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Influence of Social Status on Spatial Attention in African Cichlids (*Astatotilapia burtoni*)

by

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This thesis is dedicated to Benny, Junie, Milan, Elsie, and Julius.

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Abstract

Detection and avoidance of potential threats depend on allocating attention to biologically relevant stimuli. The aim of the present study was to test how the physiological and social variability within the male phenotypes of the African cichlid fish *A. burtoni* may affect their attention to potential threats in their visual field. In *A. burtoni*, dominant males (DOM) show aggression towards other DOMs, but also threaten and chase subordinate males (SUB) in their habitat. This task-oriented behavior in DOMs is in sharp contrast with that of SUBs, which shoal with females and flee from their dominant counterparts. Thus, we hypothesized that SUBs and DOMs will show differences in allocating attentional resources, namely a broader spatial attention in SUBs dedicated to conflict avoidance, compared to a more focused attention in DOMs. To test this notion, we developed a spatial attention paradigm where we presented visual threatening stimuli (visual looms) that were preceded by true and false spatial cues (same and different locations relative to the loom, respectively). The results show that DOMs have a discriminating response to looms preceded by a true spatial cue, indicated by a higher response rate and longer escape latencies when compared to false cue conditions and no cue controls. In contrast, SUBs showed an overall high but non-discriminating response to all three stimulus conditions. These results imply socially driven differences in vigilance to potential threats in SUBs and DOMs that influence vital behaviors.

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Startle behavior has been studied to explain responses to threatening stimuli in teleost fish, such as the zebra fish *Danio rerio* (Dill, 1974; Eaton, Bombardieri, & Meyer, 1977; Maximino *et al.*, 2010), the black goby *Gobius niger* (Turesson, Satta, & Domenici, 2009), and the goldfish *Carassius auratus* (Eaton & Emberley, 1991; Fetcho & Faber, 1988; Preuss, Osei-Bonsu, Weiss, Wang, & Faber, 2006; Weiss, Zottoli, Do, Faber, & Preuss, 2006; Zottoli, Newman, Rieff, & Winters, 1999;). Following the onset of a sudden stimulus, the startle response is initiated by a pair of bilateral neurons in the brainstem called Mauthner cells (M-cells) that receive extensive sensory information. Visual input in the ventral dendrites is derived from the optic tectum (Canfield, 2003; Zottoli, Marek, Agostini, & Strittmatter, 1987) and auditory input (e.g., sounds associated with a predator hitting the water) is received in the lateral dendrites. Firing of a single action potential (AP) in either M-cell activates the contralateral motor neurons while inhibiting the ipsilateral musculature, causing a unilateral fast-bend of the trunk and tail. The resulting formation is a c-bend, or C-start away from the stimulus (Canfield, 2003; Eaton *et al.*, 1977; Medan & Preuss, 2014; Zottoli, 1977).

Numerous studies have shown that auditory stimuli are also effective in eliciting C-start responses in goldfish (*Carassius auratus*). Szabo, Weiss, Faber, and Preuss (2006) used acoustic pressure in air to examine auditory afferents and intracellular M-cell activity, and Curtin, Medan, Neumeister, Bronson, and Preuss (2013) used underwater speakers to deliver 200 Hz sound pulses. Visually evoked C-starts can be triggered by presenting the animal with an expanding object above its view (loom), which mimics an approaching predator and has been used to examine predator-prey behavior in different species of fish (Anderson, 1988; Dill, 1974; Domenici, 2002; Fernald, 1985; Preuss *et al.*, 2006). Different methods have been used to present visual stimuli in the laboratory setting. Early techniques involved the electromagnetic

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release of objects just above the water surface, such as a ball (Dill 1990; Eaton *et al.*, 1977; Eaton & Emberley, 1991), or a combination of water (weak stimulus) and a cylinder (strong stimulus) into plastic pipes (Turesson *et al.*, 2009). Computerized looming stimuli have also been used, allowing for multiple measurements of startle responses by using looms of varying sizes and velocities (Preuss *et al.*, 2006).

