Male and female guppies differ in speed but not in accuracy in visual discrimination learning

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ABSTRACT

In many species, males and females have different reproductive roles and/or differ in their ecological niche. Since in these cases the two sexes often face different cognitive challenges, selection may promote some degree of cognitive differentiation, an issue that has received relatively little attention so far. We investigated the existence of sex differences in visual discrimination learning in the guppy, *Poecilia reticulata*, a fish species in which females show complex mate choice based on male colour pattern. We tested males and females for their ability to learn a discrimination between two different shapes (experiment 1) and between two identical figures with a different orientation (experiment 2). In experiment 3, guppies were required to select an object of the odd colour in a group of five objects. Colours changed daily and therefore the solution for this task was facilitated by concept learning. We found males' and females' accuracy practically overlapped in the three experiments, suggesting the two sexes have similar discrimination learning abilities. Yet, males showed faster decision time than females without any evident speed–accuracy trade-off. This result indicates the existence of consistent between-sex differences in decision speed perhaps due to impulsivity rather than speed in information processing. Our results align with previous literature indicating that sex differences in cognitive abilities are the exception rather than the rule, while sex differences in cognitive style, i.e., the way in which an individual faces a cognitive task, are much more common.

Keywords: cognitive sex differences; cognitive style; decision speed; discrimination learning; fish cognition; *Poecilia reticulata*.

INTRODUCTION

In many animal species, reproductive roles differ considerably between the sexes. As a consequence, males and females may be required to solve different cognitive problems. For example, often females, but not males, choose between potential mates using complex characteristics, such as coloration, courtship displays, and calls (Bateson 1983). This process arguably requires refined discrimination accuracy, learning ability and memory capacity (Bateson and Healy 2005). In polygamous voles, males have a much larger home range size than females and have therefore greater spatial orientation requirements (Gaulin and FitzGerald 1986). In nest parasite birds, often females are required to remember the exact location and the reproductive stage of many host nests which are regularly visited on the days before egg deposition (Astié et al. 1998). Sex-specific cognitive challenges may also arise because males and females frequently occupy different habitats, have different diet or different predators (reviewed in Magurran and Garcia 2000; Selander 1966; Shine 1989). For example, in the elephant seal, *Mirounga angustirostris*, females preferentially chase pelagic species such as squids, while males use a sit-and-wait strategy to capture bottom-living fish such as rays, two strategies that likely require distinct skills (Le Boeuf et al. 1993).

In all these situations, selection might act differentially on males and females, favouring the evolution of sex differences in cognition. The literature reports a few interesting cases of sex differences in cognition that appear to be associated with sex differences in reproductive roles. For example, in the polygamous voles *Microtus pennsylvanicus*, males showed increased accuracy compared to females in a spatial task (Gaulin and FitzGerald 1986). In the nest parasitic cowbird *Molothrus bonariensis*, females perform better than males in memory tasks (Astié, et al. 1998). In the lekking bird *Manacus vitellinus*, females are able to discriminate among males that differ by only few milliseconds in courtship rate, and have much more developed neural regions underlying this function (Day et al. 2011; Barske et al. 2011).

Since the situations in which males and females face difference cognitive challenges are diverse (reviewed in Bateson and Healy 2005; Magurran and Garcia 2000; Selander 1966; Shine 1989), cognitive sex differences could potentially evolve in a large number of species and in many cognitive domains. Unfortunately, previous research has focused on few species (e.g., humans and laboratory rodents) and on a limited range of cognitive tasks (e.g., spatial learning tasks; Jonasson 2005). Most of the literature in this field comes from human psychology. Men and women have been compared in virtually all domains (Halpern 2013). However, only two cognitive differences appear consistent: females show better performance in some verbal tasks such as semantic learning, while males often have better scores in some spatial tasks such as mental rotation (Halpern 2013). Arguably, the investigation of different species and different tasks appears essential for testing hypotheses about the evolution of sex differences in cognition.

The guppy, *Poecilia reticulata*, exemplifies how much males and females can differ in reproductive roles, behaviour, and ecology. Male guppies are tiny and colourful while females are larger and show a cryptic coloration (Houde 1997). Females normally forage in shoals with complex social networks, while males move from one shoal to another to search for mates (Croft et al. 2004; Griffiths and Magurran 1998). This frantic male harassment is detrimental to females and forces them to depart from preferred sites in shallow water and to occupy more dangerous deep waters (Croft et al. 2006; Darden and Croft 2008). In some rivers, male and female guppies differ in their diets, as females feed more on diatoms, while males feed more on algae (Magurran 2005). Moreover, piscine predators attack preferentially females (Pocklington and Dill 1995); thus, females express more predator inspections, and display increased antipredator response (Magurran 2005; Magurran and Garcia 2000).

The largest difference between male and female guppies undoubtedly concerns mating behaviour. Males show little selectivity, while females choose accurately among available males (Houde 1997). Female mate choice is based on multiple visual traits such as male body size, tail length, and body colouration (Houde 1997; Magurran 2005). Females demonstrate an astonishing ability to discriminate between males with subtle differences in size, shape, number, hue and intensity of colour spots (Houde 1997; Houde and Torio 1992; Kodric-Brown 1989; Long and Houde 1989). Females also learn and memorize features of males they have encountered (Dugatkin et al. 1992; Eakley and Houde, 2004) as they mostly prefer males exhibiting colour patterns dissimilar from previous mates (Eakley and Houde, 2004; Hughes et al. 1999).

We aimed to investigate the existence of sex differences in visual discrimination learning in guppies. Lucon-Xiccato and Bisazza (2014) have compared male and female guppies in a simple colour discrimination, red *versus* yellow, finding the two sexes learned the task with equal ability. In this study, we therefore investigated sex differences in three more complex visual discriminations. In the first experiment, guppies were required to discriminate between different shapes. Sex differences in the ability to discriminate objects have been investigated in rodents (e.g., 3D objects constructed with Lego® building blocks: Bettis and Jacob 2012) and humans (e.g., photographs with altered features: Barkley and Gabriel 2007), finding a female advantage in both cases. The second experiment consisted of a discrimination between a figure and its horizontal mirror image. This task appears to be particularly difficult for most vertebrates, including fish (Gierszewski et al. 2013). In humans, there is a male-advantage in recognising rotated 2D objects (e.g. Collins and Kimura 1997). The third experiment consisted of an oddity discrimination learning task. The subject was required to choose the object that differed in colour from the other four objects presented. Since the pair of colours was changed daily, this last task could be solved using concept learning (Hille et al. 2006). As primary measure of discrimination abilities in the experiments, we measured choice accuracy. However, we also measured decision speed as it is thought to be key component of discrimination processes in ecologically relevant situations (Chittka et al. 2009).

