Near-threshold equal-loudness contour estimates for harbor seals (*Phoca vitulina*) based on reaction times during audiometry studies with tonal signals

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Near-threshold equal-loudness contours for harbor seals (*Phoca vitulina*) based on reaction times during audiometry studies with tonal signals

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Abstract

Animals do not hear equally well at all frequencies. Equal-loudness functions describe relationships between the frequencies of sounds and their perceived loudness. Sounds of equal perceived loudness are assumed to elicit equal reaction times (RTs). During a psychoacoustic hearing study, the responses of two young female harbor seals to tonal signals between 0.125 and 100 kHz were filmed. For all responses, frame-by-frame analysis was used to quantify RT (the time between the onset of the sound stimulus and the onset of movements away from the listening station, made by the seals to indicate their detection of the signal). Near-threshold equal-latency contours, which represent equal-loudness contours, were estimated from RT-level functions fitted to mean RT data. The closer the received SPL was to the 50% detection hearing threshold, the more slowly the animals reacted to the signal (RT range: 188-982 ms). The equal-latency contours of the seals were similar in shape to their individual 50% detection hearing curves. Equal-latency levels were calculated relative to the RTs shown by each seal at sound levels of 0, 10 and 20 dB above the detection threshold at 1 kHz. Because 50% detection thresholds are obtained with well-trained subjects actively listening for very faint sounds which they cannot detect half of the time, when calculating audibility ranges of sounds for harbor seals in nature, it may be appropriate to consider levels at 20 dB above this threshold. At the more realistic audibility ranges resulting from this calculation, sounds would almost certainly be detected in natural situations (depending on the background noise, signal duration, animal orientation relative to the sound source, and general context).

I. INTRODUCTION

Humans and other animals do not hear equally well at all frequencies within their functional hearing range. A certain received level (above the listener's detection threshold) is not perceived as equally loud for all frequencies. To compensate quantitatively for this differential frequency response of hearing systems, frequency weighting can be applied which emphasizes or de-emphasizes the spectral components in a sound. For humans, substantial improvement in dose-response models is obtained by filtering noise through weighting functions derived from equal-loudness contours (e.g. A- and C-weighting; Kinsler *et al.*, 2000). Equal-loudness functions, expressed in phons (for humans), are used to describe the relationship between the received level at different frequencies and the perceived loudness.

An equal-loudness contour is a curve showing the varying sound pressure levels of a pure tone that has the same apparent loudness at various frequencies. Fletcher and Munson (1933) presented listeners with pure tones at various frequencies over 10 dB increments in stimulus loudness. For each frequency and loudness, the listener was also presented with a reference tone at 1000 Hz. The test tone was adjusted until it was perceived to be of the same loudness as the reference tone. The lowest equal-loudness contour, which represents the quietest audible tone, is also known as the absolute threshold of hearing. The highest contour is the pain threshold. The currently most accepted set of equal-loudness contours was based on 12 studies of humans (Suzuki and Takeshima, 2004), and was standardized in a revised version of ISO 226:2003 (International Organization for Standardization).

Underwater noise from human activities (particularly at low frequencies; Ross, 1976) has increased during the last century due to global industrialization. Noise from e.g. ships, oil and gas exploration and exploitation, wind generator parks, and some military and civil low-frequency sonar systems may affect seals by displacing them from areas used for foraging or reproduction, or by reducing their hearing sensitivity temporarily or permanently. Noise can also compromise hearing by masking signals (Richardson *et al.*, 1995).

Criteria for allowable noise exposure in humans are based on frequency-weighting functions which take into account both the frequency bandwidth of human hearing and loudness perception (Crocker, 1997). Noise exposure criteria for marine mammals should also be based on weighting functions derived from equal-loudness contours, as recommended by Southall *et al.* (2007). Behavioral effect studies with marine mammals would benefit from the development of more accurate weighting functions. Realistic weightings would improve the correlation between the dose and the response in studies of responses to broadband signals.

Thus far, equal-loudness contours derived as described above only exist for humans. It is difficult to apply loudness-matching techniques to animals, so instead, reaction time (RT, or response latency) data from psychophysical experiments, and amplitude-intensity functions from evoked potential experiments have been used to estimate equal loudness (Dent, 2000, 2005). In humans, several studies have shown that RT is a good predictor of perceived loudness. The RT-loudness relationship has been established by using loudness matching of pure tones (Buus *et al.*, 1982) and 1/3-octave bands (Humes and Ahlstrom, 1984), and by exploiting temporal and spectral loudness effects, such as loudness recalibration (Arieh and Marks, 2003) and spectral summation of loudness (Wagner *et al.*, 2004). Equal-latency contours can be derived from a subject's RT to a sound. These equal-response contours show good correspondence with equal-loudness functions derived by loudness-matching procedures in humans (Pfingst *et al.*, 1975a; Marshall and Brandt 1980). Equal-latency contours have been calculated for a few mammals and birds, including some primates (Stebbins, 1966; Pfingst *et al.*, 1975a; Green, 1975; Dooling *et al.*, 1978; May *et al.*, 2009).

So far, in marine mammals, the only published attempt at quantifying equal-latency contours is a preliminary study on loudness at frequencies of 5 to 120 kHz, based on whistle response time (acoustic RT) in hearing studies with bottlenose dolphins (*Tursiops truncates*; Ridgway and Carder, 2000). So far, no equal-loudness studies have been conducted with pinnipeds. Therefore the goal of the present study was to derive near-threshold equal-loudness estimates from RTs collected during psychoacoustic hearing studies with two harbor seals (*Phoca vitulina*; Kastelein *et al.*, 2009).

II. MATERIALS AND METHODS

A. Study animals

The study animals were two female harbor seals (codes SM.Pv.01 and SM.Pv.02), which were born at the Ecomare Centre, Texel, the Netherlands. Throughout the study, the animals were healthy. During the study they aged from 14 to 18 months and their body weight increased from around 34 kg to around 42 kg. The seals were fed four times per day, in general during research sessions.

B. Study area

The study was conducted at the SEAMARCO Research Institute in the Netherlands, in an outdoor pool (8 m (l) x 7 m (w), 2 m deep), with an adjacent haul-out space. The water circulation pump and the air pump of the bio-filter were shut off 10 minutes before and during test sessions, to reduce noise. This also reduced flow noise from the skimmers. The signal operator and the equipment used to produce the stimuli and monitor the underwater sounds were in a research cabin next to the pool, out of sight of the animals. More details of the study area are given by Kastelein *et al*. (2009).

C. Test stimuli

Two types of tonal signals were used. Between 0.125 and 0.250 kHz, pure tones were used. Between 0.5 and 100 kHz, narrow-band sinusoidal frequency-modulated (FM) tonal signals (with center frequencies of 0.5, 1, 2, 4, 8, 16, 25, 31.5, 40, 50, 63, 80, and 100 kHz) were used. The modulation range of the signals was ± 1% of the center frequency (the frequency around which the signal fluctuated symmetrically), and the modulation frequency was 100 Hz. FM signals were used because such signals produce fewer constructive and destructive interference effects (standing waves) in a reverberant pool than pure tones. The stationary portion of all signals was 900 ms, and the rise and fall times were 50 ms (to prevent onset or offset transients). The sound pressure level (SPL) at the seal's head while it was at the listening station could be varied in 5 dB increments (this step size was determined by the audiometer: 5 dB steps are generally used in human audiometry). More details about the sound generating equipment and the measurements of the background noise and test signal SPLs are given by Kastelein *et al*. (2009).

D. Experimental procedure

The seals were trained to respond ('go') in the presence of a signal and to withhold the response ('no-go') in the absence of a signal. A trial began when one of the animals was positioned with its head at the start/response buoy at the edge of the pool next to the trainer (**Fig. 1)**. When the trainer gave the animal a vocal command accompanied by a gesture (pointing downwards), the animal descended to the listening station (an L-shaped, 32 mm-diameter, water-filled polyvinylchloride (PVC) tube with an end cap), so that its external auditory meatus was 200 cm from the sound source and 100 cm below the water surface (*i.e.* mid-water**)**. Each animal was trained to position its nose against the listening station so that its head axis was in line with the projected beam axis of the transducer. The animals' positions could be viewed from above by means of an underwater camera (Mariscope, Micro) which was attached to the listening station. The images were visible to the trainer near the start/response buoy (who could not be seen by the study animal at the listening station) and to the operator in the research cabin.

