Can fear conditioning repel California sea lions from fishing activities?

ZACHARY SCHAKNER¹, THOMAS GÖTZ², VINCENT M. JANIK² & DANIEL T. BLUMSTEIN¹

¹Department of Ecology & Evolutionary Biology, University of California Los Angeles, CA
²Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, East Sands, St Andrews, Fife KY16 8LB, UK

Abstract

Marine mammal interactions with fisheries create conflicts that can threaten human safety, economic interests, and marine mammal survival. A deterrent that capitalizes on learning mechanisms, like fear conditioning, may enhance success while simultaneously balancing welfare concerns and reduce noise pollution. During fear conditioning, individuals learn the cues that precede the dangerous stimuli, and respond by avoiding the painful situations. We tested the efficacy of fear conditioning using acoustic stimuli for reducing California sea lion (Zalophus californianus) interactions from two fishing contexts in California, USA; bait barges and recreational fishing vessels. We performed conditioning trials on 24 individual sea lions interacting with bait barges. We tested for acquisition of conditioned fear by pairing a neutral tone with a startle stimulus. Avoidance was strongest in response to the startle stimulus alone, but low when paired with a neutral tone. From actively fishing vessels we tested for fear conditioning by exposing sea lions to a neutral tone followed by a startle pulse, a startle pulse alone, or a no sound control. We conducted playbacks from 146 (including 48 no sound control)
stops over two summer fishing seasons (2013, 2014). The startle stimulus decreased surfacing
frequency, reduced bait foraging and increased surfacing distance from the vessel while the
conditioned stimulus only caused a mild reduction in surfacing frequency with no other
behavioral change. Exposing animals to a pair of a conditioned stimulus with a startle pulse did
not achieve the intended management outcome. Rather, it generated evidence (in two study
contexts) of immediate learning that led to the reduction of the unconditioned response. Taken
together, our results suggest that for fear conditioning to be applied as a non-lethal deterrent,
careful consideration has to be given to individual behavior, the unconditioned/conditioned
responses, and the overall management goals.

Introduction

As part of rapid anthropogenic environmental change, wildlife are increasingly turning to
human-derived resources such as fish from fishing lines or nets (Zollett & Read, 2006),
domesticated livestock (Muhly & Musiani, 2009) or garbage cans (Baruch-Mordo et al., 2013).
Animals exploiting these resources create human-wildlife conflicts, ultimately threatening
human safety, economic interests, and their own survival (Woodroffe et al., 2005). In the marine
environment, marine mammal depredation, or the removal of fish from lines or nets, creates
scientific, management, and conservation concerns that include socio-economic losses upon
fisheries (Hamer et al., 2012), increased marine mammal entanglements, and potential (and
realized) retaliatory actions by fisherman (Powell & Wells, 2011; Read, 2008). As a consequence
of these conflicts, there is increasing demand for effective non-lethal mitigation techniques, such
as effective deterrents to reduce conflicts (Berrow et al., 2008; Forrest et al., 2009; Gordon &
Northridge, 2002; Götz & Janik, 2015, 2016).
Deterrents use aversive stimuli to prevent animals from acquiring human resources (Ramp et al., 2011). Deterrent stimuli use a variety of mechanisms to elicit defensive responses in animals (Götz & Janik, 2010; Schakner & Blumstein, 2013). A range of different presumably aversive stimuli, such as intense acoustic signals, can elicit avoidance in marine mammals (Berrow et al., 2008; Brandt et al., 2013; Cosgrove et al., 2009). However, the use of such intense acoustic signals in marine environments to prevent depredation is controversial. There are concerns about their overall efficacy, ethical and conservation concerns over potential hearing damage, and ecological impacts on non-target wildlife (Gordon & Northridge, 2002; Götz & Janik, 2013).

