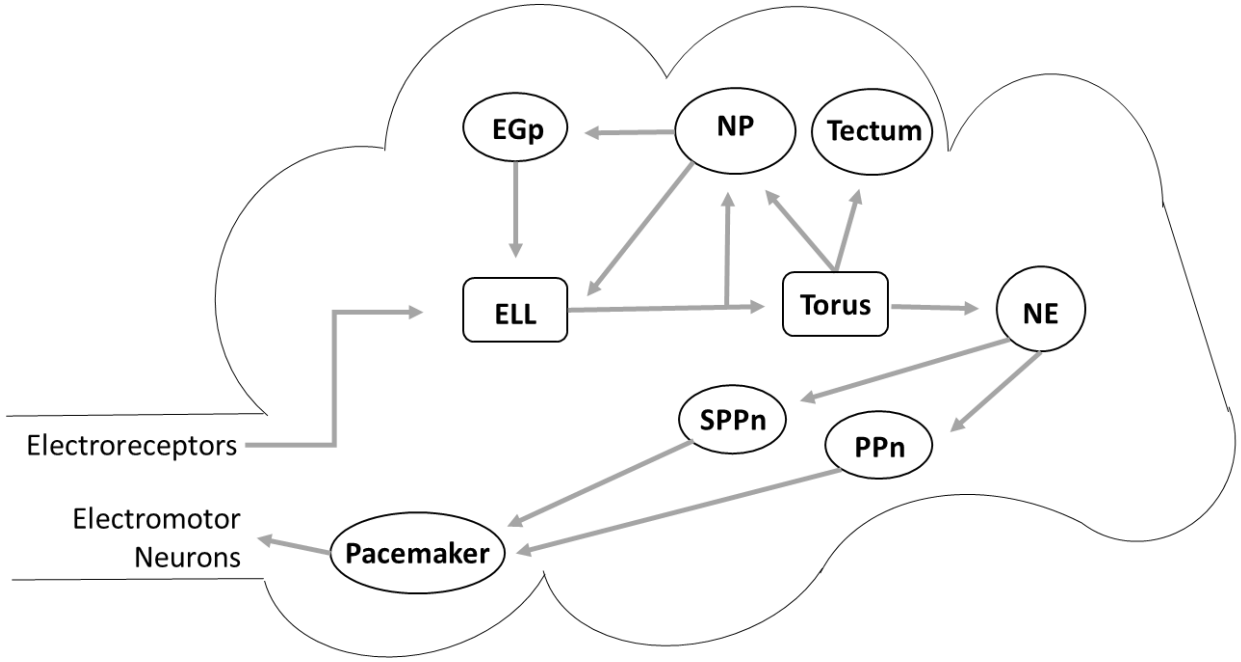

Figure 1.5 Neural circuitry of the jamming avoidance response (JAR) in *E. virescens*. ELL, electrosensory lateral line lobe; EGp, eminentia granularis pars posterior; NP, nucleus praeeminentialis; NE, nucleus electrosensorius; SPPn, sublemniscal prepacemaker nucleus; PPn, prepacemaker nucleus. Modified from Rose (2004).

1.3.4 The Experimental JAR

The jamming avoidance response has been extensively studied and thoroughly characterized in *E. virescens* (Heiligenberg, 1991; Bullock et al., 2005). Field and laboratory observations of paired weakly electric fish indicate that the JAR is a natural and reflexive social behaviour in conspecific interactions (Bullock et al., 1972a; Stamper et al., 2013). Further studies have examined the parameters of the JAR response by presenting an artificial jamming stimulus in playback experiments. In most of these studies, the fish is restrained in plastic mesh or a tube, while a sine wave (of a small DF) is presented to the fish through electrodes arranged perpendicular to the fish's body. Another pair of electrodes, arranged parallel to the fish, record the JAR as the stimulus is presented (Bullock et al., 1972a; Tallarovic & Zakon, 2005; Viete & Heiligenberg, 1991). This stimulus is sometimes 'frequency clamped', changing frequency along with the fish's shift in EODF, so that the DF between the stimulus and the fish's frequency is constant (Figure 1.6; Bullock et al., 1972b). Other studies present an 'un-clamped' jamming stimulus of a constant frequency, which does not track the change in frequency of the experimental fish (Figure 1.3; Bullock et al., 1972b, Watanabe & Takeda, 1963). Both types of stimulus presentations have their advantages. Frequency-clamped stimuli often result in a more consistent JAR behaviour, since it 'forces' the fish to continually attempt to escape a jamming stimulus (Bullock et al., 1972a). On the other hand, un-clamped stimuli are considered to provide a more natural scenario, allowing the fish to demonstrate a frequency "escape response" similar to that which occurs in paired interactions (Kramer, 1987; Watanabe & Takeda, 1963). Regardless of which type of stimulus is used, several benchmark studies on the JAR have determined that the optimal difference frequency of the stimulus is approximately -3

to -6 Hz (Dye et al., 1987; Bullock et al., 1972b), and that generally, the smaller the stimulus DF, the greater the frequency shift obtained (Bullock et al., 1972b). These studies also note that as the intensity of the stimulus increases, the magnitude of the JAR response also increases (Bullock et al., 1972b). They describe the JAR as a remarkably consistent and reproducible response, which occurs almost instantaneously upon stimulation (Bullock et al., 1972a). The JAR frequency rise is described as an approximately exponential curve, showing an asymmetric pattern as the fish's frequency falls again upon cessation of the jamming stimulus (Bullock et al., 1972a; Watanabe & Takeda, 1963). In general, since the JAR is easily and accurately quantified, and requires the experimental fish to precisely identify a conspecific or stimulus EODF, it is an especially useful tool in examining frequency detection abilities.

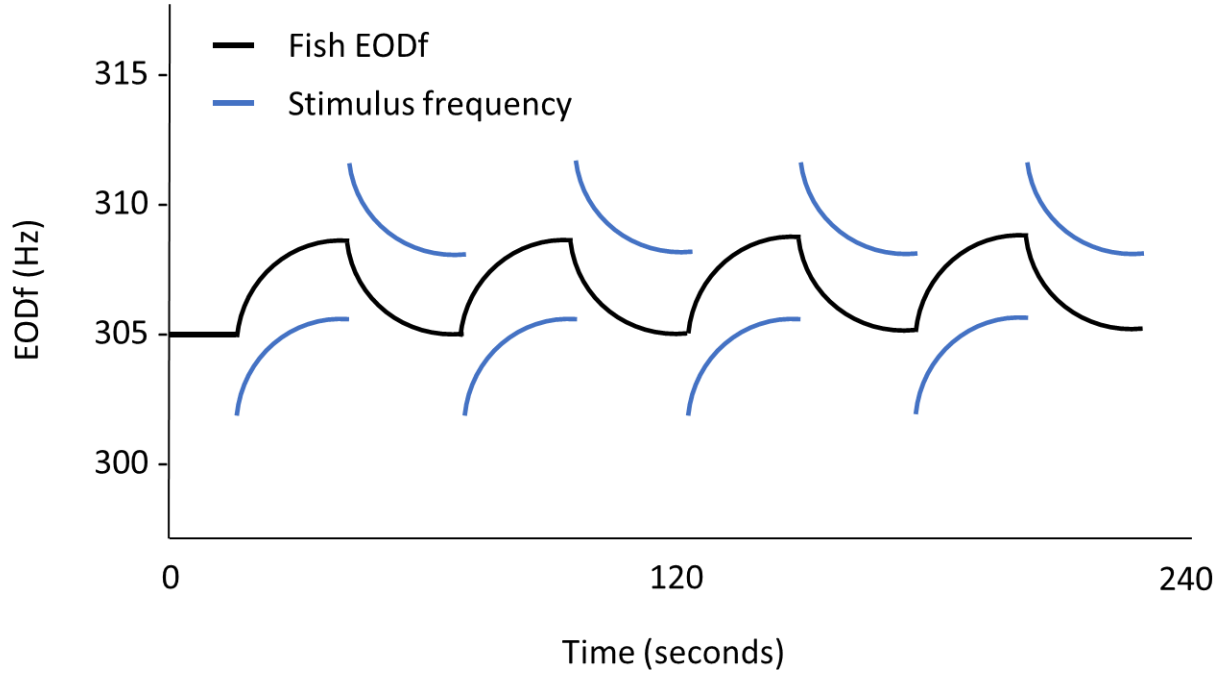

Figure 1.6 Schematic of the jamming avoidance response (JAR) when a frequency clamped stimulus is presented. Stimulus is presented for approximately 30 seconds, with an alternating -3 Hz DF and +3 Hz DF.

1.4 The Effect of Swimming Noise on EODF Identification – Previous and Proposed Study

A previous study (Yu et al., 2012) has indicated that information from the AM (indicative of conspecific EODF) and the envelope (indicative of inter-fish orientation and distance) can sometimes be conflicting. When two fish are stationary, AM information is encoded efficiently by the electroreceptors of the receiving fish; the information regarding conspecific EODF (difference frequency) is clear and unmodulated. Conversely, when a neighbouring fish is moving, the envelope causes the firing of electroreceptors to vary. This acts as a source of "noise" in the context of coding difference frequency information in the AM. Consequently, it was suggested that this noise may obscure significant conspecific identity information (Yu et al., 2012). In other words, as swimming motion increases, differentiation of the AM frequency, and therefore conspecific EODF, was thought to become more difficult as the encoding quality of the AM is degraded by 'swimming noise' at the level of the envelope. These hypotheses were first developed using experimental recordings of free-swimming *A. leptorhynchus* and experimental models (Yu et al., 2012).

Wave-type weakly electric fish like *E. virescens* are a convenient model for behaviourally examining the effects of movement noise on conspecific identification, since they robustly exhibit a behaviour that requires accurate conspecific EODF recognition: the jamming avoidance response. As previous mentioned, when two weakly electric fish with similar EODFs (DF <15 Hz) are in close proximity, the electrosensory abilities of both fish are compromised (Bastian et al., 1987a,b; Heiligenberg 1973). The jamming avoidance response requires that each fish in an interaction accurately identifies the specific EODF of its neighbour (Heiligenberg,

1991; Keller, 1988; Kelly et al., 2008). In other words, a fish will not perform a JAR if it is unable to determine the frequency of another fish with an interfering EODF.

Using the JAR as a measure of EODF identification accuracy, this study aims to examine the effect of swimming noise on conspecific EODF identification ability in *E. virescens*.

1.5 Testing the Accuracy of EODF Identification – Objectives, Hypothesis, and Predictions (Figure 1.7)

Goal: The purpose of the present study is to examine the effect of 'swimming noise' on the accuracy of conspecific EODF identification in *E. virescens*, using the JAR as a means of quantifying the precision of EODF detection.

Question: How does swimming noise affect conspecific identification abilities?

Employing established methods of stimulus presentation, a jamming stimulus mimicking a conspecific will be used in playback experiments (Bullock et al., 1971; Harvey-Girard et al., 2010; Moller, 1995). This classic stimulus will be altered, by the addition of signal noise representing various intensities of swimming motion (Yu et al., 2012). By characterizing JAR performance resulting from the presentation of stimuli with different noise levels, the effect of swimming noise on conspecific EODF determination may be quantified.

Hypothesis 1: Compromised EODF Identification

- **Hypothesis 1:** Swimming noise will reduce the ability of *E. virescens* to identify the EODF of a conspecific
- **Prediction 1:** As the degree of swimming noise increases, JAR performance will decrease: the latency to JAR will increase, the magnitude of the JAR will decrease, and the accuracy of the response will decrease as compared to when stimuli of lower noise levels are presented.

If EODF identification ability declines with rising swimming noise levels, several explanations are possible. Firstly, it could be postulated that as swimming noise levels increase, the degree of EOD jamming actually declines. As such, the 'need' to JAR would also decline, and could explain a potential decrease in JAR magnitude at high noise levels. It is also possible that gymnotiforms may actually take advantage of noise in behavioural conspecific interactions. This could involve the application of non-visual crypsis, whereby one organism is able to conceal its location and/or identity from another organism, where the sense involved in detection is not vision (Ruxton, 2009). It is well documented that gymnotiforms have electroreceptive predators, such as the electric eel (Stoddard, 1999). Furthermore, other types of electric fish have been shown to exhibit signal cloaking behaviours. For instance, the pulse-type *Brachyhypopomus* will shift the spectrum of its EOD pulse to higher frequencies that are less detectable by electroreceptive predators (Stoddard & Markham, 2008). Accordingly, it can be presumed that wave-type electric fish like *E. virescens* may have evolved their own methods of anti-predatory crypsis. Indeed, it could be proposed that gymnotiforms use the noise generated by swimming motion to disguise themselves from electroreceptive predators (a form of non-visual crypsis).

<u>Hypothesis 2: Stochastic Resonance</u>

- **Hypothesis 2:** Swimming noise will enhance the ability of *E. virescens* to identify the EODF of a conspecific.
- **Prediction 2:** When stimuli with an optimal level of swimming noise are introduced, JAR performance will be enhanced: the latency to JAR will be decreased, the

magnitude of the JAR will be increased, and the accuracy of the response will increase as compared to when stimuli with no noise and with much larger noise levels are presented.

Although initially counter-intuitive, the possibility that noise can enhance sensory processing is well-established, and is referred to as stochastic resonance (Wiesenfeld & Moss, 1995; See section 4.3). When the amplitude of a clear signal, such as a sine wave or EOD, is entirely below a detection threshold, signal detection does not occur. However, when that signal becomes 'noisy', amplitude excursions around the sine wave (due to noise) may actually cross the detection threshold, facilitating signal detection (Figure 1.7; Wiesenfeld & Moss, 1995). Hypothesis 2 stipulates that, in gymnotiforms, swimming motion will allow a sub-threshold conspecific EODF to be identified, by creating 'noisy' amplitude excursions that may cross the signal detection threshold. If so, this would be one of the first applications of stochastic resonance in an animal behaviour context, and may grant insight into the adaptive value of noise at the whole animal level (McDonnell & Ward, 2011).

<u>Hypothesis 3: No change in EODF Identification</u>

- **Hypothesis 3:** Swimming noise has no effect on the ability of *E. virescens* to identify the EODF of its neighbour
- **Prediction 3:** There is no systematic change in JAR performance at any level of swimming noise

If swimming noise is determined to have no measurable effect on the JAR, it could be postulated that *E. virescens* is able to circumvent any masking effects of swimming noise at the whole animal level – despite the fact that swimming has been shown to be a noise source at the level of a single electroreceptor (Yu et al., 2012). This possibility makes adaptive sense, as it would mean that *E. virescens* is able to balance the necessary requirements of both dynamic swimming motion and conspecific identification. Although further experimentation would be required to determine why this is possible, several hypotheses are viable (see section 4.2). For example, *E. virescens* may be able filter or average out the noise created by swimming that is encoded by the electroreceptors, by some (as of yet unconfirmed) mechanism along the JAR neural pathway (McGillivray et al., 2012; Metzen & Chacron, 2015). It is also possible that, since phase information is preserved even when swimming noise is introduced, sufficient information remains available to maintain JAR performance despite high levels of envelope noise (Carlson & Kawasaki, 2007; Shifman & Lewis, 2018).

