Notes

SEALS, SEQUENCES, AND SIGNAL DETECTION

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The sensory abilities of animals in general and marine mammals in particular are often evaluated in behavioral psychophysical experiments conducted in the laboratory (for example, see Moore and Schusterman 1987, Schusterman 1981). In this paper we are not specifically concerned with measuring physiological constraints on the sensory receptors of marine mammals, but rather with the fundamental issue of their perception. In psychophysical experiments researchers often present subjects with signal-present trials and signal-absent trials, or what have been termed "catch" trials. In these procedures animals make a series of conditioned responses indicating the presence or absence of a signal on each trial. In this context, reinforced responses are either called "hits" (the animal reports *yes* when a signal is present) or "correct rejections" (the animal reports *no* when a signal is absent). Non-reinforced responses are either "misses" (the animal reports *no* when a signal is present) or "false alarms" (the animal reports *yes* when no signal is present). In accordance with signal detection theory (Swets 1973), this receiver operating behavior is not only influenced by the strength of a signal, but also by non-sensory cues including those associated with signal probability (Terman and Terman 1972, Schusterman and Johnson 1975), and with the probability and magnitude of reinforcement for hits and correct rejections (Schusterman *et al.* 1975, Schusterman 1976). For example, if a larger magnitude of food is given for a hit relative to a correct rejection, an animal will favor a *yes* response, resulting in an increased number of hits and false alarms. This is particularly true when the detection task becomes more difficult and the animal becomes more uncertain about whether to respond yes or no.

Even when factors related to these non-sensory variables are carefully balanced to decrease or eliminate potential bias, the sequences of signal and catch trials in psychophysical tasks may still alter an animal's expectancies for trial types and thus alter its responding. For example, if a seal performing a difficult signal de-

tection task reports *no* three times in a row, he may be tempted to report *yes* on the following trial, despite remaining uncertain as to the presence or absence of the signal. Such a tactic of predicting transitions from one trial type to another is supposedly controlled for by using Gellermann series of signal and catch trials (Gellermann 1933). This type of trial series presents signal and catch trials with an *a priori* probability of 0.5 within each block of ten trials. A Gellermann series and its variants are often used in studies of marine mammal sensory capabilities to prevent subjects from using sequential cues to improve performance (*e.g.*, Moore and Schusterman 1987, Au *et al.* 1988, Griebel and Schmid 1992, Gerstein *et al.* 1999). However, this kind of constraint on so- called random presentations of trials commonly results in relatively short runs of trials (a sequence of trials of a given type). Unfortunately, the Gellermann series ignores the possibility that an animal may be able to keep track of such constrained sequences, and then use such information to increase the probability of obtaining reinforcement regardless of the signal's detectability.

Studies with young children and common chimpanzees (*Pan troglodytes*) have already shown that intelligent and experienced subjects are sensitive to run sequences of trials (Schusterman 1963). Given these observations, we suspected that marine mammals participating in psychophysical tasks could also track sequences of events in order to maximize the likelihood of obtaining reinforcement. Therefore, we analyzed the response patterns in a harbor seal (*Phoca vitulina*) during an auditory detection task to determine whether constraining the trial run length by a Gellermann series influenced patterns of responding and the subsequent detection thresholds measured.

An 11-yr-old male harbor seal (Sprouts) who had six years of experience in visual and auditory detection tasks (see Kastak and Schusterman 1998, Kastak *et al.* 1999, Levenson and Schusterman 1999, Southall *et al.* 2000) was tested in an underwater sound detection task using a 3,530-Hz pure tone. A go/no-go testing procedure was used in which the "go" response was a paddle press. Sprouts received ten "warm-up" trials in which the first signal trial level of a session was 12–15 dB higher than the test level and was attenuated after each hit by 2–4 dB steps on subsequent signal trials until the test level was reached. The test level was chosen at a value intended for 50% correct detections by the seal and was not varied within the experimental phase of a session in order to obtain d' estimates of hearing sensitivity. To encourage a high probability of responding to the test signal at this level, the seal was reinforced with two pieces of fish for a hit and one piece of fish for a correct rejection.[1] The d' value is an index of signal detectability with larger d' values indicating greater sensitivity to the signal (Swets 1973). Sprouts was also given ten "cool-down" trials at the end of each session in which the level on signal trials was 10 dB higher than the test level. Warm-up and cool-down trials were incorporated to ensure good stimulus control over the animal's behavior at the start and end of each session but were not used to determine d' estimates or in the analysis reported here.