Native to the East African Lake Tanganyika, the mouth-brooding African cichlid fish *Astatotilapia burtoni* (*A. burtoni*) is an excellent model for studying the interactions between physiological mechanisms and social behavior (Hoffman & Fernald, 2001) including the role of social status on escape behavior (Neumeister, Whitaker, Hoffmann, & Preuss, 2010; Whitaker, Neumeister, Huffman, Kidd, 2011). The social system of *A. burtoni* is characterized by two distinct phenotypes in which the males alternate between dominant (DOM) and subordinate (SUB) roles. Dominant males are brightly colored with blue or yellow hues on their scales, a prominent black stripe through the eyes and dark stripes along the body. Additionally, DOMs display aggressive behaviors to acquire and defend their breeding territories against other males. In contrast, subordinate males lack the colorful patterns of their dominant counterparts, do not defend territories, and shoal with females. But phenotypic plasticity in *A. burtoni* extends beyond behavior to reproductive physiology. The DOMs are reproductively active, spending much of their time soliciting and courting females in their environment whereas SUBs are reproductively repressed. This creates a dynamic social hierarchy where their status is in flux depending on the availability and acquisition of a breeding territory.

Previous research showed that the coloration of dominant cichlids comes with a cost with regard to their conspicuousness to predators (Maan, Hofker, van Alphen, & Seehausen, 2006). The latter notion is supported by the fact that DOMs in *A. burtoni* show higher startle escape

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rates and lower M-cell thresholds to sounds (Neumeister *et al.*, 2010, Whitaker *et al.*, 2011). As such, *A. burtoni* has been proven well suited to study socially induced plasticity in the startle escape circuit. The motivation behind the present study was to examine socially induced differences in attending to visual threats in SUBs and DOMs. As noted, dominant males (DOM) show aggression towards other males, whereas SUBs are submissive in their social interactions. Thus, we hypothesized that SUBs and DOMs will show differences in allocating attentional resources, namely a broader spatial attention in SUBs dedicated to conflict avoidance, compared to a more focused attention in DOMs.

Methods

Subjects

Twenty-nine captive-bred male *A. burtoni* were the subjects in the present study, of which 9 (31%) were DOMs and 20 (69%) were SUBs, taken from three separate cichlid communities comprised of 10-13 males and 10 females. Fish were kept in rectangular acrylic tanks (50.8 x 76.2 x 30.5 cm³) and all aquaria were outfitted with plastic aquarium plants, gravel substrate, and 5-6 terracotta pots serving as territories and spawning sites. pH (8.4-8.6), conductivity (570-640 μ S/cm), ammonia (0 ppm), carbonate hardness (179 ppm) and general hardness (268-322 ppm) were monitored weekly and fish were kept on a 12-hour light/dark cycle with lights on at 8 o'clock in the morning. Fish were fed cichlid flakes every morning ad libitum.

Each subject was given a unique marking by injecting blue dye underneath the scales on one side of the body. Bi-weekly focal observations of 10-minute sessions were performed on each male. A well-established ethogram was used to quantify dominant and subordinate behaviors in the form of a Dominance Index (DI) (Renn, Aubin-Horth, & Hofmann, 2008). The DI is calculated by adding the occurrences of all dominant behaviors (e.g., chasing, threat

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display, courting) and subtracting the subordinate behavior fleeing. The social status of subjects is determined after 5-6 continuous focal observation points and an overall DI score was calculated: a positive DI score classified a male as dominant (DOM) whereas a negative score classified the male as subordinate (SUB).

Experimental design

Subjects were tested in a circular, acrylic experimental tank measuring 73.66 cm in diameter and 30.48 cm in height (see Figure 1). To eliminate external mechanosensory cues, the tank was placed on top of an anti-vibration table and outfitted with two heaters, temperature sensors, which maintained a temperature of $27^{\circ}\pm 1^{\circ}\text{C}$, two air bubblers for aeration, and two underwater speakers (Electro-Voice UW-30). The speakers were placed on opposite sides of the arena and used to deliver sound pips (152 dB and 159 dB re 1 μPa in water) for dishabituation. The sound pips were generated by an external 8-channel stimulator (Master-8 A.M.P. Instrumental) and fed through an amplifier (Samson Servo 120). Additionally, a circular arena (38.1 cm diameter; 27.94 cm height) was constructed from white opaque netting and plastic tubing. The arena served as a separation between the fish and the peripheral equipment that may have presented visual distractions. A high-speed video camera (Olympus i-Speed 2) recorded the fish's behavior at 1000 fps from a ventral view through a mirror installed below the tank at a 45° angle.

Visual stimuli were generated using custom-designed computer software, VisLoom (version 1.0) and were displayed onto the lid of the experimental tank by a projector (DLPPlus Model #U4-131) situated 124.4 cm above. The tank was illuminated by the projector; black-out curtains were drawn to keep the area dark throughout the duration of the experiment. The loom appeared as a growing black disk with an initial size of 8 mm, a final size of 360 mm, and lasted

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for 900 ms. An additional visual cue was presented before the loom appeared as a constant black disk with a static size of 75 mm and 200 ms in duration. There was a contrast of -0.9638 between the luminosity of the background screen (83 lux on top of the lid) and the luminosity of the stimulus (3 lux). The luminance contrast was calculated using the Weber Contrast, which is often used for luminance contrast :

$$C_W = \frac{L_s - L_b}{L_b}$$

where L_s is the luminance of the stimulus and L_b is the luminance of the immediately adjacent background.