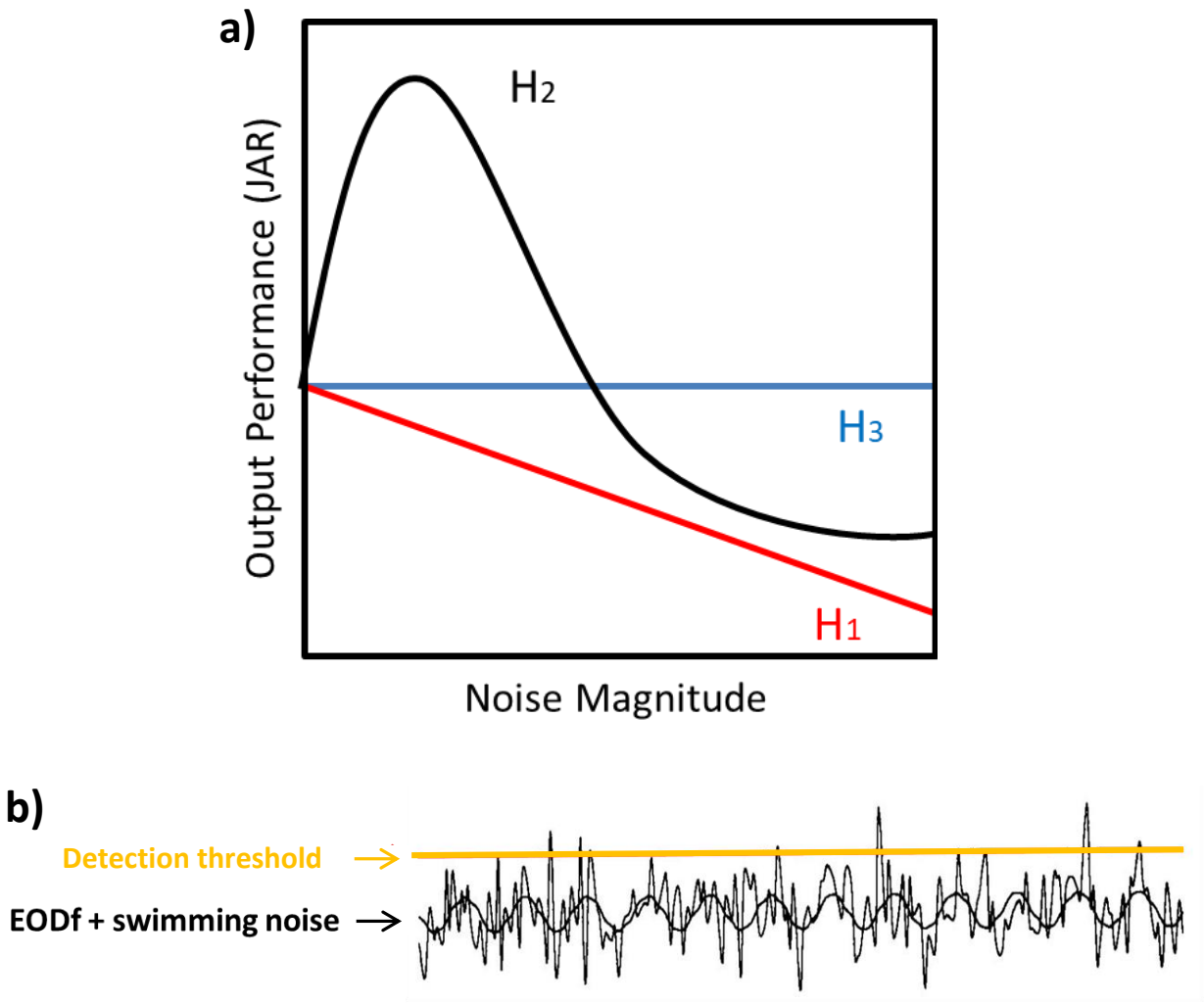

Figure 1.7 Hypotheses regarding the effect of swimming noise on conspecific identification in *E. virescens*. a) Output performance (measured by the JAR) as the amount of swimming noise increases according to the three hypotheses presented. H1, Hypothesis 1; H2, Hypothesis 2; H3, Hypothesis 3. b) Hypothetical stochastic resonance (SR) as described by hypothesis 2. The signal is detected whenever the detection threshold (yellow line) is crossed. Modified from Wiesenfeld & Moss (1995).

2. METHODS

2.1 Experimental Set-Up and Stimulus

Laboratory experiments were performed with a total of 38 specimens of *E. virescens* obtained from a tropical fish supplier. Before and after experiments, fish were be kept in 115 L flow through group tanks, held at 26-28°C, with a conductivity of 150-200 µS and on a consistent light cycle of 12 hours light: 12 hours darkness. Frozen bloodworms were fed to the fish 3 times each week.

For experiments, fish were moved to individual glass tanks (30cm x 17 cm x 13.5 cm) with a water temperature of 26-29°C and conductivity of 150-200 µS. All experiments were performed in the dark, since *E. virescens* are nocturnal. Individual fish were placed in an enclosed 'chirp chamber' for approximately 15 minutes before trials began, or until they were visually assessed to have ceased struggling (no longer swimming back and forth, trying to escape, turning, etc.) (Harvey-Girard et al., 2010; Hitschfeld et al., 2009; Zupanc & Maler, 1993). The chirp chamber consisted of an enclosed PVC tube with plastic mesh sides and ends, a pair of recording electrodes (anterior and posterior to the fish), and a pair of carbon stimulus electrodes (left and right sides of the fish). This is referred to as a "global" stimulus orientation, as the position of the stimulus electrodes (perpendicular to and across the fish's body) creates an electrical image across the whole body surface, rather than at a specific point (Figure 2.1; Metzen & Chacron, 2015). This orientation was chosen for two reasons: it is the classically used orientation to produce the jamming avoidance response, and it has been shown to be more representative of naturalistic communication signals than a more localized electrode orientation (Chacron et al., 2003; Viete & Heiligenberg, 1991). An additional pair of recording electrodes was placed outside of the chirp chamber to record the stimulus output. A grounded

electrode was also placed in the corner of the tank (Figure 2.1). All recording and ground electrodes were made with Teflon-coated silver wire, with a diameter of 0.38 mm (WPI, Inc., Sarasota, FL, USA). Electrical recordings were amplified using an AM systems model 1700 (Carlsborg, WA, USA) differential amplifier (1000x amplification, low frequency cut-off of 10 Hz, and high frequency cut-off of 1 kHz).

Recordings were sampled at 20 kHz using a dSpace Inc. (Wicom, MI, USA) DS1104 data acquisition board and dSpace Control Desk Software. The same system was used to present stimulus waveforms consisting of a sine wave (mimicking a conspecific electric fish) with varying levels of 'swimming noise' or envelope modulations (with a depth of 0-100% contrast). The stimulus frequency was set for a difference frequency of -3Hz, and was not clamped to the fish EOD; i.e. did not change during the JAR response (Bullock et al., 1972a, b). Starting from an amplitude of 0, the stimulus amplitude gradually increased as a ramp (in which amplitude rises as a cubic function of time), with the maximum amplitude occurring at the end of the 30 second stimulus presentation (Figure 2.2) (Carlson & Kawasaki, 2007). The maximum stimulus amplitude was matched to the field strength of each individual fish (measured by a pair electrodes located 3 cm lateral distance from the fish). A stimulus with an amplitude that is equal to that of the experimental fish is representative of a similar sized fish in close proximity (Carlson & Kawasaki, 2007; Hagedorn & Heiligenberg, 1985; Moller, 1995).

In this investigation, experiments were designed to determine if 'swimming noise' enhances the identification of moving conspecifics. Waveforms that mimic the envelope modulations due to swimming were generated using the model developed by Yu et al. (2012). These waveforms were scaled to different depths to produce the swimming noise stimuli at

various noise levels (Figure 2.2 a). Part One of this study featured a stimulus with an envelope frequency of 0-20 Hz (Figure 2.2 b, c). Part Two of this study used a filtered stimulus, with an envelope frequency of 2-20 Hz (Figure 2.2 b, d). Stimuli were randomly presented for periods of 30 seconds, alternating with 30 second recovery periods (in Part One) or 45 second recovery periods (in Part Two, to allow for more time for a return to baseline frequency to occur) before the next stimulus was given (Bullock et al., 1972 b). Each trial consisted of 5 thirty-second stimulus repetitions for each noise level (0%, 25%, 50%, 75% and 100% contrast), for a total of 25 thirty-second stimulus presentations per fish. During the stimulus and recovery periods, both the fish EOD and the output signal were recorded.

0% contrast stimulus (no swimming noise) acted as a control stimulus, and was always the first and last stimulus presented, to assess sensitization to the stimulus over the trial period. A separate set of control trials was performed (n=3), with a consistent stimulus of no noise (0% contrast) for one hour (30 seconds on, 30 seconds off), to examine stimulus sensitization and variability in response over the trial time.

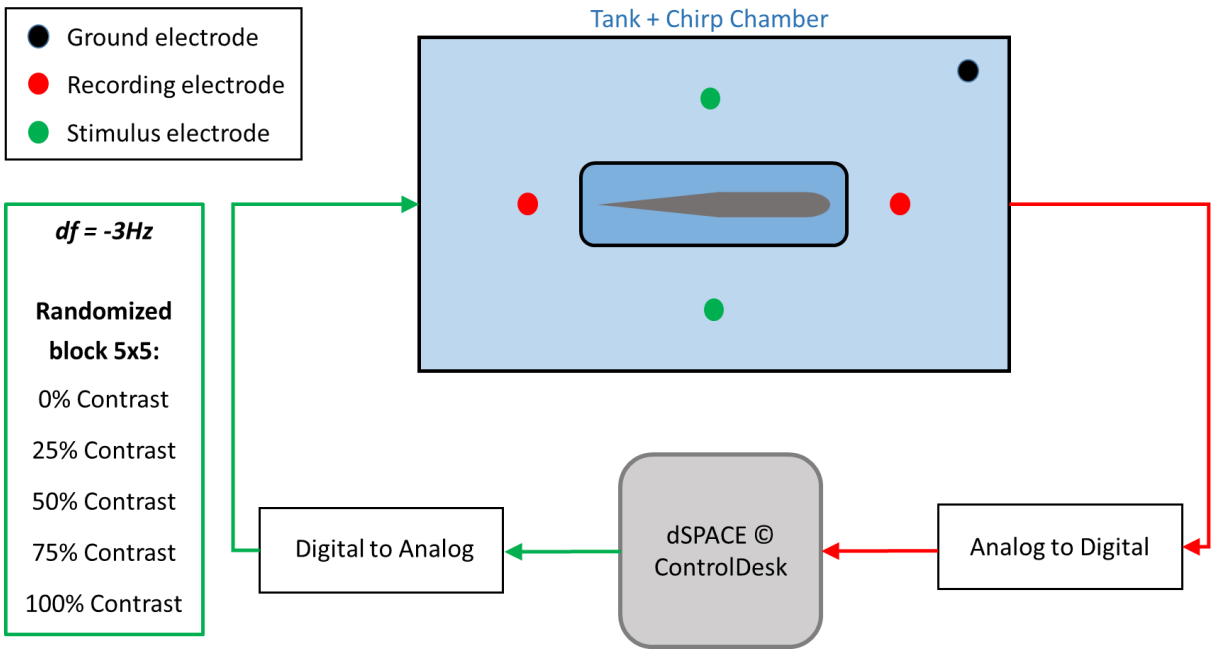

Figure 2.1 Experimental set-up. Fish was enclosed in chirp chamber within the tank, which also contained a ground electrode (black). Recording electrodes at the head and tail of the fish recorded the EODF (red). Stimulus electrodes placed left and right of the fish presented an artificial conspecific frequency, with 0-100% contrast swimming noise applied. The stimulus was set at an un-clamped DF of -3 Hz.

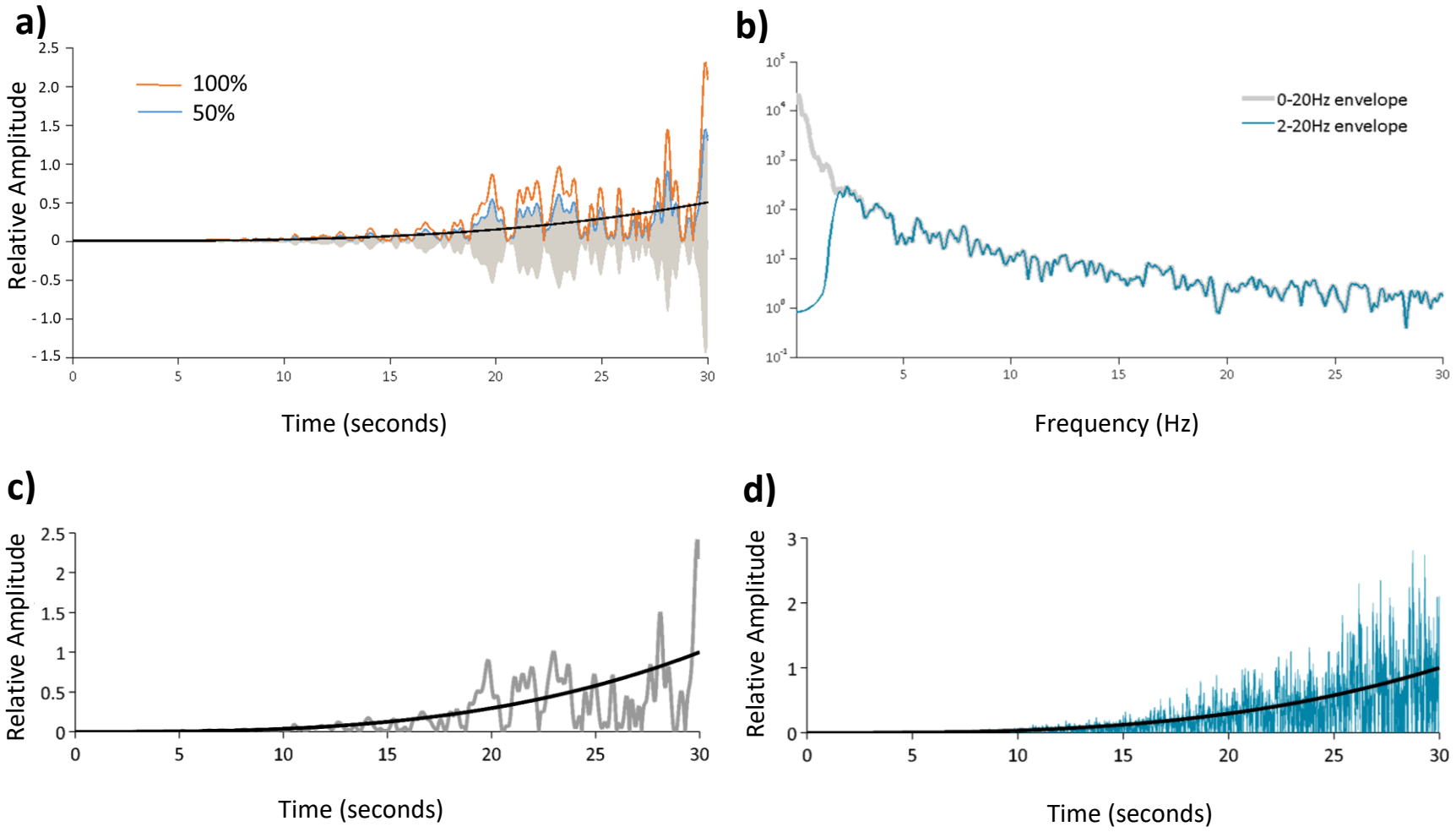

Figure 2.2 Elements of the experimental stimulus. Cubic ramp is pictured in black. a) Example of the levels of swimming noise present in the stimuli. 50% contrast and 100% contrast (the largest noise level used) in the broadband stimulus type are shown. b) Power spectra of the noise stimulus envelopes used in Part One (broadband, 0-20 Hz) and Part 2 (2-20Hz). c) Relative amplitude of the broadband stimulus (100% contrast). d) Relative amplitude of the filtered stimulus (100% contrast).