Because of the complex mate choice rules, female guppies are expected to undergo selection for the cognitive abilities that subserve visual discrimination processes. We therefore expected female to perform in general better than males (i.e., greater accuracy).

MATERIALS AND METHODS

Subjects

We used 10 male and 10 female guppies of an ornamental strain (“snakeskin cobra green”) in each experiment (30 males and 30 females overall). We observed each subject in only one experiment. Subjects were six to eight months old, and none of the females was pregnant. We measured standard length of the guppies after completion of the experiment (Supplementary materials). Guppies were bred in our laboratory and maintained in 150-litre aquaria enriched with gravel bottom, abundant natural and artificial plants to resemble natural condition (see Supplementary materials for details). Experiments comply with the law of the country (Italy) in which they were performed. The experimental procedures have been approved by Università di Padova Ethical Committee (protocol n. 09/2012).

Experimental apparatus

The experimental tanks were glass aquaria (60 × 40 × 35 cm) filled with gravel and 30 cm of water (figure 1a). By using green plastic material, each tank was divided in a front main compartment (30 × 40 cm) and a start box (10 × 8 cm). A grid prevented the subject from reaching the sector behind the start box, which was provided with abundant natural vegetation and filters. In the main compartment, a green plate (20 × 15 cm) perforated with 48 holes (Ø 1 cm, depth 0.3 cm) was placed horizontally on the gravel substratum. A transparent guillotine door controlled the connection between the main compartment and the start box.

Procedure

We used a training procedure previously adopted to study guppies' learning abilities (Bisazza et al. 2014; Lucon-Xiccato and Bisazza 2014; Miletto Petrazzini et al. 2015). All the experiments were made up of five consecutive phases (described in Supplementary materials). Phases 1–3 consisted of the habituation to the apparatus and to the procedure. Phase 4 was the experimental phase in which we evaluated discrimination learning performance. Phase 5 was a control test for the use of olfactory cues. For the entire length of the experimental phase, each subject was housed in a distinct apparatus. Outside the trials of the experiment, we provided five immature guppies (approximate standard length: 1 cm) as social companions. Subjects underwent 10 trials each day of the experimental phase (five trials in the morning and five trials in the afternoon). At the beginning of each trial, the experimenter inserted a transparent panel into the tank and gently guided the subject into the start box. Then, the experimenter closed the guillotine door and positioned a green plastic panel in front of the corridor to ensure the subject could not see the main compartment. Two (in experiments 1 and 2) or five (in experiment 3) holes of the plate were covered with small plastic discs. In experiment 2, two cards were also placed behind the discs. The discs were placed on the holes of the plate according to a scheme generated by a computer software that produces random numbers. However, we ensured that the left-right position of the rewarded disc on the plate was alternated according to a r-l-r-l-r-r-l-l sequence. The position of the discs was the same for all subjects. A food reward, consisting of a small portion of commercial crumbled food flakes, was placed into the hole under the reinforced disc using a plastic Pasteur pipette. The reinforced disc was indicated by a visual stimulus as described below. The subjects were trained to dislodge the discs during phase 3 (Supplementary materials). The experimenter added water scented with food to the apparatus to stimulate the subject in starting to search food and to prevent the use of olfactory cues to solve the task. After that, the experimenter removed the green panel, allowing the subject to observe the task from the corridor for 10 seconds, and, finally, opened the guillotine door, leaving the subject to enter the main compartment and dislodge the discs. The first disc dislodged by the subject was considered an indication of its choice to measure accuracy. Latency to dislodge a disc after entering the main compartment was recorded using a digital chronometer (see Supplementary materials for details) and, rounded to the nearest second, considered to be the decision speed as in previous literature on fish (Mamuneas et al. 2015; Wang et al. 2015). The experimenter allowed the subject five minutes to dislodge a disc; after that, the trial was considered null and repeated later. If a subject performed two consecutive null trials, the session was interrupted and the experiment continued in the following session. After dislodging an incorrect disc, the subject was allowed a further five minutes to find the rewarded disc. Other training procedures prevent subjects from finding the reward after an incorrect choice. This is not applicable with our procedure. Pilot experiments revealed that guppies ceased to participate after few consecutive trials in which they did not get the food. Perhaps because considerable effort is needed to dislodge the discs, guppies reached excellent discrimination performances in previous studies with this procedure (Bisazza et al. 2014; Lucon-Xiccato and Bisazza 2014; Miletto Petrazzini et al. 2015).

General description of the experiments

In experiment 1 (shape discrimination), two white discs with different shapes drawn in black were placed on the plate. From day 1 to 6 (60 trials), subjects had to learn to discriminate a bar from an S-shaped segment (figure 1b); from day 7 to day 12 (60 trials), they had to learn to discriminate between a triangle and a square (figure 1b). For half of the subjects of each sex the S and the triangle were rewarded; for the remaining subjects the bar and the square were rewarded.

In experiment 2 (discrimination between a figure and its mirror image), subjects were required to discriminate an E-shaped figure from an identical figure that was horizontally flipped (figure 1b). Figures were drawn on two white vertical cards (4 × 4 cm). Two identical yellow discs were placed on the plate in front of the card. The disc in front the card with the rewarded figure hid the food. We used the cards to ensure the orientation of the stimuli was fixed, irrespective of the position of the subject. For half of the subjects of each sex the E was rewarded; for the remaining subjects the mirror image was rewarded. The experiment lasted 10 days (100 trials).

In experiment 3 (oddity discrimination), five discs were displayed in a row. Four discs were of the same colour, while one was of a different colour (figure 1b) and concealed the food reward. The experiment lasted six days (60 trials), and each day the subject was administered a different pair of colours to discriminate (figure S1). The rewarded colour was flipped for half of the subjects of each sex.

At the end of the experimental phase, the subjects underwent phase 5 to test whether during the experiment they had learned to find the food by using olfactory cues. In line with previous experiments (Bisazza et al. 2014; Lucon-Xiccato and Bisazza 2014; Miletto Petrazzini et al. 2015), we found no evidence that subjects were able to detect olfactory cues from the food with this procedure (Supplementary materials).

Statistical analysis

All statistical tests were two-tailed. For each subject, we computed the "daily accuracy" (proportion of correct choices in each day of training, repeated measures variable) and the "overall accuracy" (proportion of correct choices over all training, reported as mean ± standard deviation percentage). Overall and daily accuracy were always arcsine square root transformed before conducting parametric analysis (Sokal and Rohlf 1995). Similarly, we computed the "daily decision speed" (average latency to dislodge the disc in each day of training, repeated measures variable) and the "average decision speed" (average latency to dislodge the disc over all training, reported as mean ± standard deviation). Decision speed was log transformed as the raw data had a right-skewed distribution.

We used the independent-sample *t* test to assess sex differences in standard length. Then, we used Pearson's correlation test to study relationship between standard length and the overall accuracy, between standard length and the average decision speed, and between the overall accuracy and the average decision speed.