Focusing deterrents on species-specific sensory capabilities and individual learning mechanisms can potentially limit the effects on non-target species, as well as reduce an individual’s exposure to painful stimuli (Götz & Janik, 2013). Most species can learn the cues, context, or conditions that predict threatening situations (e.g., predator attack). This suggests that a deterrent which capitalizes on learning mechanisms may enhance success while simultaneously balancing welfare concerns and potential deleterious impacts on non-target species if the aversive stimulus does not elicit avoidance responses in non-target species.

**Pavlovian fear conditioning** is a form of associative learning in which individuals are exposed to an aversive, unconditioned stimulus (US) that is paired with an innocuous conditioned stimulus (CS) (Fanselow & Ponnusamy, 2008; Fanselow, 1984). While exposure to the unconditioned stimulus alone generally generates unconditioned fear reactions, conditioned responses to a CS after conditioning are different from unconditioned response to the US itself (Blanchard & Blanchard, 1969; Fanselow, 1980; Hollis et al., 1997). For instance, rats’ unconditioned response to aversive electric shock (US) involves a burst of motor activity (Fanselow, 1982). In contrast, rats exposed to a stimulus that predicts shock or threat (CS such as
context or experimenter) react by fleeing, engaging in hyper-vigilance, or exhibiting generalized avoidance (Blanchard, 1997; Bolles & Collier, 1976; Fanselow, 1980). Conditioned responses involve behaviors like vigilance or avoidance designed to circumvent threat that can also be the target responses for an effective deterrent (Hollis et al., 1997). To use this in deterrents, a painful or aversive deterrent stimulus designed to elicit an unconditioned response is needed as a US. If effectively conditioned with a paired CS, individuals will have learned that the CS indicates an impending US stimulus so that they can learn to avoid the US stimulus entirely. Employing fear conditioning to create deterrents might be a very effective way to reduce human-wildlife conflicts in a relatively humane way, especially if the conditioned response to the target CS is avoidance (Greggor et al., 2014; Mazur, 2010; Rossler et al., 2012; Schakner et al., 2014).

The acoustic startle reflex is a response to a fast onset of an acoustic stimulus that results in eyelid closure, contraction of neck and skeletal muscles, and sympathetic activation (Koch, 1999). It also disrupts ongoing behavioral patterns, and reduces sensory and cognitive functioning (Graham, 1979). In a captive setting, Janik & Götz (2011) demonstrated that repeated startle stimuli elicited flight responses in grey seals (Halichoerus grypus) even when the seals were highly motivated to feed and in the presence of food (Götz & Janik, 2011). In field trials on harbour seals (Phoca vitulina) and grey seals, startle sounds have been used successfully to reduce seal approaches and seal depredation on salmon farms (Götz & Janik, 2015, 2016). These results suggested that a startle pulse could be used as an aversive, unconditioned stimulus. This had also previously been shown in the laboratory, when grey seals were successfully fear-conditioned with a startle stimulus as a US and a non-startling tone as a CS (Götz & Janik, 2011).

We used a fear conditioning approach with acoustic deterrents by pairing a tone, the CS, with an acoustic startle stimulus, the US, on free-living California sea lions (Zalophus californianus).
that were interacting with commercial fishing activities in southern California. By doing so, we evaluated the efficacy of fear conditioning in contexts in which it had not previously been studied.

California sea lion depredation of commercial passenger fishing vessels and bait receivers—barges and docks where live bait is sold to recreational fishers (hereafter bait barges) off the west coast of the United States has been observed for decades and has increased as pinniped populations have increased dramatically since the 1970’s (Fletcher, 2008; Keledjian & Mesnick, 2013; Lowry & Maravilla-Chavez, 2005). Our objective was to test the efficacy of fear conditioning in reducing sea lion interactions from these two commercial fishing contexts; bait barges and fishing vessels. We tested whether: (1) individual sea lions interacting with bait barges can be fear conditioned using aversive acoustic stimuli and whether fear-conditioned individuals’ responses differ from those of non-conditioned individuals and (2) fear conditioning reduces interactions between sea lions and commercial passenger fishing vessels in southern California.

