Consistency in the strength of laterality in male, but not female, guppies across different behavioural contexts

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Abstract

Laterality, the division of brain functions into separate hemispheres, is widespread across animal taxa. Lateralised individuals exhibit cognitive advantages yet substantial variation in laterality exists, particularly between the sexes. Why variation is maintained is unknown as few studies consider differences in lateralised behaviours between the sexes, and their underlying selection pressures, across different contexts. We investigated if *Poecilia reticulata* exhibited sex differences in the direction, strength and consistency of lateralisation. We assessed the turning preferences of individuals detouring around a barrier to view visual stimuli representative of different behavioural contexts: an artificial object of familiar colour, an opposite sex conspecific and a no stimulus control. While no sex differences were evident in the direction or strength of laterality, consistency in the strength of laterality varied between the sexes. Individuals of both sexes consistently detoured in one direction, but the strength of laterality exhibited by males was more predictable than females across contexts. This suggests that predictability of lateralisation across ecologically relevant scenarios represents a key, but previously unexplored, source of variation between the sexes.

Introduction

Cerebral lateralisation or ‘laterality’, the partitioning of different cognitive processes into specific brain hemispheres [1], is found in vertebrate and invertebrate taxa [2-4] and often observed as side biases in behaviour [3,5]. Laterality occurs at population and individual levels. Population level laterality results when at least 50% of a population have aligned directional biases in laterality, and is thought to arise from strong selection pressures for a specific side to become specialised for a precise function [6]. However, in populations where directional biases are not aligned, individuals can exhibit strong laterality in either direction (individual level laterality) [6]. Although the evolutionary basis of laterality at this level is unclear [6], the need for lateralisation of an individual’s brain to function efficiently suggests it is of strong importance for individual fitness.

Advantages of laterality include an enhanced neural capacity, hemisphere dominance and simultaneous processing of cognitive functions [7], which result in lateralised individuals outcompeting non-lateralised conspecifics in several behaviours [8-9]. However, despite these advantages substantial variation in laterality persists within and between species. Why variation is maintained in a seemingly advantageous trait is unclear, especially since laterality influences fitness-related behaviours, including predator avoidance, whereby lateralised individuals exhibit enhanced performance using their preferred side [3]. Thus, understanding how variation in laterality develops and why it is maintained will allow a better understanding of how this variation could impact behavioural performance and ultimately fitness.

Sex is a recognised source of variation in laterality [10-11], yet many studies remain limited to a single sex, or species where sex cannot be non-invasively identified. In species where sex differences in laterality have been studied, the patterns of lateralisation have been influenced by variation between males and females [10-11]. This variation has sometimes been attributed to individual traits such as boldness [12] and aggression [13], but largely the factors responsible for causing and maintaining sex-specific variation in laterality are poorly understood.

Behavioural variation between males and females within singular behavioural contexts is prevalent [14-15]. In many behaviours the sexes exhibit different roles and thus are subject to different selection pressures [16]. For example, during reproduction both sexes are under strong but differing selection pressures: male fitness is determined by number of successful matings and female fitness by access to resources for gamete production [17]. To date, few studies have considered the influence of sex differences in behaviour with regard to laterality.

Here we investigated sex differences in the pattern (direction, strength and consistency) of laterality exhibited in three behavioural contexts using guppies (*Poecilia reticulata*), a species in which sex differences in behaviour are well established [18]. We examined the turning preferences of individuals detouring around a barrier to view a visual stimulus, a proxy for preferences in eye use [19] and thus cerebral lateralisation. Visual stimuli represented common behavioural contexts: an artificial object to assess exploratory behaviour, an opposite sex conspecific to examine sexual motivation and a no stimulus control.

Methods

Sixty-seven adult wild-type guppies (34 males, 33 females) were selected from a laboratory population maintained at the University of Hull. To allow for individual identification, subjects were housed in small mixed sex tanks (20x20x18cm) containing three differently sized individuals captured from stock tanks following visual identification. Male and female biased sex ratios were equally balanced. Tanks were maintained at 25°±1°C on a 12L:12D photoperiod and fed daily with commercial feed.