To provide an indication of within-sex individual differences, for each subject independently we used the binomial test to compare the number of correct choices with chance level (0.5 in experiment 1 and 2; 0.2 in experiment 3) over all training period.

Daily accuracy and daily decision speed were analysed with linear mixed-effects models (LMMs) fitted with day of training, sex and, in experiment 1, discrimination as fixed effects and subject ID as random effect. In case of no significant effect of sex, we calculated an approximate Bayes factor (*BF*) according to Wagenmakers (2007). *BF* estimated the relative strength of the evidence for the absence of sex difference without the confounding of sample size (Dienes 2014).

In experiment 3, we also built a more complex model to study the two possible learning strategies adopted by subjects. We fitted the response of the subjects in each trial (correct or incorrect) in a generalised linear mixed-effects model (GLMM) with logit link function and binomial error distribution. We fitted day of training, trials of the day and sex as fixed effects and subject ID as a random effect. In experiment 3, we also analysed individual differences in the learning strategy. For each subject, we computed an improvement rate across trials within days and an improvement rate across days. The first was the Spearman ρ of the correlation between the proportion of correct choices in each trial across the days of training and the ordinal position of the trial (from 1 to 10); the second was the Spearman ρ of the correlation between the proportion of correct choices on each day and the ordinal position of the day (from 1 to 6). In experiment 3, we also performed one-sample t tests to compare the accuracy of the subjects against the accuracy expected by change (0.2). In all the mixed effect models, we performed trend analysis following Logan (2011) in case of a significant effect of day of training to study change in accuracy. Further details on statistical analysis are given in Supplementary materials.

RESULTS

Experiment 1: shape discrimination

Males and females had a comparable standard length (32.20 ± 1.93 mm and 32.40 ± 3.17 mm, respectively; independent-samples *t* test: $t_{18} = 0.170$, $p = 0.867$). There was no significant correlation between standard length and overall accuracy (Pearson's $r_{18} = - 0.066$, $p = 0.781$) or between standard length and average decision speed (Pearson's $r_{18} = - 0.266$, $p = 0.258$).

Binomial tests indicated five males and five females showed a statistically significant preference for the reinforced stimulus (figure 2a; table S1). Overall accuracy was 60.15 ± 5.67%. The LMM revealed subjects' daily accuracy was not significantly different between the two discriminations ($F_{1,198} = 3.568$, $p = 0.060$). Day of training did have a significant effect in the model ($F_{5,198} = 4.251$, $p = 0.001$), as the accuracy increased linearly with day of training (polynomial trend analysis: $p = 0.043$; figure 3). Sex had no significant effect in the model (male overall accuracy: 60.83 ± 4.98%; female overall accuracy: 59.47 ± 6.47%; $F_{1,18} = 0.099$, $p = 0.757$; figure 2a), and there was no significant sex by day of training interaction ($F_{5,198} = 0.079$, $p = 0.779$; figure 3). The other interactions in the LMM were not significant. According to Bayesian analysis, the model without the effect of sex was 198.457 times more likely to explain our data than the model with that effect.

The average decision speed was 11.84 ± 6.99 seconds. The LMM on daily decision speed revealed no effect of discrimination ($F_{1,198} = 0.080$, $p = 0.778$), but decision speed varied significantly across days of training ($F_{5,198} = 4.278$, $p = 0.001$). Moreover, the day of training by discrimination interaction was significant ($F_{5,198} = 5.739$, $p < 0.001$). Males appeared to be faster than females at making decisions in all days of the test (male average decision speed: 8.88 ± 2.84 seconds; female average decision speed: 14.79 ± 8.72 seconds; figure 5a), but this effect was not significant ($F_{1,18} = 3.602$, $p = 0.074$). Sex by day interaction was not significant ($F_{5,198} = 0.303$, $p = 0.912$), nor were the other interactions in the model. There was no significant correlation between overall accuracy and average decision speed (Pearson's r_{18} = - 0.032, p = 895). A sex-separated analysis confirmed the absence of correlation (males: r_8 = - 0.081, p = 0.823; females: r_8 = 0.065, p = 0.858).

Experiment 2: mirror image discrimination

Males and females had a similar standard length (32.30 ± 1.89 mm and 31.20 ± 1.69 mm, respectively; t_{18} = 1.374, p = 0.186). There was no significant correlation between standard length and overall accuracy (r_{18} = - 0.168, p = 0.478) or between standard length and average decision speed (r_{18} = - 0.427, p = 0.061).

Binomial tests found only one male and one female significantly learned the task (figure 2b; table S1). Considering only the last part of the experiment (from day 6 to day 10), only one female significantly learned the task. Overall accuracy was 52.74 ± 4.88%. The LMM revealed subjects' daily accuracy was not significantly affected by day of training ($F_{9,161}$ = 0.811, p = 0.607; figure 4a), suggesting guppies did not learn the task. Sex had no significant effect in the model (male overall accuracy: 52.90 ± 5.38%; female overall accuracy: 52.58 ± 14.20%; $F_{1,18}$ = 0.078, p = 0.783; figure 2b), and the sex by day of training interaction was not significant ($F_{9,161}$ = 0.968, p = 0.468; figure 4a). According to Bayesian analysis, the model without the effect of sex was 219.042 times more likely to explain our data than the model with that effect.

The average decision speed was 14.65 ± 11.61 seconds. The LMM revealed that daily decision speed changed across days of training ($F_{9,161}$ = 5.962, p < 0.001). Sex had a significant effect in the model ($F_{1,18}$ = 15.062, p = 0.037; figure 5b): males had a faster decision speed than females (9.63 ± 5.15 seconds and 19.68 ± 14.20 seconds, respectively). No significant sex by day of training interaction was found ($F_{9,161}$ = 1.746, p = 0.083). There was no significant correlation between overall accuracy and average decision speed (r_{18} = 0.277, p = 0.237). Since the sex difference in decision speed could potentially have affected the results of the correlation test, we also ran a sex-separated analysis. Again there was not statistically significant evidence of correlation (males: $r_8 = 0.553$, $p = 0.098$; females: $r_8 = 0.122$, $p = 0.738$).

Experiment 3: oddity discrimination

Males and females had comparable standard length (30.60 ± 3.13 mm and 32.90 ± 2.33mm, respectively; $t_{18} = 1.862$, $p = 0.079$). There was no significant correlation between standard length and overall accuracy ($r_{18} = 0.361$, $p = 0.118$) or between standard length and average decision speed ($r_{18} = -0.107$, $p = 0.652$).

