Chapter 17
The Mind of a Sea Lion

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Abstract The mind of a sea lion links sensory information gathered from the surrounding environment to the decision operations, or cognitive processes, that enable behavioral responses based on judgement and experience. Here, we illustrate the sea lion's impressive capabilities for complex associative learning and highlight some of the unique and essential contributions sea lions have made to our understanding of problem solving, concept formation, and memory in non-human animals. We suggest that the persistence and behavioral flexibility that allow sea lions and fur seals to exploit unpredictable environments make them particularly well suited to performing in the behavioral laboratory, and therefore, highly valuable models for comparative studies of learning and intelligence.

Keywords Sea lions · Fur seals · Otariidae · Behavior · Cognition · Learning · Memory · Neuroscience · Neurobiology

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17.1   Introduction

The otariidae are familiar to the public for high-energy participation in animal shows and their intelligence and persistence in exploiting human-made opportunities for fish predation. From these general impressions, a lay-person might sketch the sea lion's intellect as keen, and their personality as stubborn. The empirical evidence gathered over the past half century supports this impression. Given the small number of otariid research subjects featured in behavioral and cognitive sciences, there is a surprising wealth of careful, detailed studies; the majority of these feature one species, the California sea lion, *Zalophus californianus*.

Sea lions have demonstrated some cognitive and behavioral capabilities that are either unique or rarely observed in other non-human animals, including cetaceans and primates. Sea lions are behaviorally and cognitively flexible, with intense task focus and motivation, and therefore may play a disproportionately large role in comparative cognitive research. Schusterman et al. (2002) provided a comprehensive review of sea lion cognition. Here, we summarize research on perception and cognition and highlight recent findings, with particular attention to the cognitive world of the California sea lion. We also consider potentially rich avenues for future behavioral and neurobiological research, and begin with a history of behavioral research with California sea lions and other otariid carnivores.

17.2   Foundational Research

The sea lion's entry into behavioral science came largely as a response to similar research being conducted with fully aquatic odontocetes such as the bottlenose dolphin. Excitement regarding the cognitive and sensory capabilities of dolphins drove a wave of comparative research with marine mammals in the mid-twentieth century. Much of this work focused on the dolphins' remarkable ability to echolocate under water (Kellogg and Kohler 1952; Kellogg 1961). Some early researchers believed that other marine mammals might also share this biosonar capability, and a particular focus was placed on sea lions, which had been observed to navigate effectively in low-light underwater environments and produce pulsed trains of underwater sound (e.g., Poulter 1963). This interest led to federal funding in the United States and the subsequent establishment of a sea lion sensory/behavior research laboratory at the Stanford Research Institute in California (Fig. 17.1a). One of the young researchers tasked with examining echolocation in sea lions was Ronald Schusterman—a mentor to all three authors of this chapter—who would become instrumental in advancing behavioral and cognitive research with sea lions for more than 50 years (see Schusterman 1981, 2010; Schusterman et al. 2002; Fig. 17.1b). Much of his work was conducted at the Stanford Research Institute, the California State University of Hayward, and at the pinniped research facility he

Fig. 17.1 (**a**) The biosonar laboratory at Stanford Research Institute's Coyote Hills Laboratory in Fremont, California (**b**) Professor Ronald Schusterman with California sea lion *Rocky* at Long Marine Laboratory in Santa Cruz, California (**c**) California sea lion *Bibi* performing a stimulus discrimination task in which the size of the incorrect object was gradually increased

founded in 1985 at Long Marine Laboratory at the University of California Santa Cruz.

Schusterman was a behavioral scientist with training in psychophysics—the study of how physical stimuli relate to mental phenomena—and he grounded his work with sea lions in rigorous assessments of the animals' sensory capabilities (see Reichmuth 2018). By working with highly trained sea lion subjects eager to engage in carefully designed behavioral tasks in exchange for fish rewards, Schusterman and others discovered a great deal about the specific sensory capabilities and general learning strategies that sea lions could use to solve difficult problems (Schusterman 1981). They did not, however, find convincing evidence of 'echo-ranging' abilities despite an assortment of clever observations and experiments aimed at revealing such a sense (summarized in Schusterman et al. 2000a). Schusterman concluded that sea lions do not actively echolocate as cetaceans do but instead rely upon a combination of highly developed amphibious visual, auditory and tactile abilities (see Chap. 16 by Hanke et al.; Chaps. 14 and 15 by Charrier).

Schusterman's negative findings put an end to attempts to develop sea lions as subjects for biosonar and 'echo-ranging' research, but promoted sea lions as excellent models for general comparative studies of sensory biology and cognition. Healthy captive sea lions learned quickly, demonstrated high task focus, and were cooperative and enthusiastic participants in sensory and behavioral experiments. Following Schusterman's early work on sensory biology, he and other investigators continued to study sea lions in a range of behavioral and cognitive domains, including learning, memory, communication, language, and concept formation. Much of this work has been previously reviewed (see Schusterman et al. 2002; Schusterman and Kastak 2002). We highlight some of the most significant results before moving to more recent work.