2.2 Data Organization

Experiments were completed with 20 specimens of *E. virescens* from March to April of 2015 (Part One) and with 18 specimens from January to February of 2016 (Part Two). Weight, length, field strength and EOD frequency were recorded for each fish, as well as tank temperature and conductivity (Table 2.1). The average weight of the fish was 3.31 g ± 0.95 g. The average length of the fish was 11.30 cm ± 2.15 cm. The average EOD frequency of the fish was 392.21 Hz ± 66.77 Hz. The responses of individual fish to each stimulus noise level (% contrast) were visualized by plotting the change in EODF over time. Most of the fish (36 out of 38) responded to the stimuli by performing the JAR robustly. A fish was considered a non-responder if, on average, the change in EODF in response to jamming stimuli was always less than 0.5 Hz (Figure 2.3; Bullock et al., 1972b). The two non-responding fish were removed from further analysis (Viete & Heiligenberg, 1991). In the remaining experiments, the time-varying EODF was smoothed (1 sec moving average) and sampled every 100 milliseconds. The data was visually inspected for extraneous experimental noise that differed significantly from the surrounding data in frequency content. Sources of this noise were likely due to accidental movement of electrodes during recording. The data points featuring this extraneous noise were located, and smoothed using the data trajectory before and after the event. Several variables were then extracted (using custom scripts in Matlab) in order to measure and compare JAR performance among stimulus conditions (see following section).

Table 2.1 Descriptive parameters of fish used in experiments (n=38)

Fish	Weight (g)	Length (cm)	Frequency (Hz)	Water Temp. (°C)	Water Cond. (µS)
1	3.10	13	381	26.5	150
2	2.73	10	414	26.5	150
3	3.96	12	389	26.5	150
4	3.13	12	384	26.8	150
5	2.02	11	360	26.8	150
6	1.89	10	463	26.6	150
7	5.74	13.5	320	26.6	160
8	1.40	10	365	26.6	160
9	2.44	8	366	26.6	150
10	4.27	13	371	26.7	160
11	4.82	13.5	517	26.7	160
12	3.3	14	308	26.6	160
13	3.89	14	311	26.5	150
14	2.62	10	350	26.5	150
15	4.41	15	425	26.2	150
16	1.57	12	398	26.3	150
17	3.51	12	340	26.3	150
18	3.98	13	446	26.3	150
19	3.65	10	311	26.5	160
20	4.29	14	344	26.5	160
21	3.21	12	509	26.2	150
22	3.08	12	445	26.2	150
23	2.60	9	411	26.4	160
24	3.12	11	407	26.4	160
25	4.47	15	403	26.4	160
26	3.59	10	340	26.8	150
27	4.51	13	504	26.8	150
28	3.53	11	277	26.8	170
29	2.32	8	491	26.3	170
30	2.65	9	343	26.2	170
31	3.45	10	264	26.2	160
32	2.41	7	314	26.0	160
33	4.59	13.5	458	26.0	150
34	2.27	6	350	26.8	170
35	3.41	11	468	26.8	170
36	3.61	11	472	26.8	160
37	2.93	10	422	26.5	160
38	3.27	11	463	26.5	160

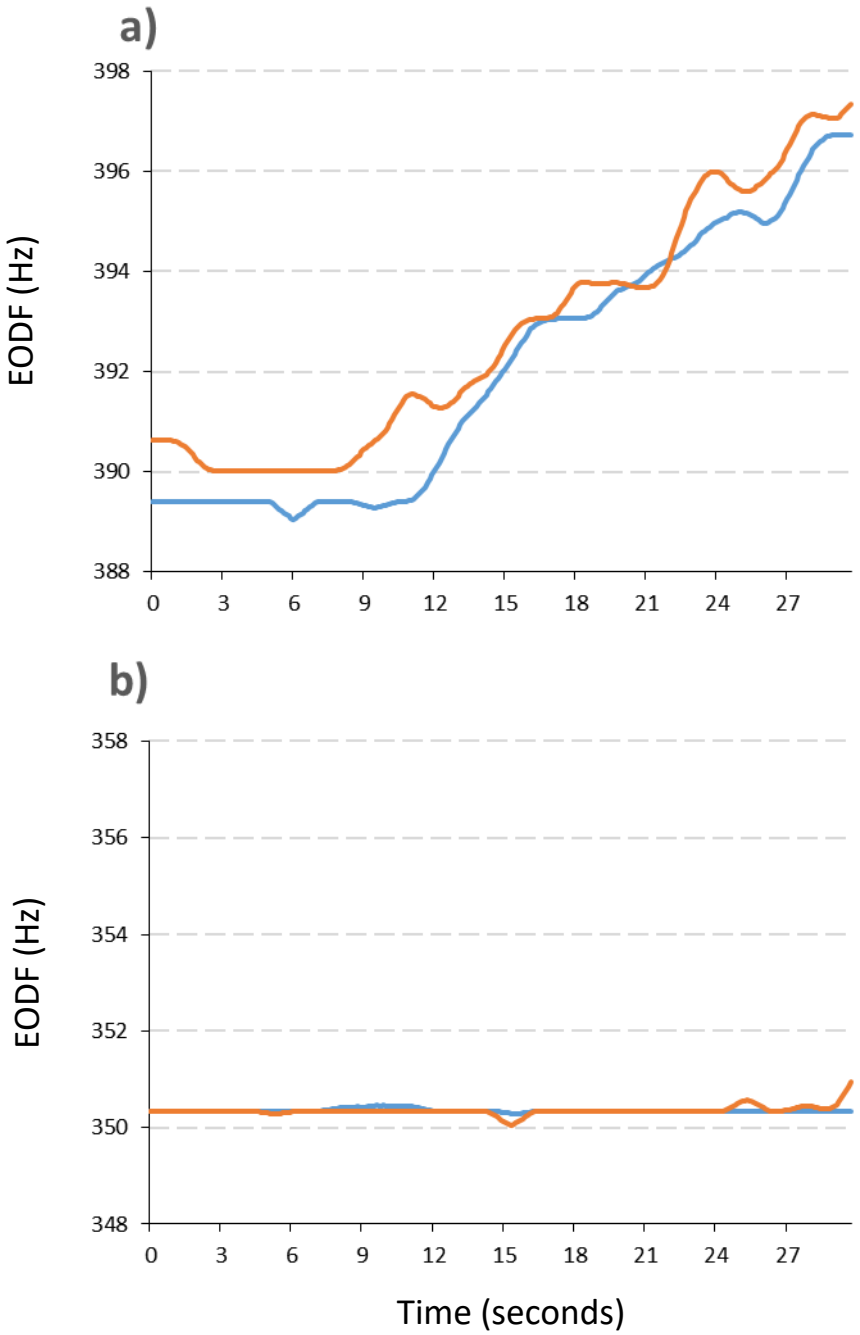

Figure 2.3 Examples of EODF (Hz) in time responses to a single 0% contrast stimuli (blue) and single 100% contrast stimuli (orange) for a) a strongly responding fish (fish #1) and b) a non-responder (fish #20).

2.3 Quantifying JAR Performance (Figure 2.4)

JAR Latency

JAR latency is a measurement of the time between stimulus onset and commencement of the JAR. Commencement of the JAR was determined on a fish-by-fish basis. Firstly, the standard deviation of each fish's baseline EODF was determined from pre-trial recordings (with no stimulus present). A JAR threshold for each fish was set at 1.96 times the standard deviation (i.e. a confidence of interval of 95%). If the fish's change in frequency (either upwards or downwards) crossed this threshold, the time point of the change was designated as the commencement of the JAR (with only a 5% chance that the change was due to normal fluctuations of the EODF) (Moss et al., 2004). Two latency values were measured from each EODF time series, referred to as *JAR latency one* and *JAR latency two*. Latency one was the time at which the absolute value of the fish's EODF first crossed the individual JAR threshold. JAR latency one measures the first supra-threshold change in EODF, whether positive or negative in direction. The latency two value is identical to the first latency measure, except for the stipulation that the EODF must rise above the threshold (in a positive direction only) *and* not return below threshold again during the stimulus period. In other words, latency one is a measure of when the fish shows signs of detecting the JAR stimulus, and latency two is a measure of when the fish has performed a correct and consistent JAR.

JAR Magnitude

JAR magnitude is the difference between the initial EODF at stimulus onset and the EODF achieved at 25 seconds after stimulus onset (near the end of the JAR stimulus period). A JAR magnitude value was measured from each EODF time series.

JAR Accuracy

JAR accuracy is a measure of the ability of a given fish to perform the JAR consistently in the correct direction (i.e. by moving upward in frequency, away from the stimulus frequency). The sign of the derivative of the EODF signal from point to point (every 100 ms) was determined. A positive derivative was denoted a value of 1, for a correct JAR decision. Negative derivatives and derivatives of 0 were both given a value of 0, for an incorrect or absent JAR decision. Using a logistic regression, these derivative values were fit (against time) to a sigmoidal function. This fit is used to determine the proportion of correct JAR decisions at 20 seconds after the start of the stimulus period. In other words, JAR accuracy represents the fraction of time, within the first 20 seconds of the stimulus, that the responding fish performed the JAR in the correct direction (upwards in frequency, away from the negative DF stimulus).

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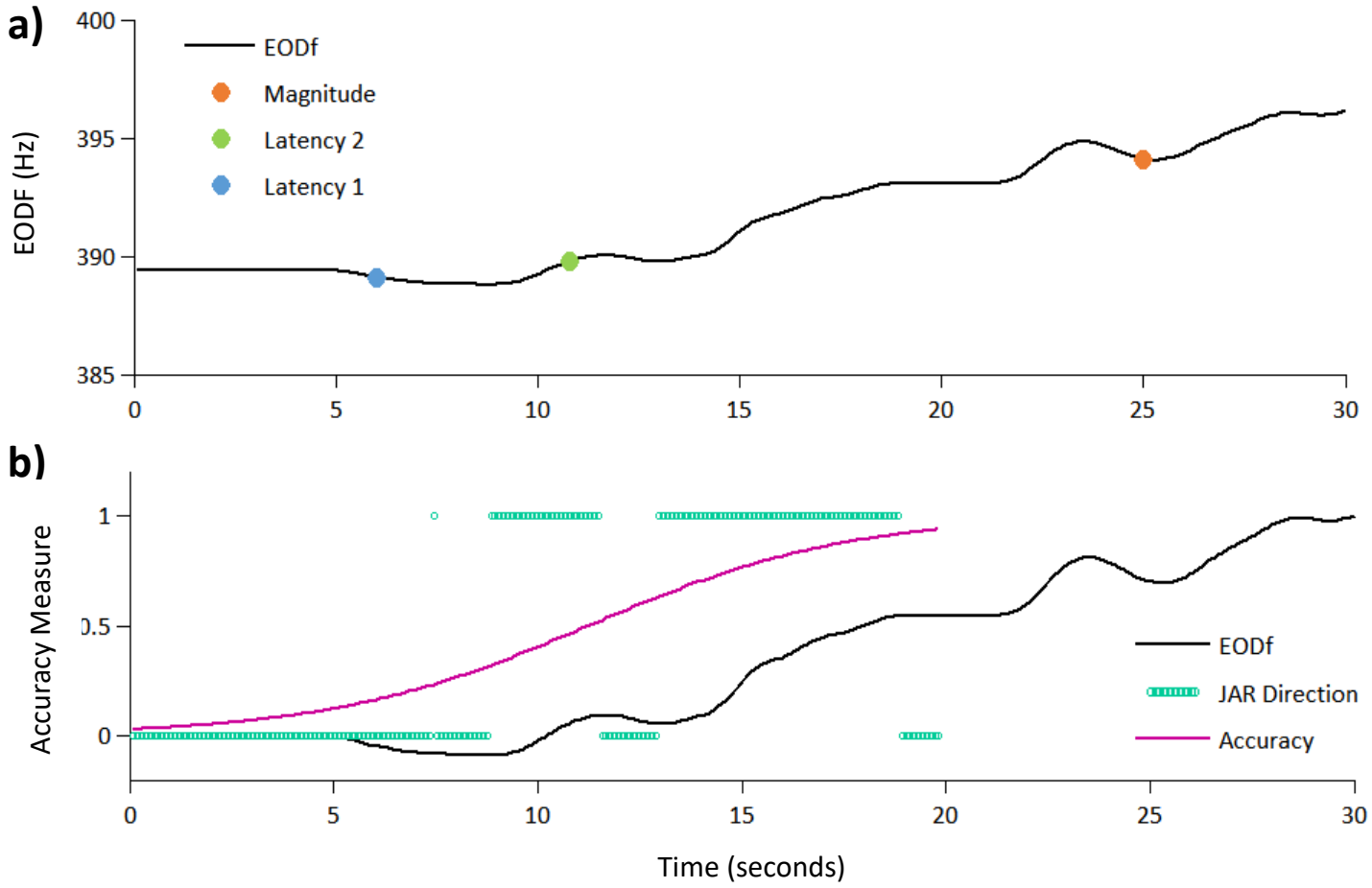

Figure 2.4 JAR performance variables using an example from a single fish (fish #1, trial #6, 100% contrast stimulus). a) Example of JAR magnitude at 25 seconds, latency one, and latency two measures on a single response. b) Example of JAR accuracy. The green circles indicate either a correct JAR (moving upwards or frequency, denoted by an accuracy measure of 1) or a null or incorrect JAR (not changing in frequency or moving downwards, denoted by an accuracy measure of 0). The sigmoid function of JAR accuracy (purple) represents the proportion of correct JAR behavior over the first 20 seconds.

2.4 Control Trials

In addition to the 38 fish used in the experimental trials, 3 fish were used in control trials to assess the presence of sensitization to the stimulus. In these control experiments, the JAR stimulus with no swimming noise (0% contrast) was repeatedly delivered to the experimental fish for 30 second intervals, alternating with 45 seconds of recovery, for one hour. Linear mixed effect models were created with time (trial number) as the fixed effect, a JAR variable (magnitude, latency, or accuracy) as the response variable, and fish id as a random factor. By comparing these models to their respective null models (with no fixed effect present) using ANOVA, the effect of time on the individual JAR variables was established. These methods indicated that within a time frame equal to that of the actual experiments (25 stimulus presentations), JAR magnitude increased significantly with time ($p = 0.01215$) and JAR latency two decreased significantly with time ($p = 0.00002513$) (Figure 2.6). This suggests that with repeated stimulus presentations, JAR performance increases. As such, time (or trial number) was accounted for in the analysis of experimental data (included as a fixed effect).

Within experiment controls (0% contrast stimulus) were also examined. The change in JAR variables over time within in an experiment was examined using responses to the 0% contrast stimulus, which was repeated 5 times throughout each experiment in a randomized block design. Again, linear mixed effect models were created with time (trial number) as the fixed effect, a JAR variable (magnitude, latency, or accuracy) as the response variable, and fish id as a random factor. These models were compared to their corresponding null models (with no fixed effect present) in a likelihood ratio test (ANOVA). This analysis revealed no significant effect of time on the JAR performance ($p>0.1$ in all cases). However, since control trials

indicated the possibility of stimulus sensitization, trial number was included as a fixed effect in subsequent analyses.