Binomial tests found nine males and seven females significantly learned the task (figure 2c; table S1). The LMM revealed subjects' accuracy was significantly affected by day of training ($F_{5,90} = 2.918$, $p = 0.0173$), but polynomial trend analysis found accuracy did not increase linearly with day of training ($p = 0.815$; figure 4b). Sex had no significant effect in the LMM (male average accuracy: 43.17 ± 11.09%; female average accuracy: 37.83 ± 11.25%; $F_{1,18} = 0.913$, $p = 0.352$; figure 2c), and the sex by day of training interaction was not significant as well ($F_{5,90} = 0.355$, $p = 0.878$; figure 4b). The model without the effect of sex was 39.243 times more likely to explain our data than the model with that effect.

This task could potentially be solved using two different strategies. This possibility was examined with the GLMM. The first strategy consisted of recurrently learning which colour concealed the food reward each day. The second strategy consisted of learning the general concept that the food reward was always concealed under the odd colour. Males and females might rely differentially on the two learning strategies, as observed for rats in spatial tasks (Rodríguez et al. 2010; Tropp and Makus 2001). We expected that subjects using recurrent learning would increase their performance across trials within each day of training; conversely, subjects adopting concept learning would increase their performance across the days of training. Therefore, if males and females adopted different strategies, we should find a significant interaction between sex and almost one among trial within day and day of training in the GLMM. GLMM results confirmed the results of the LMM on daily accuracy: day of training had a significant effect (Wald χ^2_5 = 28.166, p < 0.001), but there was no significant effect of trial within day (Wald χ^2_9 =12.651, p = 0.179) nor significant effect of sex (Wald χ^2_1 = 1.125, p = 0.289). None of the interactions in the GLMM was significant (sex by day of training: Wald χ^2_5 = 3.387, p = 0.641; sex by trial within day: Wald χ^2_9 = 7.875, p = 0.547; sex by day of training by trial within day: Wald χ^2_{45} = 30.179, p = 0.956). This GLMM analysis suggested males and females adopted the same strategy to solve the task, yet it was not clear which one. A possible explanation is that some individuals adopted recurrent learning, whereas some others adopted concept learning, irrespective of the sex. Indeed, we found a negative correlation between the improvement rates (Spearman's rank correlation: ρ = - 0.506, p = 0.023; figure S2), suggesting individual differences in the strategy adopted. Thirteen subjects (six males and seven females) showed a positive improvement rate across trials within days as predicted for the use of recurrent learning strategy; seven subjects (four males and three females) did not show positive improvement rate across trials within days, but showed positive improvement rate across days, and therefore they more likely adopted the concept learning strategy (figure S2). A new analysis (Supplementary materials) with the learning strategy shown by the subjects as fixed effect indicated no differences in the accuracy between the two groups (figure S3).

In previous analysis with GLMMs, we found a significant effect of day of training in the GLMM on the accuracy without any evidence of a linear trend. This could be explained by the fact that the colour discriminations presented on some days of training were more difficult to achieve for the subjects. Subjects chose the correct disc in 40.50 ± 11.21% of the trials, an overall accuracy that was significantly greater than the 20% expected by chance (t_{19} = 8.579, p < 0.001). A separated analysis for each day of training (corresponding to the different pairs of colour) revealed subjects achieved a significant performance in day 1 (40.00 ± 25.75%; one-sample t test: t_{19} = 3.279, p = 0.004), day 4 (54.50 ± 26.25%; t_{19} = 5.276, p < 0.001) and day 6 (47.00 ± 22.73%; t_{19} = 5.265, p < 0.001), as well as an almost significant performance in day 3 (38.00 ± 28.94%; t_{19} = 2.063, p = 0.053). By contrast, subjects did not significantly solve the task in day 2 (31.50 ± 26.80%; t_{19} =

0.698, $p = 0.494$) or in day 5 (32.00 ± 25.87%; $t_{19} = 1.131$, $p = 0.272$). Comparing within each pair the performance of subjects trained with one colour as positive and subjects with the other colour as negative, we found a significant difference in day 1 (independent-sample *t* test: $t_{18} = 7.452$, $p < 0.001$), day 2 ($t_{18} = 4.187$, $p < 0.001$) and day 5 ($t_{18} = 3.543$, $p = 0.002$) but not in the other days. Therefore, it seems reasonable that the low performance of the subjects in some discriminations was due, at least in part, to the preference for one of the two colours in some pairs.

The average decision speed was 28.86 ± 13.75 seconds. The LMM revealed that daily decision speed decreased significantly across days of training ($F_{5,90} = 4.260$, $p = 0.002$). Sex had a significant effect in the model ($F_{1,18} = 5.517$, $p = 0.031$; figure 5c): males had a faster decision speed compared to females (23.46 ± 11.05 seconds and 34.27 ± 14.55 seconds, respectively). No significant sex by day of training interaction was found ($F_{5,90} = 1.000$, $p = 0.423$). There was no significant correlation between overall accuracy and average decision speed ($r_{18} = -0.154$, $p = 0.518$). In addition, no correlation between overall accuracy and average decision speed was found in the sex-separated analysis (males: $r_8 = -0.337$, $p = 0.341$; females: $r_8 = 0.246$, $p = 0.493$).

DISCUSSION

Overall, in this study we found little evidence that male and female guppies differ in the ability to learn visual discrimination.

In experiment 1 and 2, we investigated sex differences in figure discrimination. In experiment 1, guppies initially learned the discrimination between two figures that differed in many features (S vs bar), a type of task easily performed by many fish species (Agrillo et al. 2012; Bowman and Sutherland 1970; Hemmings and Matthews 1963; Newport et al. 2013; Schluessel et al. 2012; Siebeck et al. 2009; Sovrano and Bisazza 2008); then, guppies learned the discrimination between two figures that differed only in their geometric shape (triangle vs square), a capacity reported for several fish as well (Bowman and Sutherland 1970; Newport et al. 2013; Schluessel et al. 2012; Siebeck et al. 2009). In these two discriminations of experiment 1, the percentage of correct responses reached around 60% after three days (60 trials) and steadily increased in the remaining days of training. The performance of guppies is similar to that observed in other fish species in analogous tasks after a comparable number of trials (e.g., *Danio rerio*: Colwill et al. 2005; *Pomacentrus amboinensis*: Siebeck et al. 2009), but seems lower than that of other species (e.g., *Toxotes chatareus*: Newport et al. 2014). Interestingly, guppies performed much better in colour and numerical discriminations with our training procedure (Bisazza et al. 2014; Lucon-Xiccato and Bisazza 2014). It is possible that guppies are more attuned to the latter tasks, perhaps because the cues to be discriminated are involved in situations ecologically relevant for the species, such as mate choice and predator defence (Hager and Helfman 1991; Houde 1997). Conversely, discrimination of figures might be more important for other species, resulting in better performance. For example, the archerfish, which showed enhanced figure discrimination performance, in nature needs to learn to visually discriminate a number of different edible preys from an equally large number of nonedible ones (Newport et al. 2014; Newport et al. 2015). This issue deserves attention in future research. In both discriminations of experiment 1, the two sexes had the same performance. Not only male and female guppies showed the same overall accuracy, but the temporal trend of the accuracy exhibited an almost complete overlap.