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[1] This resulted in an average ß value, an index of overall response bias (Swets 1973), of 0.80.
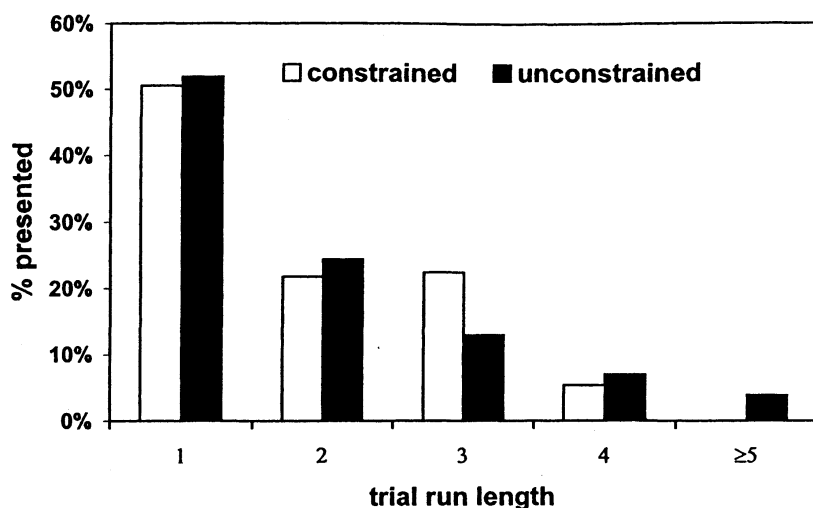
Figure 1. Trial run length probability distributions for a harbor seal in an auditory detection task. In one condition, data were collected with modified Gellermann trial series that were constrained by run length ≤ 4 (white bars); in the other condition, data were collected with unconstrained trial run lengths (black bars).

Data were collected under two different trial series conditions. In the "constrained" condition, trial series had a maximum run length of four (a modified Gellermann series). In the "unconstrained" condition, trial series had no direct constraints regarding the maximum number of trials in a run. Signal and catch trials for both conditions were presented with overall and first order conditional probabilities for a given trial type of 0.5. Although these first order conditional probabilities for trial types were the same, a different run length probability distribution between the two conditions was created by limiting the trial run length in the constrained condition but not in the unconstrained condition as depicted in Figure 1. The most notable differences in the distributions are that in the constrained condition, runs as long as three occurred about 22% of the time, but runs as long as five did not occur. In the unconstrained condition, runs as long as three occurred about 13% of the time, and run lengths as long or longer than five occurred about 4% of the time.

A one-way, repeated-measures analysis of variance was used to determine statistical differences in mean d' values between the conditions. Additionally, an analysis of responses following different run lengths of signal and catch trials was made in order to determine whether the harbor seal was anticipating transitions between trial types more under one condition than the other. For this analysis the subject's responses were categorized and pooled across experimental sessions according to the trial run length that occurred just prior to the response. A run length of one or two is hereafter referred to as a short trial run, while a run length of three or four is hereafter referred to as a long trial run. We compared these categories of responses using a two-tailed chi-square test (with a Yates correction for continuity and df = 1 unless otherwise noted).

An analysis of variance revealed a significant difference in mean d' values, *i.e.*, in detectability, between the two conditions (for constrained condition: $x = 1.44 \pm 0.86$ SD; for unconstrained condition; $x = 0.30 \pm 1.04$; $F_{1,11} = 8.90$,

$P < 0.01$). In the sessions where trial runs were constrained, Sprouts was less likely to respond *yes* following long signal trial runs than following short signal trial runs, and less likely to respond *no* following long catch trial runs than following short catch trial runs. The statistical analysis of these results show that when trial runs were constrained, Sprouts was significantly more likely to shift his response following long runs than following short runs of a given trial type (70% [64/92] *vs.* 50% [215/428], $\chi^2 = 10.6$, $P < 0.01$). This was not observed when trial runs were unconstrained (48% [38/80] *vs.* 49% [168/343], $\chi^2 = 0.013$, $P = 0.91$). Thus, the harbor seal anticipated shifts in trial types depending on his expectancies of the run series of events and was therefore able to obtain more reinforcement and a higher detectability value in the constrained condition compared to the unconstrained condition.

As in the present experiment, an animal performing a detection task may be presented with many signal trials near threshold and consequently, may be uncertain as to the signal's presence during much of the task. A decision may become more heavily influenced by non-sensory cues, including the run sequence of events. Human subjects attempting to detect weak signals in noise showed a greater *yes* response probability when a catch trial was presented on the immediately preceding trial or on the next to last trial presentation (Sandusky and Ahumada 1971). Studies which examined the effects of run lengths on responding in two choice learning tasks showed that when trial series were generated with short (≤ 5) trial run lengths, human subjects had a tendency to shift their response following successive occurrences of an event (Derks 1963, Gambino and Myers 1966, Jones and Myers 1966). The harbor seal in this study, by being able to track and estimate the number of trials in a run when it was predictable, also showed this type of response shift strategy in a signal detection task.

Gellermann (1933) intended to create well-balanced trial series by constraining the trial run length. While many marine mammal investigators adopted this procedure in an effort to avoid potential response biases, this constraint unfortunately creates a predictable run series of events. Our results showing that a single harbor seal can track sequential patterns within pseudorandom trial series suggest that other marine mammals, especially those individuals that are repeatedly used as subjects in psychophysical tasks, can potentially do this as well. If this type of bias is not carefully controlled, then an animal's sensitivity may be overestimated. Such detection measurements can be especially misleading in the marine mammal literature because few subjects generally serve as representatives for an entire species (*e.g.*, see Schusterman 1981). Therefore, we urge investigators in marine mammal psychophysics to use trial series that are generated without directly constraining the number of sequential presentations of a given trial type.

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