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Beyond the classic sensory systems: Characteristics of the sense of time of harbor seals (*Phoca vitulina*) assessed in a visual temporal discrimination and a bisection task

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Abstract

Beyond the classic sensory systems, the sense of time is most likely involved from foraging to navigation. As a prerequisite for assessing the role time is playing in different behavioral contexts, we further characterized the sense of time of a harbor seal in this study. Supra-second time intervals were presented to the seal in a temporal discrimination and a temporal bisection task. During temporal discrimination, the seal needed to discriminate between a standard time interval (STI) and a longer comparison interval. In the bisection task, the seal learnt to discriminate two STIs. Subsequently, it indicated its subjective perception of test time intervals as resembling either the short or long STI more. The seal, although unexperienced regarding timing experiments, learnt both tasks fast. Depending on task, time interval or duration ratio, it achieved a high temporal sensitivity with Weber fractions ranging from 0.11 to 0.26. In the bisection task, the prerequisites for the Scalar Expectancy Theory including a constant Weber fraction, the bisection point lying close to the geometric mean of the STIs, and no significant influence of the STI pair condition on the probability of a long response were met for STIs with a ratio of 1:2, but not with a ratio of 1:4. In conclusion, the harbor seal's sense of time allows precise and complex judgments of time intervals. Cross-species comparisons suggest that principles commonly found to govern timing performance can also be discerned in harbor seals.

KEYWORDS

interval timing, pinnipeds, scalar property, temporal judgments, Weber's law

1 | INTRODUCTION

The sensory systems provide organisms with information essential for all behaviors including foraging or orientation and navigation. Beyond the classic sensory systems, a well-developed sense of time might assist and complement the sensory systems. Many animals have been reported to adjust their behavior, such as the daily activity pattern, the onset of migration or reproduction, depending on temporal changes in the environment

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(Richelle & Lejeune, 1980; Vasconcelos, de Carvalho, & Machado, 2017). These changes occur mostly over time scales spanning from hours and days to months and years. Interval timing, which focuses on time intervals in the second-to-minute-range, helps animals to determine for example the time elapsed since the last food/prey item was found/caught or the replenishing time after a food source was depleted (Daan & Koene, 1981; Davies & Houston, 1981; Henderson, Hurly, Bateson, & Healy, 2006; Thorpe & Wilkie, 2006). These few examples already demonstrate that temporal aspects can affect animal behavior as do external stimuli that are perceived by the classic sensory systems.

The sense of time however differs from the classic sensory systems as time is not perceived by a sensory organ exclusively devoted to receiving temporal stimuli. In contrast, temporal information can probably be deduced from stimuli of any modality thus requiring the contribution of sensory organs such as the eye or the ear. Furthermore, temporal stimuli are not processed or perceived by a specific brain area, instead, different brain areas are responsible for the processing/perception of time intervals of different duration and timing task or are active depending on for example task or experimental condition (e.g., Buhusi & Meck, 2005; Merchant & de Lafuente, 2014; Tallot & Doyère, 2020). Nevertheless, the cerebellum, cortical areas, such as the supplementary motor area, and the frontal and parietal cortices as well as subcortical structures, such as the basal ganglia, seem to be main areas generally involved in timing and time perception across studies and species (e.g., Ivry & Spencer, 2004; Grondin, 2010; Merchant & de Lafuente, 2014; Grondin, 2019; for review Tallot & Doyère, 2020).

Regarding marine mammals, we could recently show that two pinnipeds species possess a well-developed sense of time (Heinrich, Dehnhardt, & Hanke, 2016; Heinrich, Ravignani, & Hanke, 2020). For this group of animals, time can be an essential parameter during foraging when energy intake is to be optimized on the basis of energy gain per time, travel duration between patches or dive duration in line with optimal foraging/dive theory (Heaslip, Bowen, & Iverson, 2014; Krebs & Davies, 1981; Thompson & Fedak, 2001). In the context of orientation and navigation, time might play a role during distance estimation (Maaß & Hanke, 2021) per se or as part of path integration (e.g., Etienne & Jeffery, 2004; Kautzky & Thurley, 2016; Mittelstaedt & Mittelstaedt, 1982) or during sun compass orientation to compensate for the position of the sun over the day (Guilford & Taylor, 2014; Schmidt-Koenig, 1990). Temporal information could be particularly vital to marine mammals in their oceanic habitat, which seems rather featureless at first sight and in which information from the classic sensory systems might be occasionally impaired or even absent. Moreover, timing/rhythm abilities of harbor seals in particular have already attracted attention in a totally different context: as harbor seals possess many characteristics including for example vocal flexibility/learning or a vocal apparatus close to humans, they could thus serve as model organisms for the evolution of speech, music, or rhythm (e.g., Kotz, Ravignani, & Fitch, 2018; Ravignani et al., 2016).