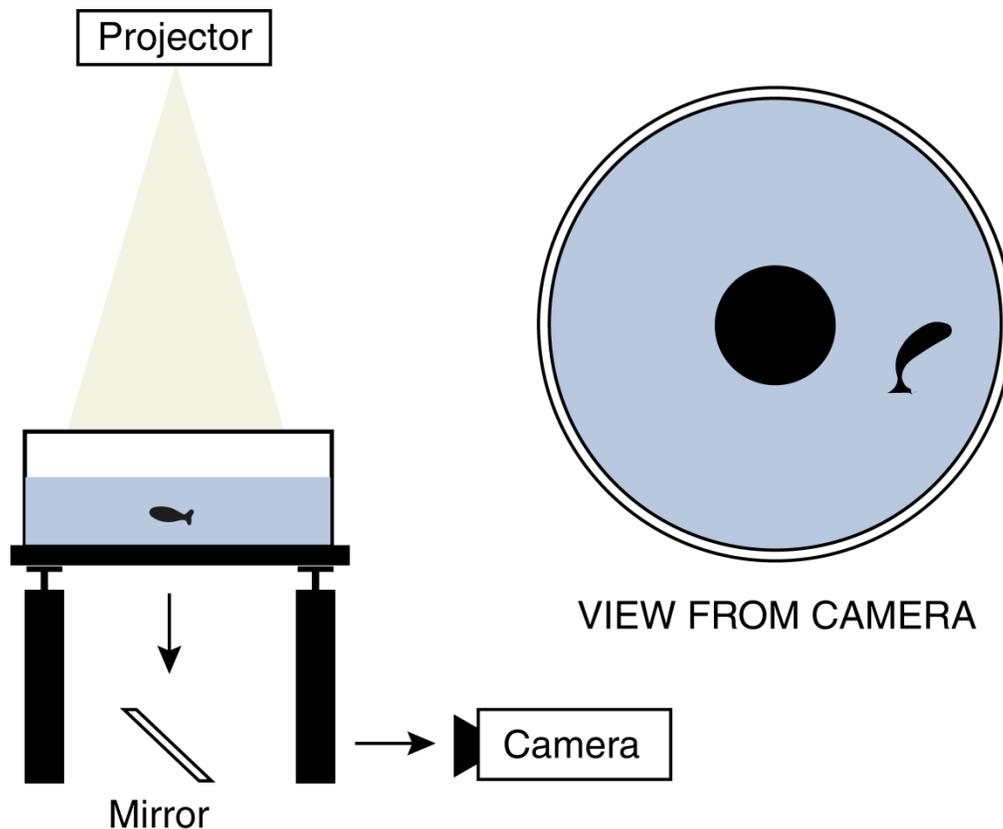


Figure 1. The experimental set-up. The loom is projected from the projector above and behavior is recorded from a ventral view below the tank.

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At the start of each experiment, water quality was examined to ensure the experimental conditions matched those of the home tank (e.g., conductivity differences did not exceed 50 $\mu\text{S}/\text{cm}$ and pH levels were within 0.5 units). The water height in the experimental tank was 6 cm ensuring a constant distance between the fish's eyes and the screen. This is an important requirement of the set-up as it limits the fish's movements to two dimensions. This method was also used in a similar experiment to examine escape responses to visual looms (Preuss *et al.*, 2006).

Procedure

All experiments were conducted between 10:00 a.m. and 3:30 p.m. (Eastern Standard Time) and each lasted between 2 to 2 hr 30 min. Once the status of a fish was confirmed stable after 5-6 continuous focal observations, it was selected for experimentation. Subjects were identified by the same individual markings used for focal observation. On the day of experimentation, the target fish was identified, transferred from its home tank to the experimental tank and given 20 minutes to acclimate to its new environment (referred to as the acclimation period). The remaining fish in the community were removed from their home tank and placed in a holding bucket containing conditioned water and an aerator for the duration of the experiment. This was done to prevent possible changes in the social hierarchy due to the removal of the male test fish.

