Harbour seals use rhythmic percussive signalling in interaction and display

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ARTICLE INFO

Multimodal rhythmic signalling abounds across animal taxa. Studying its mechanisms and functions can highlight adaptive components in highly complex rhythmic behaviours, like dance and music. Pinnipeds, such as the harbour seal, *Phoca vitulina*, are excellent comparative models to assess rhythmic capacities. Harbour seals engage in rhythmic percussive behaviours which, until now, have not been described in detail. In our study, eight zoo-housed harbour seals (two pups, two juveniles and four adults) were passively monitored by audio and video during their pupping/breeding season. All juvenile and adult animals performed percussive signalling with their fore flippers in agonistic conditions, both on land and in water. Flipper slap sequences produced on the ground or on the seals' bodies were often highly regular in their interval duration, that is, were quasi-isochronous, at a 200–600 beats/min pace. Three animals also showed significant lateralization in slapping. In contrast to slapping on land, display slapping in water, performed only by adult males, showed slower tempo by one order of magnitude, and a rather motivic temporal structure. Our work highlights that percussive communication is a significant part of harbour seals' behavioural repertoire. We hypothesize that its forms of rhythm production may reflect adaptive functions such as regulating internal states and advertising individual traits.

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Animals primarily use specialized tissue structures to generate sounds for communication or localization, such as vocal organs or modified parts in the feet, wings and even on the swim bladder. Beyond these highly specialized mechanisms, animals also produce a multitude of acoustic signals via body parts not principally adapted for sound production. These signals, be they the by-product or the aim of bodily activity, can also have communicative value, conveying information about the traits, qualities or state of the signaller. When sounds are created by repetitive bodily movements, their temporal patterning, that is, their rhythm, can elicit or enhance species-specific behavioural responses. Signal rhythmicity can aid the decoding process of the receiver, by facilitating the parsing of the auditory stream (see auditory scene analysis, Honing et al., 2015) and entraining neural oscillations (e.g. Noda et al., 2017). Moreover, secondary sound production mechanisms of the body, specifically called nonvocal acoustic behaviour in tetrapods, can extend to the visual and tactile modalities, with multimodal presentation facilitating rhythm processing (Kisilvesky & Muir, 1991).

A prominent form of multimodal and rhythmic bodily activities is percussive or drumming behaviour. It is mainly performed with limbs, but it can also involve various other body parts, such as the head and the teeth (Randall, 2001). This means that, for example, the enormous diversity of pulse-like sounds generated by fish is typically not considered percussive in the literature, as their drumming mechanism is not multimodal signalling, and it is also produced by specialized tissues. Understanding the mechanisms and functions of percussive behaviour across species is relevant not only to modern zoology but also to the comparative study of the evolution of rhythm cognition. It constitutes a testbench to probe adaptive components of rhythmic, interactive, multimodal signalling in behavioural phenomena such as human dance and musicality.

Functions of Percussive Communication across Species

Percussive behaviour has been observed in a wide range of taxonomic groups. In insects, (e.g. stoneflies, Maketon & Stewart,

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1984; Sandberg et al., 2001) or spiders (Parri et al., 1992), it is a form of sexual signalling, involving striking the abdomen against a substrate. Birds can also use drumming as part of their mating or territorial display, for example the ruffed grouse, *Bonasa umbellus* (Garcia et al., 2012; Gullion, 1966), woodpeckers (Garcia et al., 2020; Schuppe et al., 2021) and the tool-using palm cockatoo, *Probosciger aterrimus* (Heinsohn et al., 2017). Foot drumming is common in rodents and other mammals such as carnivores, ungulates, rabbits, elephant shrews and marsupials (Randall, 2001). Gorillas, *Gorilla* spp., usually drum on their chests, while chimpanzees, *Pan troglodytes*, beat on resonant objects such as tree trunks or buttresses, creating long-distance signals which seemingly coordinate the movement of dispersed individuals (Babiszewska et al., 2015; Eleuteri et al., 2022).

Mammals can thus use percussive signalling in various contexts (see Randall, 2001): to display territoriality (Narins et al., 1992; Randall, 1995) and competition, to attract mates (Demartsev et al., 2022; Kenagy, 1976), to express submission and readiness to mate (Burley, 1980), and to communicate about the presence of predators (Owings & Owings, 1979). It can also signal prey alertness to predators (Randall & Matocq, 1997). Overall, drumming increases with agitation or stress, and it can also be a ritualized displacement activity when an animal has conflicting urges (Randall, 2001). Larger species can use it to overcome the metabolic challenges of fighting and to defend their territories. Drumming can thus affect the receiver's behaviour by communicating fighting ability, sparing costly encounters (Owings & Morton, 1998), and attracting mates (Maynard Smith, 1974). In human groups, rhythmic components of dance and music can also serve to display capacities or exert emotional and social regulatory functions (Fink et al., 2021; Roederer, 1984; Sauciuc et al., 2022).

Vocal Learners in Rhythm Production Research

The most recent version of the vocal learning and rhythmic synchronization hypothesis (Patel, 2021) predicts that vocal learning abilities correlate with the degree of audio-motor neural connectivity and thus rhythmic capacities. Importantly, the inclination towards rhythmic bodily (gestural) signalling possibly constitutes another prerequisite for beat perception and synchronization, that is, entrainment to external rhythmic stimuli (Sauciuc et al., 2022). Accordingly, percussive behaviour is widely used by marine mammals (Dudzinski & Gregg, 2018; Verga & Ravignani, 2021) capable of vocal production learning, namely pinnipeds (Duengen et al., 2023; Ralls et al., 1985; Reichmuth & Casey, 2014; Stansbury & Janik, 2019) and cetaceans (Janik, 2014; Vernes et al., 2021). Pinnipeds are indeed optimal models in the study of rhythmic capacities and percussive behaviour (Ravignani et al., 2016): multiple species have been observed to produce series of nonvocal impulsive sounds typically in their breeding season. Grey seals, *Halichoerus grypus*, clap their fore flippers underwater (Hocking et al., 2020), walruses, *Odobenus rosmarus*, generate loud impulses by fore flipper cavitation (Larsen & Reichmuth, 2021) and harbour seals, *Phoca vitulina*, slap the water surface with their flippers (Boness et al., 2006; Hanlan, 1998; Hayes et al., 2004; Newby, 1973; Perry, 1993; Renouf, 1993; Renouf & Lawson, 1986; Riedman, 1991; Sullivan, 1981; Venables & Venables, 1957).

Besides showing a propensity for multimodal signalling, percussive behaviours also imply that marine mammals need signals to carry far in high ambient noise (e.g. Mooney et al., 2020) or to stand out from species-specific vocalizations (Hocking et al., 2020). The explosive acoustic nature of pinniped percussive signalling is due to several features: it consists of

remarkably brief (a few or tens of milliseconds long) sounds, which cover a broad frequency band, and it is extremely loud with an in-water source intensity exceeding 180 dB re 1 μPa (Larsen & Reichmuth, 2021; Wahlberg et al., 2002). The playback of similarly intense (170 dB re 1 μPa), short rise time noise pulses to grey seals led to sensitization in their spatial avoidance by repeatedly eliciting a startle reflex (Götz & Janik, 2011). Hence, the acoustic properties of percussive sounds together with their repetition in bouts could be employed by males to advertise physical superiority and mating potential in 'noisy' aquatic habitats, keeping other males away.