Materials and methods

Study site

We conducted two sets of fear conditioning trials. The first focused on California sea lions hauled out on bait barges in Southern California’s Mission Bay. The second focused on sea lions interacting with commercial passenger fishing vessels off Southern California. These vessels were based in San Diego Bay, Mission Bay, Dana Point, San Pedro, and Marina Del Rey.

Playback equipment and stimuli
We broadcast acoustic stimuli through a Lubell 9162T underwater loudspeaker (Lubell Labs Inc., Columbus, Ohio), using a Vibe 292 power Amplifier (Lanzar Inc.), from a Tascam DR40 player. The loudspeaker was calibrated using a variety of test signals at broadband source levels. Stimuli were adjusted digitally using Adobe Audition (Adobe® Systems, Mountain View, CA, USA) to create the desired source level. The Conditioned Stimulus (CS) was a 6 s long, 120 dB re 1 µPa sine wave tone (shaped with a 1.5 s long fade in to be non-startling), with a frequency range of 1-2 kHz (Figure 1). The Unconditioned Stimulus (US), the startle pulse, was centered around 10-11 kHz with a bandwidth from 2 kHz to 18kHz. The pulse was synthesized from white noise in Adobe Audition 2.0 software with a band-pass filter and an envelope gain function. The stimulus was played at a source level of 190 dB re 1 µPa rms, had a duration of 200 ms, and a rise time of 2 ms (figure 1). During pairings, the US was played 2 seconds after the CS.

**Experimental design**

*Conditioning trials on bait barges*

Two observers were stationed at the end of the bait barge to control the acoustic apparatus and perform focal follows. Individual sea lions were marked with non-toxic paint pellets. After marking, a focal individual was flushed into the water by walking towards it. Each individual was randomly assigned to a paired startle-pulse or control treatment. For the paired group, treatment consisted of 6 trials of CS/US training followed by a test phase of 6 trials of the CS alone (CS-) (Figure 2). Individuals in the unpaired control group were presented with the same total number of CS and US sounds (6 control-CS and 6 control-US) as the paired group in their
training phase, but in a predetermined random order so there was no consistent association between the CS and US (Figure 2). Thus, the control animals were exposed to 6 isolated CS presentations and 6 isolated US presentations. Following a 2 min pre-trial observation period, trials commenced when the focal individual surfaced within 20 m of the speaker. The stimulus was played as soon as the animal put its head underwater after being detected. Each trial consisted of a sound exposure followed by observation of the subject’s response (surface time and distance to barge measured using a laser rangefinder). The subsequent surfacing of the animal within a 20 m radius of the deterrent initiated the next trial, again playing the stimulus as soon as the head was underwater after surfacing. This continued until all trials were completed for the focal animal’s treatment.

Bait barge conditioning trials analysis

To study factors that predicted response during observation, we fitted generalized linear mixed effects models (GLMMs) with distance fled (in m) and time spent outside of a 20 m radius of the transducer (in min) as response variables, using a gamma error distribution and (log-link function). For all statistical analyses, we used R 2.14 (R Development Core Team, 2014) using the package lme4 (Bates et al., 2011). We used a two-step (Zuur et al., 2009) model selection procedure using the Akaike Information Criterion for small sample sizes (AICc). In a first step we determined the optimal random effects combination with the fully populated fixed effects. In a second step we determined the optimal fixed effects combination while using the previously determined random effects. Fixed effects that we considered included treatment (factor levels: CS/US training, CS- testing, Control US-Alone and Control CS-alone), trial number, and sex, as well as the interaction between trial number and treatment. We tested the following random
effect combinations (here shown in R notation); random intercept term for individual (1 | ID) as well as random slope terms for treatment x individual (treatment | ID) and trial number (Trial | ID) within individual.