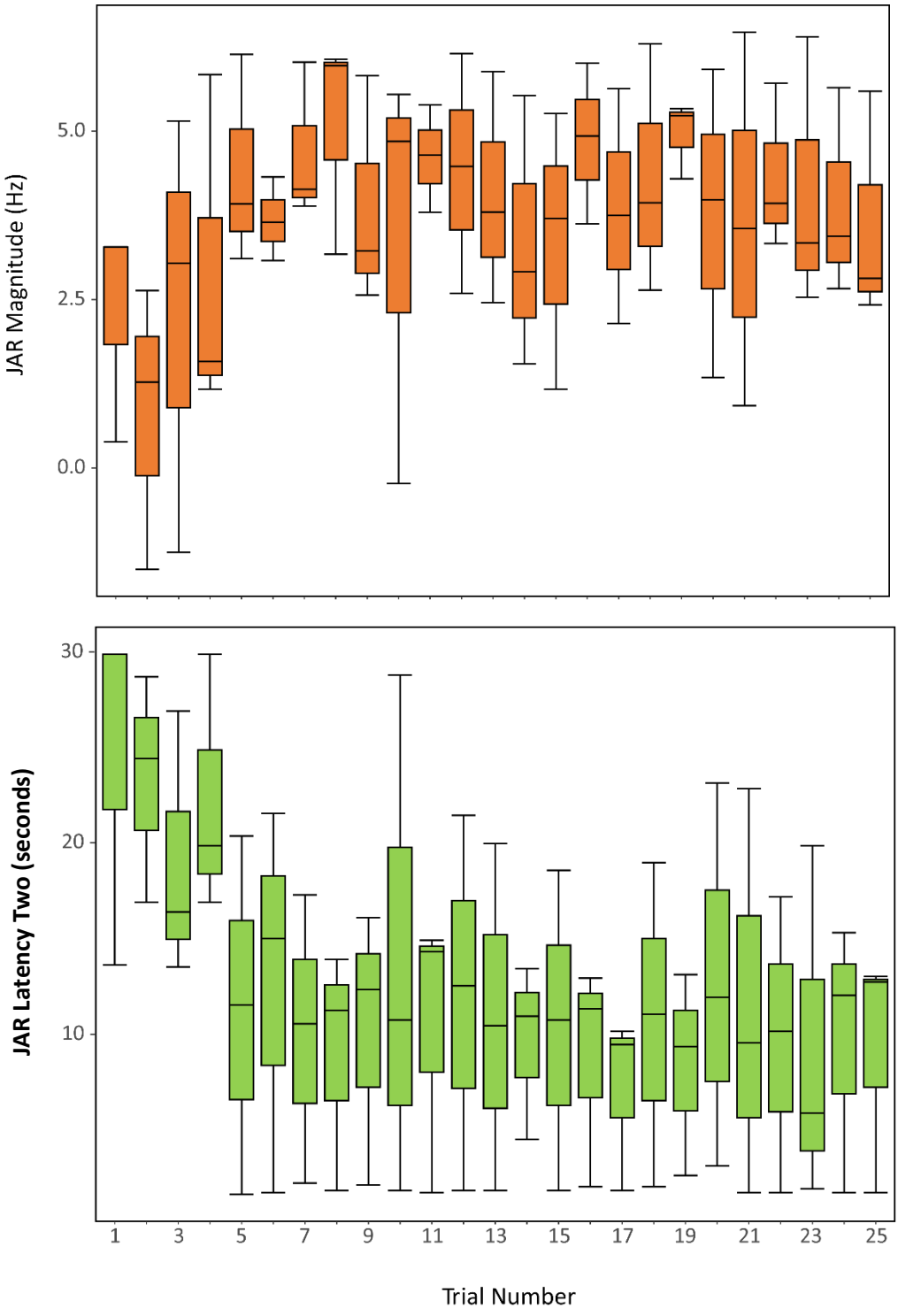

Figure 2.5 First 25 stimulus presentations of JAR Magnitude (orange, top) and JAR Latency Two (green, bottom) in control trials (0% contrast stimulus only).

2.5 Data Analysis

The effect of swimming noise level (stimulus % contrast) on JAR performance variables was examined through the use of random slope linear mixed effects models with repeated measures (*lm* and *lme4* in R statistical software) (Bates, Maechler & Bolker, 2012). This form of analysis was chosen as it provided a simple means of accounting for common statistical obstacles in animal behaviour research, such as repeated measures, variability between and within subjects, and sensitization to the stimulus over time (Dingemanse & Dochtermann, 2013; Garamszegi, 2016). A list of all of the models used can be found in Table 2.2. Within the models, stimulus condition and trial (without interaction term) were entered as fixed effects. Trial number (1-25) was included as a fixed effect, since control trial analysis indicated a significant sensitization of response over time (Figure 2.6). Fish id was used as a random effect to control for inter-subject variation. By-fish random slopes for the effects of condition and trial were also incorporated, to account for the fact that the effects of time and stimulus noise level may vary by fish. This model was deemed to be the most appropriate to summarize the data, but other more simple models were tested, with similar overall resulting trends. In some cases, the model fit failed to converge. In such an instance, the optimization method was changed to *Nelder-Mead* (from the default optimizer *bobyqa*). In some cases, this was not effective in resolving non-convergence, so data were then rank transformed (with duplicates set as average) and this resolved the fitting.

Visual inspection of residual plots, as well as qq-plots and histograms of the residuals, did not reveal any evident deviations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests (ANOVA) of the full model with the effect in question against

the model without the effect in question (the null model) (Table 2.2). By comparing the model with stimulus condition as a factor against the null model (without stimulus condition), the significance of the degree of variability that is characterized by stimulus condition was ascertained. The slope of the model was representative of the direction of change in a particular JAR variable as stimulus condition increases. The variation explained by the random effects was also reported.

Further analysis was completed in order to describe how the EOD response varied in time *in relation to the envelope modulations of the stimulus itself*. To begin, the rate of change of the stimulus amplitude and the rate of change of the EODF for each fish and stimulus condition were calculated. In order to account for any lag in time between the rise of the stimulus amplitude and the rise of the EODF, a cross-correlation analysis was completed (*ccf* function in R), using the envelope data for the highest noise condition (100% contrast). For each fish, this analysis gave a particular lag value (amount of shift of the stimulus envelope data in time, given in data points) at which the cross-correlation between the stimulus amplitude and the EODF was most prevalent (highest CCF value). The stimulus amplitude traces were then adjusted by their corresponding lag values. This was done for all fish within each stimulus noise level. A simple linear regression model (*lm* function in R) was then used to examine the degree of correlation between the stimulus amplitude and EODF (rates of change), again for each fish and stimulus condition. The p-value presented in the model summary indicated the significance of the correlation between the EODF and the stimulus envelope depth, with any lag in response accounted for. P-values were obtained for each fish within each noise level (0%-100% contrast) and noise type (filtered vs broadband stimuli). As such, it was possible to determine if any

"envelope tracking" behaviour was occurring, and compare this behaviour between noise levels and noise types (Metzen & Chacron, 2014).

Table 2.2 Linear models and linear mixed effects models used in data analysis. Models run in R Statistical Software with function *lmer* and *lm*. In most cases, likelihood ratio tests (ANOVA) were used to compare models with their corresponding null models.

	Model	Fixed Effects	Random Effects
Main Model	*lmer* (JAR variable ~ stim + trial + (1+stim|fish) + (1+trial|fish))	Stim + trial	(1+stim|fish) + (1+trial|fish)
Main Null Model	*lmer* (JAR variable ~ trial + (1+stim|fish) + (1+trial|fish)	Trial	(1+stim|fish) + (1+trial|fish)
Control Model	*lmer* (JAR variable ~ trial + (1|fish))	Trial	(1|fish)
Null Control Model	*lmer* (JAR variable ~ (1|fish))	NA	(1|fish)
Cross-Corr. Model	*lm* (envelope data ~ EODF data)	EODF data	NA

3. RESULTS

Experiment Results: Part One - Broadband Noise Stimulus

3.1.1 JAR Performance

In Part One of this study, a total of 18 experiments were analyzed. The stimulus featured an EODF with broadband swimming noise, created from a model representation of a dynamically swimming gymnotiform fish (Yu et al., 2012). The envelope of the stimulus ranged in frequency content, including modulations from 0-20 Hz (Figure 2.2 b, c). An example of an individual response to this broadband stimulus can be seen in Figure 3.1. The mean responses for each variable, along with the standard deviation of the mean and the maximum, minimum and range of the data over all fish is presented in Table 3.1.

Linear mixed effects model analysis revealed that swimming noise (at all stimulus noise levels) had no significant effect on any of the JAR variables (Figure 3.2, 3.3; Table 3.2). Model summaries indicated that residual random effects (rather than fish identity or trial number) explained the majority of the variance in the data (Table 3.2). Overall, when the broadband noise stimulus was employed, signal modulations due to movement had no significant effect on the JAR performance.

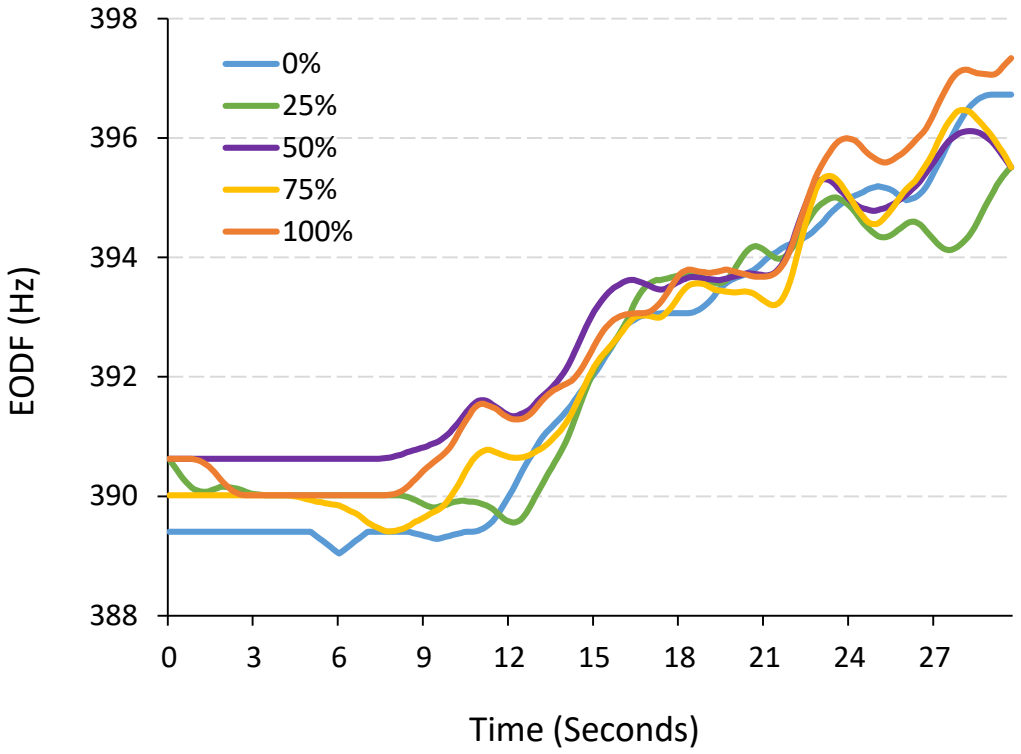

Figure 3.1 Response of fish #1 to the broadband stimulus used in Part One. Responses to all stimulus conditions (% contrast) are shown.

Table 3.1 Mean, standard deviation, maximum values, minimum values, and range of values for each JAR variable, computed over all fish in Part One (n=18).

	Latency One	Latency Two	JAR Magnitude	JAR Accuracy
Mean	8.511111	15.83622	2.060622	0.657551
SD	5.878754	4.752015	1.447809	0.136875
Max	25.7	30	9.817069	0.995028
Min	1.3	1.3	-2.5129	0.5
Range	24.4	28.7	12.32997	0.495028

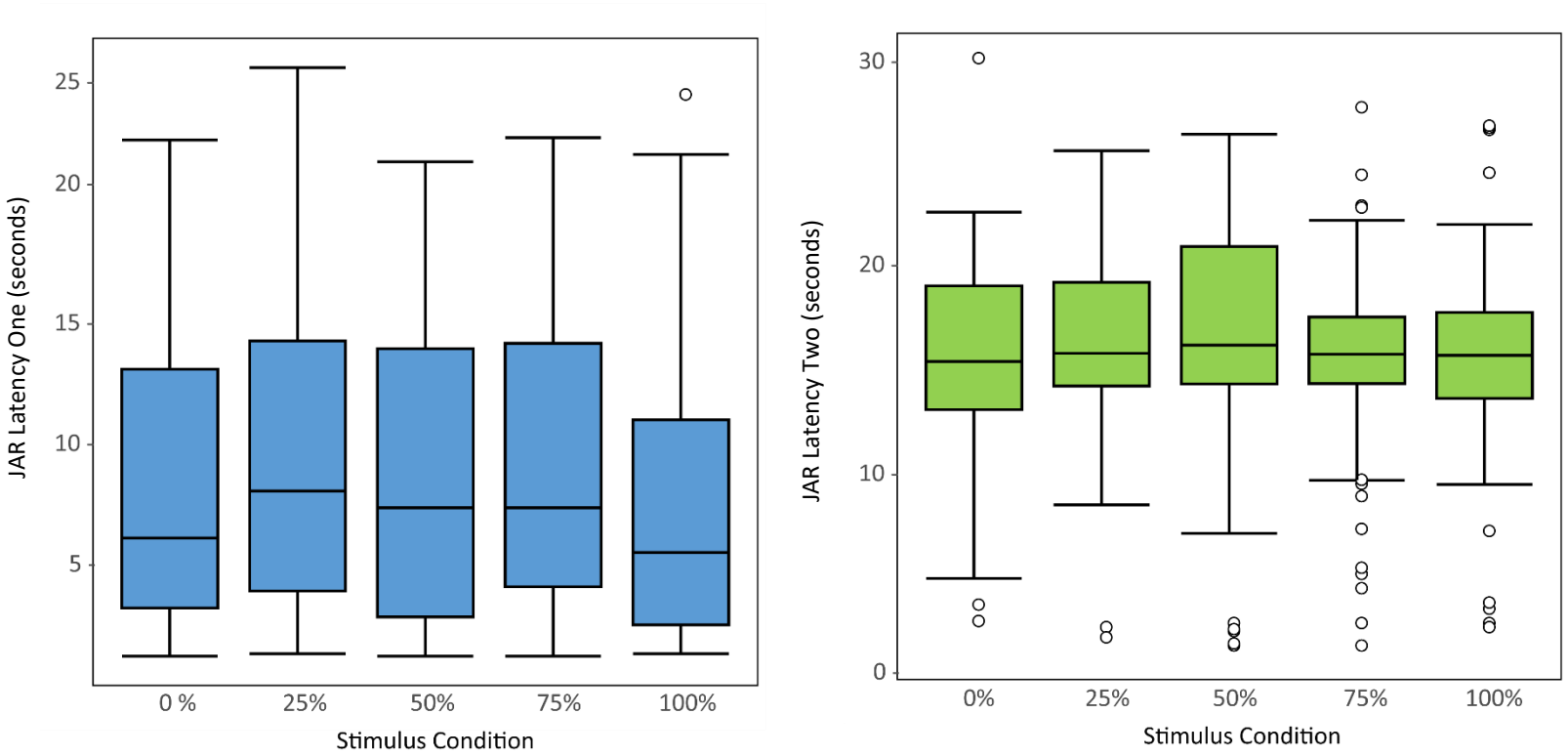

Figure 3.2 Boxplots of JAR latency variable values for all fish in Part One, in response to the broadband noise stimulus at different stimulus conditions. Left (blue) is JAR latency one and right (green) is JAR latency two, both measured in seconds. Boxes represent the interquartile range (IQR), or the spread from 25th percentile (lower hinge) to the 75th percentile (upper hinge), with a central horizontal bar denoting the median value. Whiskers encompass values within 1.5 x IQR extending from the lower and upper fences. Open circles denote data outside this range.