Behavioral testing was initiated upon the completion of the acclimation period. Each experiment consisted of 18 trials evenly distributed across three stimulus conditions: a loom-only (no cue) condition used to obtain baseline responses to the stimuli, and two conditions where cues preceded the loom; cues presented at the same location as the loom (true cue) and different locations (false cue). Four locations were assigned to the false cue condition using clock

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directions (12, 3, 6, and 9 o'clock), allowing a large area of the experimental arena to be used and preventing habituation to one cueing location. Trials involving a cue had an interstimulus interval (ISI) of 50 ms and times between trials were randomized from three to eight minutes. The sound pip used for dishabituation was given randomly via one of two underwater speakers after every three trials. These steps were taken to prevent the animal from any foreknowledge (habituation) of the type and timing of sensory stimulation (Viswanathan & Jansen, 2010).

If the loom elicited a C-start response, the recorded video clip was reviewed and 150 milliseconds (or 150 frames) of video starting from the onset of the loom was saved onto the camera's memory card before the start of the next trial. For all startle trials, information pertaining to escape latency and direction of responses (towards or away from the loom) was collected. For startle and non-startle trials, stimulus condition and the location of fish in the arena at the onset of the loom were recorded. There are three dependent variables in this study: startle probability defined as the proportion of startle responses to the total number of trials in an experiment, escape latency defined as the time between the onset of the loom stimulus and the first visible head turn of the C-start (Eaton, DiDomenico, & Nissanov, 1988; Preuss *et al.*, 2006), and directionality of the startle (towards or away from the stimulus). All experiments were conducted according to the protocols and regulations established by the Institutional Animal Care and Use Committee (IACUC) of Hunter College, City University of New York (Approval ID: TPescape 1/18-01).

Statistical Analysis

The experiment constituted a 2 (dominant/submissive) between-subject X 3 (no cue/true cue/false cue) within-subject mixed design. The repeated-measures ANOVA is typically used for such designs, but to do so, it requires that trial-by-trial data be averaged to avoid the problem of

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non-dependent data. This averaging can reduce the power of the statistical test. As an alternative, an extension of the Generalized Linear Model, the Generalized Estimating Equation (GEE), was used to model the responses while taking into account the fact that multiple responses were produced by the same subject. Latency and startle probability were analyzed using the Statistical Package for the Social Sciences (SPSS) version 21. To account for the binary responses (i.e., startle or no startle), a binary logistic GEE model was used to analyze escape probabilities. For multiple pairwise post-hoc comparisons, the Bonferroni correction was used to avoid Type I errors. In our data, the Bonferroni method computes a p -value based on 15 different hypotheses (i.e., 6 pairwise comparisons multiplied by 5 combinations divided by 2 pairs), inflating the likelihood of a Type I error (i.e., incorrectly rejecting the null hypothesis). In order to make an appropriate correction for the pairwise comparisons between the two groups across three stimulus conditions, we divided each Bonferroni p -value by 15 and multiplied by 3. This adjustment will be referred to as an *adjusted* Bonferroni for the purposes of our results. Lastly, a binomial test was used to examine the overall directionality in the responses for each stimulus condition, whether or not the number of responses *away* or *towards* the stimulus was significantly different from chance.

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Results

Escape Probabilities

A total of 514 trials, of which 307 (59.7%) responses and 207(40.3%) no responses ($M = .60$, $SD = .491$), were used to determine startle escape probabilities across three stimulus conditions: loom only, true spatial cue, and false spatial cue (see methods). One dominant fish was excluded as an outlier, having an atypical low response rate of 5.56% which was two SDs below the mean (the reason for this behavior is unknown at the moment). The binomial logistic GEE model showed a significant main effect of stimulus condition ($p < .001$) controlling for other variables in the model (false cue, $M = .51$; true cue, $M = .66$; no cue, $M = .56$). Adjusted Bonferroni post-hoc tests revealed significant differences for DOMs in the no cue ($M = .46$, $SEM = .068$) and false cue ($M = .45$, $SEM = .058$) conditions when compared against the true cue ($M = .68$, $SEM = .066$) condition. The analysis also indicated an overall higher probability of startle for SUBs ($M = .63$) compared to DOMs ($M = .53$). These main effects were qualified by a significant interaction between status and stimulus condition ($p = .002$). Results did not show differences for SUBs between the no cue ($M = .66$, $SEM = .062$), false cue ($M = .58$, $SEM = .072$), and true cue ($M = .64$, $SEM = .062$) conditions (see Figure 2).