One of the most common experimental approaches to study temporal judgments is the temporal bisection task (Church & Deluty, 1977; Vasconcelos et al., 2017). It requires the subject to learn to discriminate between two temporal stimuli of different durations, one of "short" (*S*) duration and one of "long" (*L*) duration, defined as standard time intervals (STIs). When presented with test time intervals (TTIs) with durations in between the two STIs, the subject has to continue with the response behaviors for either *S* or *L* thereby indicating its subjective perception of the TTI durations as being either similar to the *S* or the *L* STI.

In the past decades, the temporal bisection approach has been used to answer numerous questions regarding the perception and processing of temporal intervals. Data obtained in a bisection experiment are usually analyzed regarding temporal sensitivity and the location of the bisection point (BP), also known as the point of subjective equality. Moreover, these experiments determined how these two aspects change with the properties of the stimulus (Droit-Volet, Meck, & Penney, 2007; Lustig & Meck, 2011; Meck, 1984; Ortega & López, 2008; Penney, Gibbon, & Meck, 2000), the duration of the STIs (Wearden et al., 1997), stimulus ratio (Wearden & Ferrara, 1996), or the different spacing of the TTIs (Penney, Gibbon, & Meck, 2008; Raslear, 1985; Wearden & Ferrara, 1995), just to name a few modifications. This way the timing abilities in a variety of organisms, such as rats (e.g., Church & Deluty, 1977; Kim, Ghim, Lee, & Jung, 2013; Meck, 1983, 1984; Raslear, 1985; Siegel & Church, 1984), pigeons (e.g., Araiba & Brown, 2017; Fox, Prue, & Kyonka, 2016; Laude, Daniels, Wade, & Zentall, 2016; Machado & Keen, 1999; Machado & Pata, 2005; Pinheiro de Carvalho, Machado, & Tonneau, 2016; Platt & Davis, 1983), mice (e.g., Akdoğan & Balcı, 2016; Penney et al., 2008), dogs (Domeniconi & Machado, 2017), and humans of different age (e.g., Allan, 1991; Allan & Gerhardt, 2001; Droit-Volet, Clément, & Fayol, 2003; Droit-Volet & Wearden, 2001; Kopec & Brody, 2010; Lustig & Meck, 2011; Provasi, Rattat, & Droit-Volet, 2011; Rattat & Droit-Volet, 2001; Wearden, 1991b; Wearden et al., 1997) were characterized.

With the experimental paradigm of this study, including another harbor seal individual and comparing its temporal discrimination with its temporal bisection performance, we intended to (1) compare the performances of two harbor seal individuals documented with the temporal discrimination approach (Heinrich et al., 2016; Heinrich et al., 2020), and to (2) compare the results obtained in one individual but from two different experimental approaches. Moreover, documenting the timing abilities of a harbor seal in a temporal bisection task allows a better comparison of the seal's timing performance with the performance of other organisms, mainly tested using the bisection approach, to unravel similarities and differences regarding the underlying principles.

With the temporal bisection task, we also intended to determine how a harbor seal performs in a timing task with increased complexity compared to temporal discrimination. It was of particular interest to assess whether the seal would shift its response rule in the presence of two STIs, including for example both STIs into its decision process, or whether it would compare the TTI solely with the *S* STI as during temporal discrimination. Of further interest was to assess the temporal sensitivity as well as the BP for various STI pairs differing in duration as well as *S*/*L*-ratio. Altogether our results would also indicate whether sensitivity to time is proportional to the duration of the interval being timed in harbor seals, meaning the longer/shorter the time interval, the more inaccurate/more accurate seals should be in discriminating time intervals. This relationship is predicted by the Scalar Expectancy Theory (SET, Gibbon, 1977; Gibbon, Church, & Meck, 1984), one of the earliest and most common theories to explain information processing in timing, and more generally by Weber's law, a law central to sensory perception allowing meaningful comparison across modalities and tasks (Gescheider, 1976).

2 | MATERIALS AND METHODS

2.1 | Experimental animal

The experiments were conducted with a male harbor seal called "Henry" (22 years old at the beginning of the experiment). The animal was kept at the "Marine Science Center" of the University of Rostock, Germany, where it received approximately 50% of its total daily diet during the experimental sessions once or twice per day, 5 to 7 days a week. The seal was highly experienced in conducting experiments (see e.g., Bodson, Miersch, & Dehnhardt, 2007; Hanke, Miersch, Warrant, Mitschke, & Dehnhardt, 2013; Sticken & Dehnhardt, 2000; Wieskotten, Mauck, Miersch, Dehnhardt, & Hanke, 2011).

2.2 | Apparatus

Both experiments took place in an experimental chamber (3 m deep, 2 m wide, and 2 m high) which allowed keeping illumination, mediated by a fluorescent lamp (Standard FSL T8 36 W 765 Radium, Wipperfürth, Germany), constantly at 40 lx.