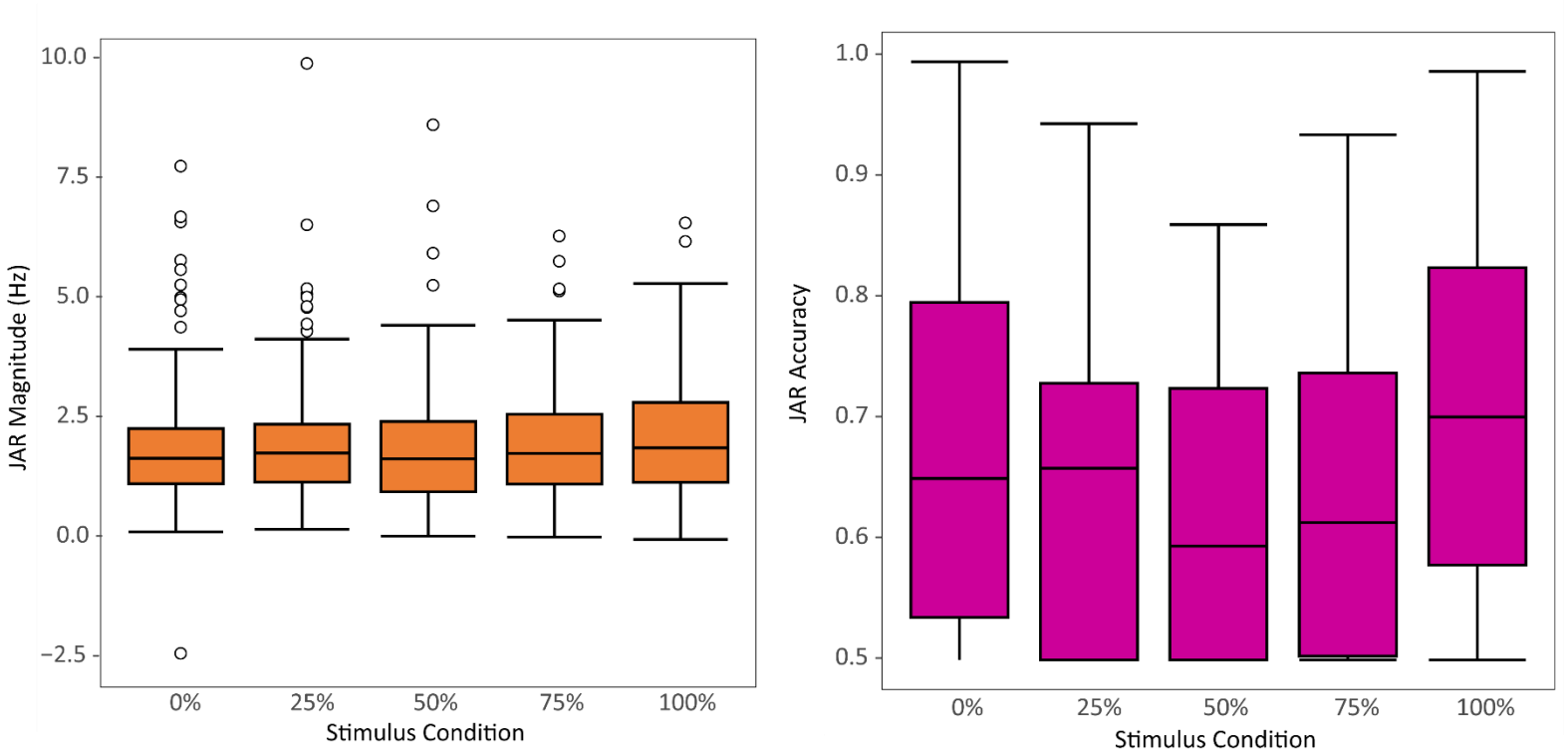

Figure 3.3 Boxplots of JAR magnitude and JAR accuracy values for all fish in Part One, in response to the broadband noise stimulus at different stimulus conditions. Left (orange) is JAR magnitude, measured in Hz. Right (purple) is JAR accuracy, measures as the proportion of the response consisting of the correct JAR. Boxes represent the interquartile range (IQR), or the spread from 25th percentile (lower hinge) to the 75th percentile (upper hinge), with a central horizontal bar denoting the median value. Whiskers encompass values within 1.5 x IQR extending from the lower and upper fences. Open circles denote data outside this range.

Table 3.2 Model summaries and results of likelihood ratio tests for Part One of this study. P-values reflect the results of likelihood ratio tests (ANOVA) performed between the model and the null model for each of the JAR variables. Standard deviation (St. Dev.) of the random effect terms (1+stim|fish and 1+trial|fish) are representative of the variance in the data explained by each of the terms in the model. Residual standard deviation (St. Dev.) represents the variance in the data that was unexplained by the model. The slope of the model indicates the direction and gradient of change in the JAR variable from one stimulus condition to the next (in order of 0%-100% contrast). The slope of magnitude is presented in Hz, the slopes of latency one and two are presented in time, and the slope of accuracy is presented in proportion of correct JAR behaviour. Re-scale/Rank indicates adjustments applied to the model or data in order to assure model convergence: N.M, Nelder-Mead optimization; Rank, data ranking.

General Model: JAR variable ~ stim + trial + (1+stim|fish) + (1+trial|fish)

General Null Model: JAR variable ~ trial + (1+stim|fish) + (1+trial|fish)

JAR Variable	St. Dev. 1+stim|fish	St. Dev. 1+trial|fish	Residual St. Dev.	Slope	Chi Square	P-Value	Re-scale /Rank
Magnitude	0.0116	0.0439	0.941	0.0377	1.4213	0.2332	None
Latency One	7.25	3.194	113.6	-5.481	1.6583	0.1978	N.M. + Rank
Latency Two	0.03223	0.1157	4.129	-0.0877	0.4035	0.5253	None
Accuracy	0.00535	0.004294	0.1101	0.0205	0.8779	0.3488	None

3.1.2 Envelope Tracking

Upon closer examination of fish responses to the broadband noise stimulus (0-20 Hz) in Part One, it was found that the EODF of some fish appeared to be "tracking" the slower envelope modulations of the noise stimulus, representative of slower and longer duration movements of the conspecific mimic (Metzen & Chacron, 2014). It appeared that the fish performed the JAR during the slow increases in envelope amplitude and then, when the amplitude of these envelope peaks decreased, the JAR ceased (Figure 3.4 a). In an attempt to quantify this pattern, the stimulus envelope data and each fish's average EOD response during 100% contrast stimulus presentations were compared.

To examine if a time delay in EOD response to envelope peak was masking a stronger correlation between the two data series, a cross-correlation analysis was completed using the *ccf* function in R Statistical Software. This analysis resulted in a significant correlation between the EODF and envelope traces in 16 out of 18 subjects examined ($p<0.05$), and in several cases this relationship was highly significant (Figure 3.4 b). In summary, the cross-correlation analysis revealed a clear "envelope tracking" behaviour among the fish used in Part One of this study.

According to Metzen & Chacron (2014), the prominence of the frequency-following behavioural response should decrease along with the depth of the envelope of the noise stimulus. In order to confirm this in *E. virescens*, EODF and broadband stimulus envelope traces were also compared for the other stimulus noise levels (0%, 25%, 50% and 75% contrast). Using the same cross-correlation time-lag adjustments as were applied to the 100% contrast stimulus data, linear models were used to examine envelope tracking behaviour in response to varying envelope depths. Consistent with behaviour seen in *A. leptorynchus*, the "envelope tracking"

response became less apparent as the depth of the envelope modulation decreased (i.e. the overall significance of the correlation between EODF response and stimulus envelope decreased along with the % contrast of the stimulus) (Figure 3.4 b). Thus, this data provides ample evidence of an "envelope tracking" behaviour in *E. virescens*. This suggests that the variables measured in Part One of this experiment were contaminated by responses to the low-frequency components of the stimulus and therefore their interpretation in the context of this study was confounded.

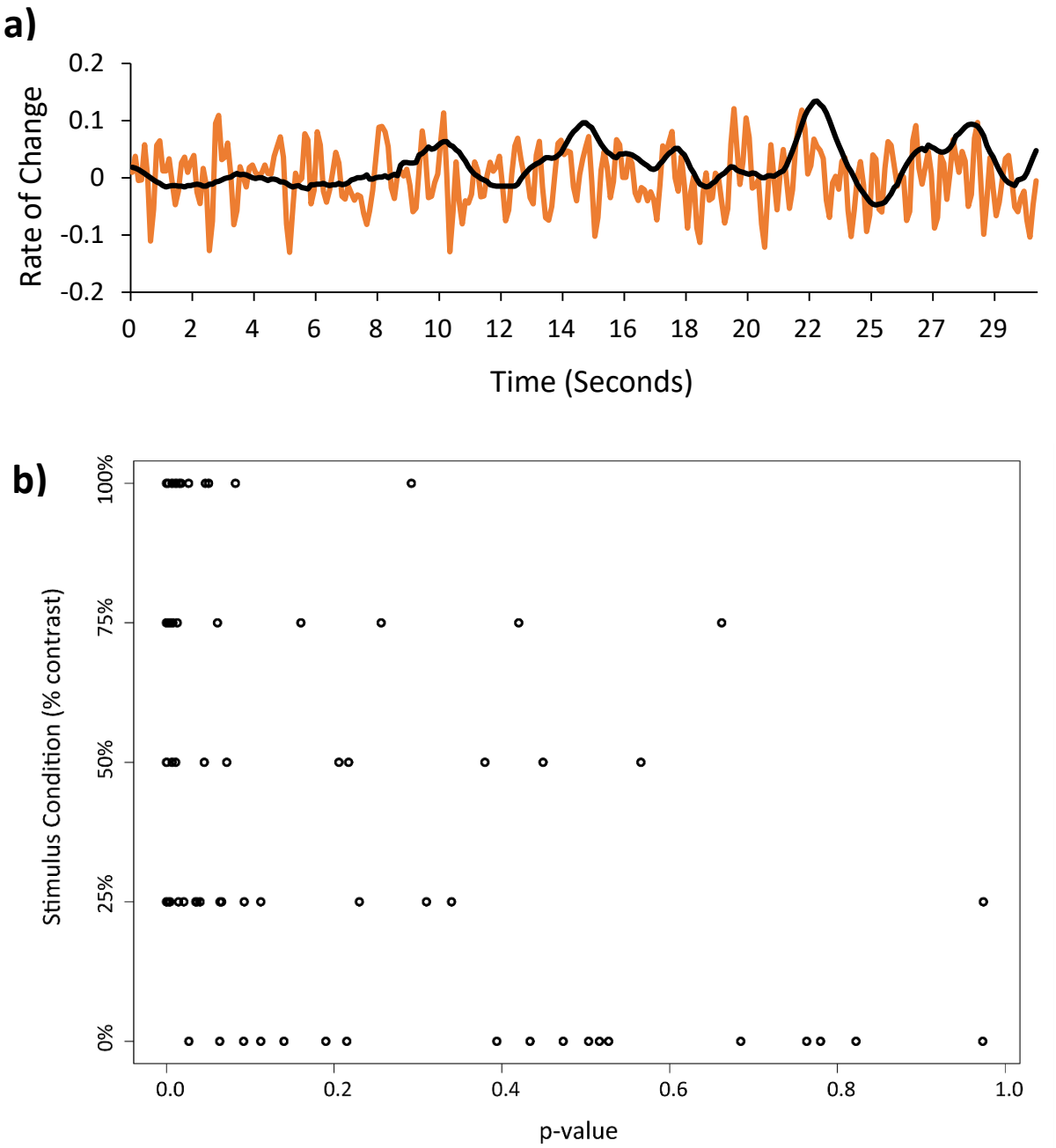

Figure 3.4 Evidence for envelope tracking behaviour with the use of broadband noise stimulus. a) Rate of change of the EODF (black) vs rate of change of the stimulus envelope amplitude (orange) over the stimulus period. Example taken from one trial (100% contrast stimulus condition) of fish #1. b) Correlation of EODF data series and stimulus envelope amplitude data series for all stimulus conditions. Data points indicate values for individual fish. P-values are representative of the strength of the correlation, and were computed using a linear regression model following cross-correlation adjustments.

3.2 Experiment Results: Part Two – Filtered Noise Stimulus

3.2.1 Jar Performance

In Part Two of this study, a total of 18 experiments were analyzed. In an attempt to circumvent the envelope tracking behaviour seen in Part One of this study, Part Two featured a filtered noise stimulus, wherein the noise spectrum was filtered to remove long and slow envelope modulations. This resulted in a stimulus with an envelope ranging from 2-20 Hz – outside the established frequency range of envelope tracking behaviours (Figure 2.2 b, d; Metzen & Chacron, 2014). The mean responses for each variable, along with the standard deviation of the mean and the maximum, minimum, and range of the data over all fish is presented in Table 3.3. An example of an individual response to this filtered stimulus can be seen in Figure 3.5. It's interesting to note that the EODF appears to fluctuate over the first 0-5 seconds of the stimulus period. This wavering in EODF has not been described with non-looming stimuli, which typically are characterized as producing a smooth and symmetric response (Bullock et al., 1972 a, b). In addition, the latency is lower for intermediate noise levels.

Like in Part One, linear mixed effects models were used to examine the effects of various levels of swimming noise on the JAR variables measured (Table 3.4). Results indicated that swimming noise level had no significant effect on JAR latency two (Figure 3.6), JAR magnitude, or JAR accuracy (Figure 3.7). However, JAR latency one was found to vary significantly with stimulus condition ($p = 0.015$). Interestingly, latency one decreases linearly along with rising levels of swimming noise (Figure 3.6). Since latency one is a measure of when

the absolute value of a fish's EODF first crosses their individual threshold for response (in either a positive or negative JAR), these results indicate that EOD detection is significantly improved by signal modulations due to movement. Accordingly with the stochastic resonance hypothesis, the stimulus modulations used appear to improve the sensory inputs required to *detect* a conspecific. However, as latency two (the time at which the EODF rises *and stays above* a fish's threshold for response) was not influenced by stimulus condition, it is difficult to interpret what this result means in terms of EODF *identification* abilities.

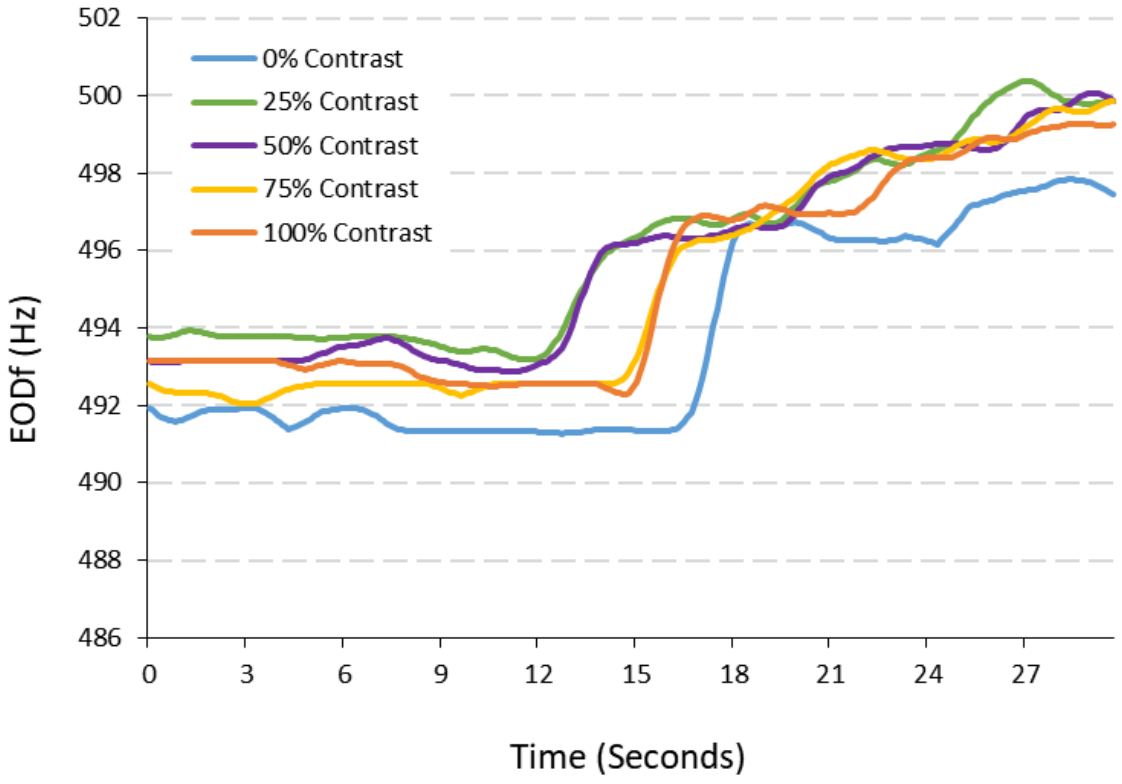

Figure 3.5 Response of fish #29 to the filtered stimulus used in Part Two. Responses to all stimulus conditions (% contrast) are shown.