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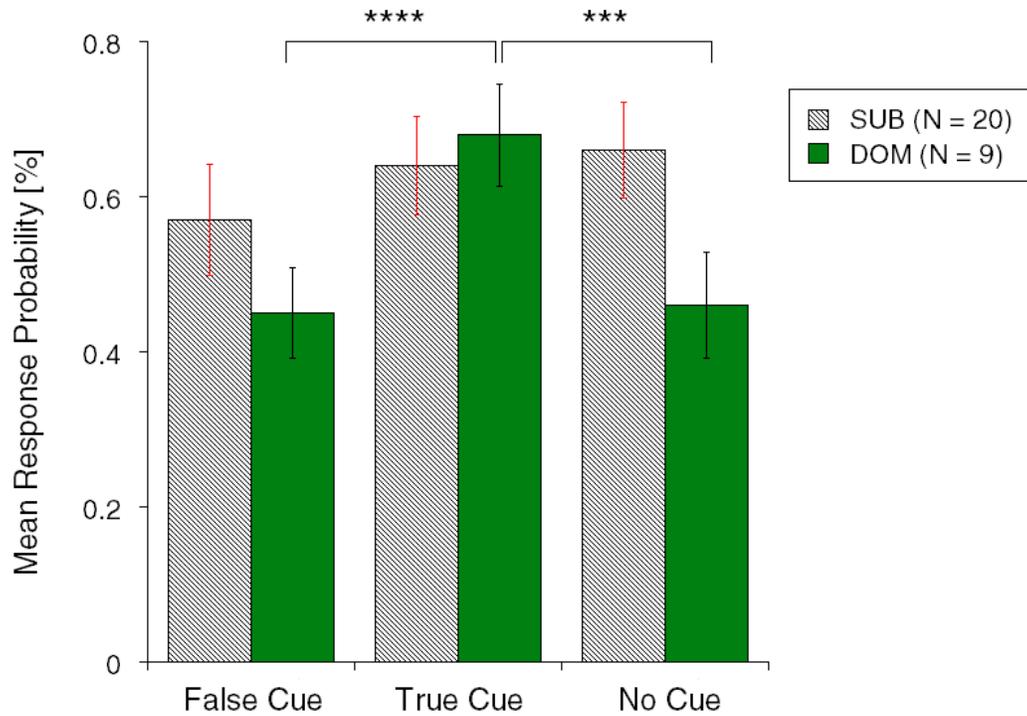


Figure 2. Estimated marginal means of startle response probabilities (\pm SEM) for DOMs and SUBs across the three stimulus conditions. Stars indicate statistical significance (DOMs: true cue vs no cue, *** $p < .001$; true cue vs false cue, **** $p < .0001$)

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Escape Latencies

Of the 514 total trials in this study, 307 (60%) C-start escapes were observed across all three stimulus conditions ($M = 673.50$, $SD = 166.657$). The GEE revealed a statistically significant main effect of stimulus condition ($p = .023$), but there was no status effect and no interaction (see Figure 3).

