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Quantitative assessment of intrinsic noise for visually guided behaviour in zebrafish

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ABSTRACT

All sensory devices, whether biological or artificial, carry appreciable amounts of intrinsic noise. When these internally generated perturbations are sufficiently large, the behaviour of the system is not solely driven by the external stimulus but also by its own spontaneous variability. Behavioural internal noise can be quantified, provided it is expressed in relative units of the noise source externally applied by the stimulus. In humans performing sensory tasks at near threshold performance, the size of internal noise is roughly equivalent to the size of the response fluctuations induced by the external noise source. It is not known how the human estimate compares with other animals, because behavioural internal noise has never been measured in other species. We have adapted the methodology used with humans to the zebrafish, a small teleost that displays robust visually-guided behaviour. Our measurements demonstrate that, under some conditions, it is possible to obtain viable estimates of internal noise in this vertebrate species; the estimates generally fall within the human range, suggesting that the properties of internal noise may reflect general constraints on stimulus–response coupling that apply across animal systems with substantially different characteristics.

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1. Introduction

Biological systems do not behave deterministically: when presented with two identical instances of an external event, they may react differently depending on their internal state at the time of stimulation (Green, 1964; Highcock & Carter, 2014). This observation applies without exception to conditions where a stimulus signal is corrupted by an external noise source, and a human participant is asked to detect the presence of the signal: identical instances of signal and noise will result in different reports on the part of the human participant on about 3 out of 4 stimulus replications (Burgess & Colborne, 1988; Neri, 2010a).

It is possible to measure this departure from deterministic behaviour and quantify the amount of internal perturbation, but this can only be done in a relative sense. Because behaviour is driven by the internal representation of the stimulus, internal noise can only be defined with relation to this internal representation, which lacks absolute units. In the dominant framework for the quantification of animal behaviour, termed signal detection theory (SDT), this issue is addressed by rescaling all perceptual quantities (e.g. sensitivity) as a function of the variability induced upon them by variations within the external stimulus (Green & Swets, 1966). The same approach can be applied to internal noise (Burgess & Colborne, 1988; Neri, 2010a), thus enabling estimates of this phenomenon that are not only quantitative, but in principle directly comparable across different species provided sensory behaviour for the species in question can be adequately modelled using the principles of SDT.

In light of the above-stated potential for comparative studies of a fundamental property of animal behaviour such as internal noise, it may seem surprising that this phenomenon has so far been quantified only in humans. To our knowledge, there have been no comparable measurements in other species, making it difficult to interpret the human measurements on a broader scale that takes into account their comparative significance. Intraindividual variability (IIV), a quantity commonly used to study related phenomena (MacDonald, Nyberg, & Backman, 2006), lacks an established theoretical framework (Biro & Adriaenssens, 2013); its potential for comparative judgements is therefore compromised by the unavailability of a common metric space across different species. The goal of our experiments was to rectify these limitations and allow for direct comparison of intrinsic behavioural noise between humans and a small vertebrate, the zebrafish, that

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has proven a useful animal model for genetic manipulations relating to a range of human pathological conditions (Norton & Bally-Cuif, 2010), some of which (ADHD in particular) are believed to stem from abnormalities associated with internal noise (Gilden & Hancock, 2007, 2009, Perry, Sagvolden, & Faraone, 2010, 2012, 2013).

2. Methods

2.1. Animals and test apparatus

Except for the visual stimuli, which were specifically designed for this study (see next section), all other procedures were identical to those described in previous work (Neri, 2012) and will only be summarized here. We used wild-type zebrafish bred and maintained by trained staff in a dedicated facility (Institute of Medical Sciences, Aberdeen, United Kingdom; see also Vargesson, 2007; Therapontos & Vargesson, 2010 for details relating to husbandry). Outside testing, fish were kept inside a 10-litre storage tank (average density two fish per litre) attached to a recirculated system (Aquatic Habitats, Apopka, FL, U.S.A.) at 27 °C on a 14:10 h light: dark photoperiod and never exposed to heterospecifics. They were fed brine shrimp twice a day (at 09:30 and 16:30). During testing, one fish was transferred from the facility to a test tank measuring 25 × 13 cm and 11 cm high. The two furthest sides of the test tank were placed against two identical LCD monitors driven by one computer allowing independent control over the images displayed to the two sides. A webcam located above the test tank acquired images at 4 Hz and stored them on the hard drive for automated offline analysis. After testing, fish were returned to the breeding stock. Ethical approval for all the research reported in this study was obtained from the University of Aberdeen Ethical Review Committee. The work, which was in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki), was deemed as nonregulated by the Home Office Inspector; however, input was received from the Home Office Inspector and the Named Veterinary Surgeon and the care of all fish was under the remit of the Animals (Scientific Procedures) Act 1986. No animal licence was required because the behavioural procedures used here were non-invasive, in accordance with natural behaviour patterns, and only involved wild-type animals. A relevant constraint imposed by ethical guidelines was that fish could not be housed individually for extended periods of time, restricting our ability to identify specific individuals across multiple testing sessions. This guideline is enforced in view of the highly social nature of zebrafish, so as to ensure that they would not be exposed to potentially harming excessive isolation from conspecifics.