The fixed and random effects combination retained in the final selected model are shown in supplementary table 1. We calculated 95% confidence intervals using the ‘confint’ function (method “Wald”) in lme4. We validated model assumptions by examining the distribution of residuals and quantile-quantile plots. Table S1 lists the information on the random and fixed effects included in the full model and distributions. All model parameter coefficients and CIs are shown on the scale of the response variable.

Insert Figure 2 about here

Conditioning trials on fishing boats

Each commercial passenger fishing vessel (CPFV) fishing trip had multiple fishing stops. At each stop, the deterrent apparatus was deployed at the stern of the fishing vessel where fishing was concentrated. The acoustic stimuli were broadcast only when sea lions were observed within 50 m of the vessel. Three conditions were randomly selected for playback: Paired stimuli (CS/US), startle-pulse alone (US), or control with no sound.

Two observers, one stationed on the observation deck and one on the stern performed behavioral observations and counts of the number of sea lions within 50 m of the vessel while scanning for other marine mammals > 50 m away. Surface distances from vessel were measured with a laser range finder. The observers focused on quantifying the following behavioral variables: bait foraging (the amount of time sea lions were within 30 m of the stern actively
taking bait from fishing lines or chum while swimming back and forth), surface take (when sea
lions removed a hooked fish as evidenced by movement on the fishing line indicating that a fish
was no longer hooked, and a sea lion surfaced immediately with a fish), surfacing behavior
(number and distance of surfacings), and the number of sea lion-vessel interactions (number of
sea lions and time spent within 50 m of vessel).

Analysis of conditioning trials on fishing boats

To study the factors that influenced sea lion surfacing behavior during playback, we fitted a
GLMM (Poisson error distribution, log link) with surfacing frequency as a response variable and
a GLM (Gamma error distribution, log link) with surfacing distance as a response variable. For
all fishing boat analyses, we first used the AICc value to select whether to use GLM or GLMM,
then we used the same two-step procedure mentioned above to find the optimal fixed and
random effect model structure. Predictor variables included were treatment (factor levels: control,
CS/US pairing, US-alone) and time spent fishing. Location and the fishing stop number were
included as random effects for all GLMMs. To study how the startle pulse influenced sea lion
bait foraging, we fitted a GLM with bait foraging presence as the binomial response variable and
predictor variables were treatment and time spent fishing. Bait foraging occurred when sea lions
were stern foraging for at least 50% time fishing at a single stop (absence defined as a sea lion
bait foraging for less than 50% time fishing at a stop).

Results

Conditioning trials on bait barges
Conditioning trials took place from September through November 2014. A total of 24 individual California sea lions were marked and used for playback (12 treatment, 12 control). The only factor to significantly predict the distance and time spent away in response to playback was the US when played alone in the control group (Table 1; Figure 2). Individual sea lions surfaced 7.7 times farther and spent nearly 8 times more time away from the bait dock in response to the US-alone (Table 1, Figure 2) than in response to the control CS. There was a trend that seals came closer in later trials. In response to CS/US paired playback, individuals surfaced 2.2 times farther away but did not spend any more time away from the transducer compared to control individuals. The interaction between trial number and CS/US treatment was significant for both distance and time spent away, suggesting that responses diminished with each successive trial (CS/US pairings) compared to control individuals. The interaction between CS-Testing x Trial and US x Trial was significant for distance, indicating somewhat diminished responses in later trials for treatment compared to control individuals.

**Conditioning trials on fishing boats**

We monitored 226 fishing stops across five locations in southern California during two summer fishing seasons (May-September 2013, 2014). Fishing time at a stop ranged from 0.08 h to 1.9 h with a mean of 0.73 h (±0.45 h SD). Over the two seasons of observations, interactions with sea lions occurred during 62% of the 226 fishing stops. Playbacks were performed on 98 fishing stops; in addition, we had 48 control (no sound) observations. Surface takes occurred too infrequently to be included in analyses.
Compared to no-sound control treatment, playback of the startle pulse (US-alone) caused sea lions to surface 2.7 times farther from the vessel and reduced surfacing frequency by 23% (Table 2). The paired playback caused a 26% decrease in surfacing but had no effect on distance surfaced compared to control treatments (Table 2). In addition more surfacings were detected during stops with longer fishing times (Table 2).