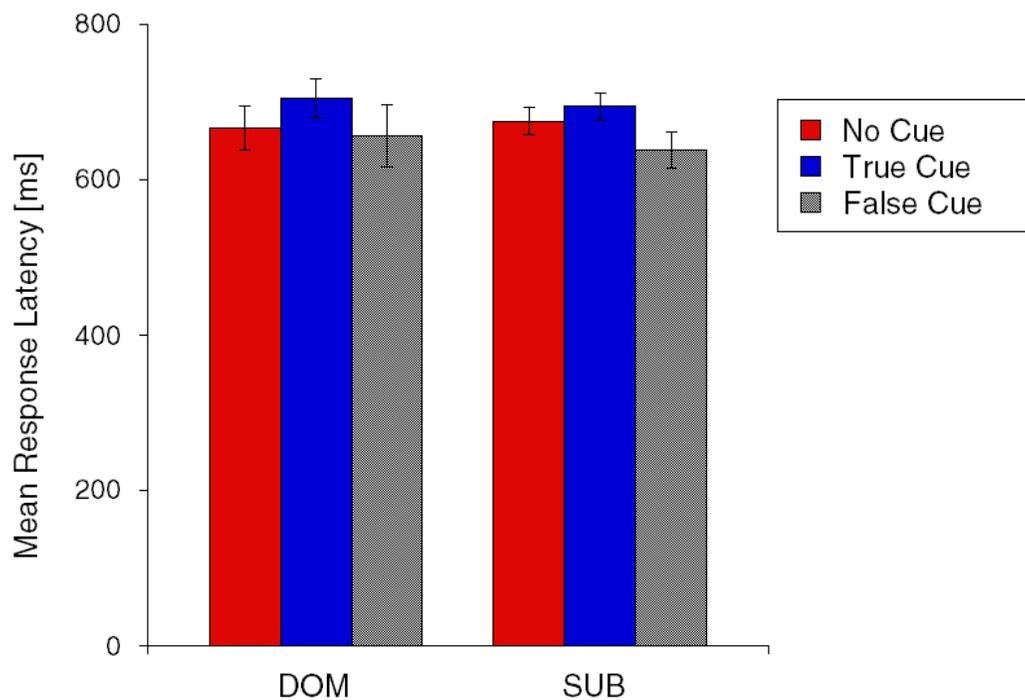


Figure 3. Estimated marginal means of startle latencies for each status across the three stimulus conditions. The fastest responses (shortest latencies) occurred in the false condition for DOMs ($M = 657.30$, $SEM = 40.550$) and SUBs ($M = 638.39$, $SEM = 29.301$). The slowest responses (longest latencies) occurred in the true condition for DOMs ($M = 705.25$, $SEM = 30.852$) and SUBs ($M = 694.43$, $SEM = 21.612$).

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To demonstrate the differences in latencies using a different perspective, we constructed cumulative response probabilities over the duration of the loom (see Figure 4). The majority of responses occurred between 50-85% of the stimulus duration indicated by the steep slope. The data shows a right-shift of the stimulus/response curve in the true cue condition for DOMs (see Figure 4A blue trace). This separation from the other curves indicates longer response times and differential treatment of the true cue. The SUBs showed a relatively consistent spread across the three conditions (see Figure 4B).

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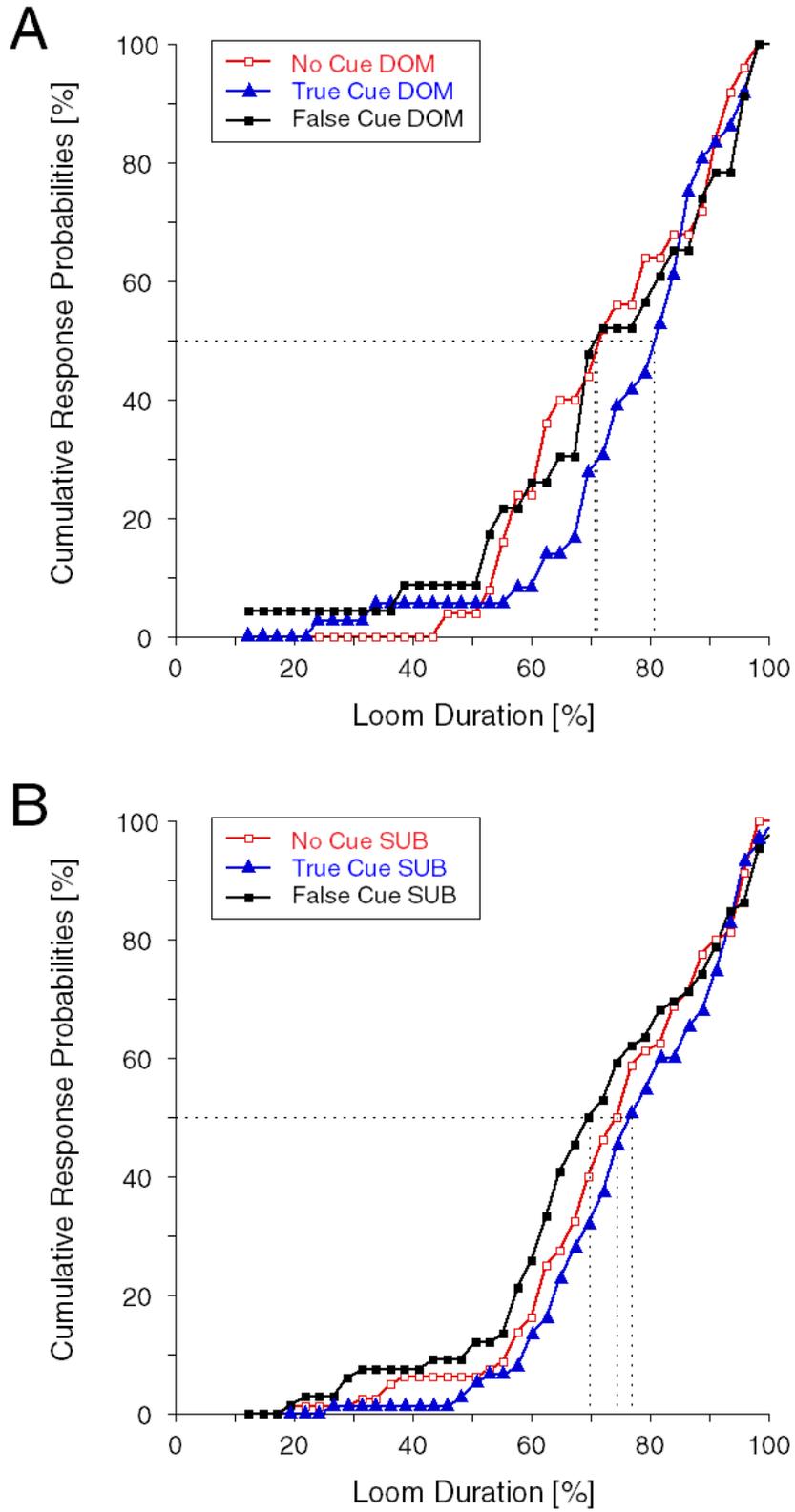


