

Lateralized Function Without Lateralization

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Lateralized function without lateralization

Abstract

In many vertebrates, the right hemisphere/left visual field is used to process information about threats while the left hemisphere/right visual field is used to process information about conspecifics. This is referred to as hemispheric lateralization. But prey that are too predictable in their response to predators could have reduced survival. We studied hemispheric lateralization in yellow-bellied marmots (*Marmota flaviventer*), a social rodent that falls prey to a variety of terrestrial and aerial predators. We first asked if they have lateralized responses to a predatory threat. We then asked if the eye that they used to assess risk influenced their perceptions of risk. We recorded the direction marmots were initially looking and then walked towards them at 0.5 m/s. We recorded the distance that they responded to our experimental approach by looking, the eye with which they looked at us, and the distance at which they fled (i.e., flight initiation distance; FID). We found that marmots had no eye preference with which they looked at an approaching threat. Furthermore, the population was not comprised of individuals that responded in consistent ways. However, we found that marmots who looked at the approaching person with their left eye had larger FIDs suggesting that risk assessment was influenced by the eye with which they used when assessing risk. These findings are consistent with selection to make prey less predictable for their predators, despite lateralized function.

Introduction

The left and right hemisphere of the vertebrate brain are specialized to carry out specific activities (Rogers & Andrew, 2002). In humans, much research has shown that the left hemisphere is responsible for interpreting language and the right hemisphere is responsible for alert responses (Rogers & Andrews, 2002). Hemispheric lateralization controlling fear responses has been shown to be an ancestral trait found in a variety of mammals including primates and rodents (Kim et al., 2012). For instance, Japanese monkey's (*Macaca fuscata*), upon hearing an alarm call, looked longer at a picture of a snake with their left eye which suggests right hemispheric dominance during visual processing of a threatening stimuli. (Masahiro, 2014). Mice (*Mus musculus*) use their right hemisphere to control observational fear learning (Kim et al., 2012). Other types of lateralization, such as handedness in inbred mice (*Mus molossinus* and *M. castaneus*) is less consistent; about half the tested population retrieved food with their left hand while the other half retrieved food with their right hand (Collins, 1985).

The advantage of a lateralized brain is that it helps individuals perform tasks simultaneously (Rogers, 2004). For example, lateralized eye use in chickens (*Gallus gallus*) permits them to forage with one eye and be alert to predators with the other eye (Rogers, 2004). However, there may be some costs of lateralization. For instance, if prey respond in consistent and predictable ways by looking at their predators, predators can learn how they escape and capitalize on this predictability (Vallortigara, 2000). Hence, it is possible that eye preference varies across individuals within a population (Vallortigara, 2000) and that, at a population level, there may be no evidence for lateralization in prey.

Animals perceive approaching humans as predators (Frid & Dill, 2002) and by walking directly towards an animal, it is possible to elicit an antipredator response. Flight initiation distance (FID), the distance between a predator and its prey at which the prey initiates flight, is a widely used method to quantify risk assessment (Cooper & Blumstein, 2015). When approached by a potential predator, the prey may change their posture and look towards the approaching

threat to monitor it. This alert response can be used to study eye preference and hence hemispheric lateralization.

Although evidence for hemispheric lateralization has been studied in many species, there are few studies of rodents (Kim et al., 2012), especially in the field. However, we know that rodents have lateralized brain function (Glick et al., 1977). Thus, our aim was to study hemispheric lateralization in a free-living rodent. We focused on yellow-bellied marmots (*Marmota flaviventer*), which are prey to a variety of terrestrial and aerial predators (Van Vuren, 2001) and asked two related questions. First, when approached by a human, did marmots respond by looking at us with their left eye. Second, did the eye with which they looked at us influence the distance at which they fled.

Methods

Study site and subjects

Between 5 June 2017 and 23 July 2017 we measured responses of adult yellow-bellied marmots (those ≥ 2 years old) to an approaching human. We studied marmots in the upper East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL; 38°77'N, 106°50'W) in Gothic, Colorado, the site of a long-term study (Blumstein, 2013; Armitage, 2014). All marmots are regularly live trapped and individually marked with ear tags, for permanent identification, and we use fur dye to mark each individual with a unique dorsal mark that permits identification from afar (Armitage, 1982).