Accordingly, harbour seal flipper slapping has been associated with male mating displays (Hanlan, 1998; Perry, 1993; Renouf, 1993; Sullivan, 1981; Venables & Venables, 1957), threat signalling (Dudzinski & Gregg, 2018; Perry, 1993) and play (Bishop, 1967; Renouf, 1993; Renouf & Lawson, 1986). As seals are amphibious mammals, water- and land-based percussive behaviour might be equally important in their nonvocal communication. Yet, the different forms and functions of harbour seal flipper slaps have only been sporadically and anecdotally reported in the literature. Further, to the best of our knowledge, fine-grained temporal features and potential rhythmic structures in seal percussive behaviour have not been described.

In this study, we aimed to determine the principal forms of percussive behaviour in harbour seals, addressing their potentially conserved temporal features, which can both advertise individual qualities and determine the main units of nonvocal acoustic communication. We described flipper slapping and attempted to infer its potential functions by using two complementary approaches. First, we aimed to provide further insights into the functions of slapping, based on our observations of zoo-housed harbour seals. We examined which individuals (pups, juveniles, adult females or males) flipper-slapped, on which occasions and on which mediums. Second, we aimed to give a temporal characterization of flipper-slapping behaviour in harbour seals to determine whether it showed rhythmicity, particularly rhythmic categories comparable across species as well as present in human music (i.e. isochrony, small integer interval ratios, see de Gregorio et al., 2021; Demartsev et al., 2022; Raimondi et al., 2023; Roeske et al., 2020). The study of rhythmic bodily signalling in harbour seals can reveal behavioural contexts, associated traits and rhythmic capacities which may help us understand the origins and function of rhythmic movements in social interactions, a key feature of musicality. In particular, one of the statistical universals in musicality is the use of percussion (Savage et al., 2015), which further stresses the importance of studying percussive signalling in a comparative framework.

METHODS

Signallers, Targets and Forms of Percussive Behaviour

In the first part of our study, we carried out long-term audiovisual monitoring at the Zoo Cleves, Germany. For the passive acoustic monitoring, we used a Song Meter 4 (Wildlife Acoustics, Maynard, MA, U.S.A.; 44.1 kHz, 16-bit resolution stereo, dynamic range: default 39 dB–126 dB SPL) equipped with two built-in omnidirectional microphones. For the simultaneous video capture, an RLC-510WA camera (Reolink, Wilmington, DE, U.S.A.; 6–30 fps depending on light conditions) was set up above the pool.

Seven to eight harbour seals were monitored for 330 h over 15 days between 6 and 20 July 2021. These individuals were two pups, two juvenile (1-year-old) males, two adult females (6 and 24 years

old) and two adult males (16 and 20 years old). We excluded 15 h of monitoring from our analysis, because for these there was no simultaneous high-quality (Song Meter 4) acoustic data available, allowing the sound monitoring of the entire pool. The seal pool's water was lowered around the second pup's birth time (day 4). After 7 days of low water (during which we obtained 136 h of recording), the pool was filled again; we then recorded the seals for 179 h over 8 days. Multiple dry platforms were also available for the seals both inside and outside the pool. These conditions made it possible to monitor percussive behaviours in both terrestrial and aquatic conditions. The camera was positioned to overview the main hauling areas where seals rested and tended to interact with each other and with zoo personnel during feeding. This means that the camera pointed to one or the other half of the facility depending on whether the pool water was permanently lowered or the pool was filled up (for 119 h versus 196 h, respectively; see Fig. A1).

Ethical Note

The harbour seals in the study were either born at the Zoo Cleves ($N = 4$) or acquired from other zoos ($N = 4$): from Zoo Duisburg (male 3 and female 2), Zoo Osnabrück (female 1) and Zoo Heidelberg (male 4). The captive individuals were housed in a 230 000-litre freshwater pool in a 300 m^2 enclosure and kept on their regular diet during the recordings.

Seals were always kept together in one facility; no seal was separated at any point during our investigation. They could roam the enclosure freely and were thus either in the pool or on dry platforms where they also interacted with zoo personnel during feeding once or twice per day.

We conducted the recordings according to the requirements of the Landesamt für Natur, Umwelt und Verbraucherschutz (LANUV) NRW, Germany, section animal experiment affairs (file number Az. 81-04.78); and the recordings did not cause any disturbances.

Audiovisual Annotation and Analysis

Upon selecting all percussive behavioural events in the videos manually, we annotated the corresponding acoustic events in 1 h recording epochs in Praat (Boersma, 2001; Boersma & Weenink, 2021). We delineated the individual slaps with their broadband impulse (see Fig. A2) as interval onset. A series (bout) of slaps was delimited and labelled with the individual performing the slapping, the medium (ground, body, object, water) of the slapping and the interaction type (seal or human). Invisible or indistinct bouts, and those overlapping with other percussive events or vocalizations (including human speech), were excluded from the analysis ($N = 236$ bouts). The delineation of percussive bouts was straightforward in most cases; a new bout started when there were multiple seconds of pauses during slapping, there was a distinct change in the slapping limb or medium or another seal took a turn at slapping.

For the analysis of the annotated slaps and bouts, we used the Python packages Parselmouth (a Python interface to Praat, version 0.4.2, Jadoul et al., 2018; Praat version 6.1.38, Boersma & Weenink, 2021), NumPy (Harris et al., 2020), pandas (McKinney, 2010) and TextGridTools (Buschmeier & Wlodarczak, 2013). For further temporal analysis of flipper slapping, slap onset times were extracted and grouped by their corresponding bout intervals. Interonset intervals (IOI) between slap onset times were calculated within each manually annotated bout and regardless of bouts within each individual.

To assess the quality of flipper slapping, we determined the signal-to-noise power ratio (SNR) estimates for each slap: 10 ms before (baseline 'noise') and 10 ms after slap onset ('signal') were selected for power calculation. The power of the baseline was subtracted from the signal power before calculating the SNR.

To assess the consistency of manual annotations, we used the upper Tukey's fence boundary (Tukey, 1977), Q3 + 1.5 × IQR (where Q3 is the third quartile and IQR is the interquartile range) to establish an interbout interval criterion in bout separation. This separation was based on the distribution of within-individual slapping intervals pooled across the 1 h recording chunks. The bout interval limits were calculated separately for land-based slaps in seal ($N = 6$ seals) and human ($N = 2$ seals) interactions as well as for water slaps ($N = 6$ seals).

We additionally annotated the target individuals and the slapping limb (right or left fore flipper) for each seal. In interactions, we defined the target as the individual towards which the slapping animal oriented its body and/or head, usually in close proximity. We used these observations for separate analyses to quantify the strength of interactions between seals, and their limb preference, respectively.

We visualized the network of percussive seal interactions with the tidyverse (Wickham et al., 2019), tidygraph (Pedersen, 2022) and ggraph (Pedersen, 2020) packages in RStudio's 2022.02.3+492 release (RStudio, PBC, Boston, MA, U.S.A., http://www.rstudio.com). Next, we used the NetworkX (Hagberg et al., 2008) Python package for the preparation and analysis of the weighted directed graph representing seals as nodes and the number of interactions as edge weights (excluding object slapping and display slaps to 'unknown' targets). Degree centrality (DC), which expresses the fraction of nodes (seals) a particular node is connected to (Hagberg et al., 2008), was calculated for each animal as follows. We weighted the graph edges (seal interactions) by the number of slapping bouts, then divided the resulting node degree (sum of connecting edges) by the total number of interactions. This quantification enabled us to compare the fraction of interactions each seal participated in and the intensity of their interactions (number of percussive events).

Measures of Complexity in the Rhythm and Form of Percussive Behaviour

We set out to quantitatively analyse the rhythmic structure of percussive behaviour (see Ravignani & Norton, 2017).