Figure 4. Cumulative response latencies with respect to stimulus duration for (A) DOMs and (B) SUBs. Dotted lines indicate where 50% of the responses occurred.

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Directionality

To further explore the influence of spatial cues on startle behavior, we also compared the directionality of escape responses between DOMs and SUBs. Each fish was classified as turning more towards the stimulus, more away from the stimulus, or neither (equal amount of turns and away from the stimulus) in each condition. A binomial test was performed on the number of fish that were classified as turning more away or more towards, and results revealed that given a hypothetical chance level of left and right turns of 50%, the SUBs turned significantly away in the no cue condition ($p = .035$), but there was no significance in directionality in the true cue ($p = .629$) and false cue ($p = .143$) conditions. Furthermore, DOMs did not show significant responses in either direction across all three conditions (no cue, $p = .727$; true cue, $p = .125$; false cue, $p = .625$) (see Table 1). However, when the statuses and stimulus conditions were combined, results indicated a significant response away from the stimulus (see Table 2).

Table 1

Frequencies of Fish and Directionality Trends for DOMs and SUBs In Each Stimulus Condition

Status	Direction	No Cue	True Cue	False Cue
DOM (N = 9)	Away	5	6	3
	Towards	3	1	1
	Neither	1	2	5
SUB (N = 20)	Away	12	10	12
	Towards	3	7	5
	Neither	5	3	3

Note. Neither = Equal number of turns away and towards the stimulus.

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Table 2

Frequencies of Fish and Directionality Trends for Statuses and Conditions Combined

Direction	All Conditions
Towards	6
Away	19*
Neither	4

* $p = .015$; binomial test

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Discussion

Our goal was to elucidate possible differences in spatial attention in two social phenotypes of *A. burtoni*. Our results showed that the true cue condition (cue appearing in the same location relative to the looming stimulus) produced differential responses in dominant males (i.e., higher response rates and longer latencies) when compared to no cue and false cue conditions (loom only and cue in different location relative to the loom, respectively). In contrast, subordinate males showed high startle escape rates and similar latencies in all stimulus conditions (i.e., a non-discriminating response to spatial cues). As such we present behavioral evidence that dominant and subordinate males may process spatial information related to threats differentially.

Previous research has shown that fish do not startle on the mere detection of a predator; the escape response is contingent on the size, distance, and expansion rate of the predator's image on the fish's retina (Anderson, 1988; Dill, 1974; Domenici, 2002; Regan & Vincent, 1995; Preuss *et al.*, 2006). Furthermore, there are costs associated with fleeing that every prey animal must face. Jones and Godin (2010) referred to the 'starvation-predation risk trade-off' as an animal's decision to forgo foraging opportunities in order to escape from an imminent predatory attack. Mistakes in predator avoidance may lead to fatal consequences, thereby making the decision to leave a foraging site more profitable for the animal's long-term fitness (Ydenberg & Dill, 1986).

Attention is defined as the selective focus on one facet of an individual's surroundings while ignoring all others (Castro & Wasserman, 2014), which assumes a need for information processing and filtering for relevant and irrelevant stimuli. Furthermore, behavioral performance is enhanced by dedicating more attention to one central task compared to dividing attention to

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multiple sensory information (Dukas, 2002). Therefore, an animal must determine the range of attention dedicated to specific tasks in its visual field since a predatory attack may come from any direction. For example, scanning a large area may impact visual acuity whereas focusing on a smaller area may enhance the detection of fine details in the environment, such as a predator shadow or other visual cues that can determine attack location (Dukas, 2004). Our behavioral results show that DOMs were significantly more attentive when they saw a visual cue in the same location as the looming stimuli, suggesting a narrow range of spatial attention dedicated to relevant tasks. Additionally, the longer escape latencies in the true cue condition may attribute to more decision-making; DOMs may be showing more judicious escapes to reduce costs associated with lost foraging opportunities. Another explanation might be related to predatory escape strategies. A small prey animal may have more success by trying to "outmaneuver" the predator than to escape. Since a large predator approaching at high speeds requires more time to adjust its turning radius, delaying the escape response by the prey will afford a narrow time for capture, thereby allowing the fish to escape successfully (Lind, Kaby, & Jakobsson, 2002).