If the animal detected the sound, it responded by leaving the listening station ('go' response) at any time during the signal's duration and returning to the start/response buoy (**Fig. 1**). If the animal had not responded approximately 2 s after signal onset, the operator indicated to the trainer that the animal had failed to detect the signal ('no-go').

A session generally consisted of 30 trials per animal and lasted for about 15 min. per animal. The seals were always tested in the same order. During experimental sessions, the starting SPL of the signal was 10-15 dB above the estimated threshold. Following each hit, the signal amplitude of the next signal-present trial was reduced by 5 dB. Following each miss, the signal level was increased for the next signal-present trial by 5 dB.

Fifty percent detection thresholds were determined for the 16 tonal signals mentioned above. To prevent the animals' learning processes from affecting the threshold levels, the test frequency was varied from day to day and adjacent frequencies were usually tested on successive days (going from low to high and from high to low frequencies, in the 'up/down staircase' method).

Usually four experimental sessions were conducted on five days per week (at 0900, 1100, 1400 and 1600 h). Data were collected between August and November 2007. More details about the experimental procedure can be found in Kastelein *et al*. (2009).

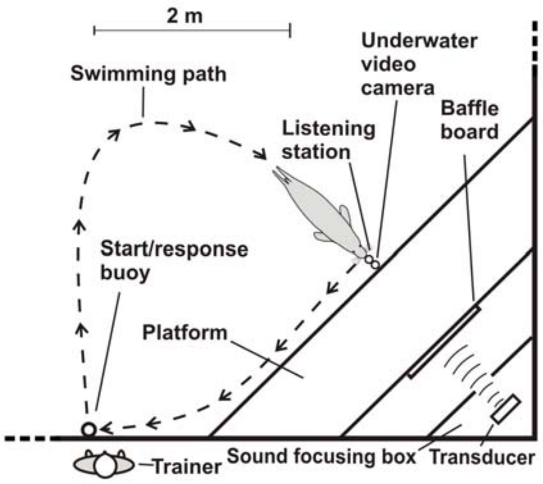
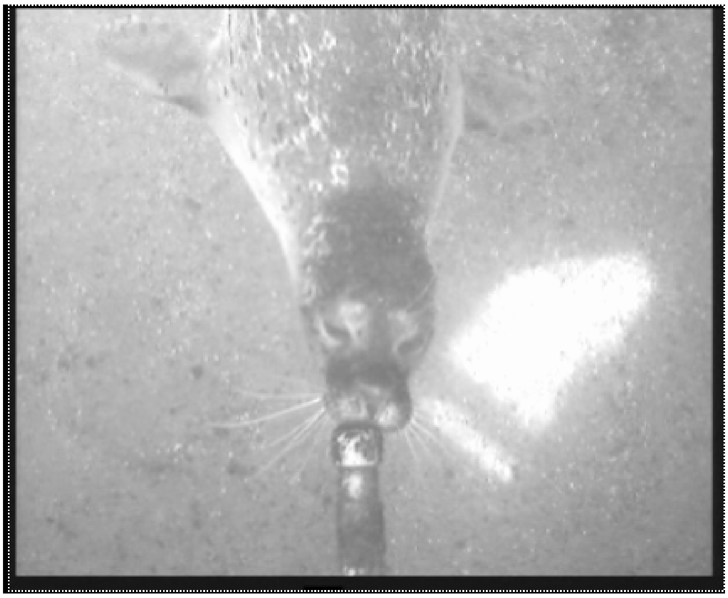


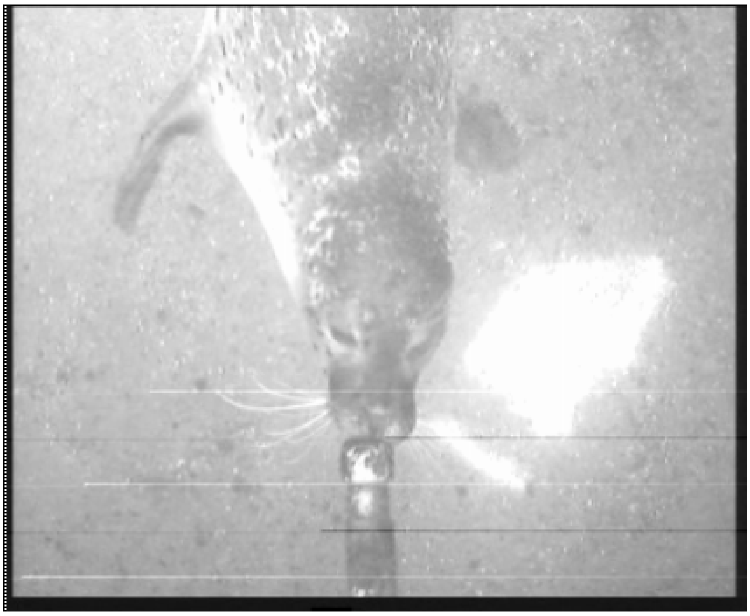
FIG. 1. Top view of the study area, with the harbor seal at the listening station. Also shown is the swimming path of the animal in response to a test signal.

E. Image recording and video analysis

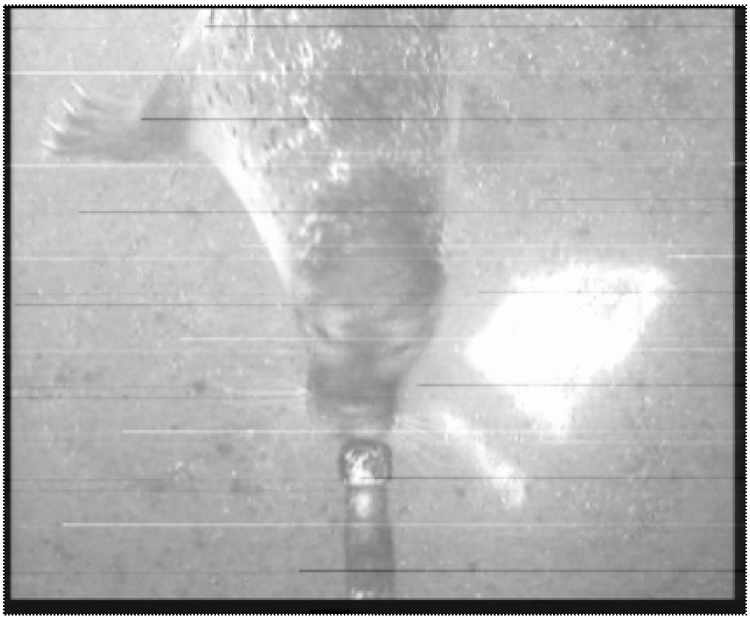
In order to calculate their RTs, the animals' movements, captured by the underwater video camera, were recorded on tape. An electrical signal, generated by the audiometer when the test signal was produced, was fed into the video recorder. The signal produced an image distortion consisting of horizontal lines on the video image, which allowed the video frames with and without test signals to be distinguished visibly in the frame-by-frame analysis. The tapes were digitized using a video analog-to-digital converter (Dazzle DVC 100 USB; Pinnacle Systems) and analyzed with a video editing program (VideoChargeSoftware, 2007). In the frame-by-frame analysis, the RTs of the seals were measured to the nearest 40 ms (this was the duration of one frame; 25 frames/s). RT was defined as the time between the onset of the signal (the video image distortion) and the beginning of the animal's head movement (**Fig. 2**). There was a small time difference between the video image distortion and the sound arriving at the animal. This time delay, caused by the travel time of sound through the water (2.0 m distance/1500 m/s speed of sound), was 1.3 ms, which is negligible in relation to the RTs found in this study (188-982 ms) and to the accuracy with which they were recorded (40 ms). One RT was measured for each trial in which the animal detected the acoustic stimulus.