Quantifying lateralization using flight initiation distance

We assumed that marmots treated humans as predators (Frid & Dill, 2002) and studied lateralization while measuring flight initiation distance (Blumstein et al., 2015). Observers were trained to approach marmots at a standardized velocity of 0.5 m/s (Blumstein et al., 2004; Runyan & Blumstein, 2004; Petelle et al., 2013). If more than one marmot was at a location, we focused on a single subject.

Once a subject was identified, we waited at least 10 minutes to ensure it was in a relaxed state, which we defined as foraging, looking, standing and looking, or lying down and looking, before we approached it. We dropped flags at the location we started the experimental approach, the location where the marmot looked towards the approaching person, and the location where it fled. We then walked to the location where the animal was when we began the experimental approach and measured the following distances (in m): starting distance (first flag to initial position); alert distance (second flag to initial position); and FID (third flag to initial position). In addition, we recorded the number of other marmots within 10 m of the focal subject, the escape substrate (dirt, stone, talus, low or high vegetation), slope of the terrain over which the marmot fled, and the distance to its escape burrow.

To quantify lateralization, we first noted the closest eye to the observer at the start of the experimental approach and quantified this as straight (looking with both eyes directly at observer), right (right eye or right shoulder toward observer), left (left eye or left shoulder toward observer) or away (its back facing toward the observer). We recorded the eye direction when the marmot alerted to us in the same way (straight, right, left, away).

Statistical Analyses

To explain variation in looking direction, we fitted generalized linear mixed-effect models (GLMER) with a binomial error structure, using the following R packages lme4 (Bates et al.,

2017), lmerTest (Kuznetsova et al., 2016), optimx (Nash & Varadhan, 2013), and ggplot 2 (Wickham and Change, 2016). We focused on those marmots that either responded by looking left or right (the few that looked directly at us were not analyzed). We then modeled the direction they looked in response to our approach as a function of their initial looking direction (left, right, straight, or away) and sex (male or female). We included a random effect of individual marmot because most marmots were approached more than once. We tested for individual consistency by comparing a model with and without the random effect of individual with a likelihood ratio test and by fitting a model with only individual marmot as a fixed effect. We plotted residuals versus predicted values and generated qq-plots to evaluate distributional assumptions.

To study variation in FID, we fitted linear mixed effects models and modeled FID as a function of alert distance, the eye with which they looked at us during the experimental approach, sex, and the two-way interactions between alert distance and sex and alert distance and looking direction. Again, marmot identity was included as a random effect, and again we plotted residuals versus predicted values and generated qq-plots to evaluate distributional assumptions.

Because risk perception may be influenced by other factors, but because our sample size was somewhat limited and we did not wish to over-fit the model by including them all at once, we systematically added distance to burrow, escape substrate (stone, dirt, talus, low vegetation, or high vegetation), and escape incline, along with their two-way interaction with alert distance, to our basic linear model.

Results

We conducted 104 flushes on 39 unique adults that either looked left or right in response to our approach (58 of these approaches generated a look with their left eye, 46 approaches generated a look with their right eye). We found no effect of prior looking direction, or of the marmot's sex on looking direction (Tables 1 and 2). Importantly, the random effect of identity explained no variation in looking direction (likelihood ratio test comparing a general linear model with the mixed effects model containing initial head position and sex, $P = 0.671$), and the model with only the random effect of marmot identity explained no significant variation in looking direction ($P = 0.245$).

However, we found that for a given alert distance, marmots that responded to an approaching person by looking at them with their left eye, fled at greater distances (Table 3, Figure 1), and we found that for a given alert distance, males fled at a greater distance than females (Table 3; Figure 2).

The three covariates tested had significant interactions between alert distance and distance to burrow ($P = 0.029$), escape substrate ($P = 0.008$), and escape incline ($P = 0.021$), but all models retained the significant interaction between look direction and alert distance ($P = 0.004$, 0.004 , 0.046 , respectively). Thus, while other variables explain some variation in FID, we can conclude that the eye with which marmots looked at the approaching human was always a significant factor.