Behavioural lateralisation was assessed using a detour test [20; Figure S1]. The apparatus consisted of a rectangular tank with a double-ended T-maze joined by an opaque plastic runway. A barrier (10x16cm) made of vertical cylindrical bars (0.25cm diameter) spaced 0.25cm apart, was placed at one end of the tank in front of a stimulus, partially obscuring it. A removable opaque plastic door separated the runway from the end sections of the T-maze. Behavioural laterality was assessed with three visual stimuli: an artificial object of familiar colour (orange test-tube bung), an opposite sex conspecific (each conspecific was unique and contained in a 8x11cm transparent cylindrical tank) and an empty environment (control) presented 48 hours apart, with the order randomly determined at the housing tank level. Water in the tank was maintained at 25°C, was 11cm deep and was replaced after every fish to avoid changes in temperature and dissolved oxygen levels, which can affect laterality [21]. The tank was evenly lit and all trials were video recorded (Lifecam Studio, Microsoft, Washington, USA, connected to a computer) from above.

Each individual was allowed to acclimatise to the test arena for three minutes before being confined to one end using the door. The barrier and visual stimulus were then placed behind the runway at the opposite end of the tank and the door removed.

Individuals were allowed 30s to independently approach the runway, after which they were gently encouraged using a small dip net. Fish swam down the runway towards the barrier forcing them to detour left or right. The detour direction was recorded and the individual confined at the end of the tank while the barrier and stimuli were moved to the alternate end (accounting for asymmetry in the set-up) and the procedure repeated for 10 consecutive trials.

For each individual, the direction of laterality (population-level) was assessed using a relative laterality index (L_R): (right – left)/(right + left) x 100 [20]. L_R ranges from -100 to 100 indicating a preference to consistently detour leftward or rightward respectively. The strength of laterality irrespective of direction (individual-level), was assessed using the absolute laterality index L_A, calculated as $|L_R|$. L_A ranges from 0 (equal number of left and right detours) to 100 (turning consistently in one direction).

Statistical analyses were conducted using R version 3.6.2 [22]. To examine whether guppies exhibited directional preferences in laterality in each behavioural context, two-tailed t-tests were used to determine whether L_R scores deviated from random choices (0). Chi-squared tests were used to examine whether fish exhibited significant individual-level laterality in each context, by determining whether there were more individuals with extreme L_A scores in the tails of the distribution than expected by chance (based on a normal approximation to the binomial distribution at p=0.5). χ^2 was calculated as ((N-1)*var(X1)/(n*0.5*0.5), where N is the number of individuals, n is number of trials per individual and X1 is the number of right (or left) turns per individual [23]. The false discovery rate method [24] was used to correct for multiple testing and adjusted p-values are reported. Linear mixed effects models (LMM), fitted using *lme4* [25], were used to examine the effect of sex, stimulus, body length, housing sex ratio and biologically relevant two-way interactions on L_R and L_A. Individual ID nested within group was included as a random factor to account for repeated measures and for each housing tank experiencing the stimuli in the same order. Residuals were assessed for homoscedasticity and a normal distribution by visual inspection of residual-fit and Q-Q plots. The model (R code format) that best explained the data for L_R and L_A, based on model simplification using likelihood ratio tests, was: $L_R/L_A \sim 1$.

We assessed consistency of laterality using 2 measures: repeatability (group-level) of L_R and L_A, and predictability (individual-level) of L_A only. Between context agreement repeatability estimates were calculated for the L_R and L_A of each sex using the *rpt* function (*rptR* package; [26]), from variance components of a LMM with individual ID as a grouping random factor. Statistical significance of repeatability was determined by likelihood ratio tests comparing the deviances of models with the grouping factor of interest to models without. Observed likelihood ratios were compared to distributions of likelihood ratios determined from parametric bootstrapping (x1000) to obtain p-values [27].

To compare predictability of L_A between sexes, we used the residuals from simplified LMMs containing context as a fixed effect and individual ID as a random intercept, for each sex separately, to calculate a measure of intra-individual variation (IIV) [28]. Context was retained in the model regardless of significance, since it was directly relevant to experimental design. IIV was calculated as the residual individual standard deviation (riSD), $\sqrt{}(\Sigma(Y_{ij}-E_{ij})^2)/N_i-1$. Y_{ij} and E_{ij} represent observed and expected values for each individual (i) at each observation (j) and N_i represents the number of observations [28]. Male and female IIV were compared using a two-sample t-test to determine if predictability of L_A varied between sexes.