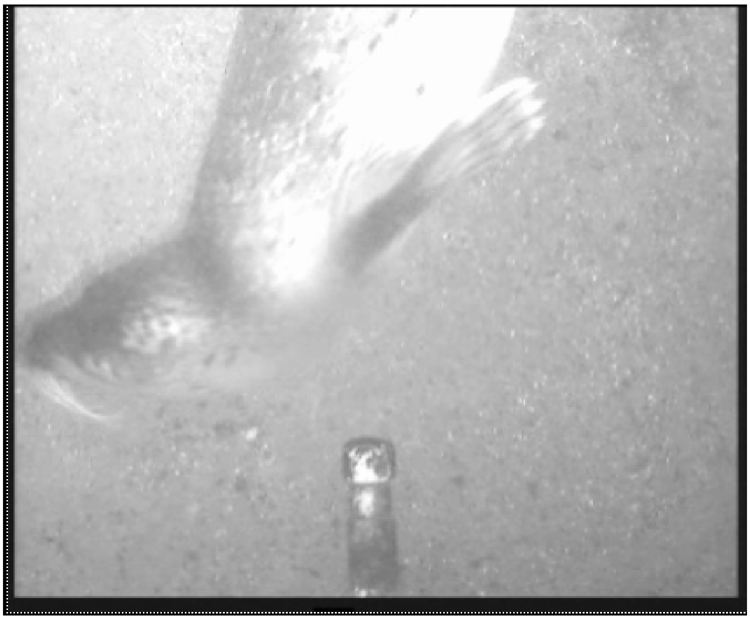
a) A seal at the listening station, waiting for a sound signal



b) A seal at the listening station at the onset of the sound signal (indicated by the image distortion in the form of horizontal lines)



c) The seal reacting after detecting the signal by moving to its right



d) The seal moving towards the response buoy, after the signal has stopped

FIG 2. A seal at the listening station waiting for a signal (a), the seal at the listening station at the onset of the sound signal (indicated by the image distortion in the form of horizontal lines) (b), the seal reacting after detecting the signal by moving to its right (c), and the seal moving towards the response buoy, after the signal has stopped (d).

F. Analysis of the reaction time (RT) data

To estimate the equal-latency contours, the RT data were evaluated as a function of frequency and Sensation Level (sometimes abbreviated as SL, but given in full here to avoid confusion with Source Level), which is defined as the received SPL in dB relative to the 50% detection threshold under the actual background noise conditions of the same animal at the same signal frequency. Because the 50% detection threshold is the average of a number of trials, the Sensation Level per trial can vary in 1 dB steps between -5 and +20 dB.

In general a session began about three 5 dB steps above the 50% detection threshold. Therefore, the RT sample size per data point increases as the Sensation Level approaches zero, i.e. as the received SPL approaches the 50% detection threshold (**Fig. 3**) as a result of the up/down staircase procedure. Mean RTs were calculated from a minimum of seven RT measurements per signal level. This minimum sample size was considered acceptable because RTs were relatively invariable at higher received SPLs.

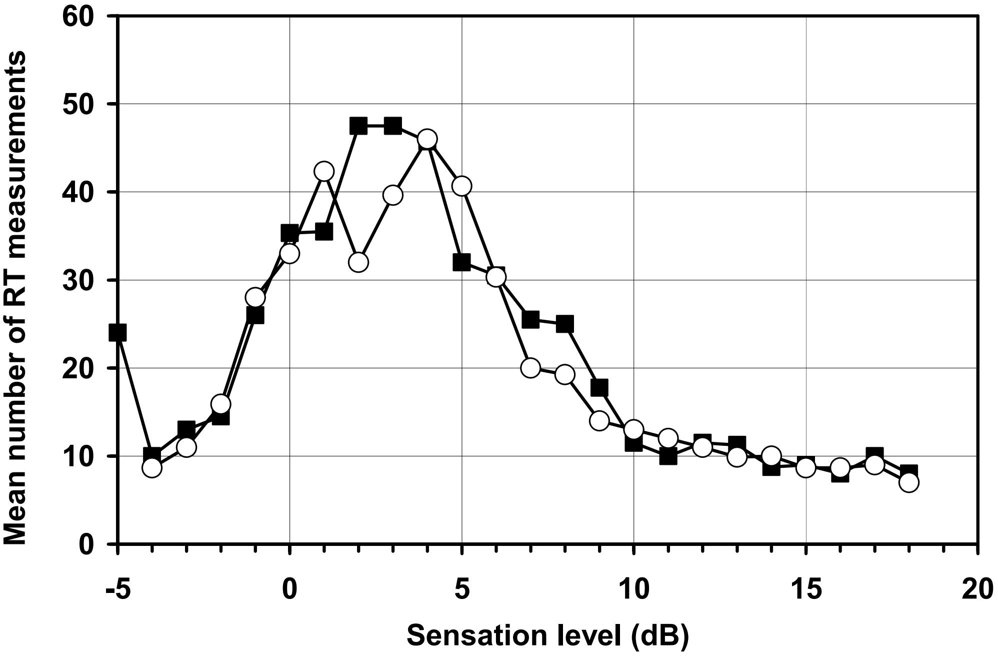


FIG. 3. The mean number (over all test frequencies) of RT (reaction time) measurements used to calculate the mean RTs, as a function of Sensation Level for harbor seal 01 (■) and harbor seal 02 (○). The sample size per data point increases as the received SPL approaches the 50% detection threshold (0 dB-Sensation Level), as a result of the up/down staircase method used.

In RT-based equal-latency contours, the SPL values that correspond with an equal RT are presented as a function of frequency. These SPL values have to be obtained by interpolation in, and extrapolation of, the data set of RT as a function of SPL at each frequency. For each frequency, the following simplified form of the Piéron function (Pins and Bonnet, 2000) was fitted to the mean RT data to obtain a set of RT-level functions:

$$RT = kI^{-\beta} \qquad (1)$$

where I is the Sensation Level converted to linear units by $10^{(\text{Sensation Level}/10)}$, and k and β are free parameters. This two-parameter power law was preferred over the more commonly used three-parameter form of the Piéron function (Piéron, 1920), because, for the majority of frequencies, RTs did not approach an asymptotic value at the higher received SPLs. In order to determine the overall difference in RT between the two seals, Equation 1 was also fitted to the mean RT data for all frequencies.

To obtain the RT estimates of the equal-latency contours, the approach used by May *et al.* (2009) was taken. As in human studies, a reference frequency of 1 kHz was chosen. For each animal, the reference RT values for the contours were obtained by evaluating the 1-kHz RT-level function at Sensation Levels of 0, 10 and 20 dB. This resulted in RTs of 675, 442, and 289 ms for seal 01, and of 780, 388, and 193 ms for seal 02. Thereafter, the equal loudness levels were calculated by matching equal RTs across signal frequency and level. **Figure 4** illustrates this process for frequencies of 0.2, 1, and 80 kHz. The SPLs at which the horizontal equal-RT lines cross the fitted RT-level functions were selected to be part of the equal-latency contours. RTs were fitted as functions of Sensation Level, not as functions of SPL, but SPL is used in **figure 4** to visualize the RT-matching procedure.