Table 3.3 Mean, standard deviation, maximum values, minimum values, and range of values for each JAR variable, computed over all fish in Part Two (n=18).

	Latency One	Latency Two	JAR Magnitude	JAR Accuracy
Mean	10.72359	17.11039	2.506673	0.709535
SD	6.362426	6.174303	1.66352	0.166534
Max	30	30	8.032808	0.999772
Min	1.4	1.6	-1.31545	0.5
Range	28.6	28.4	9.348261	0.499772

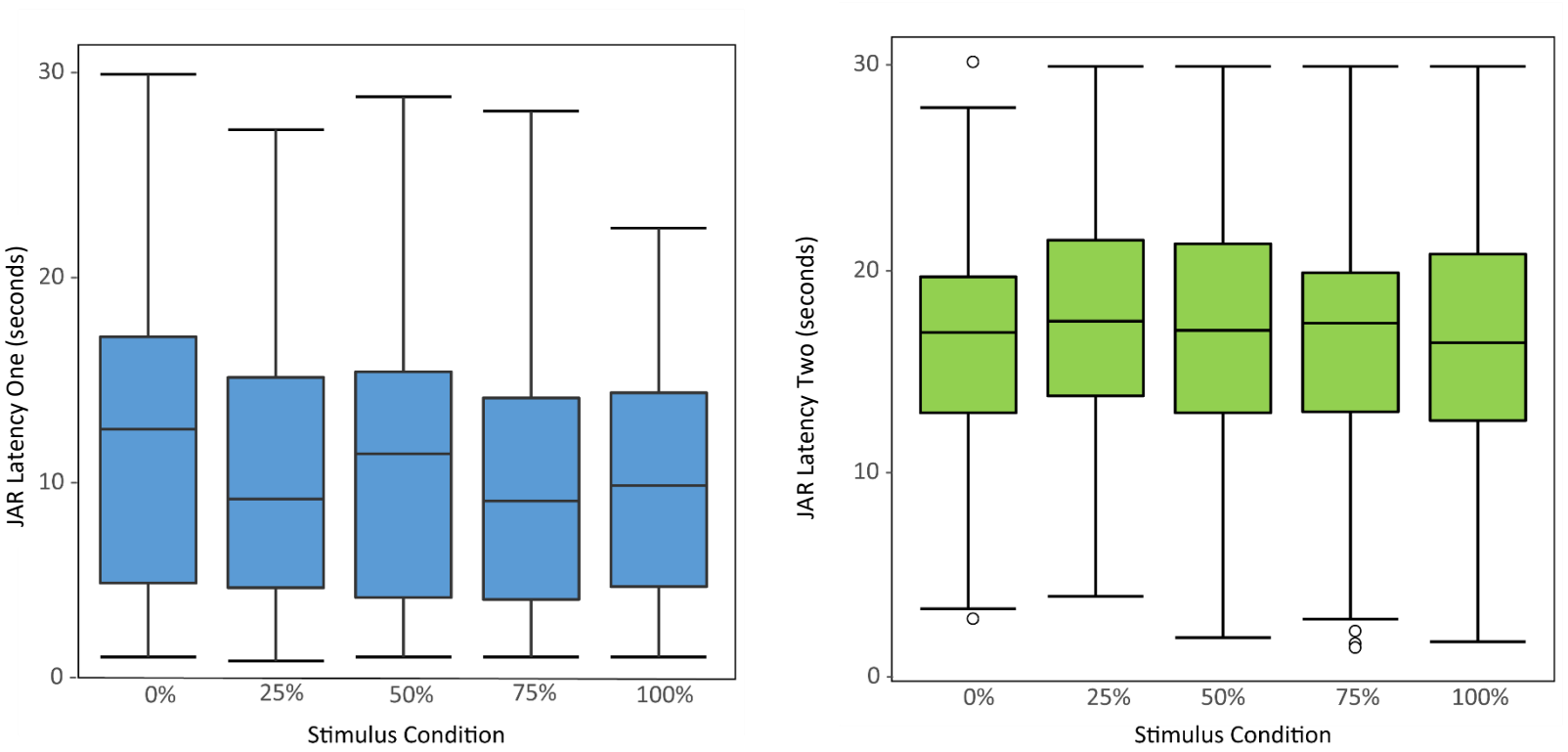

Figure 3.6 Boxplots of JAR latency variable values for all fish in Part Two, in response to the filtered noise stimulus at different stimulus conditions. Left (blue) is JAR latency one and right (green) is JAR latency two, both measured in seconds. Boxes represent the interquartile range (IQR), or the spread from 25th percentile (lower hinge) to the 75th percentile (upper hinge), with a central horizontal bar denoting the median value. Whiskers encompass values within 1.5 x IQR extending from the lower and upper fences. Open circles denote data outside this range.

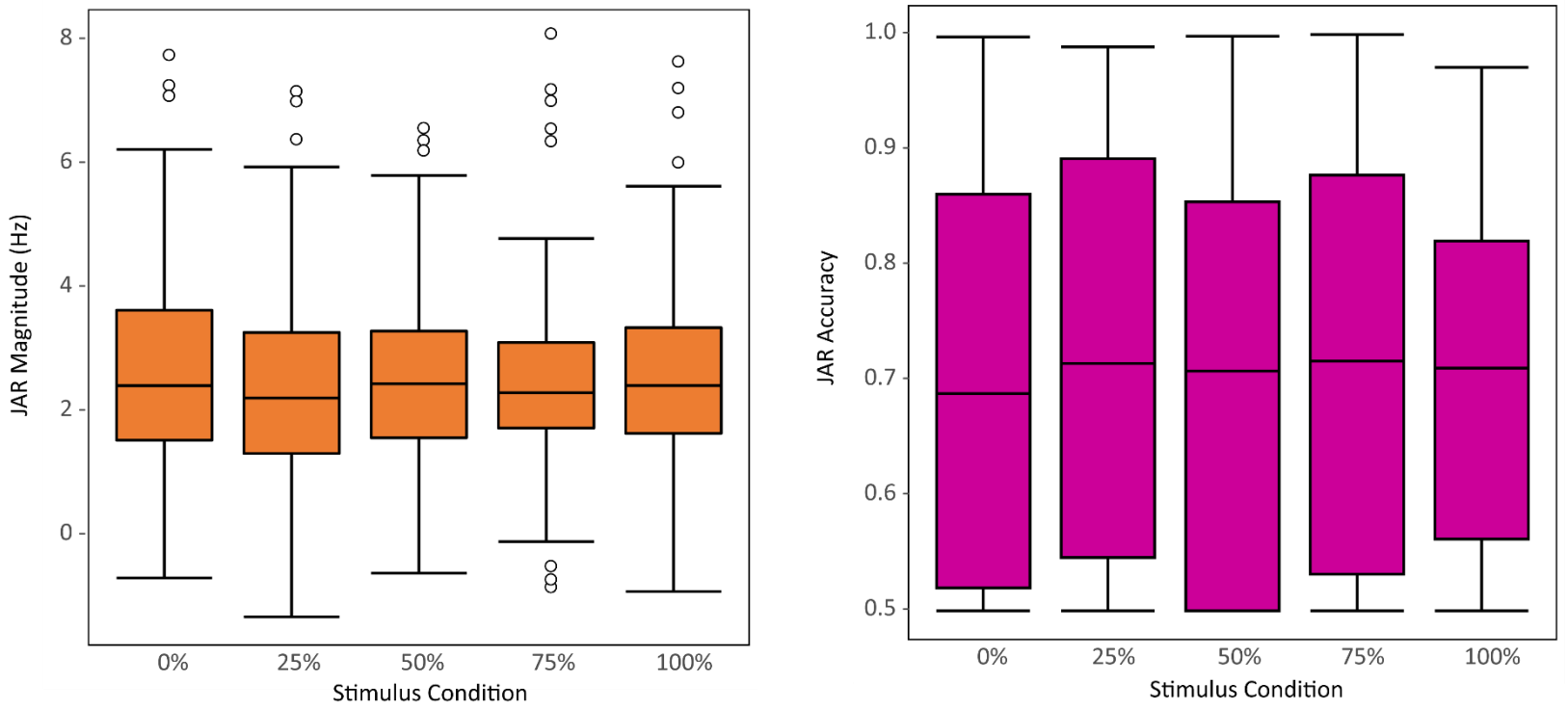

Figure 3.7 Boxplots of JAR magnitude (left, orange) and JAR accuracy (right, purple) values for all fish in Part 2, in response to the filtered noise stimulus at different stimulus conditions. JAR magnitude is measured in Hz, JAR accuracy is measured as the proportion of response with the correct JAR. Boxes represent the interquartile range (IQR), or the spread from 25th percentile (lower hinge) to the 75th percentile (upper hinge), with a central horizontal bar denoting the median value. Whiskers encompass values within 1.5 x IQR extending from the lower and upper fences. Open circles denote data outside this range.

Table 3.4 Model summaries and results of likelihood ratio tests for Part Two of this study. P-values reflect the results of likelihood ratio tests (ANOVA) performed between the model and the null model for each of the JAR variables. Standard deviation (St. Dev.) of the random effect terms (1+stim|fish and 1+trial|fish) are representative of the variance in the data explained by each of the terms in the model. Residual standard deviation (St. Dev.) represents the variance in the data that was unexplained by the model. The slope of the model indicates the direction and gradient of change in the JAR variable from one stimulus condition to the next (in order of 0%-100% contrast). The slope of magnitude is presented in Hz, the slopes of latency one and two are presented in time, and the slope of accuracy is presented in proportion of correct JAR behaviour. Re-scale/Rank indicates adjustments applied to the model or data in order to assure model convergence: N.M, *Nelder-Mead* optimization; Rank, data ranking.

General Model: JAR variable ~ stim + trial + (1+stim|fish) + (1+trial|fish)

General Null Model: JAR variable ~ trial + (1+stim|fish) + (1+trial|fish)

JAR Variable	St. Dev. 1+stim|fish	St. Dev. 1+trial|fish	Residual St. Dev.	Slope	Chi Square	P-Value	Re-scale /Rank
Magnitude	14.4	0.4774	82.09	-0.1917	0.0034	0.9536	Rank
Latency One	0.067	0.076	5.511	-0.4379	5.917	0.015*	None
Latency Two	0.363	0.00246	5.305	-0.0760	0.1561	0.6927	None
Accuracy	0.0051	0.00121	0.123	0.0025	0.3759	0.5398	None

3.2.2 Envelope Tracking

In Part Two of this study, the envelope tracking cross-correlation analysis was repeated (*see Part One – Envelope Tracking*), this time featuring a filtered noise stimulus (2-20 Hz). As expected, the degree of correlation between the EODF response and stimulus envelope was noticeably reduced compared to the correlation seen in the broadband stimulus analysis (Figure 3.8). This is consistent with the results of Metzen and Chacron (2014) in other species of weakly electric fish – where envelope tracking behaviour was evident in response to envelope frequencies below 1 Hz, and less so to envelope frequency above 1 Hz.

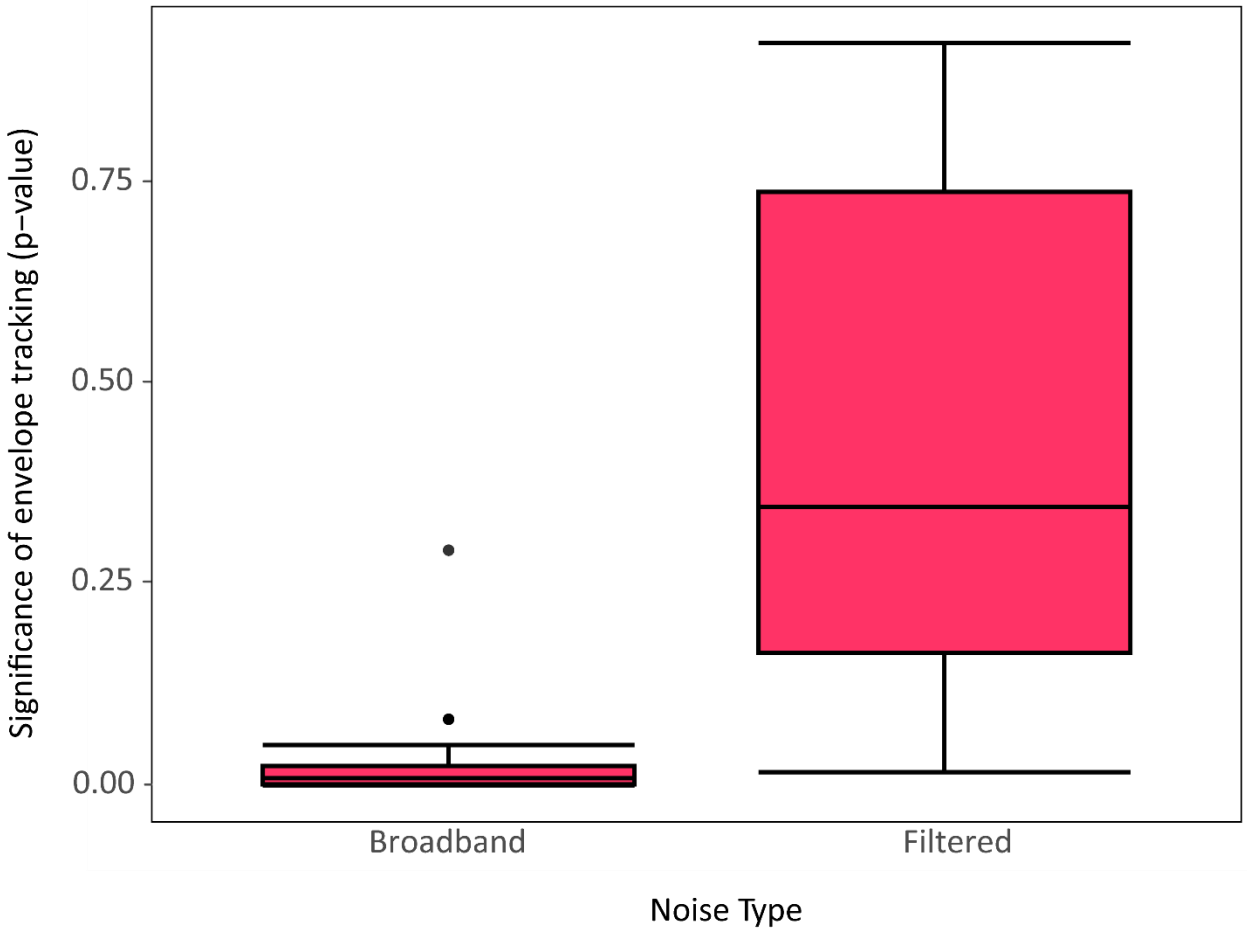

Figure 3.8 Significance of envelope tracking behaviour in response to the broadband (0-20Hz) and filtered (2-20Hz) envelope stimuli. P-values were obtained by simple regression models, and represent the significance of the correlation between the stimulus envelope and the EODF in time (following crosscorrelation adjustments). EODF data from 100% contrast stimulus condition only are represented here.