To calculate the rate of flipper slapping for each individual, we calculated slap IOI distributions. To further characterize the rhythmic structure of slapping, the 'rhythm ratios' (r) were calculated between each pair of N adjacent IOIs (i.e. IOI$_k$ and IOI$_{k+1}$ for $k = 1, 2, 3, ..., N$-1) according to the formula proposed by Roeske et al. (2020):

$$r_k = \frac{\text{IOI}_k}{\text{IOI}_k + \text{IOI}_{k+1}}$$

The distribution of these values can quantify rhythmic categories centred around the isochrony ratio (1:1 interval ratio, i.e. $r = 0.5$), and quantifies equally accelerating or decelerating intervals symmetrically around the 0.5 value of isochrony. We defined on-integer and neighbouring off-integer ratio bins following previous work on animal vocal rhythms (de Gregorio et al., 2021; Roeske et al., 2020; see the Appendix: Rhythm Ratio Methodology and Bin Calculation and Fig. A3 for more details). We also quantified the occurrence of isochronous rhythms by calculating the percentage of two-interval patterns with ratios between $\frac{1}{2.25}$ and $1-\frac{1}{2.25}$. To determine the significance of rhythm ratio (r) peaks, (1) each ratio bin count was normalized by the length of its ratio bin range, and (2) on-integer and their adjacent off-integer interval bins were compared (Wilcoxon signed-rank tests) across bouts within each individual.

Next, we characterized the overall quality and temporal features of the slapping bouts in each individual by the number and median SNR of their slaps, as well as the following temporal measures: the median, IQR and median absolute deviation of their IOIs and r

values, as well as the normalized pairwise variability index (nPVI) according to Grabe and Low (2008):

$$nPVI = \left(\frac{100}{N-1}\right) \sum_{k=1}^{N-1} \left| \frac{IOI_k - IOI_{k+1}}{(IOI_k + IOI_{k+1})/2} \right|$$

The nPVI expresses the temporal complexity of the bouts by measuring the average variation between the consecutive IOI pairs.

We ran nonparametric statistical tests on slap and bout features as distributions were skewed or multimodal. For a nonparametric, multivariate comparison of the bouts between animals, we performed mixture and flexible discriminant analysis with the mda R package (Leisch et al., 2022).

To quantify the degree of limb preference in slapping for each individual, we applied a commonly used lateralization index (LI, see e.g. Camerlink et al., 2018):

$$LI = \frac{R - L}{R + L},$$

which compares the number of bouts produced with either the right (R) or the left (L) flipper. Limb preference was probed with a series of binomial tests for each individual (with a test proportion of 0.5 for one limb), and Fisher's exact test served to test whether the medium of slapping was associated with limb preference.

We performed statistical tests and data visualization in MATLAB R2022a (The MathWorks Inc., Natick, MA, U.S.A., https://www.mathworks.com) as well as with the ggplot2 (Wickham, 2016) and tidyverse packages in RStudio's 2022.02.3+492 release.

RESULTS

Percussive Behaviour has Versatile Forms in Harbour Seals

Repetitive, nonlocomotor fore flipper movements were present in all individuals including pups, but acoustically distinct percussive signalling was only observed in juveniles and adults. Altogether, we detected 627 bouts with 4766 slaps.

Percussive slapping seemed to accompany behavioural signs of high arousal, most often in agonistic interactions with conspecifics (Videos S1, S2 and S4; see also Dudzinski & Gregg, 2018), in breeding display (Video S3a, b) or during feeding.

Agonistic, interactive events manifested as ground, body or object slapping on land, and water slapping ($N = 372$; Table A1). Display slapping was performed by adult males, leaning sideways (see also Bishop, 1967) and striking the water surface with the right flipper while circling around the pool, creating an explosive acoustic effect ($N = 23$ bouts). As display water slaps were not always on frame throughout the bout ($N = 14$ bouts) due to the partial video camera coverage of the pool, we assigned the bouts to one of the two adult males according to the visible slaps.

The two oldest individuals, male 4 and female 2, had previously been trained to flipper slap on cue. Here, they displayed percussive behaviour ($N = 228$ and $N = 4$ bouts, respectively) to the zoo personnel during feeding time, potentially as a form of anticipatory behaviour. We observed two-flipper ground ($N = 7$ bouts) and body ($N = 19$ bouts) slaps in male 4 during these interactions. In these cases, the strokes could not always be assigned to the flippers based on camera capture, so the individual slaps were not distinguished and thus not analysed further. Additionally, one juvenile produced two-flipper body slaps on one occasion.

Upon manual annotation, we validated the consistency of bout separation by calculating upper Tukey's fence boundaries (i.e. $Q3 + 1.5 \times IQR$) for slap IOIs. The boundaries were 0.4 s, 0.2 s and 4.7 s in the case of land-based slaps in seal interactions, human

interactions and water slaps, respectively (Fig. A4). These post hoc criteria revealed only a few manually annotated slaps ($N = 7$; one water, one body and one ground slap among seal-directed slaps and four human-directed slaps) the preceding IOI of which was longer than the calculated upper boundary. However, upon reinspecting these slaps in the annotations, we found no change in slapping limb or medium, and confirmed these were still part of the respective slapping bouts.

Next, we examined the target individuals of the percussive events in seal interactions which may provide information on their function (see also Table A2). As Fig. 1 highlights, the two adult females had the most extensive percussive signalling network with the largest number of interactions (the two largest weighted DC values: $DC = 0.70$ and 0.54). These encounters typically occurred when another seal approached their pups (see Hanlan, 1998). In accordance with this, the incidence rate of percussive behaviour peaked around pup birth: 40% of the bouts in our study were observed within 24 h after another pup (pup 1, pup of female 1) was born (Fig. A5).

Of the two adult males, the older (male 4, $DC = 0.33$) was rather reactive in slapping upon being targeted with flipper slaps, whereas the larger male 3 ($DC = 0.14$) actively flipper-slapped towards male 4 and showed display-like slapping to 'unknown' targets (multiple or undetermined individuals, $N = 15$). The two juvenile males (males 1 and 2, $DC = 0.15$ and 0.09) also engaged in display-like percussive behaviour ($N = 9$ and 16, respectively), which manifested as solitary flipper slapping. In one further case of female 2, we could not determine the target of percussive behaviour.

Object slapping was not included in the previous visualization, as it was only observed in the two juveniles ($N = 1$ and $N = 25$ bouts). Together with nondisplay type, interactive water slapping ($N = 21$ bouts altogether; Table A2), 43% of which consisted of a single slap, object slapping was not analysed further. In addition, we also considered that the accidental nature of percussive flipper waving on an object and the intermingling of swimming strokes with water slaps in these cases cannot be ruled out.

Percussive Signalling Shows Medium- and Individual-specific Complexity

Land-based percussive behaviours

Land-based flipper slapping showed high regularity in its interval durations. The grand median (and IQR) of slap IOIs in ground
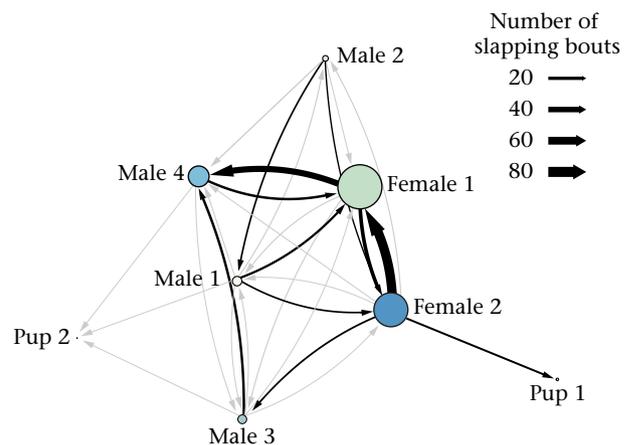

Figure 1. Directed weighted graph showing the observed percussive interactions between all seals (ground, body and water-slapping bouts). Percussive activities with unknown targets or display water slaps were excluded from this plot. The edge weights represent the number of interactions displayed with proportional line widths. Edges between seals with five or fewer bouts are shown in grey. Node size is proportional to the weighted degree centrality divided by the total number of interactions.

and body slaps fell into the 0.1−0.3 s (200−600 beats/min tempo) range in all animals (Fig. 2a), with human-directed slapping being significantly faster than the seal-directed one in the two trained animals (Wilcoxon rank sum test: $Z = 10.1$, $P < 0.001$, and $Z = 5.66$, $P < 0.001$ for the ground slaps of male 4 and female 2, respectively, and $Z = 4.8$, $P < 0.001$ for the body slaps of male 4).