In experiment 2, we tested guppies in a discrimination between an E-shaped figure and its horizontal mirror image. This task appear to be very difficult for fish (Gierszewski et al. 2013; Mackintosh and Sutherland 1963) and other vertebrates (Bradshaw et al. 1976; Riopelle et al. 1964; Todrin and Blough 1983; but see Hopkins et al. 1993). We tested guppies in a mirror image discrimination task because its difficulty could be helpful in disclosing even subtle sex differences. Guppies did not show increase in accuracy over days even though in this experiment we performed four additional days of training. Individual analysis revealed that only two subjects (one male and one female) out of the 20 tested performed above chance level. Therefore, our results suggest that in general guppies are not able to solve horizontal mirror image discrimination but only few individuals possess this capability. This experiment perhaps requires the subjects to perform a left-right discrimination, a task that is facilitated by cerebral lateralization (Chiandetti and Vallortigara 2009). Among poeciliids, strongly lateralized individual are around 10% of the population (Facchin et al. 1999). This figure is compatible with the hypothesis that in our experiment only the most-lateralised individuals were able to solve the discrimination. As in experiment 1, here we found no evidence of sex differences in the overall accuracy and in the temporal trend of the accuracy.

In experiment 3, guppies performed a task based on oddity discrimination learning (Hille et al. 2006). In each trial, we presented four same-coloured discs and one disc of a different colour; subjects had to select the odd disc to obtain the reward. We presented the same pair of colours throughout each day, but we changed the pair daily. With this design the task could be solved either by learning the concept (i.e., always choosing the odd disc) or by recurrently learning the different colour discrimination presented each day. We found guppies significantly chose the correct disc, but there was not clear evidence that guppies used concept learning or recurrent learning to solve the task. An analysis of individual performance suggested that perhaps about one-third of the subjects used concept learning, whereas the remaining recurrently learned the new discrimination each day. Individual differences in the strategy adopted to solve cognitive tasks have been previously reported in other fish species (*Gambusia holbrooki*: Agrillo et al. 2009; *Cyprinus carpio*: Mesquita et al. 2015). Moreover, in line with our results, in a previous attempt to study oddity concept learning in fish only few individuals perhaps learned the task (Newport et al. 2014). Although we did not entirely prove guppies can learn the concept of oddity, our results are promising since some individuals may show this ability. Future experiments should examine this possibility with paradigms specifically designed, such as those in which the subject performs a final probe test in which new stimuli are presented every single trial (e.g., Newport et al. 2014). In this experiment, we found no evidence of sex difference in accuracy and a roughly equal number of males and females significantly chose the correct stimulus during the training. Moreover, males and females were equally split between the two groups of subjects that apparently solved the task with different strategies, revealing the two sexes used the two strategies to the same extent.

Altogether, our results reveal a general absence of sex differences in discrimination learning abilities in guppies. Bayesian analysis provided "very strong" to "decisive" evidence (Jeffreys 1998) that males and females showed an almost identical accuracy in all the tasks. Indeed, the model without the effect of sex better represented our data and the lack of significance was unlikely to be explained by sample size. Analysis of individual performance revealed that a roughly equal number of males and females solved the tasks. In experiment 3, we examined individual differences in learning strategy, but an equal proportion of males and females used the two alternative strategies. These two results suggest that, in guppies, individual within-sex differences in discrimination learning abilities and strategies are greater than differences between the sexes. The absence of sex differences in discrimination accuracy did not confirm our hypothesis. Female guppies base their mate choice mainly on male colour patter. Several studies have evidenced females' ability to finely estimate the size, the shape and hue of the different colour spots as well as their capacity to remember and compare the quality of different males (Houde and Torio 1992; Hughes et al. 1999). Moreover, females avoid mating with males with colour patters similar to previous mates, a process that perhaps requires some degree of concept learning (Eakley and Houde, 2004; Hughes et al. 1999). Given the cognitive load imposed on female guppies by mate choice, we were expecting female advantage in visual discrimination learning.

A possible explanation for the absence of sex differences is that none of the discrimination abilities investigated are relevant for female mate choice or for other situations in which male and female guppies experience different selective pressures in their natural environment. Alternatively, it is possible we looked at basic mechanisms of learning and discrimination, and there might be strong developmental constraints that prevent differentiation of these cognitive systems between the sexes. The cognitive functions underlying visual perception and shape recognition involved in experiments 1 and 2 are probably based on phylogenetically ancient systems. Indeed, the mechanisms for representing an object present in the visual field appear fundamentally the same from fish to humans (Ben-Simon et al. 2012; Gori et al. 2014; Rischawy and Schuster 2013; Sovrano and Bisazza 2008). In addition, the same mechanisms of shape recognition are used in a number of different contexts, such as spatial orientation, foraging and predator recognition. Even if in one of these contexts males and females experience different selective pressures, the pressures imposed in the other contexts are likely to constrain the evolution of sex differences. The situation is perhaps different for experiment 3, which involved the discrimination of colours and concept learning, two abilities that are much important for female mate choice. One might therefore expect females being selected for enhanced colour discrimination and concept learning abilities. Yet, a recent study has shown males probably need the same capacity as females in estimating male body coloration, as they are able to exploit female preference by associating with males that are duller than they are (Gasparini et al. 2013). Sexual selection could therefore create similar selective pressures in both male and female discrimination learning abilities.

In our experiments, we used guppies bred in the laboratory. Rearing conditions resembled as much as possible natural conditions and were equal for males and females (absence of predators, same habitat and food sources). Minimizing environmental differences between males and females could disclose potential cognitive differentiations that have occurred through evolutionary processes. However, it is possible that sex differences in discrimination learning accuracy emerge only if males and females experience different environments during ontogeny (e.g., Ebbesson and Braithwaite 2012). Therefore, an interesting direction for future investigations is the use of wild-caught guppies or, alternatively, the study of sex by environment interaction in guppies reared in the laboratory.