During the experiments, the animal was stationed in a metal hoop affixed to a steel-plate 6 cm above the bottom (Figure 1). The experimental station ensured a constant viewing distance of 50 cm to and thus a constant viewing angle of the stimuli on the monitor (Experiment 1: Eizo, Flex scan S1721 17″, refresh rate 60 Hz, Eizo Nanao Corporation, Hakusan, Ishikawa, Japan; Experiment 2: LG IPS LED Business Monitor, 60 Hz refresh rate, LG Electronics Deutschland GmbH, Ratingen, Germany), on which the stimuli were presented. Two response targets were attached to the left and the right side of the hoop station (Figure 1).

To avoid secondary cue giving, the experimenter was hiding in a room adjacent to the experimental chamber and could only observe the animal's response behavior via a camera (HD Logitech Webcam C270, Logitech GmbH, Munich, Germany). Both rooms were connected by a window, which was closed with a black opaque slider during trials and opened for the purpose of rewarding and sometimes for correcting the animal's position.

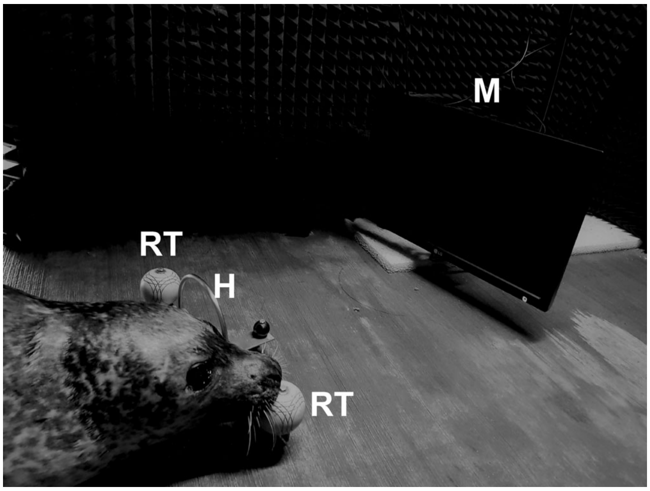

FIGURE 1 Experimental setup in the experimental chamber. In the intertrial interval and during stimulus presentation, the harbor seal was stationing in a hoop station (H) fixed in front of the monitor (M) on which the stimulus (white circle, not shown here) was presented. After the stimulus had disappeared, the seal indicated its response by moving its snout to either the left or right response target (RT; shown here; for details see Section 2)

2.3 | Stimuli

The stimuli were white filled circles of 10.5 cm diameter on black background which were displayed on the monitor (Figure 1) for a pre-determined duration.

In Experiment 1, the circle was presented either for the standard time interval (STI) of 3 s or a longer comparison time interval (CTI) of 10, 8, 6, 5, 4, and 3.5 s (Table 1; for details about the procedure see Heinrich et al., 2016; Heinrich et al., 2020). In Experiment 2, the circle was presented either for a "short (S)" or a "long (L)" standard time interval (STI) or a test time interval (TTI) with a duration intermediate to the two STIs (Table 1). For the determination of each bisection point (BP) for the seven STI pairs, five TTIs were presented. These TTIs were linearly spaced in duration between the durations of the *S* and *L* STI as in previous studies (e.g., Droit-Volet & Wearden, 2001; Rattat & Droit-Volet, 2001) and included the arithmetic (AM) and geometric mean (GM) of the STI pair.

In both experiments, the stimuli were generated in and presented with PsychoPy (Peirce, 2007, 2009; Peirce et al., 2019; script A. Ravignani, see Heinrich et al., 2020). The measured duration of the time intervals deviated on average by 25 ± 4.7 ms (Experiment 1) and 23.5 ± 4.4 ms (Experiment 2) from the programmed value (see Heinrich et al., 2016 for measurement procedure).

2.4 | Procedure

Each trial started with the experimental animal stationing calm and attentive in its hoop station, whereupon the experimenter started stimulus presentation. The subsequent response of the animal was rewarded with a fish, if it was correct. Each incorrect response was signaled with a verbal "no". The different stimulus durations were presented in pseudorandom order during each session (Gellermann, 1933).

In Experiment 1, a two alternative forced choice procedure was used to determine a difference threshold for a STI of 3 s and longer CTIs. A correct answer was defined as the animal moving its head to the left response target after the presentation of the STI or as the animal moving its head to the right response target after the presentation of a CTI (Figure 1). After the animal reached the learning criterion for a specific STI/CTI combination (76.67% correct choices in two consecutive sessions), the CTI was decreased step by step until the animal was not able to reach the learning criterion within five sessions anymore (for details about the procedure see Heinrich et al., 2016).