Early research on sensory biology in sea lions led to a variety of clever experiments that revealed important learning abilities transcending specific sensory modalities. Following work on 'errorless' learning techniques in pigeons (Terrace 1963),

Schusterman began applying similar methods for sea lions, using 'fading' (gradually reducing the salience of a stimulus over successive trials or exposures) to demonstrate that sea lions could learn new sensory discriminations with few to no errors along the way (Schusterman 1966; Fig. 17.1c). Not only could sea lions learn to reliably select one stimulus over another in this manner, but they could learn to reverse their preferences, again and again, with minimal errors throughout the learning process (Schusterman and Thomas 1966). The same was later shown to be true in spatial learning tasks with sea lions, when predictable response locations were reversed (Beach and Pepper 1974). Such 'reversal learning,' in which an animal learns to switch its selection preference depending on reward contingencies, represents an impressive display of behavioral flexibility afforded by application of basic learning mechanisms. Schusterman also demonstrated efficient, flexible, and generalizable learning mechanisms through exploration of what has been termed 'learning sets,' which represent an animal's *learning to learn* ability. This ability involves learning to solve different problems of a similar type more quickly on repeated exposure (Harlow 1949). Schusterman charted this performance improvement effect in sea lions learning successive stimulus discrimination problems with arbitrary visual shapes (Schusterman and Thomas 1966), and the results supported his ongoing belief in the importance of using many example problems during training (e.g., Kastak and Schusterman 1994). By providing experimental animals with many training problems of a given type prior to testing a specific ability or process with novel problems, Schusterman believed an experimenter could reduce the potential effects of response strategy and idiosyncratic responses on cognitive performance. These and other studies were conducted during a time when animal learning studies were developing within behavioral frameworks from the emerging field of operant conditioning (Skinner 1938; Breland and Breland 1966). Schusterman's sea lion studies were pioneering demonstrations of fundamental cognitive abilities that paved the way for systematic evaluation of animal intelligence.

The 1970s and 1980s were golden years for research in animal cognition, particularly for work with primates and marine mammals. A major focus was to establish artificial communication frameworks that would enable human-animal informational exchanges. Language-learning studies with non-human animals were centered primarily on sign language and symbol use with primates, considered of great interest due to their close relationship to humans, as well as complex vocal production learners such as parrots and dolphins. A general consensus has since emerged that while animals are capable of learning arbitrary stimulus-symbol bindings—with some primates, parrots, and even dogs capable of learning hundreds of these word-like associations (Hilix and Rumbaugh 2013; Pilley and Hinzmann 2013)—non-human animals have not demonstrated an ability to use grammar or syntax in a systematic way. Some animals, however, including great apes and cetaceans, apparently have the capability to respond appropriately to syntactic elements of signals, specifically, the order or pattern of symbol or words (Kako 1999; Shanker and King 2002). This ability has been taken by some as evidence of convergent evolution of syntactically relevant cognitive capability (e.g., Fitch 2011).
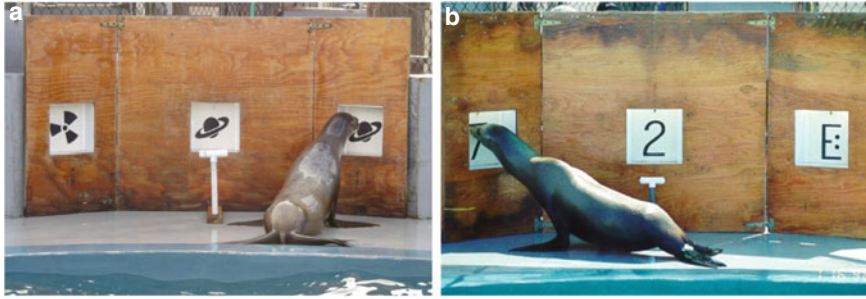
Fig. 17.2 (**a**) California sea lion *Rocky* demonstrating application of the problem-solving concept of reflexivity or 'sameness' by matching unfamiliar but identical visual shapes, see also Supplementary Video 17.2 (**b**) California sea lion *Rio* demonstrating the formation of functional stimulus categories by matching shapes belonging to the same abstract grouping ('letters'), see also Supplementary Video 17.3

While sea lions lack complicated social communication systems, they have provided an excellent 'generalist' mammalian system with which to consider the true nature of certain cognitive abilities, including those related to 'artificial' language learning. Schusterman and his colleagues built upon their strong foundation of basic studies to show that sea lions could also perform well in highly complex instructional tasks. He trained several sea lions, including star pupil *Rocky*, to learn gestural cues for objects, their descriptive characteristics, and actions that could be performed with them. *Rocky* could respond appropriately to even novel assemblies of these cues (e.g., *large white cone, black small ball fetch*—meaning "*bring the small black ball to the large white cone*"), alter her behavior in response to changes in cue order, and even answer questions about the presence or absence of specific items in her environment (Gisiner and Schusterman 1992; see Supplementary Video 17.1). Schusterman and Gisiner (1997) eventually argued that these impressive capabilities could potentially be explained not via specific language- or meaning-related adaptations, but through complex associative learning. Whether receptive syntax can be fully explained by associative learning or not, the ability of sea lions to respond appropriately to meaning carried by novel combinations of 'word' order suggests that syntax-relevant abilities are spread very widely in the animal kingdom, and not just among close relatives to primates, or complex vocal production learners such as dolphins and parrots.