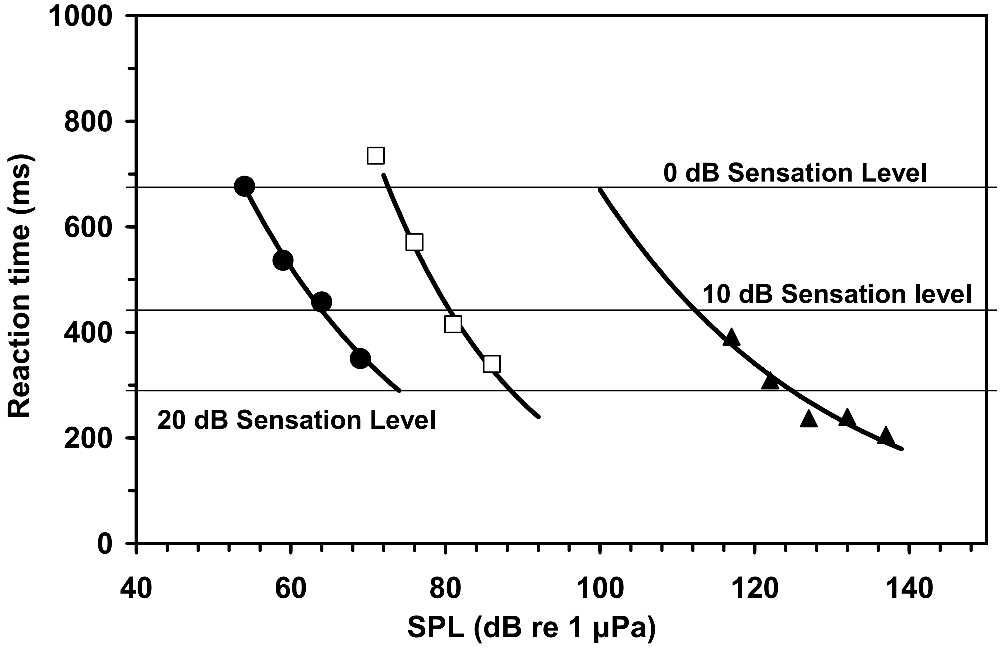


FIG. 4. Example of the RT (reaction time)-matching procedure used to derive the equal-latency contour data of harbor seal 01 for frequencies of 0.2 kHz (□), 1 kHz (● ; the reference frequency), and 80 kHz (▲). One RT-level function is shown for each of the three frequencies as a black hyperbolic (Piéron function, Eq. 1) regression line through the means of the observed RTs at 0, 5, 10 and 15 dB-Sensation Level (677, 536, 457 and 350 ms). Three RTs were obtained by evaluating the 1-kHz RT-level function at Sensation Levels of 0, 10, and 20 dB. These RTs of 675, 442, and 289 ms are shown as horizontal lines in the graph. The received SPLs that elicit equal-RT, thus the points where the horizontal and curved lines cross, are the data points that were used for the construction of the equal-latency contours.

III. RESULTS

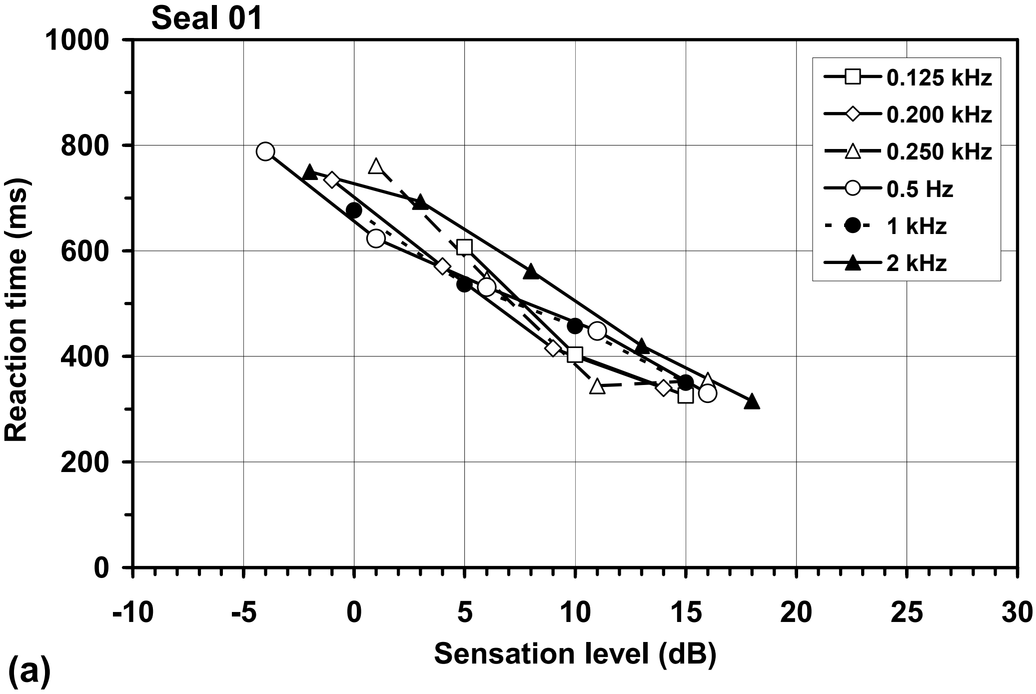
The relationship between the Sensation Level and the average observed RTs of seal 01 and seal 02 for 16 tonal signals is shown in **Fig. 5**. The RT decreased as the Sensation Level increased, and signals of higher frequency induced shorter response times. The seals responded 188 to 982 ms after signal onset to signals within the range of -4 to 18 dB-Sensation Level.

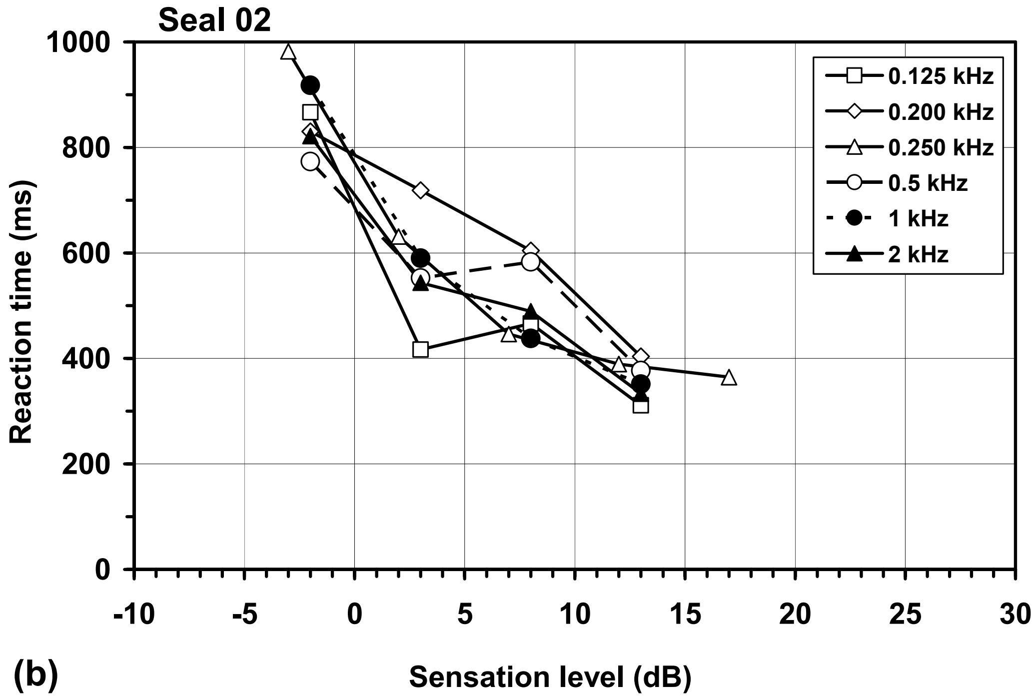
A fit of the two-parameter Piéron function (Eq. 1) to the mean (all-frequencies, and -4 to 20 dB-Sensation Level) RT data of seal 01 and seal 02 showed that harbor seal 01 had on average 33 ms slower RTs than harbor seal 02. However, the shape of the animals' RT-level function was similar: the slope coefficient β was 0.22 for seal 01, and 0.25 for seal 02. The mean RTs for all frequencies at the 0 dB-Sensation Level were 606 ms for seal 01, and 581 ms for seal 02 (at 0 dB-Sensation Level the difference is 606-581=25 ms; at 20 dB-SL the difference is 220-184=36 ms. The slopes of the RT-Level functions are similar but not identical).

The near-threshold equal-latency contours of the seals, based on RT-matches at 16 frequencies, are shown in **Fig. 6**. Also shown are the underwater behavioral 50% detection thresholds of the same animals obtained during the same research sessions (Kastelein *et al.*, 2009).