In Experiment 2, a correct response was defined as moving the head to the left response target after the *S* STI was presented and moving its head to the right response target after the *L* STI was presented (L response). Although, the animal got feedback after its response

TABLE 1 Overview of the stimuli and results of Experiment 1 and Experiment 2

Experiment 1

STI (in s)	CTI (in s)	Difference threshold ΔS (in s)	Weber fraction c
3	10, 8, 6, 5, 4, 3.5	0.8	0.26

Experiment 2

S/*L*-ratio of STI pair	STI pair (in s)	Difference L-S (s)	TTIs (in s)	BP (in s)	GM (in s)	AM (in s)	Weber fraction	K_1	K_2
1:4	1/4	3	1.5; 2; 2.5; 3; 3.5	2.81	2	**2.5**	0.12	1.40	**1.12**
	2/8	6	3; 4; 5; 6; 7	4.56	4	**5**	0.17	1.14	**0.91**
	3/12	9	4.5; 6; 7.5; 9; 10.5	7.31	6	**7.5**	0.25	1.22	**0.97**
1:2	2/4	2	2.5; 2.75; 3; 3.25; 3.5	2.70	**2.83**	3	0.11	**0.95**	0.90
	3/6	3	3.5; 4; 4.5; 5, 5.5	4.29	**4.24**	4.5	0.11	**1.01**	0.95
	4/8	4	5; 5.5; 6; 6.5; 7	5.42	**5.65**	6	0.11	**0.96**	0.90
	5/10	5	6; 7; 7.5; 8; 9	7.31	7.07	**7.5**	0.11	1.03	**0.98**

Note: For Experiment 1, the STI, the presented CTIs in the suite of presentation, the difference threshold ΔS, and the Weber fraction c are depicted. For Experiment 2, the STI pairs, for which bisection points (BP) were determined, are listed together with the presented TTIs. The STI pairs are listed according to the sequence of testing. The STI pairs had a short/long (S/L) ratio of 1:2 or 1:4. The temporal difference between S and L and the TTIs for each STI pair are noted. For all tested STI pairs the calculated BP, the arithmetic mean (AM), the geometric mean (GM) as well as K_1, and K_2 (see Section 2 for details) are listed. The GM and K_1 or AM and K_2 is written in bold to signify if the BP is closer to the GM or AM (the closer K_1 to 1.0 or K_2 to 1.0, the closer the BP to the GM or AM).

following a STI, no feedback was given after its response following a TTI.

The animal needed to pass a learning phase (learning criterion: 90% correct choices in three consecutive sessions) during which it learnt to respond correctly to the new STIs. During this learning phase, each session was composed of 30 trials including 15 trials in which the *S* STI and 15 trials in which the *L* STI occurred. In the subsequent testing phase, TTIs were introduced during 15 sessions. Each testing session consisted of 30 trials including 10 trials for each of the two STIs and two trials for each of the five TTIs. After completing data collection for one STI pair, the next STI pair was introduced.

2.5 | Analysis

For Experiment 1, the difference threshold ΔS was determined via linear interpolation from the mean performance of the last two sessions above 75% correct choices and the mean performance of the first five sessions below 75% correct choices. The Weber fraction *c* as measure for the animal's temporal sensitivity was calculated as $c = \frac{\Delta S}{S}$ (see also Heinrich et al., 2016; Heinrich et al., 2020).

For Experiment 2, for each STI pair, the number of *L* responses was pooled for every STI and TTI over the testing sessions. From this psychometric function (Figure 2a), the following parameters were determined:

(1) The BP, defined as the stimulus duration at which the animal showed 50% *L* responses, calculated by linear interpolation between the last data point above and the first data point below 0.5 proportion *L* responses. To assess whether the BP lies at/is closer to the AM or the GM, $K_{1,}$ (quotient of BP and the GM), and K_2 (quotient of BP and AM) were determined.

(2) The Weber fraction *c* was calculated as:

$$c = \frac{\Delta S}{BP}$$

with

$$\Delta S = \frac{\text{proportion of } L \text{ responses at } 75\% - \text{proportion of } L \text{ responses at } 25\%}{2}$$

and the *BP* of the STI pair.

We also analyzed whether three important prerequisites for the SET (Allan, 1991; Gibbon et al., 1984) are met:

(1) The Weber fractions determined for all tested STI pairs should be constant.

(2) The BP lies closer to the GM.

(3) The psychometric functions for STIs with the same S/L-ratio should show superimposition (Figure 2b, c; e.g., Gibbon, 1981; Penney et al., 2000). To assess the degree of superimposition, the *L* responses were plotted against normalized time intervals, STIs and TTIs, divided by the calculated BP for each STI pair (Allan, 1991; Wearden & Ferrara, 1996). Visual observation was used for a first estimation of superimposition (e.g., Droit-Volet et al., 2003; Droit-Volet & Wearden, 2001; Penney, Yim, & Ng, 2014; Wearden et al., 1997). However, for a detailed analysis of the degree of superposition, the influence of the specific STI condition on the probability of an *L* response was tested using a logistic regression model. For each of the two ratio conditions of the STI pairs, two models were compared. The first model (M0) only takes the normalized time intervals into account with the equation