Following the era of animal language studies, Schusterman and colleagues shifted to exploring the mechanisms that underpin apparently complex cognitive behavior. These studies examined what can be considered as concept learning or 'rule-governed' learning. For example, trained sea lions were able to solve novel problems based on strategies learned from experience with similar examples solved by trial and error (Kastak and Schusterman 1992). These problem-solving strategies included using the process of elimination or 'exclusion' (Schusterman et al. 1993a), as well as rules of logic, including sameness matching or 'reflexivity' concept (Kastak and Schusterman 1994; Fig. 17.2a, see Supplementary Video

17.2), interchangeability of arbitrary cues or 'symmetry' concept, and the more complicated rules of transitive inference and stimulus equivalence (Schusterman and Kastak 1993). These logical *if...then* rules can be expressed in mathematical terms as: *if* A = A and B = B...*then* C = C (reflexivity), *if* A = B...*then* B = A (symmetry), if A = B and B = C...*then* A = C (transitivity), and finally A = B and B = C...*then* C = A (stimulus equivalence, which combines all three logical rules). In these experiments, the stimuli were arbitrary visual shapes, having no prior meaning to the sea lions. Examining the ability of sea lions to make these logical inferences with arbitrary items enabled, for the first time, a systematic analysis of the learning skills that support complex behavior, including some of the behavioral performances described in artificial language studies. These evaluations of concept learning have implications that extend beyond laboratory studies of animal cognition. For example, the concept of stimulus equivalence can be used to explain the complex behavior of wild sea lions, including multimodal recognition between mothers and their dependent pups (Schusterman et al. 1992; Schusterman and Kastak 1998), the 'dear enemy' phenomenon observed in male territorial sea lions, and even how sea lions and other animals classify individuals into functional categories such as 'friends' and 'foes' (Schusterman et al. 2000b). Each of these examples require individuals to use information about familiar stimuli to solve unfamiliar problems.

Learning experiments conducted with trained sea lions provided insight into how sea lions and other animals remember and recall information over both short and long periods of time. For example, in language-learning tasks, sea lion behavior is influenced by 'priming' from recent behavioral experiences (Schusterman et al. 1993b). In other stimulus association tasks, sea lions could hold information about visual shapes in working memory for at least two minutes without a decrement in problem-solving (Schusterman and Kastak 2002). On a much longer time scale, a highly trained California sea lion called *Rio* showed a memory ability exceeding that of any other animal who had been tested over multiple years. *Rio* had taken part in systematic studies of concept formation as a young adult, and later showed she was capable of remembering previously learned concepts—as opposed to memorizing specific solutions to familiar problems—for periods of 1–10 years (Reichmuth Kastak and Schusterman 2002). To date, *Rio's* remarkable memory performance remains among the best formal evidence concerning the longevity and complexity of animal memories.

It may seem intuitive that long-lived and sentient animals like sea lions must solve novel problems and remember essential information for extended periods of time. For example, sea lions and fur seals show astounding natal site fidelity, with females sometimes giving birth within a few meters of their pupping sites from prior years (see Chap. 1 by Gentry). Fur seals also show the ability to learn and remember the location of productive foraging sites, which they return to over successive at-sea trips (e.g., Bonadonna et al. 2001). In a social context, female otariids recognize the calls of their pups for multiple years, well beyond the period of maternal dependency, and pups seem equally able to remember the features of their mothers' voices (Chap. 14 by Charrier; Insley 2000; Mathevon et al. 2004; Pitcher et al. 2010).

Competing neighboring males can recognize and remember their territorial neighbors over multiple years, and treat these individuals differently than unfamiliar rivals (Chap. 1 by Gentry). Despite many examples of natural behavior that seem to call upon advanced cognitive abilities, there are few species for which complex behavior observed in nature can be linked to explicit learning and memory abilities demonstrated in controlled experiments. It is possible that behaviorally flexible animals such as otariids have greater pressure for associative learning or long-term memory than animals relying on instinct or less changeable circumstances. Thus, yet another aspect of otariids that sets them apart from other animals is our ability to view their behavior clearly from the standpoints of both natural problem-solving and cognitive capability (see Schusterman et al. 2002).

In the years since Schusterman et al. (2002) summarized the cognitive abilities of sea lions, otariids have contributed to a number of advances in comparative cognition. We focus in the next sections on more recent studies of otariid cognitive capabilities.

Box 17.1: Brain and Behavior

Recent research has expanded our understanding of otariid neurobiology and its potential relevance to behavior and cognition. For much of the history of sea lion research, these animals were not considered to have a nervous system predictive of high intelligence or advanced cognitive performance. This was on account of their Encephalization Quotient or 'EQ': a measure of how a species' ratio of brain size to body size compares to typical trends across species, which has been considered by some to be representative of a species' raw intellectual capabilities (Jerison 1977). Sea lion EQ has been measured close to 1 or 1.1 (Worthy and Hickie 1986), suggesting they have a typical brain-to-body ratio for a mammal, though note that due to sexual dimorphism, female sea lions have a higher EQ than males. The EQ measure for sea lions and other otariids is lower than for some other highly productive model species such as dolphins and non-human apes. However, as addressed below, contemporary neuroscientists no longer believe EQ to be a strong correlate to cognitive capability.

The impressive success of sea lions in cognitive tasks—some of which animals with much higher EQs failed or struggled to complete—has been attributed to the importance of simple associative mechanisms, broadly conserved across vertebrate species, rather than specializations of brain structures (Schusterman et al. 2002). Perhaps sea lions weren't necessarily smarter than other animals (or why the relatively low EQ?), but rather just highly motivated and allied with persistent trainers. This is a difficult interpretation to reconcile with contemporary knowledge of brain and behavior, which has cast doubt on the relevance of EQ in predicting species intelligence. EQ likely does not equal IQ, despite the fact that many species considered to be highly intelligent have

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Box 17.1 (continued)