Results

L_R and L_A were not influenced by sex, stimulus, housing sex ratio, body size or their interactions (Table 1). Thus, males and females exhibited similar patterns of laterality in the detour test regardless of behavioural context.

Table 1: The effect of sex, stimulus, body length, housing sex ratio and biologically relevant two-way interactions on a) L_R and b) L_A. The intercept represents females, from female biased tanks, in the conspecific treatment.

	estimate	**s.e.**	**df**	**t**	**p**
a) Direction of laterality (L_R)					
Intercept	26.408	39.855	63.365	0.663	0.510
Sex (male)	82.242	80.546	62.853	1.021	0.311
Stimulus (control)	-7.058	8.109	130.000	-0.870	0.386
Stimulus (artificial object)	-1.176	8.109	130.000	-0.145	0.885
Body length	-0.922	1.348	61.370	-0.684	0.497
Sex ratio (male-biased)	-7.299	8.581	26.592	-0.851	0.403
Sex (male) * Stimulus (control)	-5.668	11.554	130.000	-0.491	0.625
Sex (male) * Stimulus (artificial object)	-3.066	11.554	130.000	-0.265	0.791
Sex (male) * Body length	-2.713	2.806	61.986	-0.967	0.337
b) Strength of laterality (L_A)					
Intercept	38.224	20.045	59.328	1.907	0.061
Sex (male)	-61.213	40.631	57.143	-1.507	0.137
Stimulus (control)	-4.705	5.470	129.995	-0.860	0.391
Stimulus (artificial object)	-9.411	5.470	129.995	-1.720	0.087
Sex ratio (male-biased)	5.255	5.600	23.440	0.938	0.357
Body length	-0.078	0.669	54.250	-0.118	0.906
Sex (male) * Stimulus (control)	5.311	7.795	129.995	0.681	0.496
Sex (male) * Stimulus (artificial object)	13.654	7.795	129.995	1.752	0.082
Sex (male) * Body length	1.860	1.413	55.877	1.317	0.193

Individuals exhibited significant laterality (L_A) in the detour test (Table 2b). Thus, guppies tended to detour consistently leftward or rightward in each behavioural context (Figure 1). However, individual preferences were not aligned amongst individuals as no overall population-level directional bias (L_R) was observed in any behavioural context (Table 2a).

Table 2: one-sample t-tests and x^2 tests examining if a) L_R and b) L_A differed from random choices in each behavioural context. Adjusted p-values are reported and if significant highlighted in bold.

		a) Direction of laterality (L_R)		**b) Strength of laterality (L_A)**	
Stimulus	**df**	**t**	**p**	**χ^2**	**p**
Conspecific	66	-0.224	0.823	124.704	**<0.001**
Control	66	-2.224	0.089	109.026	**0.001**
Artificial object	66	-0.821	0.621	98.591	**0.006**

Figure 1: L_A for a) female and b) male guppies detouring around a barrier to approach an empty environment (blue), an opposite sex conspecific (orange) or an artificial object (green). Boxplots display the median and IQR for each sex while individual points represent the L_A of each individual in each context and dashed lines represent between context consistencies.

L_R was repeatable across contexts in both sexes (Males: R=0.324±0.116, 83% CI=0.162-0.471, p=0.001; Females: R=0.363±0.115, 83% CI=0.19-0.506, p<0.001; Figure 2a) however; L_A was only significantly repeatable in males, not females (Males: R=0.252±0.11, 83% CI=0.081-0.390, p=0.011; Females: R=0.124±0.095, 83% CI=0-0.255, p=0.134; Figure 2a). Females were significantly less predictable (larger riSD) at the individual level than males (t=3.267, df=62.169, p=0.001; Figure 1 & 2b).

Figure 2: a) repeatability of L_R and L_A for females (triangles) and males (circles) with associated 83% CI (L_R=dashed, L_A=solid) as recommended by Payton et al [29].

b) riSD of L_A for females (red) and males (yellow). Asterisks indicate significant differences between groups at p<0.05.