Land-based slaps exhibited isochrony in all animals: $69 \pm 9\%$ of ground and $90 \pm 10\%$ of body slap interval pairs in seal−seal interactions were in the isochrony on-integer range (Fig. 2b). In the two trained animals, flipper slap intervals in seal−human interactions did not display a significantly different rhythm ratio distribution from those in seal−seal interactions for ground or body slaps (Wilcoxon rank sum test: $Z = 0.34$, 0.35 and 0.61 with $P = 0.73$, 0.73 and 0.55, respectively).

In the bouts of seal-directed ground slapping, all animals except male 4 showed a significant isochrony on-integer peak (Wilcoxon signed-rank tests: $P < 0.01$; see Table A3), whereas small integer ratios outside the isochrony range were not significant. However, in human-directed slapping, strong isochrony peaks were present in male 4 but not in female 2. These differences can possibly be attributed to the low number of bouts in the nonsignificant categories.

Seal-directed body slapping bouts had significant isochrony peaks in the case of the three younger animals (males 1, 2 and female 1; Wilcoxon signed-rank tests: $P < 0.05$; see Table A3), which produced at least 10 bouts. In addition, the median SNR of body slaps in seal interactions showed a strong negative correlation (Spearman rank correlation: $r_S = -0.99$, $P = 0.006$) with age. We suggest that this might potentially be attributed to different flipper sizes. Flippers of different sizes would in turn result in different positions of the flipper on the body during slapping (closer or further from e.g. the ground or shallow water), leading to different sound quality and temporal characteristics.

Importantly, the measures of IOI regularity such as IQR (Spearman rank correlation: $r_S = -0.03$, $P = 0.55$), median absolute deviation (Spearman rank correlation: $r_S = -0.004$, $P = 0.93$) or nPVI (Spearman rank correlation: $r_S = -0.04$, $P = 0.41$) were not significantly correlated with the used SNR power estimate. This suggests that the presence of noise likely did not impose a bias on the annotations, thus influencing the IOI dispersion.

Below, we compare seal-directed percussive behaviours across individuals.

Seals exhibited different degrees of flipper preference in slapping. Only one seal showed an association between slapping medium and limb preference (male 2; Fisher's exact test: $P = 0.006$). Taking this together with the fact that body slaps were less numerous ($N = 50$ bouts, <5 bouts in half of the animals) than ground slaps ($N = 274$ bouts), body and ground slaps were pooled at the bout level (Table A4, Fig. 3a). Female 2's strong left limb preference may have been due to training; however, male 3 displayed an absolute preference for the right fore flipper, despite no training or past injury. Further, the majority of display-like events originated from this male both on land and in water, in which he used his right flipper to produce single slaps or double/triple repetitions.

Ground-slapping bouts had adequate sample size across all animals, and were therefore used for a multivariate comparison of individuals. We focused on five bout features: the median and IQR of IOIs, the median of the rhythm ratios, the nPVI and the median SNR (63.4% model accuracy in mixture and flexible discriminant analysis, mDA; MANOVA: $F = 5.95$, $P < 0.001$). Importantly, the accuracy of discrimination due to a signature can be confounded with anatomical constraints of age and sex, as well as the number of bouts. Nevertheless, the first canonical variable (CV1, 52.5% contribution) was highly reliant on the median SNR (Spearman correlation: $r_S = 0.81$, $P < 0.001$), while CV2 (30.2% contribution) was highly correlated with complexity measures such as the interquartile range of the IOIs (Spearman correlation: $r_S = -0.90$, $P < 0.001$) and the nPVI (Spearman correlation: $r_S = -0.71$, $P < 0.001$).
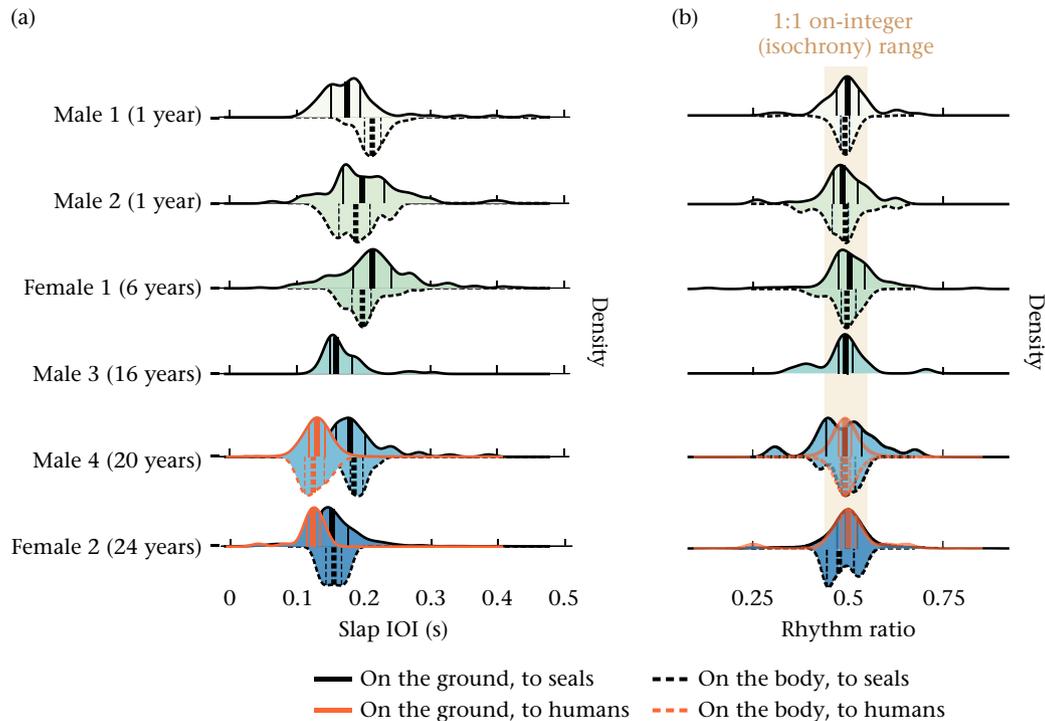