Discussion

We found no effect of eye preference when marmots were approached by a human, nor did we find that individual marmots had a consistent bias in the eye used to monitor approaching threats. This lack of a visual bias is striking because many studies (Santi et al., 2002, Hook-Costigan

& Rogers 1998, Lippolis et al., 2002) have reported hemispheric lateralization of antipredator responses. However, it may be costly for prey to be too predictable in their antipredator response (Briffa, 2013). A predator may learn a bias in how prey respond to their attacks and use this to their advantage. Therefore, there may also be strong selection on prey to respond to predators in an unpredictable manner.

Our results are consistent with selection for this unpredictability. Yellow-bellied marmots at our study site are preyed upon by a variety of predators, including terrestrial ones (coyotes (*Canis latrans*), badgers (*Taxidea taxus*), American martens (*Martes americana*), black bears (*Ursus americanus*), and long-tailed weasels (*Mustela frenata*), Van Vuren, 2001) and aerial ones (golden eagles (*Aquila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsoni*), and goshawks (*Accipiter gentilis*), Van Vuren, 2001). It is possible that vulnerability has selected marmots to be unpredictable with their eye use, despite having lateralized function.

Other studies have reported that predictable prey may be more vulnerable to predation. For instance, proactive jumping spiders (*Portia labiata*) captured more prey that responded predictably than unpredictable prey while docile spiders captured more unpredictable prey (Chang et al., 2017). Furthermore, hermit crabs (*P. bernhardus*) that fled in response to a predator (*C. maenas*) had unpredictable reemergence times, a finding consistent with this random response being an antipredator behavior (Briffa, 2013).

Yet, our results are also consistent with hemispheric lateralization influencing marmots' escape behavior. The eye marmots used to monitor an approaching predator was associated with the distance at which they fled the approaching predator. Because lateralized eye use seems to be an ancestral and wide spread trait for risk perception in vertebrates (fishes--Dadda et al., 2010; birds--Andrew, 1991; rodents--Kim et al., 2012; and primates--Shibasaki, 2014)), we expected to see a greater FID when the left eye monitored approach because this was the eye that was associated with right hemispheric processing of risk-related stimuli. Therefore, when the right eye was used for risk assessment we expected that marmots would tolerate closer approaches. For example, a teleost fish (*Cymatogaster aggregate*) with lateralized escape behavior responded faster to a threat that was monitored with their left eye (Dadda et al., 2010). Similarly, fish who shared the same turning direction as the school, had a better escape behavior (Chivers et al., 2016).

It is possible that our predator manipulation was insufficiently risky to generate a lateralized response. Levels of predator exposure influence lateralization in fish, where individuals with the greatest risk of predation were the most lateralized (Ferrari et al., 2015) (Lucon-Xiccato, 2017) (Heuts, 1999).). Thus, lateralization is not fixed but can change from environmental pressures with experience and development. Proved in research on chicks in that their visual lateralization changed over time with development (Rogers et al., 2013) and with light exposure (Chiandentti, et al. 2005).

However, and taken together, yellow-bellied marmots' response to threats may be selected to not be predictable to predators but because they nevertheless have lateralized function, may pay a cost for this response if the longer time required before flight is costly. The precise costs in marmots remains to be formally studied. And, the broader question of whether prey are less likely to have lateralized responses remains to be determined.

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Table 1. Generalized linear mixed-effect models fitted in R to explain variation in looking direction and to test for random effect of individual marmot.

Description	Model	AIC
Model with only random effect	Looking direction $\sim (1 uid)$	146.433
Mixed effect model	Looking direction $\sim$ Initial head position + sex + $(1 uid)$	149.683
Fixed effect only model	Looking direction $\sim$ Initial head position	146.5
Fixed effect only model	Looking direction $\sim$ Initial head position + sex	148.320

Table 2. ANOVA table for linear mixed effects model explaining variation in looking direction.

	z-value	P value
Intercept	0.033	0.974
Starting_headL	-1.615	0.106
Straing_headR	-0.153	0.878
Starting_headS	-0.044	0.965
SexM	0.425	0.671
Intercept	0.218	0.8273
Starting_headL	-1.678	0.0933
Straing_headR	-0.178	0.8586
Starting_headS	-0.124	0.9013

Table 3. Linear mixed-effect models explaining FID based on the eye used

Estimates	df	Pvalue
Intercept	38.48	0.2404
Looking_headR	78.56	0.2841
SexM	28.19	0.1713
AlertDist	65.62	<2e-16
Looking_headR:AlertDist	94.16	0.0304
SexM:AlertDist	57.53	0.0446
Intercept	53.32	0.5078
Looking_headR	81.17	0.2574
AlertDist	81.18	<2e-16
Looking_headR:AlertDist	95.51	0.0277

Figure Legends

Figure 1 Relationship between alert distance and FID for left and right eye. The plus signs represent the right eye and dots left eye. For any given distance, the right eye (bold line) had a shorter fleeing distance than the left eye (thin line).