The US-alone treatment reduced the presence of sea lion bait foraging behavior causing an 83% reduction in the number of events when bait foraging was present (more than 50% of the time). There was no significant effect of the paired playback on bait foraging behavior (Table 3).

Discussion

The purpose of our study was to investigate whether individual sea lions could be fear-conditioned using aversive acoustic stimuli and whether fear conditioning reduces interactions between sea lions and commercial passenger fishing vessels in southern California.

From bait docks, playback of startle pulses evoked strong, unconditioned behavioral responses in California sea lions that included rapid flight and increased surfacing distances. These results are consistent with earlier studies that showed avoidance responses to startling stimuli in grey seals (Götz & Janik, 2011) and harbor seals (Götz & Janik, 2015, 2016). The pairing of a neutral tone with the startling pulse produced conditioned responses in individual sea lions interacting with bait barges. However, this response was not as strong compared to the startle pulse alone, and it diminished with successive CS/US pairings. Thus, we found evidence for prominent behavioral responses to the unconditioned stimulus, and moderate to weak
12

responses to the pairing of CS and US, as well as in response to CS (after training). From the
vessels, sea lions clearly responded to the startle pulse by increasing the distance from the boat
and by decreasing their time spent bait foraging, while showing minor responsiveness to pairing.
It appears the presence of the CS effectively removed the ability of the deterrent (the US) to
reduce the behavior we aimed to reduce—bait foraging.

According to adaptive-evolutionary perspectives on learning theory, the nature of the
conditioned response is determined by the unconditioned stimulus (Fanselow & Lester, 1988;
Timberlake, 1994). Learned responses are tailored to the particular US. For instance, response to
sickening food involves taste aversion (Garcia et al., 1955), whereas responses to CS preceding
tactile pain, like a shock, include the avoidance of the context where pain occurred. For our study,
the unconditioned stimulus was a startle-eliciting acoustic pulse. We found that the behavioral
responses to the startle pulse included avoidance of the site of sound exposure, as observed in
captive experiments (Finneran et al., 2003; Götz & Janik, 2011). However, once conditioned
with a paired CS, individuals showed weaker responses to the US, eventually diminishing any
responsiveness with successive trials. A possible explanation for this is that the animals
developed strategies to reduce hearing sensitivity that could not be observed behaviorally. In
some cetacean species for instance, the Pavlovian response to a warning signal preceding intense
acoustic stimuli reduces hearing sensitivity (Nachtigall & Supin, 2014, 2013), a possibility that
has not been explored with pinnipeds. In contrast to previous studies, we used a relatively long
CS tone that may have provided the animals with a relatively long warning period. Thus, the
specific duration of the CS might have helped sea lions develop successful avoidance strategies.

For the purpose of reducing pinniped/fisheries conflict, our startle pulse changed the
behavior of sea lions interacting with fishing vessels but the deterrence range was limited
because the average distance of surfacing during playback was still within the 50 m of boats. It may be that individuals surfaced further out to avoid being near the sound source while stern foraging. However, we found bait foraging to be reduced by 83%. The increased surfacing distance elicited in response to the startle pulse may be useful in other commercial fisheries (e.g., bottom set gillnets), or on fish farms where predators need to spend a significant amount of time underwater, close to the fishing apparatus to obtain prey (e.g., by manipulating nets).

In some cases, the startle deterrent did not influence sea lion behavior. This also happened with some of the grey seals in a previous study, possibly due to elevated hearing thresholds in the subjects (Götz & Janik, 2011). Identifying the specific mechanisms underlying the lack of response (habituation, increased motivation, higher hearing thresholds, or indeed a high turnover of animals) requires further investigation. Generally speaking, one problem with otariids (which include California sea lions) is that they have less sensitive underwater hearing than most phocid seals (which include grey seals) limiting the applicability of acoustic startle devices (Schusterman, 1981). The lack of the ability to mark individual sea lions foraging in the open ocean remains a major limitation of our and other studies that require individual identification (e.g., studies of habituation to repeated exposure of stimuli).