4. DISCUSSION

4.1 General Discussion

This study examined the effect of amplitude modulations of the EOD due to motion (swimming noise) on conspecific EODF identification ability in *Eigenmannia virescens*. Three alternate hypotheses were proposed:

1. Swimming noise reduces the ability of *E. virescens* to identify the EODF of a conspecific
2. An optimal level of swimming noise enhances the ability of *E. virescens* to identify the EODF of a conspecific
3. Swimming noise has no effect on the ability of *E. virescens* to identify the EODF of a conspecific

The jamming avoidance response (JAR) was used as a measure of EODF identification, since a correct performance of the JAR requires *E. virescens* to accurately identify the frequency of a conspecific's EOD relative to its own. The JAR was quantified through several variables:

- Latency One: The time of the first change in EOD above the baseline discharge frequency, in either a positive or negative direction (the time required to *detect* a conspecific signal, but not necessarily identify the difference frequency, DF, accurately)
- Latency Two: The time required to raise the EOD above the baseline discharge frequency, in the correct (positive) direction only, *while* remaining above this threshold for the remainder of the trial (the time at which a fish *identifies* a conspecific signal correctly)

- Magnitude: The change in EOD from the start of the trial to the end of the trial (measured at 25 seconds)
- Accuracy: A measure of the proportion of the response spent performing the "correct" JAR (moving upwards in frequency, away from the stimulus frequency)

The stimulus delivered was designed to mimic the EOD of a conspecific, with a DF of -3 Hz in order to elicit a JAR. Various levels of swimming noise (envelope modulations with a depth of 0%-100% of the fish's own EOD amplitude) were delivered in a randomized block design. In Part One of this study, the envelope frequency content of the stimulus ranged from 0-20Hz (Figure 2.2 b, c). Analysis revealed that changes in JAR performance were not apparent across levels of swimming noise, delivered by a broadband (0-20 Hz) stimulus envelope (Figure 3.2, 3.3; Table 3.2).

However, upon further examination of the experimental trials in Part One, it became evident that the fish were responding to the stimulus envelope in a stereotyped manner over the 30 second stimulus periods (Figure 3.4 a). Cross-correlation analyses between the stimulus amplitude and the EOD response (over time) revealed that the fish were changing frequency in tandem with the long duration and slow amplitude modulations of the noise stimulus envelope. This behaviour became significantly more prevalent as the stimulus noise level (25-100% contrast) increased (Figure 3.4 b). As such, it was determined that *E. virescens* was clearly exhibiting an 'envelope tracking' response, previously described by Metzen & Chacron (2014) in *A. leptorhynchus*. As a result of this behaviour, the JAR variables measured in Part One of this study were deemed to be an unreliable measure of EODF identification ability.

With this in mind, a new stimulus was developed, wherein the long duration and slow amplitude modulations of the noise envelope (<2 Hz) were removed. This resulted in a stimulus that eliminated envelope tracking behaviour (Figure 2.2 b, d; Figure 3.8). The JAR variables were re-examined in experiments featuring the filtered noise stimulus (n=18). In this case, JAR latency two, JAR magnitude, and JAR accuracy were unaffected by swimming noise (Figure 3.6, 3.7; Table 3.4). However, JAR latency one decreased as the swimming noise level increased, providing evidence for Hypothesis 2 (Figure 3.6; Table 3.4).

This result is especially interesting given that JAR latency two did not change significantly with stimulus noise level, nor is there any evidence that this variable follows the same trend as latency one. As described previously, there is an important distinction between the latency measures, and the difference in their response to swimming noise may provide particular insights into the behaviour of *E. virescens.* JAR latency two is a true measure of certain *EODF identification*: a JAR must be performed (requiring a detection of a conspecific stimulus), the JAR must be positive (requiring the correct identification of the sign of a conspecific DF from information contained in the AM), and the JAR must be maintained above threshold for the remainder of the trial (there is no uncertainty of conspecific EODF). On the other hand, JAR latency one is a measure of *EODF detection* only. Again, a JAR must be performed, requiring the fish to detect the presence of a conspecific signal. However, this JAR behaviour may be in the correct direction (upwards away from negative DF) or in the incorrect direction (downwards towards the negative DF). Additionally, the response may be inconsistent – even if a fish performs the correct JAR, it may demonstrate uncertainty by lowering its frequency below threshold again during the trial period. As such, JAR latency one indicates that

a fish has indeed *detected* a conspecific signal, but not necessarily that it has *identified* the DF of this signal accurately. Considering this, the discrepancies found in this study between JAR latency one and JAR latency two may provide some insight into the overall JAR strategy employed by *E. virescens*. More specifically, it could indicate the involvement of a random search for the correct response, wherein 1) a signal is detected, 2) EODF is randomly changed (in either JAR direction) 3) jamming is either improved or worsened based on the actual sign of the DF 4) JAR direction is re-evaluated and the process is repeated. This is in line with theoretical models of value based decision making, wherein outcome evaluation is used to improve a response, and is an interesting avenue of further research in the context of the jamming avoidance response (Rangel et al., 2008).

Overall, two central inferences can be made from the JAR latency variables examined. First, assuming that the measures and analysis used were sufficient in describing the data, it can be inferred that swimming noise has no effect on the ability of *E. virescens* to accurately *identify* the EODF of a conspecific. Despite large modulations of the AM signal, *E. virescens* is able to obtain sufficient information regarding the DF of a conspecific (Hypothesis 3). Secondly, although EODF identification abilities are unchanged by swimming noise, EODF *detection* abilities actually improve as greater modulations are applied to the AM signal (Hypothesis 2).

4.2 Swimming noise does not interfere with accurate conspecific EODF identification

As previously stated, this study suggests that swimming noise has a positive effect on signal detection, but has no influence on signal identification in *E. virescens*. A signal with swimming noise may notify a fish of the presence of a conspecific earlier than a noise-free signal. However, it does not appear to help nor hinder their ability to identify the specific EODF of that individual, since the time at which the correct and consistent JAR occurs (JAR latency two) is not influenced by the stimuli presented. This is supported by the measure of JAR accuracy, which was also found to be independent of swimming noise level. Analysis of JAR accuracy indicated that the proportion of the response consisting of a 'correct' JAR (EODF moving upwards) was neither increased nor decreased by the introduction of signal noise. If EODF identification was occurring sooner, or more reliably, this proportion is likely to have increased. Conversely, if identification was occurring later, or less reliably, this proportion is likely to have decreased. Since neither scenario was observed in response to a variety of swimming noise stimuli, this could provide further evidence that EODF identification abilities are preserved, but not enhanced with swimming noise. JAR magnitude was similarly unaffected by stimulus noise level, indicating that the magnitude of the JAR may be more related to the time spent performing the correct JAR (and therefore the time of stimulus identification) than the time at which the stimulus is first detected. It is important to note that the JAR magnitude and accuracy results could simply be due to high variability of the data set, which may conceal a measurable effect of swimming noise.

Although it is evident that swimming noise does not alter EODF identification abilities, at least as was measured here, exactly *how* this behaviour is preserved despite naturalistically high levels of swimming noise remains unclear. Several hypotheses about how this behaviour is so well maintained are plausible. Perhaps most notably, although swimming noise may mask information regarding the frequency and depth of the AM, other information may be available to indicate DF. To perform the JAR, a fish must first determine the sign of the DF; it does so by analyzing the interference that results from the combination of their own EOD and that of a conspecific. This interference is described by both the AM and the phase of the combined signal. As described previously, the fish determines the DF by comparing the time-varying signal received (both amplitude and phase) between different locations on their body's surface (Figure 1.4; Heiligenberg 1991; Carlson & Kawasaki, 2007; Kawasaki, 1997). Although swimming noise at the level of the envelope may occlude the information provided by the AM, phase information (whether the phase at one location on the body is leading or lagging relative to another) is preserved (Shifman & Lewis, 2018). There is evidence that non-jamming or "phantom jamming" stimuli, consisting of only amplitude or only phase information, can induce a JAR in natural situations. Although amplitude is encoded by P-unit electroreceptors, and phase by T-unit electroreceptors, the spike times of each afferent time are slightly affected by the opposing stimulus (Carlson & Kawasaki, 2006; Carlson & Kawasaki 2007). This means that at a "phantom" AM can be perceived in response to a stimulus composed of only phase information (and vice versa). Of particular importance here is that a signal consisting purely of information regarding sinusoidal differences in phase creates a jamming stimulus that can be mistakenly perceived as a negative DF. Thus, if phase information of a conspecific signal is not

degraded by swimming noise, a negative DF may be perceived even if AM information is indistinguishable from noise (Carlson & Kawasaki, 2007). In this manner, JAR performance could be preserved despite the significantly varying envelopes that are a result of dynamic swimming motions. To test this experimentally, the effect of 'phase noise' (as well as the AM noise employed here) would have to be determined. The difficulty of this proposition lies in the stimulus design, as it would be challenging to produce naturalistic signal variations that would selectively degrade phase information. Nevertheless, it offers an interesting avenue for further exploration, and may provide some insight into how *E. virescens* is able to maintain EODF identification abilities despite swimming noise.

Another hypothesis stipulates that *E. virescens* may be able filter or average out the motion related noise that is encoded by electroreceptors. The neural mechanism of the JAR in *E. virescens* has been fairly well described, yet some specifics remain in question, and may provide some insight (Metzner, 1993; Heiligenberg 1991). For instance, there is some evidence that (in *A. leptorhynchus*) pyramidal cells in the ELL (sensitive to P-unit firing) may be especially capable of encoding information contained in the envelope (Middleton et al., 2006; McGillivray et al., 2012). However, this has not been tested in *E. virescens*, nor has it been considered over the full natural range of envelope stimuli that may be elicited from movement. Perhaps of greater significance to the current study, there is some evidence demonstrating that (in *A. leptorhynchus*) different peripheral electroreceptor neurons (P-unit) may vary in their response to envelopes caused by movement (Metzen & Chacron, 2015). In fact, the sensitivity of these neurons did not depend on frequency content of the envelope or of the AM stimulus itself, but to the timing of the stimulus envelope, providing more evidence that phase may be key in the

preservation of JAR performance despite high contrast swimming noise (Metzen & Chacron, 2015). Although all of the P-unit afferents measured responded in an equal manner to changes in the frequency of the AM, their responses to changes in the stimulus envelope were heterogeneous, partially due to a difference in baseline firing rates. Some afferents were found to be "ON-type", with a low baseline firing rate. These p-units respond with an average increase in firing rate in response to a stimulus envelope (due to rectification) – and therefore respond in phase with the envelope. Conversely, "OFF-type" P-units were shown to have a high baseline firing rate. These p-units responded with an average decrease in firing rate in response to a stimulus envelope (due to saturation), and so respond out of phase with envelope. A P-unit with an average baseline firing rate did not respond to envelope information, as no change in firing rate is elicited by the phase of the envelope (in this case the increase in firing rate due to rectification and the decrease in firing rate due to saturation offset one another) (Metzen & Chacron, 2015). This neural heterogeneity, if also present in *E. virescens*, may demonstrate a method by which signal-to-noise ratios are optimized, and information about both conspecific identity and movement patterns may be obtained simultaneously.

It is certainly arguable that further investigation of the neural underpinnings of the JAR could give some insight into how *E. virescens* is unaffected by swimming noise. To fully explain the results of this current experiment, it is especially important that future related neurophysiological studies use *E. virescens* as their model. Recent work seems to focus on *A,leptorhynchus*, including the work that motivated this study (Yu et al., 2012). However, *E. virescens* and *A. leptorhynchus* differ in neuroanatomy required for the JAR, as well as in the origin of their electric organ (myogenic in *E. virescens* and neurogenic in *A. leptorhynchus*)

(Bennet, 1971; Rose, 2004). There is also some indication that *E. virescens* possesses a "higher signal-to-noise ratio for JAR-related sensory inputs" than *A. leptorhynchus*, perhaps due to the relatively lower degree of spatial heterogeneity and complexity of *E. virescens*' electric field (Shifman & Lewis, 2018). With these differences in mind, it may be ineffectual to compare electroreceptive and behavioural responses between these two species, despite their other similarities (Metzner, 1999; Rose, 2004). As such, further experiments into the effects of swimming noise on signal retention at the electroreceptor level in *E. virescens*, along with the possible noise filtering properties of the neural JAR mechanism, may provide a stronger understanding of the behavioural evidence presented here.

4.3 Swimming noise improves conspecific detection

Although further experimentation is required to support this thesis, it provides evidence of one of the first applications of stochastic resonance in an animal behaviour context, and may grant insight into the adaptive value of noise at the whole animal level in *E. virescens* (McDonnell & Ward, 2011). Stochastic resonance is often described as a counter-intuitive phenomenon. Most generally, it refers to any sort of signal-processing that is enhanced by noise (variability resulting from "random or unpredictable fluctuations or disturbances" in the system) (Faisal et al., 2008). In other words, stochastic resonance is said to occur when the transmission or processing of a signal in a non-linear system is improved when an intermediate level of noise is present, as compared to when it is absent or very high amplitude (McDonnell & Abbott, 2009). In this scenario, noise may promote the detection of a weak signal, or increase the amount of information being transferred (Moss et al., 2004). This study suggests that in *E. virescens*, the former appears to be occurring.

The classic definition of stochastic resonance requires the presence of a detection threshold, a sub-threshold stimulus, and noise in a non-linear system (Figure 1.7 b; Gingl et al., 1995; McDonnell & Abbott, 2009). The experiments performed here meet all of these criteria. Information about the sub-threshold stimuli is discerned only when the signal crosses the detection threshold. On its own, the stimulus is entirely below threshold, and no detection occurs. When noise is added to the system, threshold crossings will occur, allowing the stimulus to be sampled. As the signal noise increases in amplitude (from 25% contrast to 100% contrast stimulus in this study, for example), threshold crossings due to noise are more likely to occur,

allowing the stimulus to be detected more reliably (Figure 1.7 b; McDonnell & Abbott, 2009). Although information transfer may be more irregular than when a stimulus is supra-threshold, sequences of threshold crossings due to noise may contain a large degree of information about the stimulus (Moss et al., 2004). This irregularity - a rise and fall of the noisy stimulus around the detection threshold - may explain why the JAR latency one variable was the most sensitive to SR behaviour: a response was not limited to a consistent (or correct) JAR. When an AM 'peak' of the stimulus crosses the detection threshold, the fish may very briefly detect the presence of a conspecific, and thus performs the JAR (perhaps pre-emptively). As the amplitude of the swimming noise level drops again below threshold, EODF may return to baseline, as the conspecific is no longer detected. This describes perfectly the 'wavering' behaviour seen over the 0-5 seconds of the stimulus (in Part Two), an occurrence that has not been described with non-looming stimuli (Figure 3.5).

However, in theory, noise will only have a beneficial effect up to a certain intensity, at which it begins to degrade the signal. This is what is meant by the term 'resonance' in SR. This terminology becomes clear when examining the theoretical signal-to-noise ratio (SNR) of an output signal against the intensity of noise present in the input signal when stochastic resonance is occurring (Wisenfeld and Moss, 1995). At low noise intensities, the SNR will be small, as not enough threshold crossings are occurring for adequate signal transfer. Similarly, the SNR will also be small at high noise intensities, since the large degree of noise threshold crossings essentially masks the sub-threshold signal. However, at an intermediate, optimal level of noise, the SNR will be maximal, as signal transfer is enhanced by noise (Figure 1.7 a: *H2*). Because this plot is so similar to those seen in frequency-dependent systems, with a peak

output response at a particular 'resonant frequency', the term resonance is used to describe this phenomenon (although in this case, resonance is caused by noise, rather than the input stimulus itself) (McDonnell & Abbott, 2009). Although this thesis demonstrated that signal detection improves linearly with the addition and augmentation of swimming noise, it failed to exhibit the concept of "resonance". It is possible that if a higher resolution of swimming noise levels (ex: 10%, 15%, 20%, etc. contrast) were applied, a deterioration of signal detection abilities would be observed, and an optimal "peak" of envelope modulation could be established. This is an important avenue for further study, as it may fully solidify the presence of behavioural SR in *E. virescens*.