Discussion

Our results provide the first evidence of a sex difference in the consistency of laterality across different behavioural contexts. Individuals of both sexes consistently turned left or right, but males were more predictable than females in the strength of laterality exhibited across contexts. Although our study does not allow consistency across contexts to be distinguished from consistency in general (i.e. both within and across contexts), previous work has shown within-context consistency of laterality in female guppies [30]. Little is known about the relationship between laterality and other behaviours in guppies, but we propose three key factors that may drive the observed difference in consistency: laterality as the subject of sexual selection, variation in sexual motivation, and sex differences in the strength of selection resulting from predation.

Sex differences in the consistency of parental care behaviours are found in house sparrows (*Passer domesticus*), whereby males exhibit strong consistency not observed in females [31]. Male consistency in this case acts as an indicator of male quality for female mate choice and has direct implications for sexual selection [31]. The increased consistency of L_A in male guppies could result from laterality being under direct sexual selection, or correlated with sexually selected traits, but this is currently unknown.

Secondly, sexual motivation could impact the strength of laterality exhibited in the detour test and thus the consistency of L_A across contexts. In guppies, both sexes are under strong sexual selection [18]: male fitness is driven by number of successful matings [17] while female fitness is driven by access to resources for gamete production [17]. As guppies live-bear, gravid females are likely less sexually motivated than non-gravid females [32-33], while selection for males to pursue mating opportunities results in high levels of sexual harassment towards females [34]. Sexual motivation across males is thus likely more consistent, while in females sexual motivation likely varies with reproductive status.

In female guppies deprived of males, strong lateral biases have been shown, that are not present in females with access to males [35]. Here, female reproductive status and associated sexual motivation was unknown, but could have influenced variation in female L_A both within and across contexts. For example, live bearing is associated with enhanced cognition especially in tasks involving spatial learning [32] that are important for successful foraging and offspring survival [36]. Thus, heavily gravid females may exhibit stronger lateralisation with artificial objects or in empty environments relative to non-/less gravid counterparts, as a result of enhanced cognition in spatial tasks associated with carrying young.

Finally, male guppies experience stronger predation pressures than females owing to brighter colouration and smaller size [37]. Increased predation pressure could have a strong stabilising effect on L_A in males, driven by natural selection, which causes them to exhibit consistency in L_A across behavioural contexts. In some fishes, increased predation pressure is associated with stronger lateralisation [19,38], which has been linked to enhanced escape reactivity [39] suggesting that individuals exhibiting strong predation pressures would benefit from consistent hemispherical biases regardless of context.

Despite no overall sex differences in the direction and/or strength of laterality, our results demonstrate variation between the sexes in the consistency of L_A across contexts. Several factors could underpin this variation, the majority of which have yet to be studied in the context of laterality. Thus exploration of the effects of sexual selection, reproductive state and predation pressure on the evolution and expression of lateralisation within and between contexts in guppies is needed. Future studies should also investigate the generality of this finding by examining laterality in both sexes across a variety of behavioural contexts and species.

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Competing interests

We have no competing interests.

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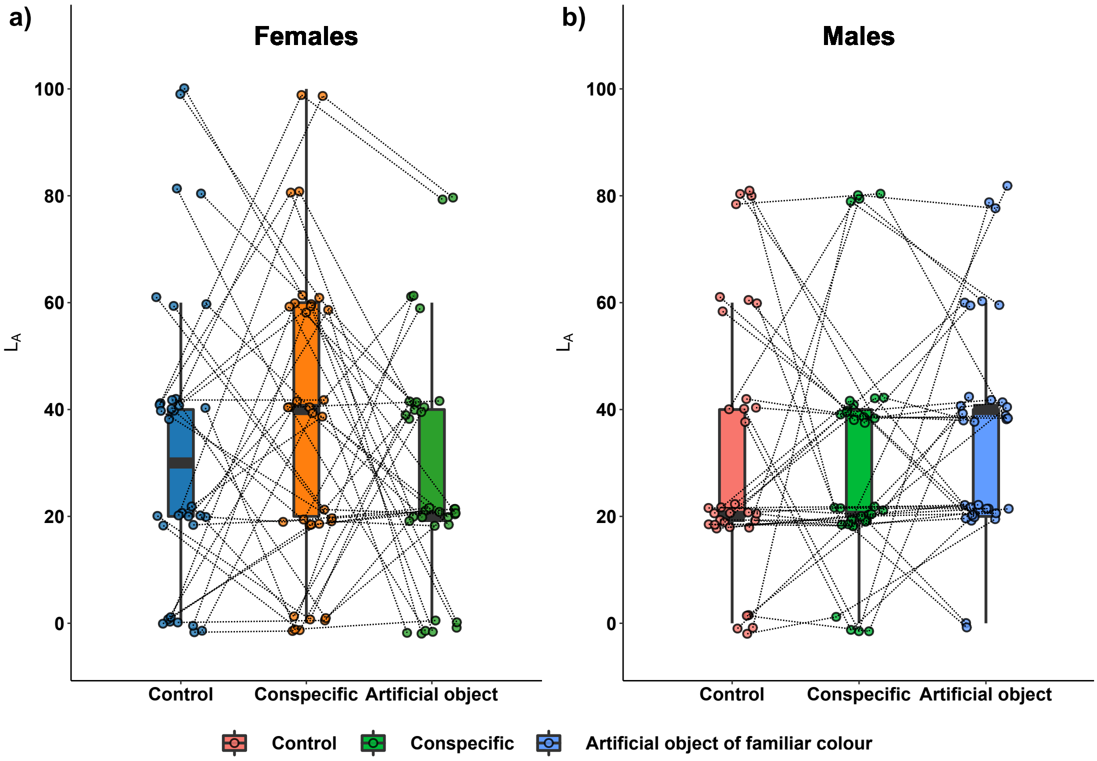
Figure 1