Our observations suggest that the conditioned response to acoustic stimuli failed to create the desired management goal (avoidance) in this particular fishery. However, the unconditioned stimulus we used on its own holds potential because the startle pulse elicited strong responses. The addition of the CS, introduced to minimize the overall impact on the animal, and indeed may prevent the development of contextual fear by providing time for an individual to engage in other responses. Thus, while we were able to induce mild fear conditioning in individual Californian sea lions interacting with commercial fishing activities, we were unable to create the desired
avoidance necessary to mitigate the predation problem in the tested industries by using a CS/US pairing.

Taken together, the pollution of an effective acoustic US with a warning CS reduced the efficacy of the US for controlling sea lions interacting with recreational fishing activities in our study. For the fear conditioning method to have promise for development of non-lethal deterrents in other contexts, careful consideration has to be given to the behavior of individuals, the unconditioned/conditioned responses, and the overall management goal when designing these acoustic deterrents.

Acknowledgments

Z.S. was supported by a NSF predoctoral fellowship and by a grant from the LaKretz Center for California Conservation Science. D.T.B. was supported by the NSF during manuscript preparation. We are indebted to Ken Franke and the members Sportfishing Association of California for both funding and allowing testing to occur from their vessels. Also, we thank the following volunteer field observers for their hard work: Emily Ferrari, Neeti Jain, Matt Petelle, Alexis Earl, and Clara Liao.

Appendix A. Supplementary material

A table specifying specific models and transformations used can be found in the online version.

References


Generalized linear mixed effects models for individual California sea lion responses (time spent away and distance fled) during conditioning trials on bait barges. Model coefficients for fixed effects are presented on the scale of the response variable. Significant (p < 0.05) variables are highlighted in bold.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Model</th>
<th>Coefficient</th>
<th>95% CI</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(intercept)</td>
<td>time</td>
<td>1.96</td>
<td>1.17, 3.28</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>10.11</td>
<td>6.4, 15.95</td>
<td>6.4x10^{-29}</td>
</tr>
<tr>
<td>Treatment: US-Alone</td>
<td>time</td>
<td>7.92</td>
<td>4.47, 14.00</td>
<td>1.2x10^{-12}</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>7.74</td>
<td>3.59, 16.65</td>
<td>6.9x10^{-7}</td>
</tr>
<tr>
<td>Treatment: CS/US training</td>
<td>time</td>
<td>1.60</td>
<td>0.79, 3.27</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>2.32</td>
<td>1.20, 4.37</td>
<td>0.02</td>
</tr>
<tr>
<td>Treatment: CS- Testing</td>
<td>time</td>
<td>0.73</td>
<td>0.36, 1.47</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>time</td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------</td>
<td>----------</td>
<td>------------</td>
<td>-------</td>
<td></td>
</tr>
<tr>
<td><strong>Trial number</strong></td>
<td>1.71</td>
<td>1.16</td>
<td>0.014</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.93, 3.14</td>
<td>1.03,1.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>US-Alone × Trial number</strong></td>
<td>1.22</td>
<td>0.88</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.08,1.37</td>
<td>0.75,1.03</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.016</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CS/US × Trial number</strong></td>
<td>0.80</td>
<td>0.82</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.69, 0.93</td>
<td>0.71,0.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CS-Testing × Trial number</strong></td>
<td>0.77</td>
<td>0.92</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.66, 0.89</td>
<td>0.80,1.06</td>
<td>0.216</td>
<td></td>
</tr>
</tbody>
</table>
Table 2

Generalized linear mixed effects models for sea lion surfacing behavior (surfacing frequency – surf.frequency and distance) during playback from active fishing vessels. Model coefficients presented on the scale of the response variable. Significant (p < 0.05) variables are highlighted in bold. ‘nr’ indicates the variable was not retained in the model selection process.