Figure 2. Temporal measures of land-based percussive behaviour across all individuals (sorted by age, in parentheses). (a) Interonset interval (IOI) distributions of ground and body slaps with the quartiles. Kernel bandwidths are 0.01 s. (b) Rhythm ratio (r) distributions of ground and body slaps with the quartiles. Kernel bandwidths are 0.02 s. Kernel density estimates are normalized per seal.
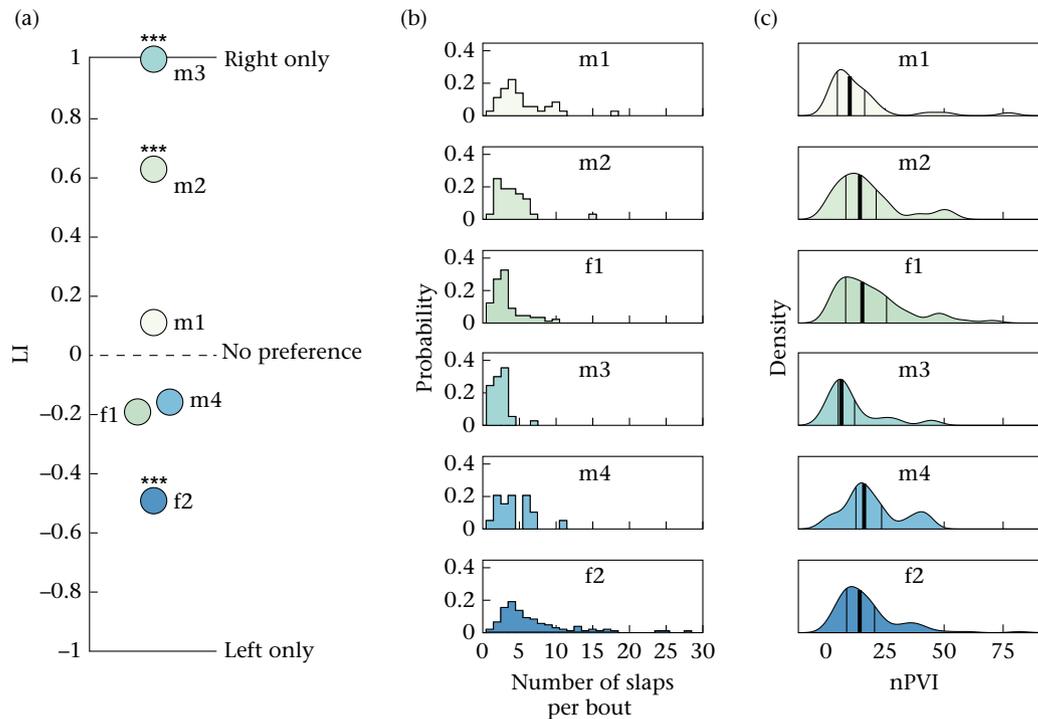
Figure 3. Measures of complexity in land-based percussive bouts. (a) Lateralization index (LI) showing forelimb preference in slapping bouts. m: males; f: females. ***$P < 0.001$, binomial tests. (b) Distributions of the number of slaps per bout. (c) Distributions of the normalized pairwise variability index (nPVI) calculated from the slap intervals in each bout. Kernel bandwidths are 4. Kernel density estimates are normalized per seal.

In both canonical variables, male 3 could most clearly be differentiated from the rest of the animals (Fig. A6). Accordingly, his overall land-based percussive behaviour showed conservativeness. His slapping bouts had the lowest complexity with the smallest median nPVI (6.52 (IQR: 8.18); Fig. 3c), the lowest variability in the number of slaps within a bout (IQR = 1 slap; Fig. 3b) and slaps with a median SNR higher by one order of magnitude (19.26 (IQR: 34.51)) than the rest of the animals (see also above the results of mDA).

Aquatic percussive behaviour

Display water slaps were performed by the two adult males (male 3: $N = 16$ bouts; male 4: $N = 7$ bouts; Fig. 4a). These events showed distinctive temporal features with IOIs occurring on two timescales (Fig. 4b), leading to 'semiflexible' rhythms (Roeske et al., 2020) with slow-paced beats (>1 s IOI median: 2.31 s, i.e. 26 beats/min; IQR: 0.72 s) and an order of magnitude shorter intervals (<1 s IOI: 0.25 s, i.e. 240 beats/min; IQR: 0.10 s). These manifested as double or triple slapping.

Accordingly, the percentages of isochrony on-integer rhythm ratios were only 49% and 31% in males 3 and 4, respectively, and they also displayed rhythm ratios (26% and 40%) outside the small integer ratio (1:2–4) range. This temporal organization resulted in three peaks in the rhythm ratio distribution (Fig. 4c), but only male 3 showed significant isochrony (Wilcoxon signed-rank test: $W = 2$, $P = 0.004$; see Table A5). Since the peaks in the water slap rhythm ratios were derived from two IOI peaks with medians of 1:9 ratio (see above and Fig. 4c), we additionally examined the corresponding ratio range (1:10). The on-integer boundaries in this high ratio range corresponded to $\frac{1}{9.75}$ and $\frac{1}{10.25}$, while off-integer boundaries were $\frac{1}{9.5}$, $\frac{1}{10.5}$. However, these peaks were not significant in this range ($P > 0.1$ or no data in range).

These results, taken together with the median nPVI values of the water-slapping bouts (male 3: 46.38 (IQR: 60.27); male 4: 57.76 (IQR: 66.23)), highlight that display water-slapping behaviour represents a more complex organization than land-based percussive behaviours.

DISCUSSION

Temporal Regularities may Reflect the Adaptive Features of Percussive Signalling

In our study, based on eight captive harbour seals, we detected a multitude of percussive acoustic events in juvenile and adult animals in high-arousal conditions. Ground and body slaps were widespread in agonistic encounters in both sexes; they were also typically produced in close interaction with the possibility of multimodal integration. In contrast, display water slapping was a solitary action and restricted to adult males.

Although both land- and water-based forms of flipper-slapping behaviour are constrained by limb anatomy and the medium used, percussive behaviour, typically of the nontrained seals, showed unitary temporal features, such as a predominance of isochrony, with a relative lack of rhythm ratios in other small integer (1:2–4) ranges. Hypothetically, a high (200–600 beats/min) tempo and a limited number of slaps in interactive percussive encounters could put sensorimotor constraints on temporal complexity (see also Roeske et al., 2020). The high temporal regularity of land-based slapping also raises the possibility that percussive behaviour in harbour seals reflects stereotyped motor patterns. We indeed observed further repetitive flipper movements beyond percussive events, which included pup stroking in mothers, waving and grooming. Often, waving and grooming were involved in or led to agonistic encounters and slapping.

The capacity for consistent production of isochronous patterns can also be a salient feature in communication and isochrony has also been suggested to constitute a building block for the evolution of musical rhythmic behaviour (Ravignani & Madison, 2017; Savage
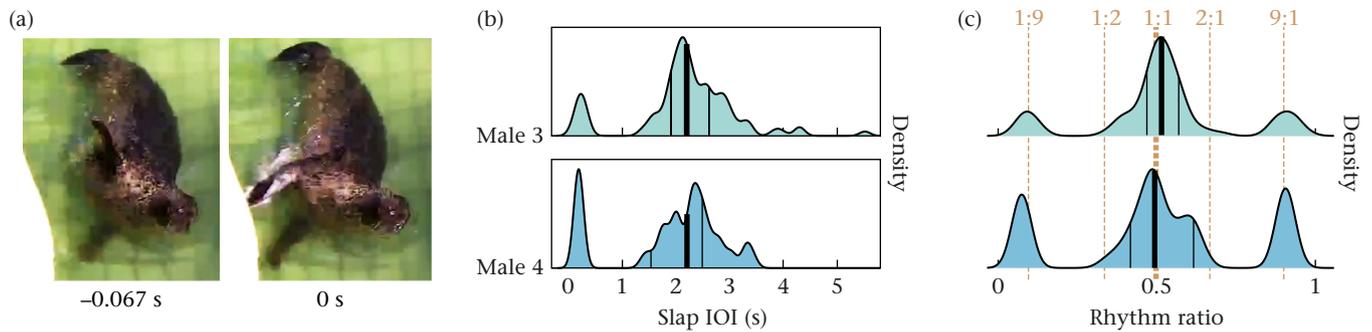
Figure 4. Temporal measures of display water slaps in the adult males. (a) Characteristic posture during water slapping is shown in two representative images of male 3 before and during a slap in two consecutive frames of the 15 fps video recording. Note that the water slap is produced by the right flipper, while the other one stays underwater. Image contrast was increased (+50) in Adobe Photoshop 23.5.1. The source video excerpt (Video S3a) can be found in the Supplementary Material. (b) Interonset interval (IOI) distributions of water slaps, with the quartiles indicated by lines. Kernel bandwidths are 0.1 s. (c) Rhythm ratio (r) distributions of water slaps showing the quartiles. The ratios above the plot show the corresponding interval ratios. Kernel bandwidths are 0.04 s. The kernel density estimates are normalized per seal.