A very different result emerged considering the latency of males and females to choose the preferred disc after entering the experimental compartment. In experiments 2 and 3, males were significantly faster than females and a similar difference was observed in experiment 1 although here it only approached statistical significance. This difference is unlikely to reflect sex difference in swimming speed as guppies could easily cover the distance between start box and discs (15 cm) more than ten times faster (approx. one second; Karino et al. 2006) than the latency we observed in our experiments (18 seconds on average). In addition, female guppies have been observed to swim faster than males (Karino et al. 2006). Observation made during the trials evidenced that guppies spent most of the time carefully inspecting the stimuli. Therefore, this sex difference is likely to reflect the time required for a fish to make a decision. Interestingly, decision speed was not related to the accuracy. This indicates that our decision speed is not a measure of cognitive abilities, such as information processing speed, but more likely reflects consistent individual differences in impulsivity (Sih and Del Giudice 2012). Perhaps, males were faster than females in deciding which option to choose because they devoted less time to collect information. A faster decision by males in cognitive tasks has been observed in another fish species (Mamuneas et al. 2015) and may reflect the existence of different cognitive styles in the two sexes (Mamuneas et al. 2015; Shettleworth 1999; Sih and Del Giudice 2012).

Decision speed does not appear to be the sole sex difference in cognitive style in the species studied. Previously, Reader and Laland (2000) found a greater innovation tendency in females than in males and Lucon-Xiccato and Bisazza (2014) reported greater cognitive flexibility in females in a reversal learning task, despite a lack of sex differences in discrimination learning abilities *per se*. In both these situations, males appear to pay a cost for their reduced flexibility, being less ready to modify their behaviour in response to environmental change. We did not detect a similar cost in our study as we found no speed-accuracy trade-offs in males, but this may be due to a limit in our procedure.

How can we explain the existence of this sex differences in decision speed? Similarly to our hypothesis on accuracy, sex differences in decision speed might depend on sex differences in reproductive roles. Male guppies court or make sneak copulatory attempts with virtually each female they encounter (Magurran and Seghers 1994) and even in the presence of several potential mates no delay in mating behaviour is observed. Conversely, females carefully evaluate many potential mates, using multiple indicators, a process that may require hours. On the other hand, it is possible that comparative and decisional processes are shaped in other contexts, such as foraging. Female guppies devote most of their time to foraging; in sharp contrast, male guppies are almost continuously involved in sexual activity (around one sexual act per minute) and invest only 20% of their time in foraging (Magurran and Seghers 1994). Because of this time constraint, males might be adapted to make quicker foraging decisions.

An alternative possibility is that the sex difference in decision speed is a by-product of other selective pressures acting on the two sexes. A recent study on sticklebacks, *Gasterosteus aculeatus*, has found bolder individuals (usually males) faster than shyer ones (usually females) in choosing which arm to enter to reach a food reward in a T-maze (Mamuneas et al. 2015). Similar links between personality traits and cognitive style have been reported widely in other species (e.g., Carazo et al. 2014; Titulaer et al. 2012). Accordingly, some authors have suggested that individual differences in cognitive style are related to individual differences in behaviour (Sih and Del Giudice 2012). Since in the guppy males are in general bolder than females (Harris et al. 2010; Irving and Brown 2013), it is possible that the sex difference we observed in decision speed is the by-product of the sex difference in personality. However, this hypothesis remains to be tested.

Sex differences in cognitive style rather than abilities are a common finding in mammals and birds. For example, in humans and rats, males and females use different cues in spatial navigation (Rodríguez et al. 2010; Tropp and Makus 2001). In the domestic chick, *Gallus gallus domesticus*, males and females showed the same abilities in learning to discriminate between two objects differing in both colour and position; however, males were discriminating based on position, whereas females were using colour (Vallortigara 1996). Our evidence of sex differences in cognitive style in fish indicates a more widespread phenomenon across vertebrate taxa.

In summary, our study confirms a general indication of the literature that sex differences in cognitive abilities are uncommon. Conversely, there is emerging evidence, confirmed by this study, that vertebrate males and females often have different styles of solving cognitive problems. This appears to be a distinctive trait in guppies as it applies to performance in several cognitive tasks (Reader and Laland 2000; Lucon-Xiccato and Bisazza 2014).

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Figure 1

(a) Aerial view of the apparatus and **(b)** representation of the stimuli used in the three experiments. Stimuli of experiment 3 exemplify only one out of the six pairs of colour.

Figure 2

Overall accuracy of males and females guppies in **(a)** experiment 1, in **(b)** experiment 2, and in **(c)** experiment 3. Data points represent percentage of correct choices of each subject. Box represent mean ± SEM percentage of correct choices of males and females. Dashed line is chance performance.

Figure 3

Daily accuracy of males (grey) and females (dark) in the **(a)** first and the **(b)** second discrimination of experiment 1. Data points represent mean ± SEM percentage of correct choices. Dashed line is chance performance.

Figure 4

Daily accuracy of males (grey) and females (dark) in **(a)** experiment 2 and in **(b)** experiment 3. Data points represent mean ± SEM percentage of correct choices. Dashed line is chance performance.

Figure 5

Average decision speed (mean ± SEM seconds) of males and females guppies in **(a)** experiment 1, in **(b)** experiment 2, and in **(c)** experiment 3.

Figure 1

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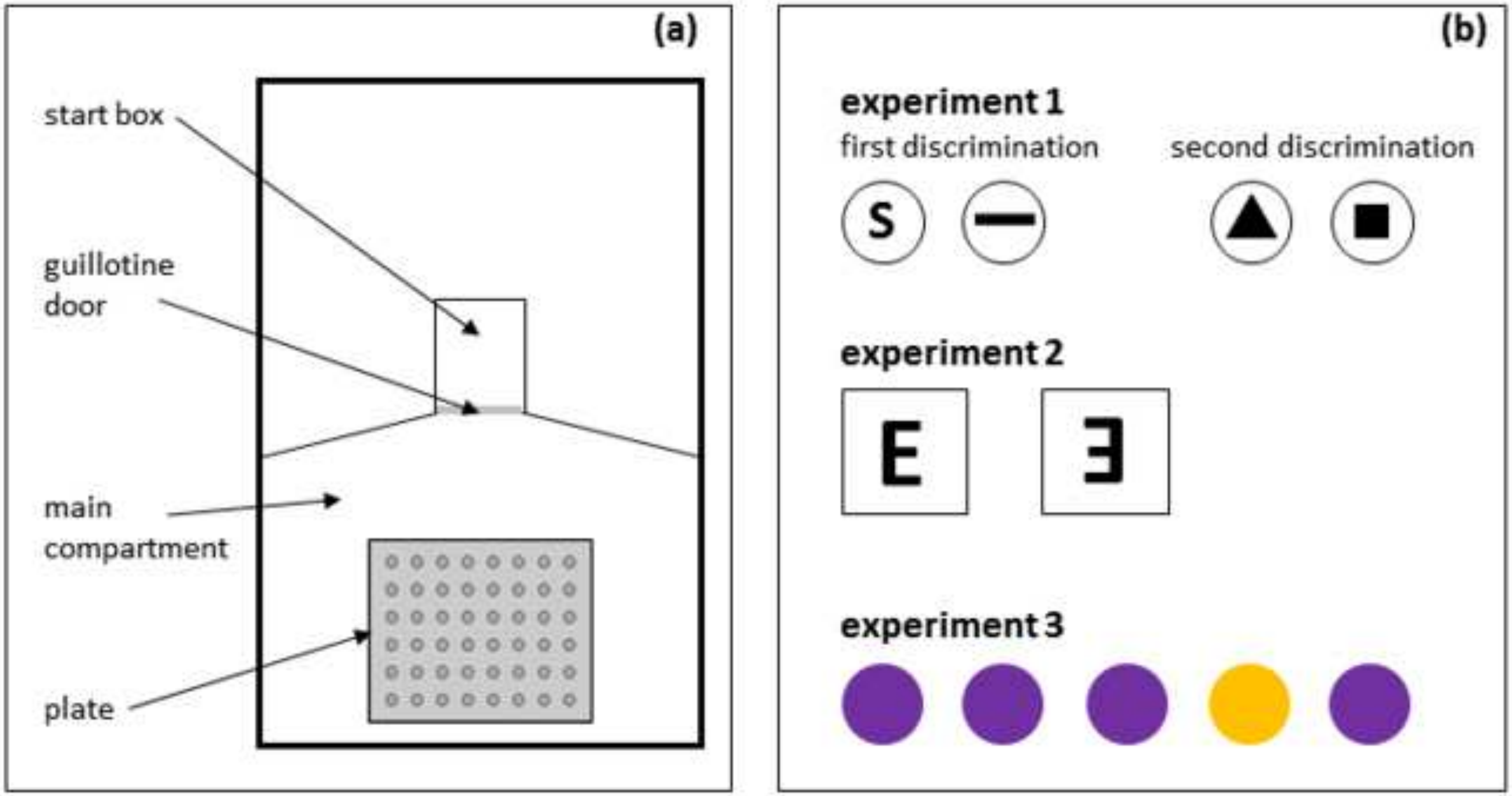