EQ > 1. Some studies have found that overall brain size is more predictive of cognitive capability than EQ when assessed in closely related species (Deaner et al. 2007). Despite their unremarkable EQ, sea lions actually have large brains, between 300 and 400 cm^3 as measured in well over 40 California sea lions (Montie et al. 2010; Cook et al. 2015). In terms of absolute size, their brains are similar to those of chimpanzees,[1] and four to five times larger than the brain size of most dogs (Horschler et al. 2019). More important than size is likely total number of neurons, particularly cortical neurons, which vary greatly across species, and correlate only loosely with gross brain size. We do not have cell counts for sea lion brains, but large pinnipeds like walruses are estimated to have in the range of 4 billion cortical neurons, far higher than the numbers found in terrestrial carnivores.[2] Yet another perspective acknowledges the brain as a complex and dynamic network for information processing. The features of that network should be most predictive of how information is processed, rather than overall size (Buzsáki and Draguhn 2004; Sporns and Honey 2006). Indeed, neurobiological evidence suggests that brain network features, such as conduction speed and distance between processing areas may be most predictive of intelligence. Primates excel in these measures, with carnivores close behind (Roth and Dicke 2017), suggesting a link to social or ecological (predatory) problem solving.

In humans, there is growing evidence that the organization of the brain's connections—more than brain size or number of neurons—is perhaps most relevant to determining intelligence (Wu et al. 2013). Such analyses have yet to be conducted for sea lions, but, anecdotally, assessment of neural tractography suggests dense and varied cortico-cortical connection pathways (P. Cook, unpublished data—see Fig. 17.3). Different types of cognitive and behavioral tasks rely differentially on different brain structures and networks. Along these lines, and also anecdotally (P. Cook, unpublished data), sea lions have an apparently enlarged caudate nucleus compared to primates and many carnivores. This structure, found in both brain hemispheres, is predominantly featured in reward learning and motor learning (Brovelli et al. 2011)—and so may be related to the sea lions' often noted drive and motivation for task-based learning.

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[1]The largest carnivores, like the polar bear (*Ursus maritimus*) or Steller sea lion (*Eumetopias jubatus*), have brain weights around 500 g and are expected to have at least a billion cortical neurons. Due to higher neuron packing density, carnivores have more cortical neurons than ungulates of the same brain size (Herculano-Houzel 2012; Kazu et al. 2014).

[2]African lions and domestic dogs have approximately 500 million cortical neurons (Jardim-Messeder et al. 2017). Humans have approximately 16 billion (Herculano-Houzel 2018).
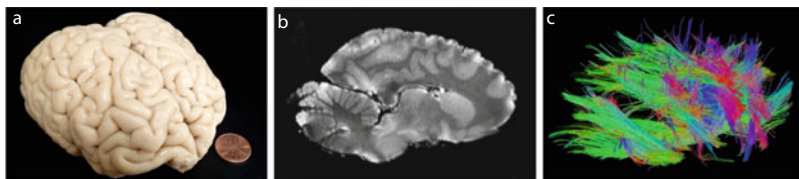
Fig. 17.3 Three views of a sea lion brain. (**a**) An extracted brain, viewed with coin for size reference (image provided by Eva Sawyer). The extensive convolutions of the sea lion brain are particularly notable. Whether the convolutions are functionally relevant remains to be determined. (**b**) A T2-weighted sagittal MRI slice of a post-mortem sea lion brain (image provided by Peter Cook). Traditional structural neuroimaging allows us to assess distribution of gray matter (cell bodies), distribution of white matter (connections between cell bodies), and to visualize and measure gross structures. The anterior (front) portion of the brain is oriented to the right of the image. Lighter tissue is gray matter (high in cell bodies) and darker tissue is white matter (myelinated axons, or communication channels between processing regions). The complexity of the cortical convolutions is apparent, even in this slice near sagittal midline. The extremely large caudate nucleus is visible near the front middle of the image, a large light gray oval. This structure, central to motor learning and reward, tends to be particularly large in canid carnivores such as the sea lion. (**c**) Deterministic fiber mapping of a post-mortem sea lion brain in sagittal view (image provided by Peter Cook). This type of image is produced from diffusion tensor imaging (DTI), a brain imaging protocol that maps large connective pathways in the brain, revealing characteristics of brain organization that are not accessible with typical structural MRI. Each colored thread is a representation of likely white matter tracts connecting processing regions. Tracts oriented front to back of the brain are shown in green (the brain stem, at the back bottom of the image contains a particularly visible green set of tracts). Tracts oriented right to left are shown in red (parts of the corpus callosum, connecting left and right hemispheres of the brain, are visible in the upper middle portion of the image in cross section). Tracts oriented up and down are shown in blue. The complex pattern of interwoven tracts is evident in sea lion cortex. Many of these represent cortico-cortical tracts connecting different cortical processing regions with each other. It is likely that complexity of cortico-cortical connections is correlated with breadth of cognitive capability

17.3 Concept Formation

After the rigorous study demonstrating flexible formation of concept classes by Schusterman and Kastak (1993), subsequent research demonstrated sea lions' facility with mental manipulation of abstract classes of visual shapes. Two sea lions were able to form large categories composed of alphanumeric symbols on the basis of their common function in a reversal learning paradigm, and later were able to link stimuli belonging to the same category in a matching task (Reichmuth Kastak et al. 2001; Fig. 17.2b, see Supplementary Video 17.3). The sea lion subjects subsequently expanded these concept classes of "letters" or "numbers" not merely through direct positive association between new stimuli and prior exemplars, but also through the logical process of exclusion (Reichmuth Kastak and Schusterman 2002). Here, sea lions were given new problems where a novel shape was presented as a possible match for a familiar class member along with a familiar shape that was not related to that class. Sea lions *Rocky* and *Rio* immediately selected the novel object by process of elimination. More notably, when the previously novel objects

were used in follow-up transfer tests, the sea lions correctly paired them with every stimulus belonging to the same class as that of the initial match. In other words, having determined by the process of elimination that a novel stimulus must belong to a particular concept class, sea lions immediately integrated the new stimulus into the broader class with no further training required.