$$\widehat{p} = \sigma(\beta_0 + \beta_1 x),$$

where $\widehat{p}$ is the probability of an *L* response, $\sigma(\cdot)$ the sigmoid function, β_0 the intercept, β_1 the slope with respect to *x*, and *x* denotes the normalized time intervals. M0 does not factor in the specific STI condition the observation came from (i.e., the nonnormalized observed time interval). The second model (M1) takes both the normalized time intervals and the specific STI pair condition of the observation as input. The model equation for M1 is

$$\widehat{p} = \sigma\left(\beta_0 + \sum_{i=1}^{n-1} \beta_{0i} y_i + \left(\beta_1 + \sum_{i=1}^{n-1} \beta_{1i} y_i\right) x\right),$$

with $y_1, \ldots, y_{n-1}$ being one-hot encoded variables giving the exact standard interval condition of an observation. All other parameters are defined in M0. Obviously, M0 is obtained by restricting M1 such that $\beta_{0i} = \beta_{1i} = 0$ for all *i*. Thus, the models are nested. For both models, the parameters that maximized the model Likelihood were determined. Subsequently, a Likelihood-Ratio test was calculated to compare the two models. If M0 and M1 had similar model Likelihoods at the α-level of 0.05, the

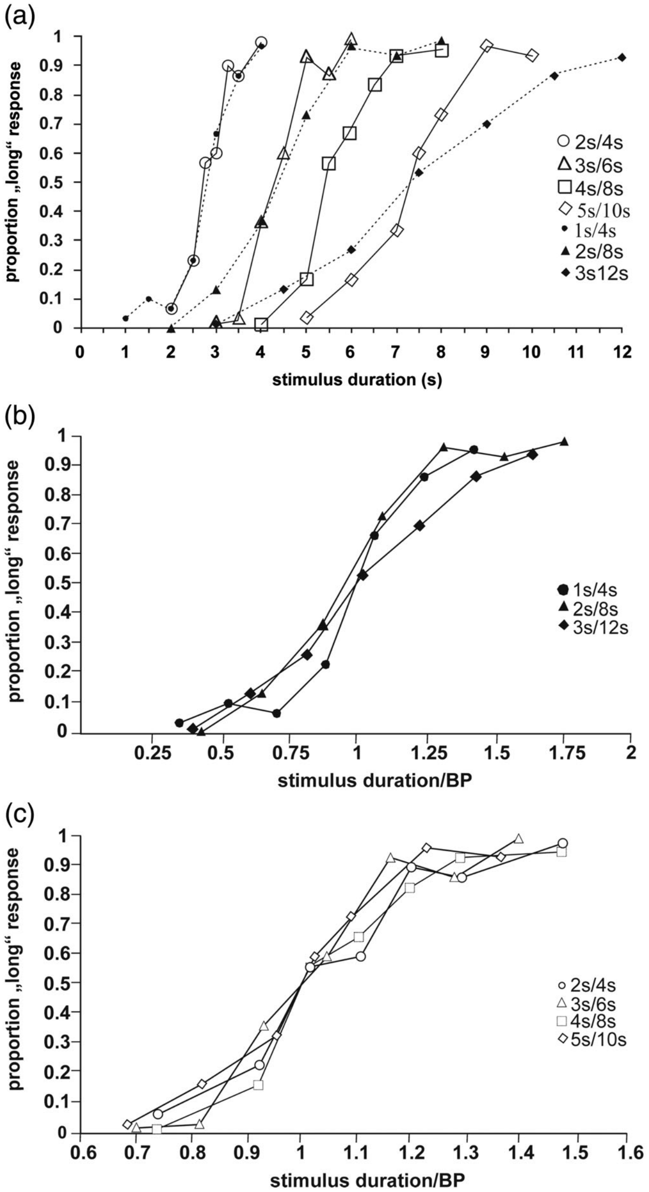

FIGURE 2 (a) Psychometric functions showing the proportion of *L* responses as a function of the duration of the STIs' and TTIs' stimulus duration (in s) for all tested STI pairs as separate curves. The data points for the STIs represent averages from 150 stimulus presentations, the data points for the TTIs average the performance of the animal over 30 stimulus presentations. Continuous lines with open data points represent the data for STI pairs with an *S*/*L*-ratio of 1:2. Dashed lines with filled data points represent the data for STI pairs with an *S*/*L*-ratio of 1:4. (b,c) Test of superimposition of the psychometric functions of (b) *S*/*L* ratios of 1:4 and (c) *S*/*L* ratios of 1:2. Proportion of *L* responses is plotted as a function of the quotient of stimulus duration of the STI pairs/TTIs and the calculated BP. The different symbols mark the different *S*/*L* ratios

influence of the STI condition on the probability of an *L* response is found to be non-significant.