a)
Females
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b)
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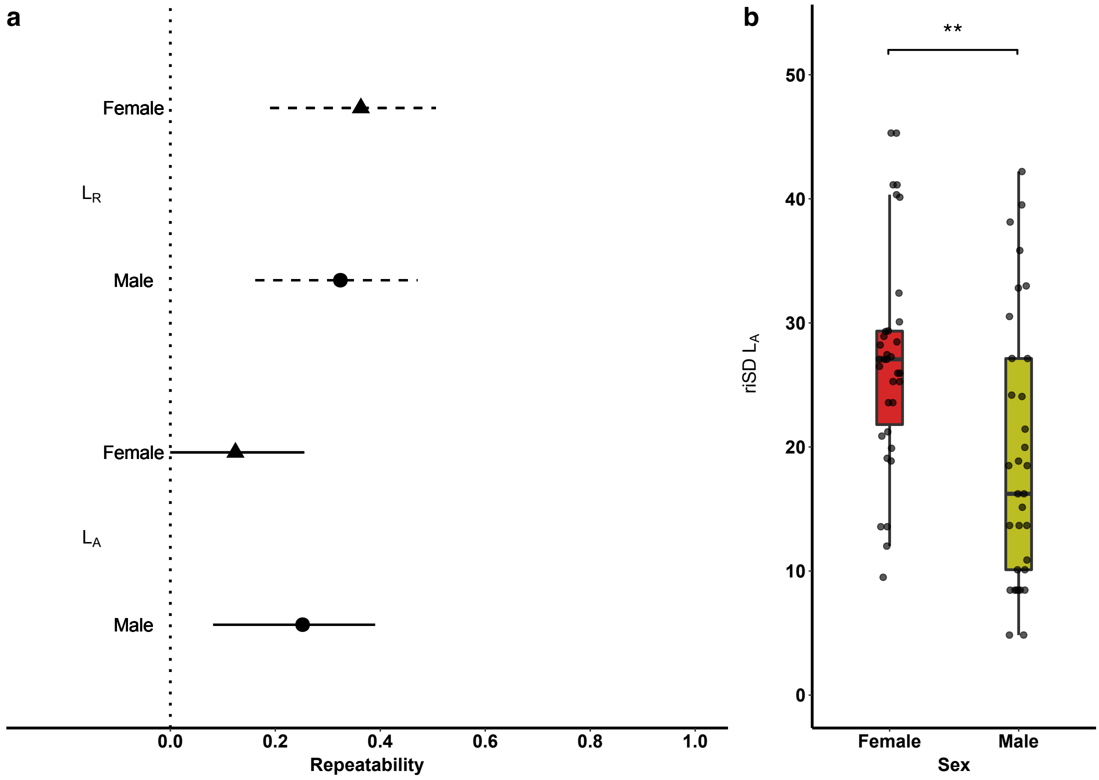
Control
Conspecific
Artificial object
Control
Conspecific
Artificial object of familiar colour

452 Figure 2



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Supplement 1: Diagrammatical representation of experimental tank (detour test)