Figure 2

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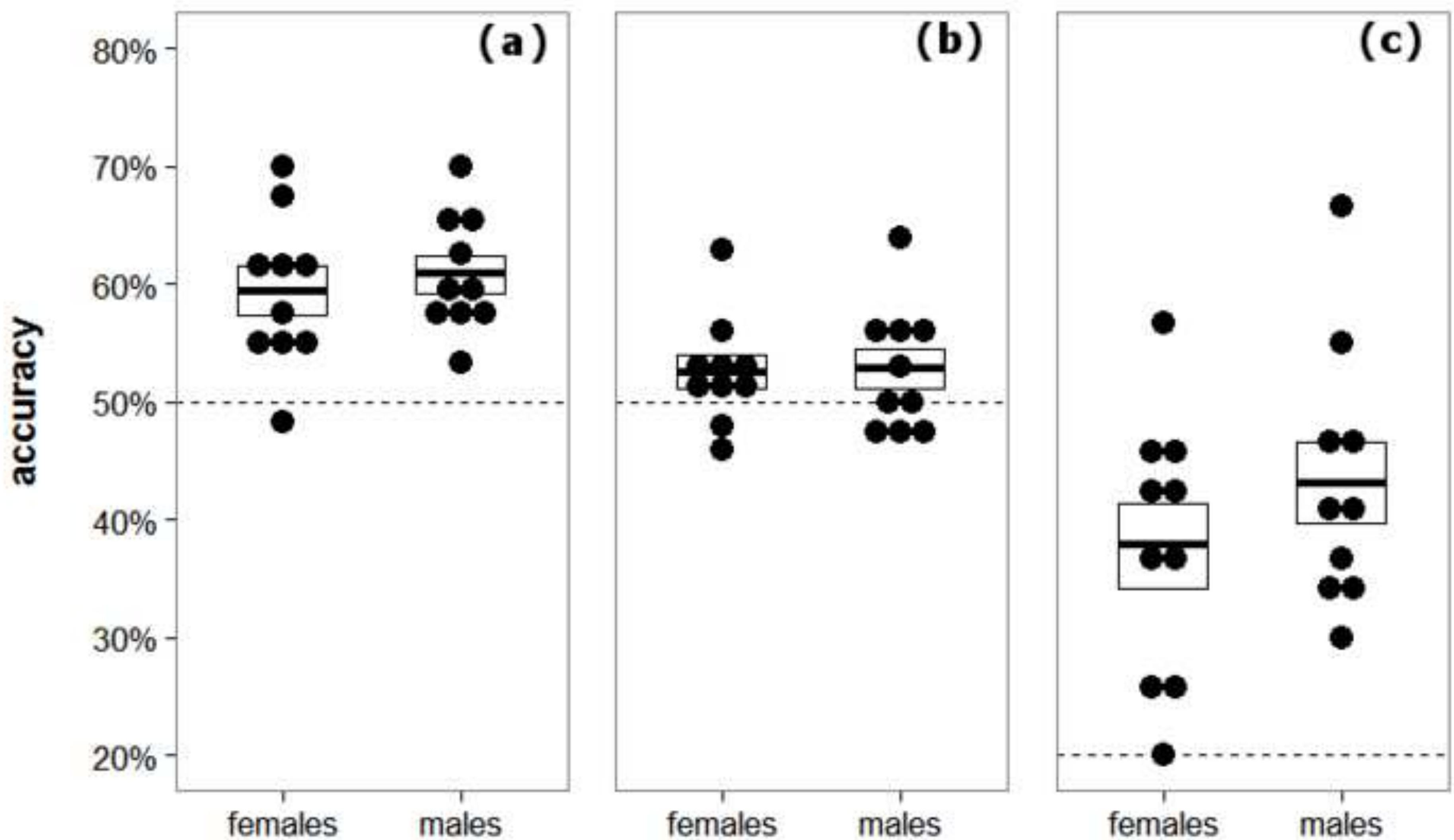
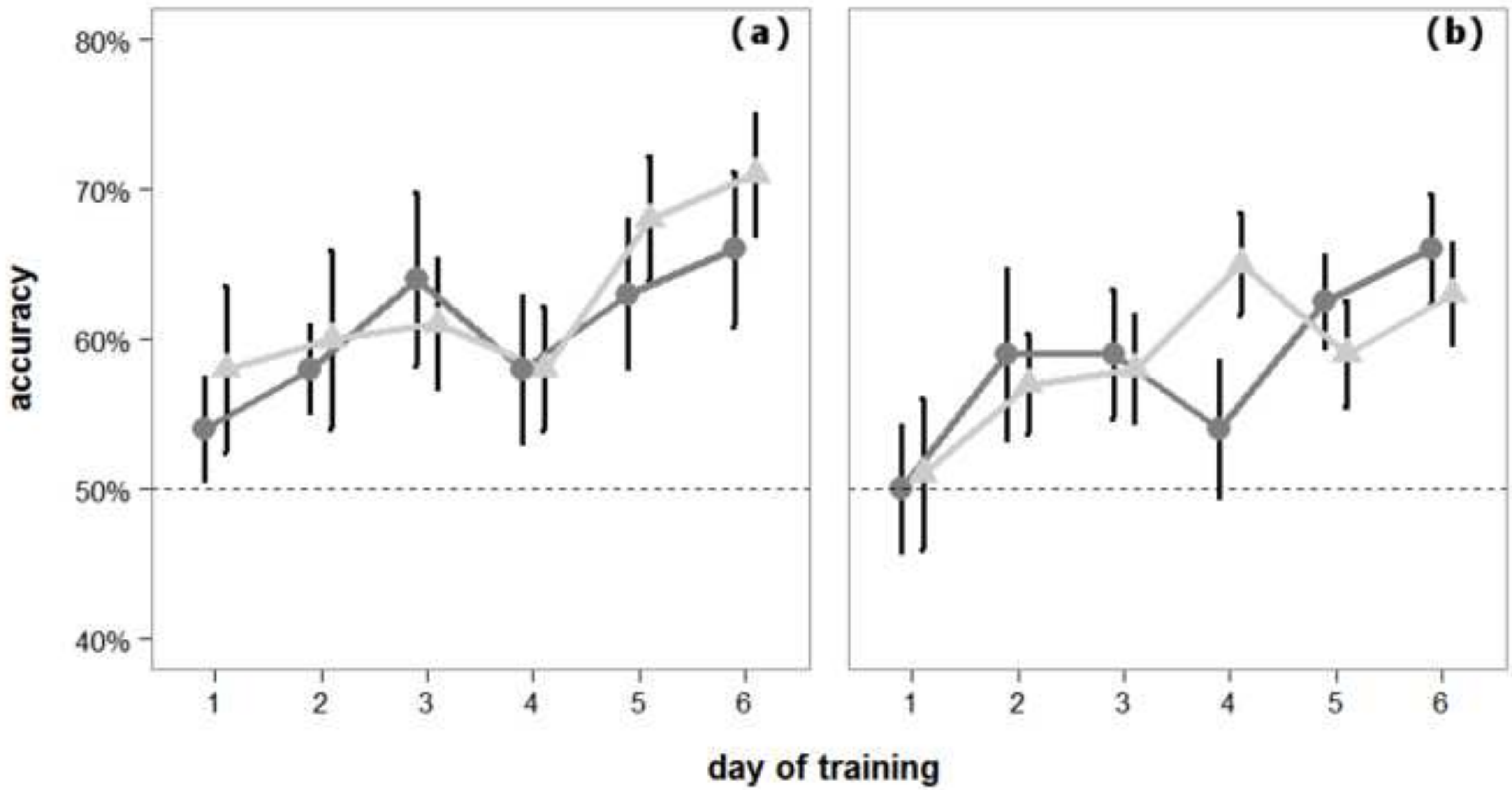