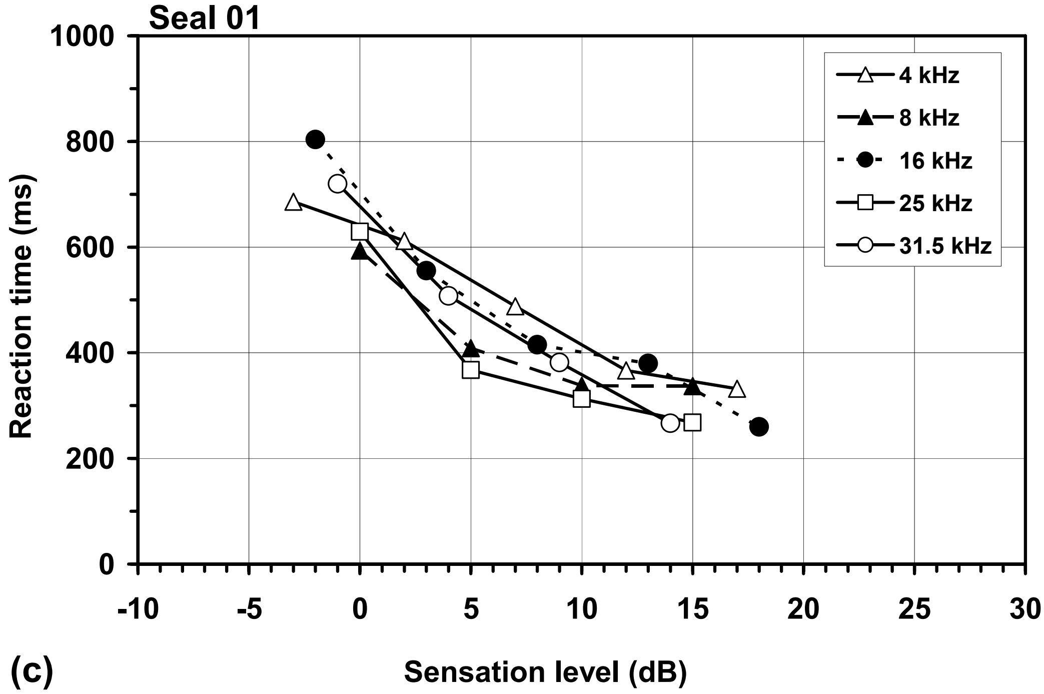
For seal 01, the three equal-latency contours correspond well with the 50% detection thresholds, with slightly less spacing between the curves at frequencies below 0.5 kHz and above 8 kHz. The 0 dB perceived loudness levels and the 50% detection thresholds for 0.125-40 kHz are within 4 dB of one another, and fall below the 50% detection threshold near the high-frequency cutoff (**Table I**).

For seal 02, the shapes of the equal-latency contours and the 50% detection thresholds are similar, but the spacing between the curves is more variable. The 0 dB perceived loudness levels and the 50% detection thresholds for frequencies of 0.125-4 kHz are within 3 dB of one another, and fall below the 50% detection threshold at frequencies above 4 kHz (**Table I**).

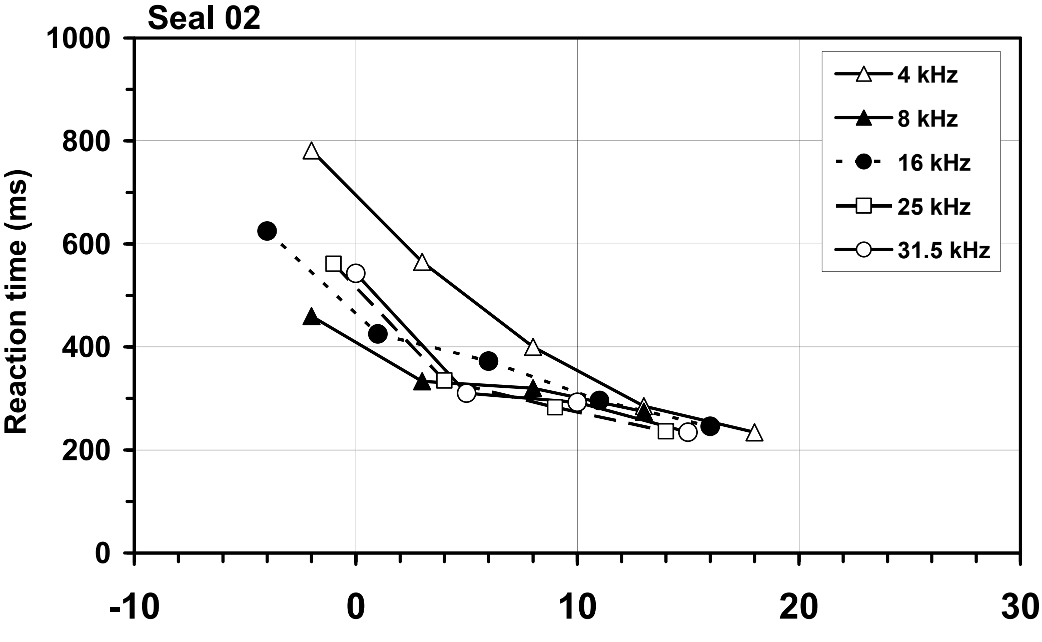



Seal 02
Reaction time (ms)
1000
800
600
400
200
0
-10
-5
0
5
10
15
20
25
30
Sensation level (dB)
0.125 kHz
0.200 kHz
0.250 kHz
0.5 kHz
1 kHz
2 kHz

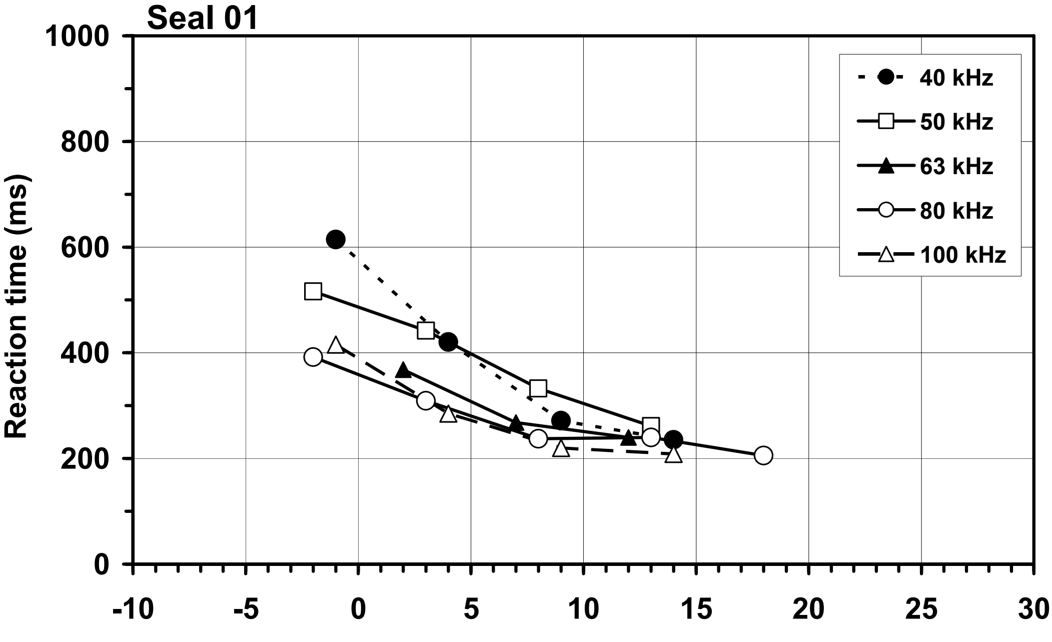
(b)


Seal 01
Reaction time (ms)
1000
800
600
400
200
0
-10
-5
0
5
10
15
20
25
30
Sensation level (dB)
4 kHz
8 kHz
16 kHz
25 kHz
31.5 kHz