2.2. Automated tracking of animal position

We wrote software specifically tailored to the images collected during the experiments; the algorithm was therefore robust and efficient in the absence of any human intervention. Readers are referred to (Neri, 2012) for details. Briefly here, the software implemented motion detection via thresholded subtraction methods (McIvor, 2000) and applied cluster analysis to identify the test animal. The location of the cluster centroid between automatically detected end-points for the tank was used as position marker (see red/blue dots in Fig. 1E). To determine whether the test animal preferred one or the other side of the tank on a specific trial, we simply averaged all position values over the duration of that trial (see red/blue lines in Fig. 1E); preference was assigned to the side of the tank closest to this average value. We also explored other methods for assigning preference, for example the % time spent on either side of the tank, but this had no appreciable impact on our results. Furthermore, we were not able to expose any systematic relationship between the specific value of mean (or median) shift displayed by the animal on individual trials and the mean contrast difference of the stimuli presented on those same trials. In other words, although the mean contrast difference systematically modulated the preference as assessed via probability of binary choice, it did not appear to modulate the mean shift on a given trial, or at least not within the resolution of our measurements.

2.3. Visual stimuli and presentation protocol

All stimuli were generated by adding the same small icon of a zebrafish to a grey background. Ten individual icons were initially placed within the image at random spatial locations and made to drift horizontally at a constant speed of 6.5 cm/s without any further element of animation (i.e. except for drifting and occasional occlusion by other elements, icons did not undergo any modification). We have demonstrated in previous work that results obtained with actual footage of zebrafish colonies are reliably replicated using the artificial stimulus adopted here (Neri, 2012). Half the icons moved to the left and half to the right. When two icons overlapped within the image, the icon added more recently was painted over the other icon. All movies lasted 16 s and were generated using a cyclical structure: the end of the movie matched the beginning of the movie, so that the movie could be played smoothly for multiple repetitions without glitches. For a given movie, the contrast of each icon was randomly drawn from a Gaussian distribution with mean μ_j and standard deviation σ, where j is 1 for the movie with higher mean contrast and 2 for the movie with lower mean contrast (i.e. $\mu_1 > \mu_2$). Both high and low mean-contrast movies were presented during each trial on opposite sides of the tank; which side contained the high contrast movie was randomly determined. On a given test lasting ~14 min, the animal was presented with 1 block of 20 trials. Each trial lasted 30 s, and trials were separated by a 10-s gap during which both monitors displayed blank screens. Each block was associated with a specific parameterization (μ_1, μ_2 and σ values) of the contrast distributions defining the two stimuli; each parameterization corresponds to a different signal-to-noise ratio (SNR) $(\mu_1 - \mu_2)/\sigma$. We tested 4 different SNR values: 4 defined by μ_1 = 70%, μ_2 = 30% and σ = 10% contrast (Fig. 1A); 6 defined by μ_1 = 80%, μ_2 = 20% and σ = 10% contrast (Fig. 1B); 12 defined by μ_1 = 80%, μ_2 = 20% and σ = 5% contrast (Fig. 1C); ∞ defined by μ_1 = 100%, μ_2 = 0% and σ = 0% contrast (Fig. 1D). Each block was divided into two 'passes': the first pass from trial #1 to trial #10, the second pass from trial #11 to trial #20. The stimulus samples presented during the first pass were independently generated: on trial #1, the stimulus on the right side of the tank may contain 10 fish with contrast values randomly drawn from the distribution with higher mean μ_1, while the stimulus on the left side would then contain 10 fish with contrast values randomly drawn from the distribution with lower mean μ_2 (see icons on top row of Fig. 1E); on trial #2, the stimulus on the right may still draw from the contrast distribution with higher mean (see icons on second row of Fig. 1E), but it would be a different random sample, and so would be the stimulus on the other side; on trial #3, the stimulus on the right side may now draw from the contrast distribution with lower mean (see icons on third row of Fig. 1E), and so on. The second pass was an exact replication of the first pass: the same stimulus samples were presented on the same side of the tank as during the first pass.

2.4. Number of test animals and data mass

We tested three different cohorts. The first cohort consisted of 7 animals (age range 1.5–2 years old) which we could identify

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