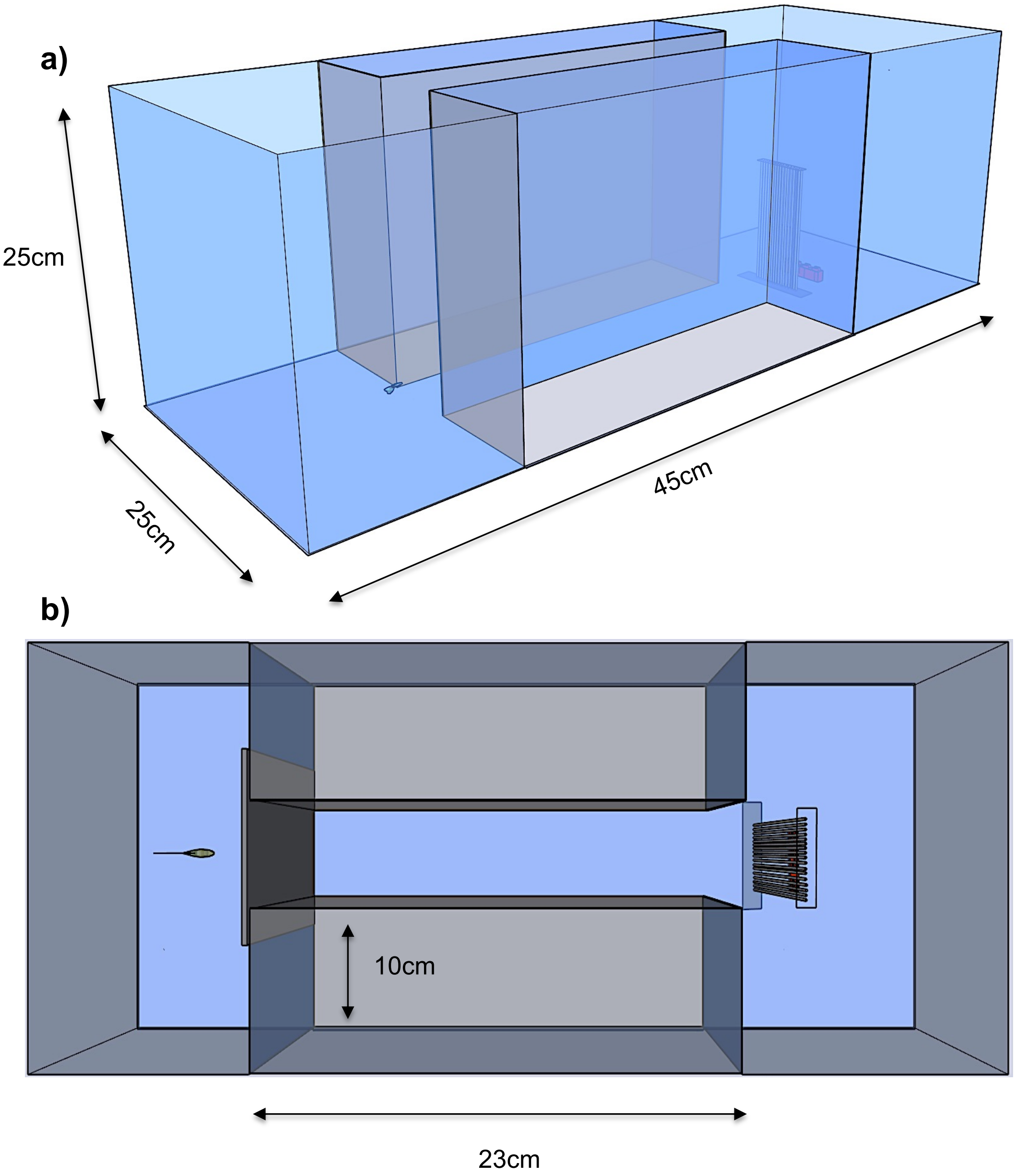

Figure 1S: Diagrammatic representation of the detour test used to examine behavioural laterality: a) side view and b) from above. Fish swam along a runway (alternatively in opposite directions) to detour around a barrier while viewing a visual stimulus (here an artificial object). The portable door used to confine individuals at either end of the T-maze before beginning each new trial is depicted in figure 1Sb.