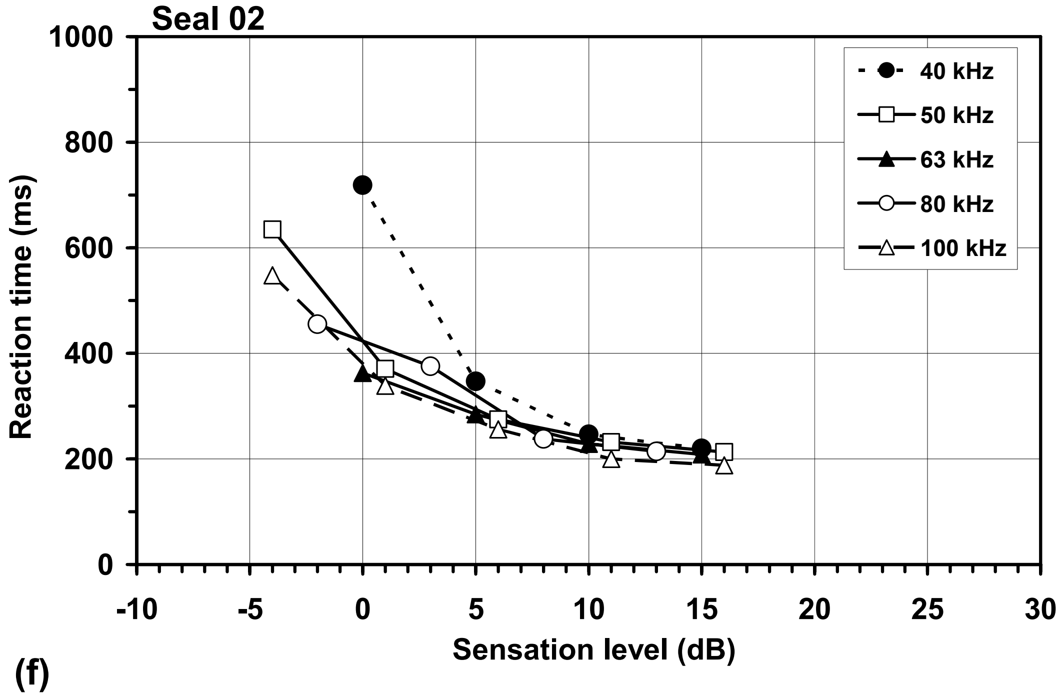
(c)


Seal 02
Reaction time (ms)
1000
800
600
400
200
0
-10
0
10
20
30
Sensation level (dB)
4 kHz
8 kHz
16 kHz
25 kHz
31.5 kHz

(d)


Seal 01
Reaction time (ms)
1000
800
600
400
200
0
-10
-5
0
5
10
15
20
25
30
Sensation level (dB)
40 kHz
50 kHz
63 kHz
80 kHz
100 kHz

(e)



(f)

FIG.5. The relationship between the Sensation Level (received SPL relative to the 50% detection threshold) and the average RT (reaction time) of harbor seals 01 and 02. The RT decreases as the received SPL increases. The sample size per data point increases as the received SPL approaches the threshold, as a result of the audiometric up/down staircase method used. In some cases (on average in three levels per frequency) the sample size for signals with levels below the 50% detection threshold was too low (< 7) for the data to be included. In general a session began about three 5 dB steps above the 50% detection threshold (i.e., 0 dB-Sensation Level).
a) seal 01 for signals of 0.125-2 kHz, b) seal 02 for signals of 0.125-2 kHz, c) seal 01 for signals of 4-31.5 kHz, d) seal 02 for signals of 4-31.5 kHz, e) seal 01 for signals of 40-100 kHz, and f) seal 02 for signals of 40-100 kHz.

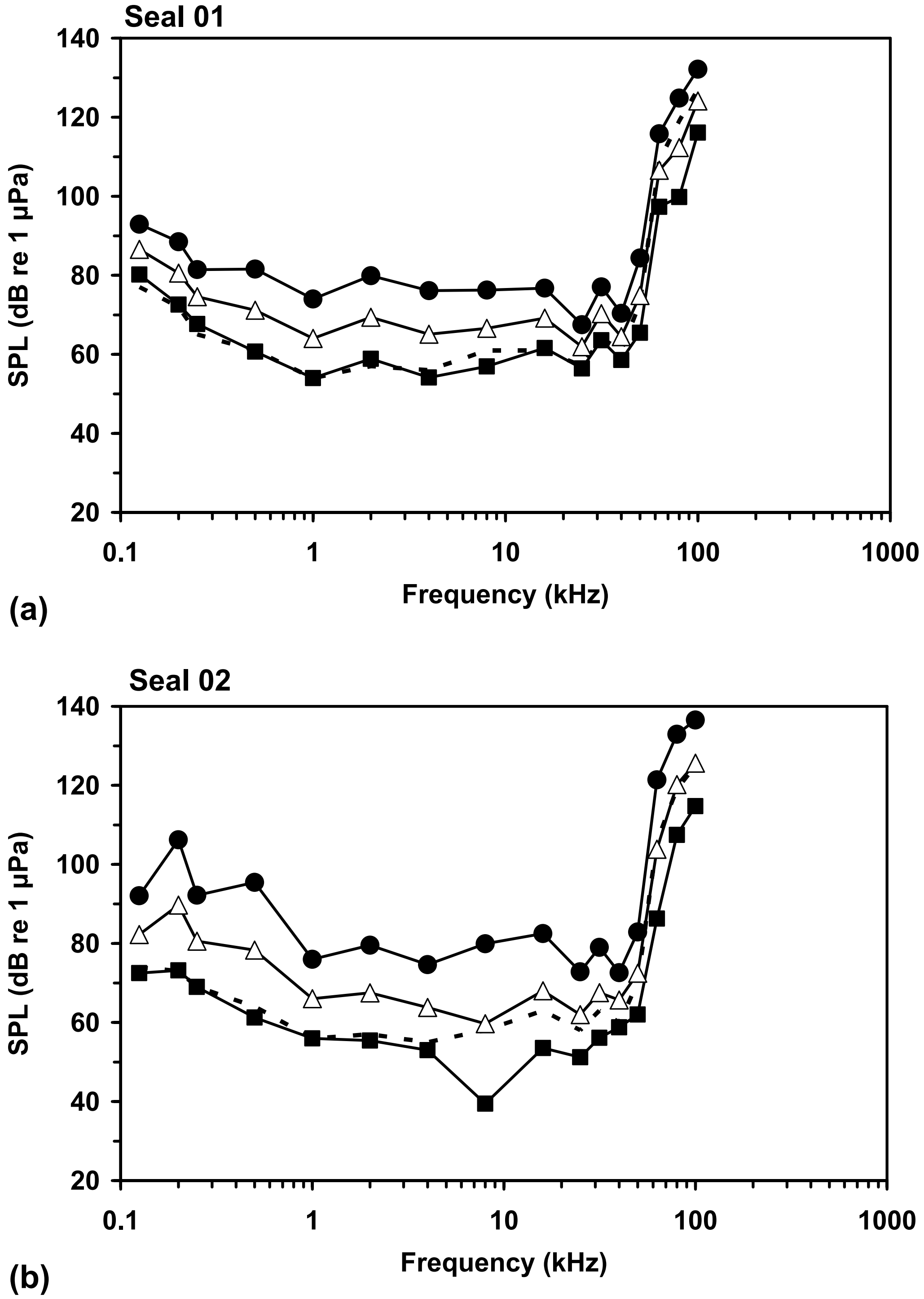


FIG. 6. The relationship between RT (reaction time), frequency and received SPL near the absolute hearing threshold of (a) harbor seal 01 and (b) harbor seal 02 for 16 tonal signals. The 0 dB (■), 10 dB (Δ), and 20 dB (●) equal-latency contours are shown (corresponding to equal-loudness contours; RTs are 675, 442, and 289 ms for seal 01, and 780, 388, and 193 ms for seal 02), together with the behavioral 50% detection hearing thresholds of the animals (the dashed lines; Kastelein *et al.*, 2009). To calculate realistic (i.e., 100%) detection ranges of sounds by harbor seals, the 20 dB contour may be a better level than the 50% detection threshold level.