More recent follow-up work has shown that sea lion *Rio* was able to expand learned concept classes of visual shapes to include arbitrary sounds, suggesting a robust, cross-modal representational faculty. Lindemann-Biolsi and Reichmuth (2013) added novel sounds to the visual sets the sea lion had previously learned. After linking one sound and one shape through direct training, *Rio* demonstrated the ability to group the sounds with visual shapes from the same set appropriately, on the very first exposure of each stimulus combination. This level of functional categorization is among the most complex demonstrated thus far by non-human animals.

In research expanding earlier studies of a 'reflexivity' or 'sameness' concept—that is, matching items that are alike, sea lions have also been shown capable of visual 'oddity' learning—that is, matching items that are *not* alike (Hille et al. 2006). In this experiment, multiple visual shapes were presented, and the sea lion was rewarded for selecting the item that is not like the others. Following training, the sea lion was able to perform the oddity task with novel problems. Relatively few mammals have demonstrated the ability to perform stimulus matching of novel items based on the concepts of 'sameness' or 'difference'; in addition to humans, these include harbor seals (Mauck and Dehnhardt 2005; Scholtyssek et al. 2013), several monkey species, chimpanzees (*Pan troglodytes*), and a dolphin (*Tursiops truncatus)* (for review, see Katz et al. 2007).

Collectively, the ability of sea lions to acquire abstract concepts indicates a robust conceptual mechanism whereby sea lions maintain long-term, flexible representations of stimulus groupings that cross sensory boundaries. They can integrate new information into established stimulus classes, even when the new information is quite different in form from prior class exemplars. Why sea lions have been uniquely successful at demonstrating concept formation compared to other animals is not clear, as parallel data are still largely lacking for other species. Their success could be due in part to the need to respond rapidly and appropriately to complex stimuli, as sea lions are fast-moving, predatory animals that operate in three-dimensional underwater environments. They use an assortment of sensory cues in an adaptable manner as they move from shore to sea and back again (Chap. 16 by Hanke et al.). Their robust performance in cognitive studies may also be due to their persistence as experimental animals and their impressive task focus, and may be related to aspects of their neurobiology (see Box 17.1). Sea lions are clearly capable of a high degree of complex associative learning. Whether additional cognitive specializations come into play is at yet unknown.

17.4   Learning in the Vocal Domain

The ability of sea lions to relate novel sounds to classes of items suggests a degree of what is termed vocal 'comprehension' learning (Janik and Slater 1997; Lindemann et al. 2006). Learning to respond differentially to different sounds is one way in which learning may influence vocal communication in animals. Contextual control of sound production is also well developed in sea lions. For example, Schusterman's early studies of sound production (for review see Schusterman 2008), showed that sea lions could be readily trained to emit vocalizations and to inhibit them on cue; sea lions could also learn to vocalize in the presence of certain objects and respond vocally to sets of objects.

While some forms of vocal comprehension learning and vocal contextual learning are fairly common among animals, evidence for vocal production learning (learning to vary emitted sounds and learn new call types) is much less common. Sea lions have a relatively simple vocal repertoire that is linked to predictable situations and socio-emotional factors (e.g., Schusterman et al. 1966; Peterson and Bartholomew 1969; Chap. 14 by Charrier). Their calls are often stereotyped and repetitive. Even so, wild otariids can learn to recognize and respond to the calls of other individuals (Insley et al. 2003). Sea lions can also learn to modulate the production of calls both in captivity and on breeding rookeries in response to social cues (see Schusterman 2008). In terms of learning to produce sounds or calls that are not typically part of the vocal repertoire, there is less evidence for vocal plasticity. While trained sea lions appear to have limited ability to vary the complexity or "phonemic" characteristics of their calls, they do have substantial flexibility and control over call rate, which has apparent relevance for social interactions (Schusterman 1977). While sea lions maintain some long-term social relationships mediated by the exchange of vocal signals, they apparently do not possess the ability to learn entirely new vocalizations, as observed in phocids, walruses, and cetaceans (see Reichmuth and Casey 2014). It is unlikely that this limitation reflects upon otariids' general cognitive capacities. While vocal production learning is rare in the animal kingdom, and predominantly found in animals with relatively complex brains and flexible behavior (Jarvis 2006), it is virtually absent in non-human apes, and likely depends on specific social evolutionary pressures (Marler and Mitani 1988; Locke and Snow 1997; Owren et al. 2011). There is also conjecture that prior breathing and foraging adaptations may have subserved evolution of vocal learning in the pinnipeds (Reichmuth and Casey 2014; Schusterman 2008).