Conversely, the similar startle rates in the no cue and false cue conditions seem to suggest equivalent treatment of those conditions from the DOMs. One parsimonious explanation might be that DOMs simply do not attend to it. The latter notion seems to be supported by the fact that the mean latencies for both false cue and no cue conditions are similar. Furthermore, the dissection of the evoked latencies over stimulus duration (see Figure 4) suggests no apparent differences for the stimulus period where most of the responses occurred (i.e., 50-80% of stimulus duration). We conclude that the DOMs were efficient in their anti-predatory strategies coupled with a conservative decision-making approach.

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In comparison, SUBs appear less discriminating to cues in their visual field evident in the similar response rates across all stimulus conditions. In other words, they appear more attentive to potential threatening cues in their environment (i.e., it implies higher levels of vigilance). One possible explanation is a need for more global attention in order to avoid social conflict with conspecifics. Indeed, social conflict has been shown to induce anxiety-related behaviors (Blanchard, McKittrick, & Blanchard, 2001). Studies of social dominance hierarchies found higher levels of cortisol, a widely used measure of stress (Bonga, 1997), in subordinates than dominant individuals (Fox *et al.*, 1997; as cited in Greenberg *et al.*, 1984). Thus, social stress may be a likely cause for the observed overall increase in startle rates and shorter latencies in SUBs.

Social context in escape behavior may also elucidate differences between DOMs and SUBs. DOMs generally do not escape from conspecifics, whereas SUBs frequently perform escape responses during social conflict, therefore requiring a wider range of dedicated attention to their environment. This notion seems to be supported by the overall higher escape rates of SUBs in our results. Considering a different social context, shoaling experience may also influence startle escape latencies. Individuals in shoals are presumed to have anti-predator advantages over solitary fish since the likelihood of visually detecting a predator increases with group size (as cited in Godin, 1986). Described as the Trafalgar Effect, information pertaining to a predator's location is transmitted across a shoal through the initiation of an escape response by the individual that first detects the threat. As a consequence, this response begins a chain reaction from nearby shoal mates in order to avoid collisions with one another. This phenomenon may explain why individual freshwater teleost fish in shoals showed lower startle escape latencies than solitary fish (Webb, 1980) because the escape response is triggered more

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quickly when more individuals attend to the environment. Subordinate *A. burtoni* have such experience in shoaling with other SUBs and females, which might explain their shorter escape latencies.

Studies in startle directionality have shown that fish typically turn away from auditory stimuli (Domenici & Blake, 1993; Foreman & Eaton, 1993; Hale, 2002; Mirjany, Preuss, & Faber, 2011; Zottoli *et al.*, 1999). In comparison, escape responses were consistently away from visual stimuli when compared to sound stimuli in herring (*Lupea harengus* L.) larvae (Batty, 1989) and directionality in cichlids can be influenced by visual stimuli as modulating inputs (Canfield, 2003). The results of our study show that directionality trends are consistent with auditory-evoked responses. However, the link between stimulus location, social phenotype, and directionality remains unclear.

Conclusion

The results of the present study imply that there are differences in spatial attention between dominant and subordinate fish. Although we were unable to show significant differences between the two phenotypes for all visual cue conditions, our results provide evidence that dominant fish have a discriminating response to spatial cues. The inferior temporal (IT) cortex in primates is the area of the brain associated with high-order processing such as object and cue recognition. For example, studies have shown neuronal activity in the IT of macaque monkeys when given visual search tasks such as cue and target matching (Chelazzi, Duncan, Miller, & Desimone, 1998; Desimone, 1998). In zebrafish, analogue areas of visual processing have been identified in the dorsal pallium (Mueller, Dong, Berberoglu, & Guo, 2011; Northcutt, 2011). Additionally, teleosts have been shown to have tri-chromatic vision and capacities to discriminate multidimensional shapes (as cited in Salva, Sovrano, & Vallortigara,

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2015). Taken together, the higher reactivity corresponding to visual cues matching threat locations could indicate neuronal activity in specialized areas of the fish brain, but without further examination this assumption remains largely speculative. In summary, the contrasting behavioral tendencies of SUBs and DOMs in our study strengthen the prevailing notion that social experience provides a powerful source for adaptive neural plasticity, including the sensory processing of environmental cues.

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