TABLE I. Sound pressure levels of the 50% detection thresholds (Kastelein *et al*., 2009) of seal 01 and 02 and the 0, 10 and 20 dB equal-latency contour data for each of the two harbor seals (see also **Fig. 6**).

Frequency	Seal 01				Seal 02			
	50% Detection threshold	Equal latency contours			50% Detection threshold	Equal latency contours		
		0 dB	10 dB	20 dB		0 dB	10 dB	20 dB
kHz	dB re 1μPa	dB re 1μPa	dB re 1μPa	dB re 1μPa	dB re 1μPa	dB re 1μPa	dB re 1μPa	dB re 1μPa
0.125	77	80	87	93	74	73	82	92
0.2	72	73	81	88	73	73	90	106
0.25	65	68	75	81	69	69	81	92
0.5	61	61	71	82	64	61	78	95
1	54	54	64	74	56	56	66	76
2	57	59	69	80	57	55	68	80
4	56	54	65	76	55	53	64	75
8	61	57	67	76	58	39	60	80
16	61	62	69	77	63	54	68	83
25	57	56	62	67	58	51	62	73
31.5	64	64	70	77	63	56	68	79
40	61	59	64	70	60	59	66	73
50	73	65	75	84	70	62	72	83
63	109	97	107	116	106	86	104	121
80	119	100	112	125	119	107	120	133
100	127	116	124	132	125	115	126	137

IV. DISCUSSION AND CONCLUSIONS

A. Evaluation of the data

On average, seal 01 responded more slowly than seal 02. Because both seals were tested within the same session, the differences in RT between the two animals were probably due to differences in the seals' physiology or psychological state, and were not caused by differences in equipment, equipment settings, methodology, personnel, or background noise. Variability between subjects is common in RT studies, which means that equal-latency contours derived from RTs averaged across individuals, or from averaged contours with arbitrarily chosen latencies, are questionable. Using the seals' own 1-kHz response latencies compensates for such inter-subject variability, and makes comparison between equal-loudness contours derived from loudness-matching procedures and equal-latency contours derived from RT-matching procedures more appropriate (May *et al*., 2009).

At 0 dB-Sensation Level, the seals' responses to high frequency signals were generally faster than their responses to 1 kHz signals (**Fig. 5**). As a result, the RT-level functions were often extrapolated to find the data for the 0 dB contour (for example at 80 kHz for seal 01; **Fig. 4**), which in turn resulted in the 0 dB equal-loudness contour dropping below the animal's own 50% detection hearing threshold in the high frequency range (**Fig. 6**). Some of the extremely low values are likely to be artifacts of the RT-matching procedure (e.g. at 8 kHz for seal 02), and the reason for the difference in RT between signal frequencies remains unknown.

B. Other studies on loudness and RT

RTs to near-threshold stimuli are sometimes considered to be of little value (Abel *et al*., 1990). Close to the threshold, RTs tend to become more variable, reflecting uncertainty, confusion, and hesitation in the subject presented with stimuli with low signal-to-noise ratios (Sanders, 1998). In comparison to the relation between loudness and supra-threshold RT (e.g., Buus *et al*., 1982; Humes and Ahlstrom, 1984; Arieh and Marks, 2003; Wagner *et al*., 2004), the effect of loudness on near-threshold RT has received relatively little attention. The few available data show that threshold and near-threshold contours measured with RT procedures agree closely with non-human audiograms (Pfingst *et al*., 1975a-b; Dooling *et al*., 1978). Once day-to-day variation is accounted for, RT is a good predictor of detection threshold in humans (Heil *et al*., 2006). The similarity between the behavioral audiogram and the 0 dB contour found in the present study at the low and middle frequencies is consistent with these conclusions. Data were collected over four months, and around 40 RT measurements were used to calculate the mean RTs near the threshold (**Fig. 3**). The mean RTs at higher Sensation Levels were calculated from fewer observations.

There is a positive relationship between the increase in loudness relative to the increase in SPL, and the spacing between equal-loudness functions; less spacing corresponds with a steeper increase of loudness. In humans, this effect is mainly observed at low frequencies, outside the range of most sensitive hearing (Suzuki and Takeshima, 2004). Harbor seal 01 showed a similar trend. In both seals, less spacing between the equal-latency contours was also observed for a number of high frequency signals, as shown by the compressed range of data points in **Figure 6**. Whether this is a sign of rapid loudness increase with smaller SPL changes, or that the relationship between equal-loudness and equal-RT is obscured for these frequencies, is difficult to judge without loudness-matching data.

Most RTs recorded for the harbor seals in the present study are longer than the acoustic RTs (times taken to respond to a sound by whistling underwater; 145-448 ms) of bottlenose dolphins (Ridgway *et al*., 1991). The dolphins responded to sounds of higher amplitude than those presented to the harbor seals in the present study, and different muscles and brain-muscle distances were used in the behavioral response. When pure tones of comparable sensation level (within a range of 20 dB of a masked hearing threshold) and frequency (0.2-100 kHz) were presented to bottlenose dolphins and beluga whales (*Delphinapterus leucas*), the mean acoustic RT of the dolphins (430 ms) was very similar to the mean motor RT of the seals (435 ms), but the mean acoustic RT of the beluga whales (640 ms) was longer (Blackwood *et al*., 2002).

The closer the SPL of the signal to the 50% detection threshold, the later (and the more slowly) the seals moved away from the station. When measuring acoustic responses to acoustic stimuli in bottlenose dolphins, Ridgway *et al.* (1991) also found that RTs varied with stimulus amplitude, as well as with stimulus duration. Signal duration was held constant in the present study and cannot have played a role in determining RT, as all the measured RTs were shorter than the signal duration.

C. Estimating the impact of anthropogenic noise

Fifty percent detection thresholds are obtained by using well-trained subjects who are expecting a familiar sound to occur within a specific time period. At the threshold level, the signal is so quiet that the attentively listening subject cannot detect it half of the time. Animals in the wild, at varying ambient noise levels, are not always consciously listening for quiet sounds, and differences in detection ranges probably exist between expected sounds such as sounds made by conspecifics, prey or predators, and unexpected sounds such as anthropogenic sounds. For SPLs near the threshold (0 dB-Sensation Level), the seals in this study did not indicate that they could hear the tone, the duration of which was 0.9s, until over a half second after its onset. At 10 dB-Sensation Level, the average decision time was reduced by 0.25s, and at 20 dB-Sensation Level by a further one eighth of a second to just over 200 ms. Once the signal was 20 dB above the 50% detection threshold, the seals were able to hear it and respond very quickly in quiet conditions.

Terhune and Turnbull (1995) quantified the apparent certainty of detection by a single harbor seal of sounds with SPLs between 0 and 20 dB above the calculated 50% correct detection threshold. At the threshold level (0 dB-Sensation Level), the animal responded correctly 54% of the time; this increased to 89%, 10 dB above the threshold and to 98%, 20 dB above the threshold. The study was conducted by using a 'yes-no' constant stimulus technique, and the subject was presented with a higher proportion of above-threshold SPLs than were the animals in the present study. The data for all three harbor seals (the one used by Terhune and Turnbull (1995), and the two used in the present study) suggest that if a signal's SPL is about 20 dB above the 50% detection threshold, the subject is almost certain to detect it. This suggests that 20 dB above the threshold, or even better, the 20 dB contour derived in the present study, should be used as the sound detection threshold level when calculating audibility ranges at sea. A level 20 dB above the threshold has already been used to calculate audibility ranges in two studies, in one case to estimate the detection range of an acoustic harassment device (AHD; Jacobs and Terhune, 2002); in the other to estimate the communication range of harp seal (*Pagophilus groenlandicus*) underwater calls (Rossong and Terhune, 2009). Whether the 50% detection threshold (0 dB-Sensation Level) or the 98% detection threshold (20 dB-Sensation Level) is used leads to a large difference in the estimated hearing range, because the conversion from level difference to range difference is non-linear. Assuming spherical spreading, the 20 dB-Sensation Level distance is 10 times smaller than the 0 dB-Sensation Level distance.