17.5   Rhythmic Behavior

Sensitivity to repetition rate during streams of redundant calls may be one reason sea lions have been shown so capable of perceiving and motorically matching a periodic beat in an auditory signal, also known as 'beat keeping' behavior (Repp and Su

2013). Specifically, exhaustive and progressive experiments with the trained sea lion *Ronan*[3] provided convincing evidence that she could (1) learn to bob her head in time to a rhythmic beat of a given tempo, (2) transfer that beat keeping ability to novel tempos, and (3) entrain her rhythmic movements to complex, musical stimuli (Cook et al. 2013).[4] This research has significant implications for the origins of what has been termed 'biomusicality' in animals (see Honing 2019). Prior to *Ronan's* unequivocal beat keeping performance, this entrainment capability had been observed only in humans and parrot-type birds—both of which are highly developed vocal production learners (Janik and Slater 1997). Some scientists had suggested that evolutionary changes to sensorimotor neural circuits in vocal production learners might also allow beat keeping to complex stimuli such as music (Patel et al. 2009a, b). However, the evidence for beat keeping in sea lions, including entrainment to dynamic musical stimuli at novel tempos, has challenged this theory (Rouse et al. 2016; Wilson and Cook 2016) as they are not considered to be vocal production learners. Once again, sea lions have played an outsize role in a contentious domain of comparative cognition.

We suspect that beat keeping capability in sea lions is probably due to strong general motor control and high motivation (Wilson and Cook 2016), as opposed to a unique neurobiological adaptation specifically supporting vocal motor control in species with complex vocal communication. The ability to judge temporal patterns is fundamental to animal behavioral ecology (DeCoursey 2004), and sensorimotor entrainment is unlikely to be restricted to rarified phylogenies, regardless of the current dearth of strong experimental evidence (Ravignani and Cook 2016). While relatively little is known about how animals perceive time, emerging evidence from a South African fur seal *Arctocephalus pusillus* suggests they can discriminate time intervals extremely well (Heinrich et al. 2020). Even for those species with fine-scale timing abilities, training animals to move in time to a beat is potentially difficult and may require highly capable research animals with dedicated trainers. Perhaps such 'high-performance' animals can more easily learn complicated sensorimotor tasks. Others have wondered whether sea lions, as relatives of other pinniped species with some evidence of vocal production learning, may have something like a vestigial vocal production learning brain circuit supporting their beat keeping (Patel 2014).

Resolving the evolutionary bases of rhythmic behavior in sea lions and other animals will require two parallel lines of evidence: behavioral data on beat keeping behavior in a range of other species (as called for in Ravignani and Cook 2016) and mapping the neural circuitry of pinniped brains. The latter is currently being explored (P. Cook unpublished data). Regardless, given the capability of sea lions to perceive and entrain to rhythmic sounds, future work in this domain should further probe these abilities with a wider range of acoustic stimuli, including the types of

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[3]*Ronan* is a young female sea lion raised in captivity following stranding and rehabilitation; she was named in honor of Dr. Ron Schusterman.

[4]Video examples of *Ronan's* beat keeping performance can be found at https://youtu.be/6yS6qU_w3JQ and https://youtu.be/qwcR5LSsTUI.

heavily syncopated and metered musical stimuli that humans are able to resolve (Fitch 2013) and the rhythmic streams of repeated communicative calls that are relevant to sea lions in the wild (Schusterman 1977).

17.6   Temperament and Self-Regulation

The experimentally demonstrated cognitive capabilities of sea lions likely have something to do with temperament. Collectively, otariids are curious, eager, opportunistic, and gregarious animals whose lives are patterned by the ebb and flow of the seasonal, temperate environments where they live. As with most mammals, they demonstrate meaningful individual differences in temperament (Ciardelli et al. 2017)—which can be loosely defined as consistent behavioral differences in the way different individuals react to changes and challenges in the environment (Manteca and Deag 1993). Individual traits related to temperament that may contribute to learning abilities are explored by DeRango and Schwarz (Chap. 19). Well-developed learning abilities are also related to executive function and cognitive control—the cognitive processes involved in behavioral self-regulation. In humans, these processes are considered 'mental faculties' that help individuals to filter distractions, prioritize tasks, set and achieve goals, and control behavioral impulses.

There are several reasons that sea lions are interesting from the dual perspectives of temperament and executive function. As described in Box 17.1, otariids have large brains with complicated corticocortical connection patterns. They also show robust ability to manipulate abstract concepts and integrate and generalize concepts across sensory boundaries. These cognitive attributes suggest dense 'polysensory' cortical adaptations, which may be linked to enhanced fronto-parietal behavioral control mechanisms (Jonides et al. 1998). Sea lions appear to have a high capacity for motor inhibition, an ability which is fundamental to self-control and related to working memory (Roberts et al. 1994; Borella et al. 2008). By inhibiting or overriding behavioral impulses, sea lions can consider and select from a wider range of potential responses that may be informed by prior experience. Anecdotally, there are many instances in which individual sea lions appear to exhibit cognitive control. For example, adult breeding males chase juvenile males within their territories, but rarely if ever attack them, while adult competitors in the same areas face extreme aggressive consequences for intrusion (Gentry 1970). During development, sea lions may show role reversal during play with individuals taking turns in status and position during sparring (Chap. 20 by Llamazares-Martín and Palagi). In captivity, we observed that a young sea lion occasionally placed her open mouth on the hand or arm of a trainer, but did not bite or break the skin; this occurred predominantly when the animal was asked to endure extended close contact training sessions (P. Cook, unpublished data). One possible interpretation of these examples is that sea lions sometimes inhibit aggressive impulses—for example, beginning an aggressive signal (biting), by using top-down inhibitory processes to avoid

completing the aggressive action. Empirical studies here are limited, but suggest meaningful capability for complex, top-down executive control mechanisms.