et al., 2015). As Miller (2000) pointed out, a well-sustained rhythm could signal aerobic fitness, coordination and cognitive abilities, which are advantageous for hunting. These traits are also beneficial for fighting and reproductive capacities, and harbour seal percussive behaviour could convey this information (Dudzinski & Gregg, 2018; Hanlan, 1998; Larsen & Reichmuth, 2021; Perry, 1993; Renouf, 1993; Sullivan, 1981; Venables & Venables, 1957). Relatedly, we observed most of the land-based, seal-directed flipper-slapping behaviour in pup-guarding females, which could promote their expression of vigour in agonistic interactions, potentially leading to spatial avoidance in conspecifics. Finally, our data on harbour seals provide one more datapoint supporting cross-species hypotheses that link isochrony and vocal learning (Ravignani, 2021; Rouse et al., 2021; Verga et al., 2022).

The consistency in male 3's land-based flipper-slapping behaviour, that is, the lateralization and the lowest level complexity in the group, points towards another intriguing direction. Future work could test whether there are dominant temporal characteristics in captive and wild populations, that is, signatures or motives, potentially transmitted by observational learning. Darwin (1871) highlighted the significance of mating displays in the origins of musical rhythmic behaviour, as rhythms can convey information about individual fitness. Anthropology (Merriam, 1964) provides examples of competitive musical behaviour, for example drum contests. The 'conservative' properties of male 3's flipper slapping potentially highlight this adaptive feature in percussive behaviour, which can also be driven by a hormone-related seasonality.

In contrast, display water slaps occurred on two timescales, and showed unique 'ornamental' (Roeske et al., 2020) temporal structure. This complexity might result from its solitary mode of presentation; thus, it is less restricted by potential percussive interactions with other seals. Furthermore, as previously suggested (Sullivan, 1981), 'splashing' displays can be ritualized swimming or steering movements, which can serve as an assessment of fitness for females. Sensory biases and constraints (see sensory exploitation hypothesis, Arnqvist, 2006) similar to those that might have evolutionarily shaped this behaviour could also lead to a further universal structural feature in music: motivic patterns on the main beat, which, together with isochrony, can ultimately facilitate cue processing in receivers (Ravignani et al., 2017; Savage et al., 2015). But the ornamental elements could also simply be attributed to the biomechanics of double or triple stroke production, rather than precise motor control. Roeske et al. (2020) also pointed out that high ratio 'fused' rhythms in human musical performances are often produced by a single gesture.

Based on these results, important questions arise about the production and perception mechanisms of percussive behaviour in harbour seals. Future research could test (1) whether the degree of slap interval regularity is state dependent or even shows maturation and plasticity, (2) how different degrees of slapping regularity can change a conspecific's physiological state and behavioural responses, and (3) whether drumming behaviours can be derived from other habitual movements, for example grooming or swimming. We can speculate that the rate and level of regularity in flipper slapping is determined by stereotyped motor programs and tuned by physical constraints as well as the current state of the animal; however, more flexible motor control may be exerted over this behaviour in certain conditions, for example when the animals take turns with a conspecific (Okobi et al., 2019; Raimondi et al., 2023), or produce faster slaps in anticipation of reward from human trainers as a result of conditioning (see Fig. 2a). Answering the questions given above with controlled experiments could help identify the level of motor control as well as the adaptive significance of isochrony and motivic patterns in percussive seal behaviours.

Overall, the forms and temporal features of harbour seal flipper slapping may indicate a function in signalling the level of behavioural arousal to conspecifics. Accordingly, percussive interactions were often elicited by movements or approach of a nearby conspecific and terminated by animals turning away or leaving the place of the interaction (Videos S2, S4). In our study, high-arousal occasions seemingly ranged from playfulness (Video S1), agitation and overt aggression (Video S2) to male territorial display (Videos S3a, b). In interactions, seals often took turns (Videos S2, S4) or interrupted each other (Video S2) with slapping, sometimes only with silent waving (see female 2 on the right in Video S2), while orienting their heads and/or bodies towards each other when in proximity. Among the potential affective traits and behaviours that accompanied percussive behaviour, we also noted vocalizations (see Fig. A2 and Video S2), not analysed in the present study, for example guttural and hissing sounds.

We also cannot exclude the possible interpretation that the observed slapping interactions and displays testify to territoriality in the group of seals studied: (1) older and larger (adult) animals dominated agonistic interactions over juveniles and pups (Fig. 1; see also Neumann, 1999); (2) male 3 was a potential dominant male with a higher propensity for aquatic displays (see Sullivan, 1981), circling and slapping around the pool. Given his further attributes in land-based flipper slapping, that is, the lateralization and the consistency of his slapping bouts, we can speculate that male 3 exhibited percussive behaviour to reinforce his place in the hierarchy, using singular and salient signalling in his interactions. However, we must stress that the recordings were done during the pupping/breeding season when the temporary increase in the

arousal level of sexually active animals could increase their territoriality and percussive behaviours (Hanlan, 1998; Perry, 1993; Renouf, 1993; Sullivan, 1981; Venables & Venables, 1957), leading to spatial avoidance in the other conspecifics.

Outlook: Flipper-slapping Mechanisms and the Origins of Percussive Behaviour

The question arises whether the propensity to exploit different mediums, that is, the ground or the body, has behavioural significance in a natural environment, such as serving as a basis for recognition and/or a measure of fitness. In addition, comparing the kinematic mechanisms of flipper slapping to other behaviours, for example swimming strokes (Sullivan, 1981), grooming or waving, and examining the anatomical prerequisites for slapping, can ultimately help tackle the evolutionary origins of the motor patterns that support percussive behaviour in harbour seals.

Flipper-slapping behaviour might also have the potential to form the basis of interactive rhythmic activity where animals mutually regulate each other's internal state and behaviour. This potential can be found in musical rhythmic behaviour, exerting beneficial physiological–emotional effects on the signaller and the receiver (Koelsch, 2014), which could be linked to the stress-relieving effect of repetitive movements (Chamove, 1989; Lameira et al., 2019). Studying the dynamics of acoustic interaction in harbour seal percussive behaviour may also unveil the relationship between the temporal features of flipper slapping and behavioural regulation.

Overall, it is important to understand the form and function relationship (Bryant, 2013) in percussive behaviour: in particular, how affective modalities, such as arousal and valence, can be encoded in and processed from the temporal organization and production mechanisms of slapping. Addressing these questions with controlled behavioural experiments can help further the understanding of the affective and sensorimotor underpinnings of rhythm cognition.

Author Contributions

Kinga Kocsis: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Software; Validation; Visualization; Writing – Original draft; Writing–Review & editing. **Diandra Duengen**: Conceptualization; Data curation; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing–Review & editing. **Yannick Jadoul**: Data curation; Methodology; Software; Supervision; Validation; Visualization; Writing–Review & editing. **Andrea Ravignani**: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing–Review & editing.

Data Availability

The preprocessed data sets and videos supporting this article are available in the Supplementary Material.

Declaration of Interest

The authors have no interests to declare.