Figure 3



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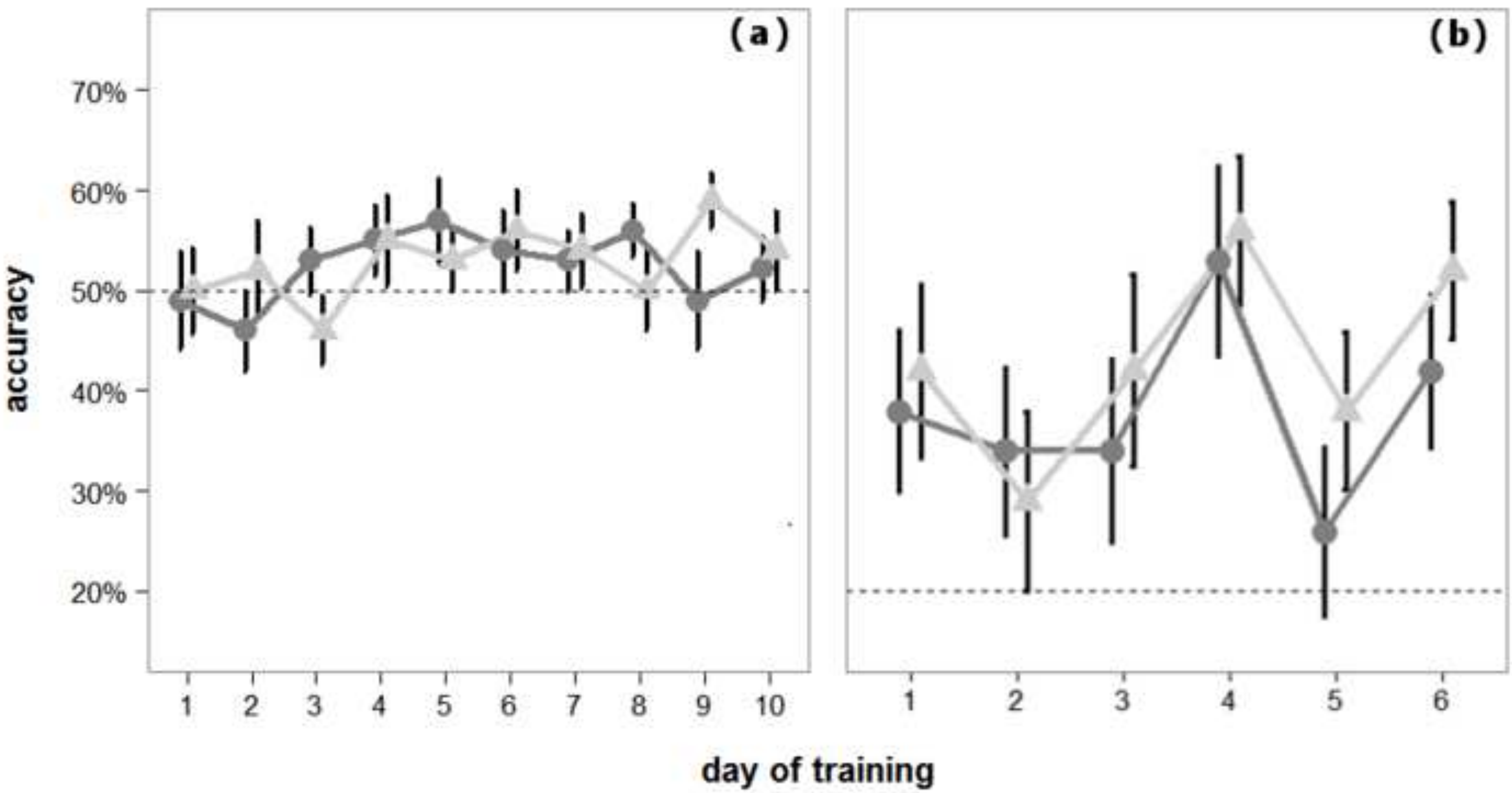

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