It is evident that studies of behavioural SR, such as the one completed here, may provide new insight into the connections between signal processing and behaviour (Moss et al., 2004; McDonnell & Abbott, 2009). The elements required for stochastic resonance to occur – a detection threshold, a sub-threshold stimulus, and noise – are common in both natural and man-made systems. As a result, SR is broadly applicable to many scientific fields. For over 25 years, research in SR was concentrated in the field of physics. However, applications in a variety of domains are becoming increasingly prevalent. SR has been used to describe financial models, climate change, chemical reactions, social systems, and much more (McDonnell & Abbott, 2009). Interest in the relevance of SR in biology was sparked in the early 1990's, when it was described in sensory neurons affected by external noise (Longtin, 1993). Since then, the study of SR in biology has expanded, and rightly so; biologically relevant sources of noise are ubiquitous, ranging from, for instance, the fluctuation of membrane potentials in neurons due to the gating of ion channels, to visual clutter in the external environment (McDonell & Ward,

2011). As such, it is only natural that in some circumstances, organisms have adapted to use noise to their benefit, at many levels (McDonnell & Ward, 2011). In the case of *E. virescens*, the adaptive value of SR is especially clear. As they rely on a distance-limited electric field to sense their surroundings, these fish must be able to swim extremely dynamically, and do so at great speeds (Lannoo & Lannoo, 1993). At the same time, the detection of conspecifics is a priority – for example, to avoid jamming, recognize a potential mate, or discern a threat (Bullock et al., 2005). Thus, their apparent ability to balance these two demands is hardly surprising.

The majority of work on stochastic resonance in biological systems has focused on demonstrating the occurrence of SR in neurons. For instance, noise enhancement of signal transfer has been documented in the crayfish mechanoreceptor, the cercal system of the cricket, and in shark multimodal sensory cells (Braun et al., 1994; Douglass et al., 1993; Levin & Miller 1996). It is more difficult, however, to determine whether this noise-enhanced signal transfer has any broader functional or behavioural benefits for the whole animal. Psychophysical studies of SR in human sensory systems have begun to bridge this gap. Cutaneously applied electrical and mechanical noise has been shown to enhance tactile sensation in humans, resulting in promising clinical applications of SR (Collins, 1995; Ribot-Ciscar et al., 2013). These applications, including the implementation of vibrating insoles, can enhance balance control and postural stability in the elderly, stroke victims, patients with diabetic neuropathy, and those with functional ankle instability (Dhruv et al., 2002; Gravelle et al., 2002; Liu et al., 2002; Priplata et al., 2003; Ross, 2007). SR has also been shown to play a role in human vision and hearing, where noise can lower the detection threshold of a pixelated image or a sub-threshold sound (Zhang-Cai et al., 2004; Simonotto et al., 1997; Zeng et al.,

2000). This has led to a better understanding of how the human visual system processes noisy visual environments, and the development of enhanced cochlear implant stimulation strategies, amongst other practical uses (Chatterjee & Robert 2001; Simonotto et al., 1997; Stocks et al., 2002).

Human psychophysical studies are useful in determining the functional roles of noise and SR, since humans are able to report the sensation of 'detecting' or 'identifying' a stimulus to researchers. However, determining the behavioural benefits of SR in non-human subjects is much more difficult, as methods of measuring whole animal signal detection are often less straight-forward. A few previous studies have circumvented this potential complication. In a study of the feeding behaviour of paddlefish, researchers found that an optimal level of electrical noise (most likely generated from swarm movement of Daphnia prey) enhances the hunting success of the paddlefish, successfully demonstrating a behavioural application of SR (Collins, 1995; Russel et al., 1999). More recently, SR has been shown to play a role in the mating behaviour of the Southern Green Stink Bug, which uses a tymbal organ to generate vibrations on plants in order to coordinate sexual interaction with a proximal conspecific of the opposite sex. Specifically, particular optimal intensities of natural environmental noise amplify the mating signal, improving communication between individuals and maximizing the behavioural 'mating' response (Spezia et al., 2008). The study completed here has continued along these lines, to further our limited understanding of the functional role of SR at the behavioural level. This novel approach to the study of SR takes advantage of a natural behavioural indication of 'detection' (JAR), and provides some evidence for the presence of SR behaviour in *E. virescens.*

As previously mentioned, further study on behavioural SR in *E. virescens* may focus on broadening the degree of swimming noise presented. It is possible that an optimal "resonance peak" for the JAR may be established, if un-tested levels of swimming noise reveal a reduction in signal detection abilities. Further work may also involve altering the experimental methods to allow direct comparison with previously published work on SR. As in other SR studies in human systems (ex: Dhruv et al., 2002; Gravelle et al., 2002; Liu et al., 2002; Priplata et al., 2003; Ribot-Ciscar et al., 2013; Ross, 2007; Simonotto et al., 1997; Stocks et al., 2002; Zhang-Cai et al., 2004), the detection threshold for each individual fish could be determined before trials begin, using the JAR. Stimuli could then be designed according to that threshold, with various levels of noise that either remain below, slightly cross, or greatly cross the fish's individual threshold for identification. JAR parameters in response to each signal could be measured in the same manner applied here, although it is possible that other additional or more appropriate measures exist that were not considered in this study.

4.4 Envelope Tracking Behaviour

Although this is the first time that envelope tracking behaviour has been documented in *E. virescens*, Metzen and Chacron (2014) demonstrated a similar envelope frequency following response in *A. leptorhynchus*. Both experiments found that the EOD of the experimental fish rises and falls with the peaks and troughs of a "noisy" envelope. However, in the study performed here, *E. virescens* was presented with stimuli that induced both amplitude modulations (AMs) and phase modulations (PMs) of the EOD, as would occur in a natural interaction. In Metzen and Chacron (2014), stimuli were artificial mimics – amplitude modulations were introduced, but the stimulus was phase locked to the EOD of the experimental fish (no differential phase modulations were present). Envelopes used in the 2014 study only covered a small range of frequencies (0.001-4 Hz), but overlapped with those applied in Part One of this experiment (0-20 Hz). In both experiments, a chirp chamber was used, with recording and stimulus electrodes oriented in the same manner (head to tail, and transverse to the fish, respectively). In both cases, a variety of envelope modulation depths were applied, over a comparable range (10%, 40%, 70% and 90% contrast in Metzen & Chacron (2014), versus 25%, 50%, 75% and 100% in the current study). Both this study and the 2014 study confirmed that, as the depth of the envelope modulations increased, so too did the depth of the tracking behaviour (Figure 3.4 b).

Despite the general similarities in stimuli and results between these two evaluations, differences arose when it came to the specific definition of 'envelope tracking'. Metzen & Chacon define this behaviour as completely distinct from the JAR. In fact, in a separate part of

their study, they apply a stimulus with an envelope frequency greater than 1 Hz, and note that "behavioral responses consisted almost exclusively of an increase in EOD frequency", devoid of tracking behaviour (2014). However, in Part One of this thesis, where no delineation was made between low frequency 'envelope tracking stimuli' (<1 Hz) and high frequency 'JAR stimuli' (>1Hz), the clear distinction between the two behaviours made by Metzen and Chacron seems illogical. More specifically, the envelope tracking behaviour found in this study was simply interpreted as a form of JAR, which was apparent due to the ramping nature of the stimulus. During the early phase of the ramp (when the overall stimulus amplitude is low), long and slow amplitude modulations (<1Hz) appear relatively distinct, and as they rise, may cross the receiving fish's threshold for signal amplitude detection. As this occurs, the fish detects a signal that was previously sub-threshold, and rises in frequency to avoid jamming. As the amplitude modulation falls downwards and below detection threshold yet again, the receiving fish simply stops the JAR, as the interference recedes (Figure 3.4 a). Metzen & Chacron propose that this downward phase of envelope tracking is an active behaviour, but our work sees no evidence to support this stipulation. Instead, we suggest that envelope tracking be viewed as an extension of the JAR behaviour. This may simply imply that a looming conspecific (indicated by a long and slow increase in amplitude like those seen at envelope frequencies <1-2Hz) provokes the JAR, whereas a waning conspecific (indicated by the fall of said amplitude) removes the threat of a jamming stimulus, allowing the receiving fish to naturally return towards baseline frequency. However, under either definition, this study presents clear evidence of envelope tracking behaviour in *E. virescens*. Although this is a fascinating insight, it complicated the interpretation of results in Part One of this study, since it appeared as though the broadband noise itself was

acting as a signal. As such, the JAR variables examined in Part One were considered to be contaminated by envelope tracking behaviour, and therefore unreliable measures of EOD identification ability in the context of the hypotheses being tested.

4.5 Shortcomings

It is important to acknowledge that this study, like most behavioural research, faced many challenges and was limited in scope. It is possible that an effect of swimming noise on EODF identification (and not just detection), could exist, but remained unobserved because of experimental or analytical constraints. The most difficult challenge lay in the variability of the data obtained. Model summaries indicated that, although a proportion of variance in the data was due to inter-fish variability and stimulus sensitization, the largest majority of the variance remained unexplained (Table 3.2, 3.4). Many studies on the JAR seem to imply that it is an exceptionally reliable and replicable measure, with shifts in frequency upwards of 5 Hz not uncommon (Bullock et al., 1972 a,b; Hagedorn et al., 1992). However, at least in terms of the variables measured, this study indicates that JAR performance is highly inconsistent. This may be due to the ramping nature of the stimulus, or perhaps because fish were not fully immobilized in the chirp chamber. Although most fish did perform a JAR in reaction to the stimuli presented, it was often not a smooth response nor was it robust in terms of magnitude, and the high degree of residual variability made overall responses difficult to surmise. In the future, a higher sample size may allow a stricter criteria of JAR behaviour to be applied, so as to remove a maximal amount of extraneous variability. Additionally, a frequency clamped

stimulus, although less behaviourally realistic, may result in a more stereotyped and comparable JAR behaviour, rather than the single DF stimulus applied in this study (Kramer, 1987).

The variability due to fish id, although not as high as the unexplained variation, was still noteworthy. As previously mentioned, this may be reduced by selecting only those fish who would be considered 'robust' JAR performers prior to repeating this study, with an even stricter criteria than was applied here. This could include a higher minimum JAR magnitude, and perhaps measures regarding the latency and smoothness of the response to noise-free stimuli. It would also be interesting to assess the behavioural type of the fish used. To our knowledge, no role of EODF or the JAR in dominance hierarchies has been explored in *E. virescens*. A better understanding of the behavioural types, group dynamics and possible social signalling related to relative DFs and the JAR could provide insight into the inter-fish response variability measured in this study. For instance, it could be speculated that a 'bolder' fish may be more likely to perform the JAR quickly at the time of detection (even perhaps without specifically identifying the sign of the DF). On the other hand, a 'shy' fish may be hesitant to reveal itself to a conspecific by performing the JAR, thereby putting an end to the 'jamming' effect that mask the sensory abilities of the neighbouring fish (see section 1.5; hypothesis 1) (Shank, 2013; Ruxton, 2009). Overall, a reduction in variability of the data, or simply a better understanding of what underlies this variability, could improve the ability of this study to discern differences in EODF identification and detection abilities with added swimming noise.

On another note, it is possible that the stimulus was not optimally designed to elicit the JAR or to facilitate the extraction of subtle differences in behaviour. It is especially difficult to

design a stimulus that is both naturalistic and behaviourally relevant, but also efficient in provoking a standardized response. For instance, Part One of this study featured a stimulus with a broadband spectrum of swimming noise. This closely mimicked the signal of a swimming conspecific, including short and fast movements as well as longer and slower looming or waning motions (Yu et al., 2012). However, as previously described, the low frequency components of the envelope resulted in a 'stimulus tracking' behaviour that made any measures of JAR performance unreliable (Metzen & Chacron, 2014). As such, Part 2 of this study featured a filtered stimulus, with the longer and slower movements extracted. Although arguably less representative of dynamic swimming motions, this stimulus avoided the envelope tracking response, and JAR performance variables were quantifiable. A similar trade-off lies in the choice between a single frequency stimulus and a frequency clamped stimulus. Many studies provide evidence that the JAR is extremely robust in response to a stimulus that maintains a constant DF, thereby chasing the fish upward (or downward, in the case of *E. virescens*) in frequency (Bullock et al., 1972b; Hagedorn et al., 1992; Kramer 1987). Despite its reliability in producing a response, this stimulus is not representative of a true interaction – therefore a single frequency stimulus was used here (Kramer, 1987). It may be worthwhile to attempt this study with a frequency clamped stimulus, to see if the effects of swimming noise can be better discerned. It may also be interesting to reconsider the range of noise applied in the stimulus (see earlier section), as it is possible that the 'optimal' level of noise was missed (Wiesenfeld & Moss, 1995; see Hypothesis 2). Finally, the rate at which the ramp of the looming stimulus rises in amplitude may also be worth re-considering. A slower, more gradual onset of the stimulus might make it easier to measure behaviour changes around a fine signal detection and EODF identification

threshold. In this study, the JAR commenced in as little as 1.4 seconds after stimulus onset, when the amplitude of the stimulus was still very small (Table 3.1, 3.3). As such, a more gradual ramp may be useful in more carefully pinpointing latency values, and in allowing a more detailed description of behaviour over this sensitive stimulus amplitude range.

4.6 Conclusion and Overall implications

Overall, this study demonstrated the following in *E. virescens*, a gymnotiform weakly electric fish:

- The EODF of *E. virescens* tracks the rise and fall of low frequency components of movement envelopes (0-2 Hz); no such tracking behaviour occurs in response to high frequency envelope components (2-20Hz).
- Variations in AM due to swimming (swimming noise) had no discernable effect on EODF identification abilities.
- Swimming noise improved EOD detection abilities; the time required to detect a signal improved linearly with increased depths of swimming noise, suggesting a novel example of behavioural stochastic resonance (SR)
- These findings satisfy the objectives of our study, providing evidence in support of hypotheses 2 and 3

This study has provided evidence that *E. virescens* is able to perfectly maintain EODF identification abilities (important for individual, sex, and species recognition) despite high levels

of signal noise caused by dynamic swimming. What is more, it has been demonstrated that swimming noise may in fact be beneficial in the detection of a conspecific signal. Although these results are astounding considering the sheer extent of noise applied to the signal, they are logical in an adaptive sense. Swimming noise is unavoidable for *E. virescens*, especially when we consider that dynamic movement is essential to sample the surrounding environment. A neurological system that did not adapt to, or perhaps even take advantage of this noise would simply be inefficient. This being said, future studies should focus not only on behavioural investigations into the beneficial effects of swimming noise on signal detection (using precise methods to confirm the presence of behavioural SR), but also on the exact neurophysiological mechanisms behind this ability to uphold EODF identification in the face of noise.

Neuroethological studies such as this one are an important link between neurophysiological data and behavioural observations. As we have demonstrated here, they can provide invaluable information to help frame future hypothesis about underlying neural mechanisms, as well as provide a better understanding of why a particular behaviour occurs. This study is a clear example of the benefit of neuroethological research, as it has clearly demonstrated that specific neurophysiological findings (i.e. swimming noise degrades signal clarity at a single electroreceptor) do not necessarily translate to the whole animal level (i.e. swimming noise is, at the least, innocuous in conspecific identification). Furthermore, this study points towards a completely novel example of behavioural SR in sensory and communication biology. Although examples of SR at the neural level are common, documented instances of adaptive noise in animal behaviour are extremely rare (Collins, 1999; Russel et al., 1999; Spezia et al., 2008). Its presence here may motivate augmented exploration of the adaptive value of

noise in behavioural systems beyond the weakly electric fish, and help us understand how biological systems have evolved to not only deal with, but use natural sources of noise to their advantage.

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