<table>
<thead>
<tr>
<th>model</th>
<th>Model Coefficient</th>
<th>95% CI</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(intercept)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surf. frequency</td>
<td>22.1</td>
<td>14.2, 34.2</td>
<td>4.4x10^{-44}</td>
</tr>
<tr>
<td>Distance</td>
<td>19.1</td>
<td>13.6, 27.1</td>
<td>6.4x10^{-9}</td>
</tr>
<tr>
<td>Treatment: US-Alone</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surf. frequency</td>
<td>0.77</td>
<td>0.71, 0.83</td>
<td>2.6x10^{-11}</td>
</tr>
<tr>
<td>Distance</td>
<td>2.70</td>
<td>1.99, 3.62</td>
<td>1.3x10^{-10}</td>
</tr>
<tr>
<td>Treatment: CS/US training</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surf. frequency</td>
<td>0.74</td>
<td>0.67, 0.80</td>
<td>2.3x10^{-9}</td>
</tr>
<tr>
<td>Distance</td>
<td>1.06</td>
<td>0.75, 1.50</td>
<td>0.72</td>
</tr>
<tr>
<td>Time spent fishing</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surf. frequency</td>
<td>1.08</td>
<td>1.02, 1.10</td>
<td>5.0x10^{-3}</td>
</tr>
<tr>
<td>Distance</td>
<td>nr</td>
<td>nr</td>
<td></td>
</tr>
<tr>
<td>Stop N</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surf. frequency</td>
<td>nr</td>
<td>nr</td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>0.88</td>
<td>0.78, 0.99</td>
<td>0.051</td>
</tr>
</tbody>
</table>
Table 3
Influence of startle pulse on sea lion foraging behavior during active fishing.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>CI (95%)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>5.40</td>
<td>2.27, 15.9</td>
<td>5.0x10^-4</td>
</tr>
<tr>
<td>Treatment: US-alone</td>
<td>0.27</td>
<td>0.08, 0.72</td>
<td>0.015</td>
</tr>
<tr>
<td>Treatment: CS/US pairing</td>
<td>6.30</td>
<td>0.94, 124.5</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Figure Legends

Fig. 1. Conditioned Stimulus (CS) and Unconditioned Stimulus (US) playback sounds.

Fig. 2. Reinforcement schedules for individuals in paired playback or control treatments from bait docks. Red dotted lines refer to US and black solid lines represent CS.

Fig. 3 Boxplot for sea lion responses (time spent away from bait barge) during bait barge trials. Boxes show median (line within the box) and upper (25%) and lower (75%) quartiles, whiskers indicate outermost data points within a 1.5 interquartile range, and circles are outliers.
Fig. 1

Fig. 2
Fig. 3

Appendix A. Full generalized linear (mixed) models with random and fixed effects that were evaluated during model selection

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Factors</th>
<th>Random Factors</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conditioning trials on bait barges</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time away from dock</td>
<td>Sex, trial, treatment</td>
<td>(1</td>
<td>ID), (treatment</td>
</tr>
<tr>
<td>Distance fled from dock</td>
<td>Sex, trial, treatment</td>
<td>(1</td>
<td>ID), (treatment</td>
</tr>
<tr>
<td>Conditioning trials on fishing boats</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bait Foraging (GLM)</td>
<td>treatment, time spent</td>
<td>n/a</td>
<td>Binomial Poisson distribution with log-link function</td>
</tr>
<tr>
<td>Surfacing Frequency</td>
<td>fishing</td>
<td>(1</td>
<td>stop), (1</td>
</tr>
<tr>
<td>Surfacing Distance (GLM)</td>
<td>treatment, time spent</td>
<td>n/a</td>
<td>Gamma distribution with log-link function</td>
</tr>
</tbody>
</table>