Acknowledgments

This work was promoted by the Bourse Région Mobilité Internationale and Erasmus+ SMP (scholarships for K.K.) as a research project for the International Master of Bioacoustics at the Université Jean Monnet in Saint-Étienne, France. The Comparative Bioacoustics Group was supported by the Max Planck Independent Research Group Leader funding to A.R. The Center for Music in the Brain is funded by the Danish National Research Foundation (DNRF117). A.R. is funded by the European Union (ERC, TOHR, 101041885). We thank the personnel of the Zoo Cleves (Tiergarten Kleve) for the opportunity to study their harbour seals, as well as for their generous support and professional help which facilitated our recordings. We also thank Dr Chiara de Gregorio (Università degli Studi di Torino) and Dr Taylor Hersh (Comparative Bioacoustics Group, MPI, Nijmegen) for their code material used in the rhythm ratio analysis.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.09.014.

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Appendix

Rhythm Ratio Methodology and Bin Calculation

The following section dives deeper into the details of the rhythm analysis described in the Methods: Measures of Complexity in the Rhythm and Form of Percussive Behaviour. This methodology is based on previous studies by de Gregorio et al. (2021) and Roeske et al. (2020), and the following description is adapted from their work.

We divided the rhythm ratio (r; $r_k = \frac{IOI_k}{IOI_k + IOI_{k+1}}$, see Methods) space into on-integer and off-integer ratio ranges. On-integer ranges were centred around $\frac{1}{2}$ (0.5), $\frac{1}{3}$ (0.33), $\frac{1}{4}$ (0.25) and also $\frac{1}{10}$ (0.1) in the case of water slaps. Off-integer ratio ranges were centred around $\frac{1}{2.5}$, $\frac{1}{3.5}$, $\frac{1}{4.5}$, $\frac{1}{9.5}$ and $\frac{1}{10.5}$. The boundaries of the ratio ranges were determined with the following harmonic spacing: $\frac{1}{2.25}$, $\frac{1}{2.75}$, $\frac{1}{3.25}$, $\frac{1}{3.75}$, $\frac{1}{4.25}$, $\frac{1}{4.75}$, $\frac{1}{9.75}$, $\frac{1}{10.25}$. We took two similarly sized off-integer intervals around the centre ratio values (see Fig. A3 for illustration) for both acceleration (e.g. 3:1) and deceleration (e.g. 1:3). Occurrences were then counted within the 'on-' and two neighbouring 'off-integer' bins and normalized by the length of the respective interval bin. This latter was necessary to account for the unequal length of the intervals in each ratio range.

Table A1
The number of single-flipper percussive bouts and slaps (in parentheses) with their medium and context (directed to seals or to humans) across all slapping individuals

	Ground slaps to seals	Ground slaps to humans	Body slaps to seals	Body slaps to humans	Water slaps	Object slaps
Male 1	21(89)	–	15(106)	–	5(13)	25(139)
Male 2	22(90)	–	10(40)	–	6(13)	1(11)
Female 1	73(241)	–	16(55)	–	1(1)	–
Male 3	35(82)	–	1(3)	–	18(119)	–
Male 4	15(68)	169(1742)	4(15)	33(419)	7(66)	–
Female 2	108(735)	4(26)	4(12)	–	7(17)	–

Table A2
The number of percussive interactions (bouts) between seals

Signaller/Target	Male 1	Male 2	Female 1	Male 3	Male 4	Female 2	Pup 2	Pup 1	Unknown
Male 1	–	3	12+*3*	2	2	9	0+*1*	0	8+*1*
Male 2	7+*2*	–	2	0	5	6	0	0	12+*4*
Female 1	3	0	–	3	54+*1*	29	0	0	0
Male 3	0+*1*	0	1	–	18	2	0+*1*	0	15
Male 4	0	0	17	1	–	0	1	0	0
Female 2	1	3	84 +*3*	9+*4*	2	–	0	12	1

The number of land-based flipper-slapping bouts is shown in regular type and the number of interactive water-slapping events in italics.

Table A3
Comparison of on- to off-integer rhythm ratio distributions in land-based slapping bouts

	Ground slapping					Body slapping				
	1:3	1:2	1:1	2:1	3:1	1:3	1:2	1:1	2:1	3:1
Seal-directed										
Male 1	NA	1 (2)	**0.002 (10)**	1 (3)	NA	NA	1 (1)	**0.003**	NA	NA
Male 2	1	1 (1)	**0.007 (12)**	1 (2)	NA	NA	1 (1)	**0.02**	1 (1)	NA
Female 1	0.37	1 (5)	**0.002 (176)**	0.62 (14)	NA	NA	NA	**0.04 (7)**	NA	NA
Male 3	NA	1 (2)	**0.007 (15)**	1 (1)	NA	NA	NA	1	NA	NA
Male 4	NA	1 (1)	0.62 (27)	0.79 (2)	0.18	NA	NA	0.17	NA	NA
Female 2	0.37	0.81 (73)	**<0.001 (380)**	0.44 (93)	1 (1)	NA	NA	0.50	NA	NA
Human-directed										
Male 4	0.10	0.70 (60)	**<0.001 (161)**	0.33 (63)	0.59 (10)	NA	0.41 (1)	**<0.001 (1)**	0.20 (1)	NA
Female 2	1	NA	0.098	1	NA	–	–	–	–	–

P values and Wilcoxon signed-rank test statistics (in parentheses, if different from zero) are listed. NA indicates ranges with no interval data. 1:1 represents the isochrony range. Significant values are shown in bold.

Table A4
The number of seal-directed percussive bouts according to the slapping flipper's side

	Ground slapping				Body slapping				Ground and body slapping		
	R	L	Binomial test (P)	LI	R	L	Binomial test (P)	LI	Binomial test (P)	LI	Fisher's exact (P)
Male 1	13	8	0.38	0.24	7	8	1	−0.07	0.62	0.11	0.50
Male 2	21	1	**<0.001**	0.91	5	5	1	0	**0.0005**	0.63	**0.006**
Female 1	30	43	0.16	−0.18	6	10	0.46	−0.25	0.09	−0.19	1
Male 3	35	0	**<0.001**	1	1	0	1	1	**<0.001**	1	1
Male 4	6	9	0.61	−0.20	2	2	1	0	0.65	−0.16	1
Female 2	29	81	**<0.001**	−0.47	0	4	0.13	−1	**<0.001**	−0.49	0.57

Outcomes of the binomial tests assessing the significance of lateralization as well as the lateralization indices (LI) are given separately for ground and body slaps as well as for both types together. Results of the Fisher's exact tests, calculated to test the association between the slapping medium and limb preference, are also reported. In the case of female 2, two ground-slapping events (one right (R), one left (L)) were added due to a flipper switch in two bouts. Significant P values are shown in bold.

Table A5
Comparison of on- to off-integer rhythm ratio distributions in display water-slapping bouts

	Display water slapping						
	1:9	1:3	1:2	1:1	2:1	3:1	9:1
Male 3	0.37 (3)	**0.03**	0.85 (6)	**0.004 (2)**	1 (5)	NA	NA
Male 4	1	0.10	1 (1)	0.45(9)	0.20 (9)	NA	0.37(3)

P values and Wilcoxon signed-rank test statistics (shown in parentheses, if different from zero) are listed. NA indicates ranges with no interval data. 1:1 represents the isochrony range. Significant results are shown in bold.