The equal-loudness data of the present study may also be used to extrapolate data from dose-effect studies with signals in a particular frequency range, to sounds in other frequency ranges. This may reduce the number of behavioral response studies that need to be conducted, thus improving efficiency.

E. Suggestions for future research

Literature shows that RTs continue to decrease with increasing loudness. With sufficient numbers of test levels, sufficient sample sizes per level, and the correct equipment, such a decrease in RT could be detected. As the differences between the levels decline, the variation around the mean is predicted to decrease, so the trend would be detectable. Wagner *et al.* (2004) described a decrease of ~50-100 ms from 30 to 90 dB-Sensation Level, which suggests that the 40 ms resolution used in the present study was not sufficient to detect such changes. It should be noted that in the study by Wagner *et al.* (2004) a decrease in RT was seen in 5 of the 6 test subjects, so the phenomenon does not occur in all subjects.

The present study illustrates the potential for using the relationship between RT and perceived loudness to obtain frequency-weighting functions for marine mammals. The data used in the present study were collected to determine detection thresholds in harbor seals and not for a study of equal-loudness contours. In future studies the seals could be exposed to higher Sensation Levels to enable the calculation of higher level equal-latency contours. As the decrease of RT is expected to decline at higher Sensation Levels (and RT is also expected to become less variable), it is important for future researchers to use a recording system with high time resolution, to allow more precise determination of the animal's RT. A high-speed camera could be used to record the responses, or a switch could be triggered by the animal itself after signal detection.

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Abel, S. M., Rajan, D. K., and Giguere, C. (**1990**). "Stimulus parameters in detection and reaction time," Scand. Audiol. **19**, 229-235.

Arieh, Y, and Marks, L. E. (**2003**). "Recalibrating the auditory system: a speed-accuracy analysis of intensity perception," J. Exp. Psychol. Hum. Percept. Perform. **29**, 523-536.

Blackwood, D. J., Ridgway, S. H., and Evans, W. E. (**2002**). "A window on perception: response times of odontocete cetaceans in audiometric tests," J. Acoust. Soc. Am. **111**, 2370-2371.

Buus, S., Greenbaum, H., and Scharf, B. (**1982**). "Measurements of equal-loudness and reaction times," J. Acoust. Soc. Am. **72**, S94-S94.

Crocker, M. J. (**1997**). "Rating measures, descriptors, criteria, and procedures for determining human response to noise," in *Encyclopedia of Acoustics*, edited by M. J. Crocker (John Wiley & Sons, New York), Vol. **3**, 943-965.

Dent, M. L., Brittan-Powel, E. F., Dooling, R. J., and Lohr, B. (**2000**). "Estimating equal-loudness contours in animals," J. Acoust. Soc. Am. **107**, 2784-2784.

Dent, M. L. (**2005**). "Estimating loudness in animals," J. Acoust. Soc. Am. **117**, 2583-2583.

Dooling, R. J., Zoloth, S. R., and Baylis, J. R. (**1978**). "Auditory sensitivity, equal loudness, temporal resolving power, and vocalizations in the house finch (*Carpodacus mexicanus*)," J. Comp. Physiol. Psychol. **92**, 867-876.

Fletcher, H., and Munson, W. A. (**1933**). "Loudness, its definition, measurement and calculation," J. Acoust. Soc. Am. **5**, 82-108.

Green, S. (**1975**). "Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*)," J. Exp. Anal. Behav. **23**, 255-264.

Heil, P., Neubauer, H., Tiefenau, A., and von Specht, H. (**2006**). "Comparison of absolute thresholds derived from an adaptive forced-choice procedure and from reaction probabilities and reaction times in a simple reaction time paradigm," J. Assoc. Res. Otolaryngol. **7**, 279-298.

Humus, L. E., and Ahlstrom, J. B. (**1984**). "Relation between reaction time and loudness," J. Sp. Hear. Res. **27**, 306-310.

Jacobs, S.R., and Terhune, J.M. (**2002**). “The effectiveness of acoustic harassment devices in the Bay of Fundy, Canada: seal reactions and a noise exposure model,” Aquat. Mamm. **28,** 147-158.

Kastelein, R. A., Wensveen, P. J., Hoek, L.,Verboom, W. C., and Terhune, J. M. (**2009**). “Underwater detection of tonal signals between 0.125 and 100 kHz by harbor seals (*Phoca vitulina*),” J. Acoust. Soc. Am. **125**, 1222-1229.

Kinsler, L. E., Frey, A. R., Coppens, A. B., and Sanders, J. V. (**2000**). *Fundamentals of Acoustics* (John Wiley & Sons, New York), Forth edition.

May, B. J., Little, N., and Saylor, S. (**2009**). “Loudness Perception in the domestic cat: reaction time estimates of equal-loudness contours and recruitment effects,” J. Assoc. Res. Otolaryngol. **10**, 295-308.

Marshall, L., and Brandt, J. F. (**1980**). “The relationship between loudness and reaction time in normal hearing listeners,” Acta Otolaryngol. **90**, 244-249.

Pfingst, B. E., Hienz, R., Kimm, J., and Miller, J. (**1975a**). “Reaction time procedure for measurement of hearing. I. Supra-threshold functions,” J. Acoust. Soc. Am. **57**, 421-430.

Pfingst, B. E., Hienz, R., and Miller, J. (**1975b**). “Reaction time procedure for measurement of hearing. II. Threshold functions,” J. Acoust. Soc. Am. **57**, 431-436.

Piéron, H. (**1920**). “Nouvelles recherches sur l’analyse du temps de latence sensorielle et sur la loi qui relie le temps a l’intensité d’excitation,” [New studies on sensory latency and on the law that relates latency to stimulus intensity]. Ann. Psychol. **22**, 58-142.

Pins, D., and Bonnet, C. (**2000**). “The Piéron function in the threshold region,” Percept. Psychophys. **62**, 127-136.

Ridgway, S. H., Carder, D. A., Kamolnick, P. L., Skaar, D. J. and Root, W. A. (**1991**). “Acoustic response times (RTs) for *Tursiops truncatus,*” J. Acoust. Soc. Am. **89**, 1967-1968.

Ridgway, S. H., and Carder, D. A. (**2000)**. “A preliminary study of loudness at frequencies of 5 to 120 kHz based on whistle response time (RT) in a dolphin,” J. Acoust. Soc. Am. **108**, 2515-2515.

Rossong, M.A., and Terhune, J.M. (**2009**). “Source levels and communication-range models for harp seal (*Pagophilus groenlandicus*) underwater calls in the Gulf of St., Lawrence, Canada,” Can. J. Zool. **87,** 609-617.

Sanders, A. F. (**1998**). *Elements of human performance: reaction processes and attention in human skill* (Lawrence Erlbaum Associates, New Jersey).

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R. Jr., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., and Tyack, P. L. (**2007**). “Marine Mammal Noise Exposure Criteria: Initial Scientific Recommendations,” Aquat. Mamm., **33**, 411-521.

Stebbins, W. C. (**1966**). “Auditory reaction time and the derivation of equal loudness contours for the monkey,” J. Exp. Anal. Behav. **9**, 135-142.

Suzuki, Y., and Takeshima, H. (**2004**). “Equal-loudness-level contours for pure tones,” J. Acoust. Soc. Am. **116**, 918-933.

Terhune, J. and Turnbull, S. (**1995**). “Variation in the psychometric functions and hearing thresholds of a harbor seal,” in *Sensory Systems of Aquatic Mammals*, *edited by* R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall (De Spil Publishers, Woerden), pp. 91-93.

Ulrich, R., and Miller, J. (**1994**). “Effects of truncation on reaction time analysis,” J. Exp. Psychol. General **123**, 34-80.

Wagner, E., Florentine, M., Buus, S., and McCormack, J. (**2004**). “Spectral loudness summation and simple reaction time,” J. Acoust. Soc. Am. **116**, 1681-1686.