Calculation of all parameters was done in Excel 2016 (Microsoft, Redmond, WA). Statistical analyses were performed in IBM SPSS Statistics Version 27 (IBM, Armonk, NY), the logarithmic regression models were calculated in R (R Core Team [2017], R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/).

3 | RESULTS

In Experiment 1, the harbor seal needed an acquisition phase of 1,867 trials in total to meet the learning criterion for discriminating two time intervals. These trials included phases in which the harbor seal did not learn the discrimination task including an STI of 5 s and CTIs of first 15 s, then 10 s. After changing the STI to 3 s and testing it against a CTI of 10 s, the animal learnt the task within only 346 trials; these trials are also included in the 1,867 trials mentioned above. Threshold determination was ended, after the seal was not able to reach the learning criterion in six consecutive sessions. Its performance in the last two of these six sessions was however high with 76.7% correct choices, a performance above significance level ($p < .01$), and 73.3% correct choices, one error too much to achieve a performance above significance level; thus, the seal almost met the learning criterion for the STI/CTI combination of 3 s/3.5 s. The ΔS for the 3 s STI was determined as 0.8 s with a corresponding Weber fraction of 0.26 (Table 1).

After shifting from Experiment 1 to Experiment 2, the animal was able to discriminate the new STI pair of 1 s/4 s without any learning phase. In general, our data indicate that the animal was able to discriminate *S* and *L* STIs well. This is illustrated by a small proportion of *L* responses ranging from 0.01 to 0.06 (chi square $p < .001$) for *S* STIs and a high proportion of *L* responses for the *L* STIs ranging from 0.87 to 0.99 (chi square $p < .001$; Figure 2a). For the TTIs, the proportion of *L* responses increased the longer the duration of the TTI (Figure 2a).

For all STI pairs, excluding the STI pairs of 2 s/8 s and 3 s/12 s, a mean Weber fraction of or very close to 0.11 was determined (Table 1). No difference was found regarding the Weber fractions for these STI pairs although *S* and *L* had different ratios. The seal's temporal sensitivity can be described as constant by a Weber fraction of 0.11 for all STI pairs with an *S*/*L*-ratio of 1:2. A Weber fraction of 0.12 was determined for the STI pairs of 1 s/4 s with an *S*/*L*-ratio of 1:4. The temporal sensitivity for the remaining STI pairs with 1:4 *S*/*L*-ratio, 2 s/8 s and 3 s/12 s, was albeit lower characterized by Weber fractions of 0.17 and 0.25, respectively. A linear relationship between the temporal difference between *S* and

L and the Weber fraction for the STI pairs of 1:4 ratio ($r^2 = 0.98$) thus constitutes a violation of Weber's law for these STI pairs.

For STI pairs with an S/L-ratio of 1:4, the BP was located above the AM indicated by a K_2 value of 1.12 for the STI pair 1 s/4 s, between GM and AM, but laying closer to the AM indicated by K_2 values of 0.91 and 0.97 for the STI pairs 2 s/8 s and 3 s/12 s (Table 1). In contrast, the BP for the STI pairs with an S/L-ratio 1:2 is closer to the GM, which is illustrated by the K_1 values ranging between 0.95 and 1.01. The STI pair 5 s/10 s is the only STI pair with an S/L-ratio of 1:2 for which the BP is located between the GM and the AM, but slightly closer to the AM as illustrated by a K_2 value of 0.98 (Table 1).

For the STI pairs with a 1:2 S/L-ratio, the scalar property of temporal sensitivity is supported by the constant mean Weber fraction (Table 1), the BP lying closer to the GM, except for the STI pair with the longest durations for S and L, 5 s/10 s. Additionally, a first visual inspection of the psychometric functions (Figure 2c) suggested good superimposition of the psychometric functions of the different STI pairs. A detailed analysis, comparing M0 and M1, did not find a significant influence on the probability of an L response of the different STI pair conditions for the ratio of 1:2 ($p = .056$). For the STI pairs with a 1:4 S/L-ratio, the scalar property of temporal sensitivity is violated: The Weber fraction is not constant but increases from 0.12 to 0.17 and finally to 0.25, and the BP lies closer to the AM (Table 1). Additionally, although the psychometric functions seem to superimpose well (Figure 2b), the Likelihood-Ratio test favored the model M1 over M0 ($p = .011$), which leads to the suggestion, that the different STI pair conditions of the ratio 1:4 have a significant impact on the probability of an L response.