Figure 2 Relationship between alert distance and FID for males and females. The triangles represent females and dots males. For any given alert distance, females (thick line) tolerated closer approach compared to males (thin line).

Fig. 1

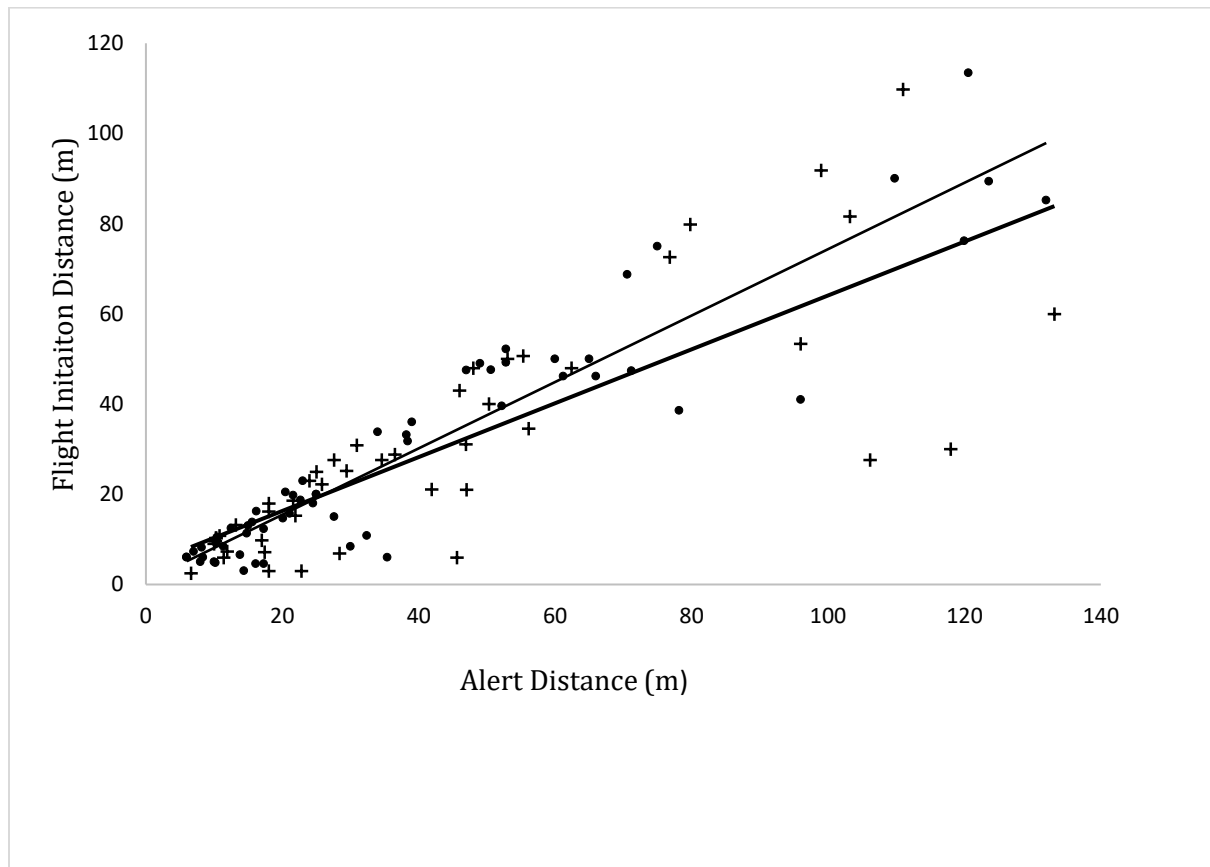


Fig. 2