One study with trained California sea lions has explored self-control directly (Genty and Roeder 2006). In this case, sea lions showed apparently greater inhibitory control than that observed by non-human primates in similar studies. Four sea lions were trained on a reverse reward contingency task in which they were presented with two arrays of fish: one containing five fish, the other only one. To receive the five fish, a subject had to select the array containing only one, while selection of the larger array was reinforced with the smaller reward. Prior to training, the sea lions showed an unsurprising preference for the array containing five fish. With additional experience however, three of the sea lions learned to select the smaller array to receive the larger reward, and they learned the reversed-reward task almost perfectly in less than 200 trials. The sea lions' performance rivaled that previously observed by orangutans *Pongo pygmaeus*, and was better than that observed in other non-human primates. The authors speculated that the sea lions' performance might be related to their non-competitive foraging ecology, which might not require the same strength of competitive impulse to seize food when presented. Others have suggested their success on the task might be attributed to subtle features of experimental design (Beran 2018). Further study of inhibitory control in otariidae is warranted.

Self-control can be considered from the perspective of working memory, which relies on similar neural substrates as inhibitory control in humans and other mammals (Engle and Kane 2004; Singer et al. 2013). In addition to early work by Schusterman and colleagues with trained sea lions that showed durable memory (spanning at least 2 min) in delayed matching procedures (see Schusterman et al. 2002), newer findings have continued to probe a range of working-memory processes in sea lions. For example, Abramson et al. (2011) demonstrated a primate-like capability for numerosity (number) discriminations in South American sea lions *Otaria flavescens*. Discriminating between different values is believed to rely on complex working memory processes in humans and other animals (Botvinick and Watanabe 2007; Ditz and Nieder 2016). Other work indicates that sea lions have an apparently impressive capability for mental manipulation of visual representations. Trained sea lions are quite good at relating rotated shapes to their static counterparts in visual matching tasks (Mauck and Dehnhardt 1997; Stich et al. 2003). Further—as is the case with humans, but not with a number of other species tested—sea lions take longer to make their choice when the angle of disparity between the rotated and static shape is greater. In humans, similar performance has been attributed to 'mental rotation' of a simulated object until it meets (or does not meet) the orientation of the choice stimulus. This type of performance displays robust working memory, using cognitive control processes to manipulate sensory representations. Interestingly, sea lions differ from humans in that while their accuracy and speed of response vary by axis of rotation, performance is better and faster when objects are rotated around what has been termed the 'skew' axis (Stich et al. 2003), which has more relevance for underwater motion than terrestrial motion. This finding echoes an old suggestion of Schusterman and Thomas (1966): that visual processing in marine mammals

adapted to move freely in three dimensions will function somewhat differently from that of land-based animals moving predominantly in two dimensions.

Some related studies support the view that sea lions are capable of some degree of mental transposition of visual information. Hill et al. (2015) showed that some sea lions have the ability to locate hidden objects viewed in a mirror's reflection. In a further demonstration of the ability to use cues to indirectly navigate the environment, Scheumann and Call (2004) showed that South African fur seals *Arctocephalus pusillus* could follow a graded range of pointing gestures from a human experimenter to obtain food rewards. Point following has been readily observed in domestic dogs cued by their trainers (Soproni et al. 2002) but has proven difficult to demonstrate in primates, leading some to speculate that the ability to follow gestural cues may be related to domestication by humans. However, the ease with which otariids demonstrate point-following in research and training contexts suggests that an evolutionary history entangled with humans is not required. It may be that the interpretation of pointing cues by sea lions is supported by early training history in human care, strong inhibitory control, low impulsiveness, or possibly a reliance on joint attention for traveling and hunting with conspecifics, but, here again, otariids have spoiled an evolutionary 'just-so' story regarding the uniqueness of certain capabilities in the animal kingdom.

While sea lions may be capable of using mirror reflections in practical ways, they have not shown clear evidence of self-focused or self-recognition behavior when presented with mirrors (Delfour and Marten 2001). Rather, they appear to treat their own reflection as a social stimulus (Schusterman 1966, 1967). Mirror 'self-recognition' is a controversial phenomenon that has been observed in some primates and dolphins (Gallup 1977; Reiss and Marino 2001), and has been suggested as an analog or at least a component of self-conception. Interestingly, but as yet anecdotally, exploratory examination of sea lion limbic connectivity via DTI imaging of the brain has shown remarkably sparse connectivity in a brain region called the cingulate cortex (P. Cook, unpublished data). This is one of the central regions involved in self-conception among human subjects, but the neurobiological basis of this ability has not been extensively studied in other species. Perhaps the lack of neural development in this part of the brain is reflective of a reduced capability for treating one's self image as an object of complex mental processes.

While a full range of higher cognitive faculties has yet to be explored in sea lions, these intriguing studies suggest that sea lions may be strong candidates for more rigorous experimental research.

17.7 Sea Lions as Natural Models for Studying Brain and Behavior

We have reviewed several laboratory studies, field observations, and anecdotes that demonstrate the short- and long-term memory capabilities of otariids. While lab studies are constrained by small sample size, and field studies may lack robust

controls, a confluence of recent events has allowed in-depth study of sea lion memory capabilities and their neurobiological substrates with relatively large sample sizes. This unexpected research opportunity has arisen from what can only be considered an unfortunate series of events for some free-ranging California sea lions.

For decades, sea lions along the California coast have been stranding in distress, suffering disorientation and seizures. The mysterious cause of these striking and increasingly frequent natural events was eventually linked to exposure to domoic acid, a neurotoxin produced by invasive algae *Pseudonitzchia* spp. (Scholin et al. 2000). Domoic acid is a glutamate agonist that leads to overactivity in the medial temporal lobe of the brain—and, in many cases, chronic epilepsy and gross hippocampal damage (Silvagni et al. 2005). In humans, similar exposures of domoic acid accumulated through the ingestion of seafood can lead to amnesic shellfish poisoning, an irreversible condition that may involve permanent loss of experiential memory (Perl et al. 1990).