4 | DISCUSSION

In Experiment 1, the performance of harbor seal Henry seemed at first glance inferior to the performance of harbor seal Luca in Heinrich et al. (2016). First, in the acquisition phase, Henry needed eight times longer than Luca to reach the learning criterion. Most likely this difference in learning was caused by the different experimental experiences of both seal individuals; whereas Luca had participated in numerous visual as well as visual cognitive experiments (Scholtyssek, Kelber, & Dehnhardt, 2008; Scholtyssek, Kelber, & Dehnhardt, 2015; Scholtyssek, Kelber, Hanke, & Dehnhardt, 2013), Henry had participated in many scientific experiments, however, addressing numerous sensory modalities (see e.g., Bodson et al., 2007; Hanke et al., 2013; Sticken & Dehnhardt, 2000; Wieskotten et al., 2011) but was inexperienced regarding visual cognitive experiments. Second, the difference threshold of 0.8 s and the corresponding Weber fraction of 0.26 for a 3 s STI were two times higher than the corresponding threshold of Luca; Luca had achieved a Weber fraction of 0.14 for a 3 s STI. However, having a closer look at seal Henry's performance of 76.7% and 73.3% correct choices in session 5 and 6 during threshold determination, this seal almost met the learning criterion (see Section 2) needed to lower the CTI to 3.25 s, which would have resulted in a threshold as low as Luca's threshold. Furthermore, the temporal sensitivity documented for seal Henry in the bisection task was comparable to the performance of seal Luca (Heinrich et al., 2016). In the bisection task, the temporal sensitivity of Henry was characterized by a mean Weber fraction of 0.11 for many STI pairs; the temporal sensitivity only decreased for the STI pair 2 s/8 s (Weber fraction of 0.17) and for the STI pair 3 s/12 s (Weber fraction of 0.25), which will be discussed later. We thus conclude that there is a good correspondence across seal individuals and across different methods addressing temporal abilities.

The temporal sensitivity assessed during temporal bisection allows inter-specific comparisons as bisection data are available for numerous other species. In general, the harbor seal's temporal sensitivity is within the range of results obtained for example in pigeons or humans for which Weber fractions approximately between 0.1 and 0.4 were determined. This comparison is complicated by methodological differences including for example differences in duration of the S and L tested. To give examples, the seal's Weber fraction is comparable to the Weber fractions obtained in adult humans of different age for STI pairs of 2 s/8 s (Ortega & López, 2008) or 3 s/6 s (Lustig & Meck, 2011; Penney et al., 2000; Penney et al., 2014), however, the seal's timing performance is worse for an STI pair of 4 s/8 s (Zélanti & Droit-Volet, 2011); comparing seals with children again changes the picture as the children's performance is far inferior when tested with STI pairs of 1 s/4 s and 2 s/8 s (Droit-Volet et al., 2003; Droit-Volet & Clement, 2001; Rattat & Droit-Volet, 2001). Pigeons and seals perform comparably precise for an STI pair of 1 s/4 s, whereas seals are outperformed by pigeons for an STI pair of 2 s/8 s (Fox et al., 2016). Nevertheless, our bisection results further strengthen the overall impression obtained in previous seal timing studies (Heinrich et al., 2016; Heinrich et al., 2020) that timing in seals compares favorably with the timing performances of other species, and differences in performance can most likely be attributed to the fact that the studies differ in experimental details and not that the timing abilities differ systematically.

Additional results further imply that processes underlying temporal bisection are comparable across species

(Allan, 1991; Wearden et al., 1997). The first aspect is the dependency of the temporal sensitivity on temporal difference between *S* and *L*. In our study, the mean Weber fraction as a measure of sensitivity was calculated as 0.11 for the STI pairs with a ratio of 1:2 as well as for the STI pair 1 s/4 s with a ratio of 1:4. In contrast, the Weber fraction increases, thus temporal sensitivity decreases, with increasing difference between *S* and *L* for the STI pair 5 s/10 s and for the STI pairs with a ratio of 1:4. Most likely, the reduced temporal sensitivity for STIs with large differences between *S* and *L* resulted from the reduced difficulty of the task with *S* and *L* being far apart in duration in line with results/conclusions of studies including rats and humans (Church & Deluty, 1977; Kopec & Brody, 2010; Wearden et al., 1997). Alternative explanations can most likely be ruled out in our experiment: (a) the ratio of the STI pair, if the ratio had an influence on temporal sensitivity, we would not have expected to find an equivalent sensitivity for the STI pairs with a ratio of 1:2 and the STI pair of 1 s/4 s, (b) the absolute duration of the STIs, if the absolute duration had influenced temporal sensitivity, we would have expected the temporal sensitivity for the STI pair 5 s/10 s to be inferior than assessed, as 10 s was the second longest STI, and (c) different cognitive processes and timing mechanisms underlying the timing of different durations of time intervals ((Buhusi & Meck, 2005; Ivry & Spencer, 2004), as these are usually thought to be different for sub- and supra-second time intervals, however, we only used intervals in the second range, and, for intervals in this time range, the temporal sensitivity of harbor seals has already been shown to be constant (Heinrich et al., 2016). Although we have evidence, that the temporal difference of the tested *S* and *L* affects temporal sensitivity after testing seven STI pairs in the second range, which is more than usually tested in bisection tasks, it would be necessary to collect comparable data in a number of species, to consolidate the conclusions drawn on the basis of the current results obtained in harbor seals.