(a)

(b)

Figure A1. Monitored areas of the seal facility. (a) View of the seals' enclosure from above. Image courtesy: Zoo Cleves. Rectangles represent the placement of the Song Meter 4 for passive acoustic monitoring; circles show the positions of the camera. Black dashed lines delineate the approximate camera angles. Brown symbols indicate the first positions around the time of pup 1's birth when the pool water was removed. Light blue symbols show the second position when the pool was partially filled. 'h' shows the respective monitored hauling spaces. (b) Example snapshots from the two camera positions (indicated with matching colours).
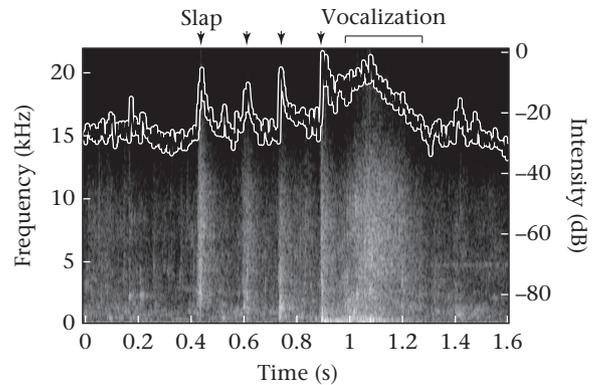

Figure A2. Spectrogram of a ground-slapping bout from female 2, with the intensity curve overlaid. Window size: 5 ms; dynamic range: 60 dB; minimum pitch setting to extract the intensity curve: 1 kHz (with mean pressure subtracted). Lighter colours in the spectrogram indicate higher power values. Note that the bout consists of four percussive slaps, and is followed by a broadband vocalization.
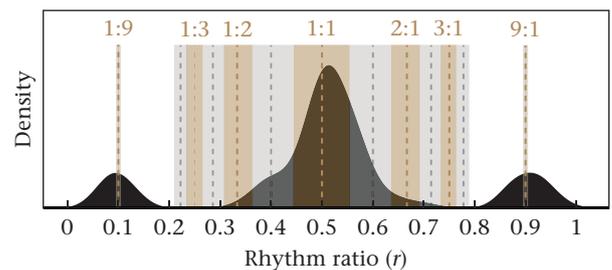

Figure A3. Rhythm ratio (r) ranges used for rhythm analysis, based on de Gregorio et al. (2021) and Roeske et al. (2020). 'On-integer' (in brown) and 'off-integer' (in grey) rhythm ratio bins are shown with a sample r distribution (top panel from Fig. 4c). Centre values for the bins are indicated with dashed vertical lines. The ratios above the plot show the corresponding interval ratios.
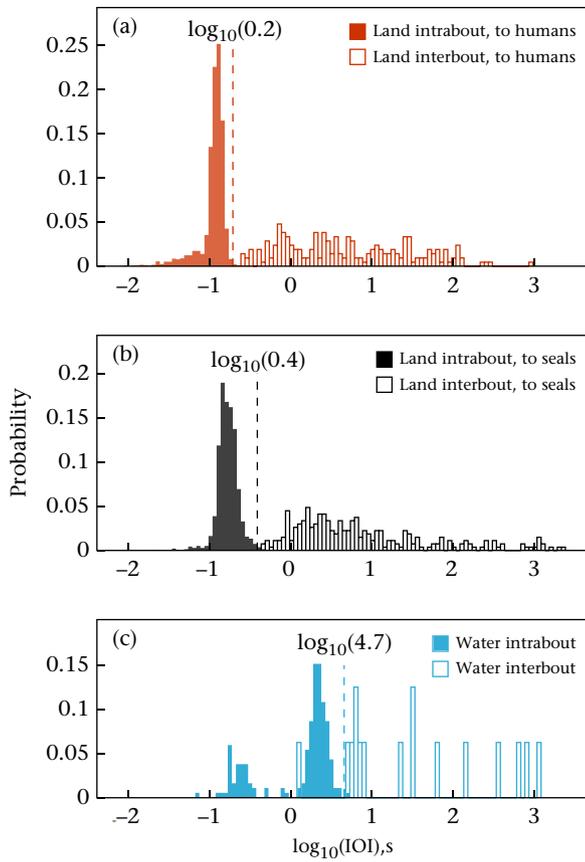
Figure A4. Interonset interval (IOI) distributions for each of the three main forms of percussive behaviour: (a) land-based human- and (b) seal-directed slapping, as well as (c) water slapping. Intrabout slap onset and interbout slap onset interval distributions from the 1 h recording epochs are presented separately. The calculated bout criteria for each category (dashed lines in the corresponding colour) highlight the separation of intra- and interbout interval distributions. Bin width is 0.05 on a logarithmic scale.
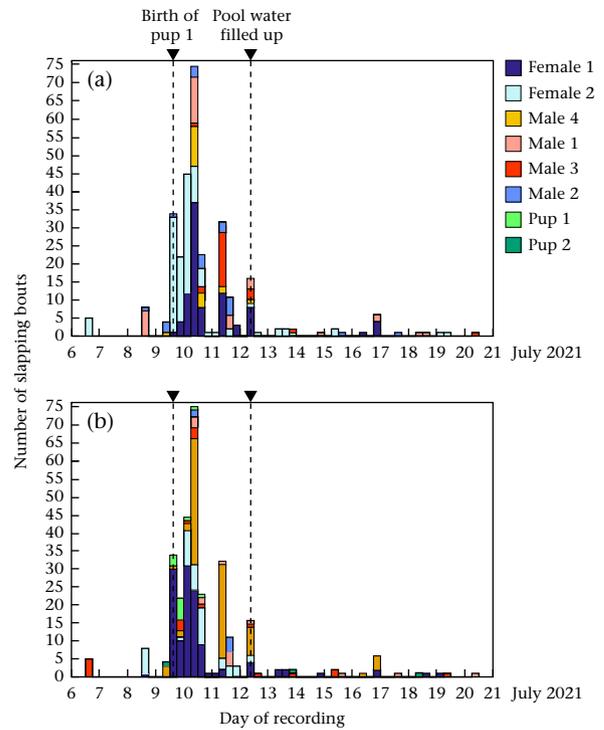
Figure A5. Temporal distribution of interactive percussive activities between seals. (a) The number of flipper-slapping bouts performed by each seal to a conspecific throughout our monitoring period (6—20 July). (b) The number of flipper-slapping bouts where the respective animals were the target of percussive interactions. Bar graphs are stacked. Seals in the key are sorted by decreasing degree centralities in the network of slapping interactions. Tick marks indicate the beginning (midnight) of each day; bin size is 6 h. The birth time of pup 1 (pup of female 1) and the time when the pool was partially filled with water are marked with dashed vertical lines.
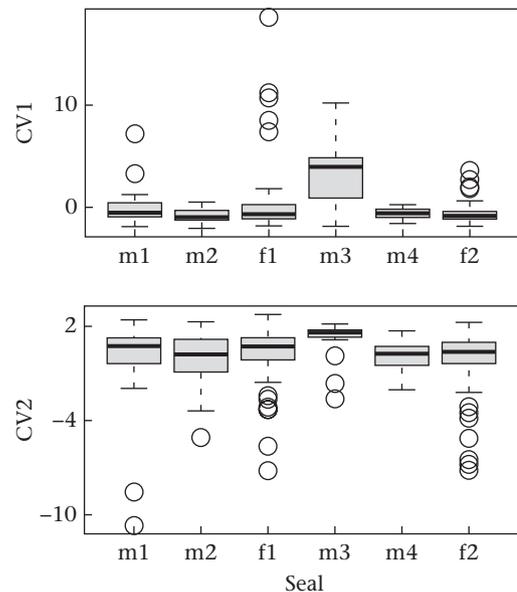
Figure A6. Distributions of the first two canonical discriminant variables (CV) in all flipper-slapping individuals. The box plots show the quartiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers. m: males; f: females.