The large numbers of stranded sea lions entering rehabilitation facilities and the subset of animals that survived domoic acid exposure created a situation that allowed for follow-up neurobehavioral study. In vivo structural brain imaging revealed gross hippocampal damage in individuals who showed symptoms of exposure to the toxin (Montie et al. 2009). This finding motivated subsequent research that combined brain imaging and comprehensive behavioral assessments in the same individuals, in an effort to improve understanding of the behavioral consequences of brain damage, if present. Cook et al. (2013) systematically evaluated 30 wild sea lions that entered rehabilitation following stranding events. They discovered impairment in spatial working memory and reference memory tasks in sea lions that was correlated to the extent of damage to hippocampal structures, where most brain lesions were found. Notably, the greatest impairment was observed in animals with damage to the dorsal right hippocampus, a region which is specialized for spatial memory in humans. These sea lions showed additional evidence of disrupted functional connectivity (active communication) between the hippocampus and thalamus (Cook et al. 2013). Finally, in brains obtained from individuals that did not survive, there was evidence of white matter pathology in the fornix, a brain pathway that connects the hippocampus and mammillary bodies, both structures essential for supporting spatial and experiential memory across a range of species (Cook et al. 2018). As in humans, amnesic shellfish poisoning may be fatal to sea lions. In addition to brain damage and permanent memory loss, sea lions can also experience altered habituation and apparent sensitization to environmental stimuli (Cook et al. 2011, 2016), which has also been observed in rats exposed to these types of toxins in the laboratory (Zuloaga et al. 2016).

These findings with stranded sea lions are relevant to understanding neurotoxic environmental exposure in wild animals, and to treating affected sea lions. In addition, because sea lions (like humans) are large-brained, long-lived animals that may be exposed to marine toxins repeatedly, sea lions are also a promising neurobiological model for understanding low-dose effects of marine toxins in humans, including exploration of developmental effects following maternal exposure. While the circumstances surrounding the periodic exposure of sea lions, humans, and other

animals to marine toxins remain a problem with few solutions, neurobehavioral data arising from these cases continues to broaden our comparative knowledge of epilepsy, the biology of memory, and behavioral regulation as well.

17.8   Conclusions

It is worth considering some of the evolutionary and ecological factors that may contribute to otariids' performances in laboratory behavioral science, along with the behavioral and physiological traits we have discussed. Their sensory faculty, which is highly developed across multiple senses and expressed cross-modally as they shift between land and water, provides them with incoming sensory streams rich with environmental information (see Chap. 16 by Hanke et al.). A large, densely packed brain with apparently complex patterns of cortico-cortical connectivity can support complex and flexible behavior across a range of contexts. Their well-developed sensory and cognitive abilities, combined with their agile, responsive, and muscular bodies, make them formidable predators on a wide variety of fish and cephalopods. Moreover, due to their high maneuverability in water, and their size and speed on land, they are capable of evading predation themselves. They are not overwhelmed on the raucous, densely crowded rookeries where they are often found, but are able to focus on attending to their own needs and the behavior of their offspring, neighbors, competitors, and mates. Despite decades of study, subtle aspects of their sociobiology continue to be revealed (e.g., Chap. 19 by DeRango and Schwarz; Wolf et al. 2007) and much remains to be learned. It seems likely that the ease with which they transition between the weightless, three-dimensional, aquatic realm and the terrestrial rocky shorelines poses specific challenges to their cognitive and neurobiological systems. Otariids have exploited productive, coastal waters as they have evolved and radiated from the north Pacific over the last 5 million years while at the same time developing an extraordinary degree of plasticity in their central-place foraging behavior (e.g., Bearzi 2006; Chap. 2 by Costa and Valenzuela Toro; Lowther et al. 2013; Staniland et al. 2010). This flexibility can also be seen in real time, as at least some species can manage the transition to living alongside humans (Chap. 18 by Schakner and Blumstein). Some of their success may be related to their apparent 'sangfroid'; their ability to cope with novel situations is clearly part of why they encounter humans so frequently, inhabit wharfs and jetties, interact with fisheries, and hunt fish at dams far upriver despite extensive efforts to dissuade them. Sea lions may be adapted to exploit unpredictable environments, and their persistence and drive may be temperamental tools to help them succeed in doing so.

   To date, otariids have overperformed in the behavioral laboratory. As traditional behavioral comparative laboratories adapt for continued relevance in the twenty-first century, sea lions are well situated to continue contributing to our understanding of sensory biology, behavior, cognition, and neurobiology in long-lived, big-brained, and gregarious mammals. They excel in laboratory settings where careful, longitudinal work is required to establish an existence proof of a complex ability. Their

spatiotemporal predictability, neophilia, and bravery make them relatively easy to study in the wild, in stark comparison to terrestrial carnivores. Their ability to learn rapidly across a wide range of contexts suits them for opportunistic assessment in zoos and aquaria, as well as rehabilitation settings. Sea lions also serve as a sentinel species, representing an accessible model to improve understanding of neurobehavioral impacts and challenges of rapid environmental change and near-shore habitat degradation. Sea lions and other otariids continue to demonstrate how much can be accomplished with careful training methods and a willing animal partner. Studies with other carnivores, including domestic dogs (e.g., Bensky et al. 2013; Miklósi 2014), are only starting to catch up to Schusterman's legacy of sea lion research.

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