The second aspect, that suggests that the processes underlying seal timing are comparable to other species, relates to the location of the BP being affected by the relative spacing of the STIs. We found the BP for all STI pairs with an *S*/*L* ratio of 1:2, except for the STI pair 5 s/10 s, to be closer to the GM than to the AM. In contrast, the BP was assessed to be closer to the AM for the STIs with a ratio of 1:4. These findings are in line with results from previous studies, including humans and rats, in which an L/S ratio $\leq$ 2:1 resulted in the BP lying closer to the GM, and an L/S ratio > 4:1 caused the BP to shift closer to the AM independent of methodical differences (for review Allan, 2002b; Kopec & Brody, 2010; Raslear, 1985; Siegel & Church, 1984; Wearden & Ferrara, 1996). As already discussed in Kopec and Brody (2010), the ratio of the STIs, which also has an impact on the location of the GM and AM of the specific STI pair, seems to influence the location of the BP, with only one exception.

Third, many of our results support one of the most common timing theories, the SET (Gibbon, 1977), which is also applicable for other species' timing abilities: (a) the temporal sensitivity can be described by a constant Weber fraction, (b) the psychometric functions for an *S*/*L* ratio superimpose well, and (c) the location of the BP is close to the GM. These aspects were found for the STI pairs 2 s/4 s, 3 s/6 s, and 4 s/8 s with an *S*/*L* ratio of 1:2. In contrast, the SET prerequisites are not met for the STI pairs 5 s/10 s and the STI pairs with an *S*/*L* ratio of 1:4. These observations illustrate, as assumed in earlier studies, that the SET is not able to explain how all temporal stimuli are dealt with, reflecting that timing abilities and temporal categorization are affected by numerous parameters, such as memory processes, attention (e.g., Meck, 1984), response bias (e.g., Gibbon et al., 1984; Raslear, 1983; Raslear, 1985) and other non-temporal factors (e.g., Akdoğan & Balcı, 2016; Allan, 2002b; Allan & Gerhardt, 2001; Allman, Teki, Griffiths, & Meck, 2014; Jozefowiez, Polack, Machado, & Miller, 2014; Penney et al., 2014).

Lastly, our results suggest, that the animal used both STIs for the categorization of the TTIs, as the location of the BP was different for the STI pairs with the same S, such as 2 s/4 s and 2 s/8 s or 3 s/6 s and 3 s/12 s and with same *L*, such as 2 s/8 s and 4 s/8 s. If the animal had only used one STI for its decision such as the S, as during temporal discrimination, we would have expected the location of the BP to be unchanged for STI pairs with the same *S* (aspect also discussed in Allan, 1991). This categorization mechanism, taking both STIs into account, was considered in different timing theories (Allan, 2002a; Araiba & Brown, 2017; Killeen, Fetterman, & Bizo, 1997; Kopec & Brody, 2010; Meck, 1983; Ng, Tobin, & Penney, 2011; Wearden, 1991a; Wearden & Bray, 2001; Wearden & Ferrara, 1995) which might thus also apply to harbor seal timing. Assessing the harbor seal's temporal bisection performance, we can show that a harbor seal is even able to solve a timing task with increased complexity, compared to a temporal discrimination task, with ease. In conclusion, the timing abilities of harbor seals also allow solving a complex timing task, and the decision process seems to include both STIs.

In conclusion, a harbor seal, although unexperienced regarding visual cognitive experiments, could successfully solve a temporal discrimination and a complex temporal bisection task with ease. It achieved a performance comparable to another seal individual and other species, and several results indicate that timing in seals is governed by generally described processes. Its performance partially supports the SET, while at the same time illustrating that numerous parameters influence timing performance. Altogether, our results imply that harbor seal timing is well-developed.

Future studies will need to address whether time can also be inferred from stimuli of modalities other than vision. Stimulus modality could have an influence due to for example different neuronal processing of the respective signal. However, we expect sensitivity of timing in seals to be equally precise irrespective of stimulus modality allowing seals to have access to temporal information under different environmental conditions with different sensory systems predominantly or exclusively in operation. Moreover, ecologically motivated studies might help to clarify the role timing plays during navigation, orientation, and foraging thereby complementing or sometimes even substituting the classic sensory systems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Tamara Heinrich: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; validation; visualization; writing-original draft; writing-review & editing. **Alexander Lappe:** Formal analysis; methodology; writing-review & editing. **Frederike Hanke:** Conceptualization; funding acquisition; resources; supervision; validation; writing-review & editing.

ETHICS STATEMENT

The experiments carried out in this study were in accordance with the European Communities Council Directive of November 24, 1986, (86/609/EEC) and the German Animal Welfare Act of 2006. The individual used in the study was not subject to pain, suffering or injury therefore no approval or notification was required.

DATA AVAILABILITY STATEMENT

All data are included in the manuscript. Detailed learning performances are available from the authors upon reasonable request.

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