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**Vocal learning in the grey seal (*Halichoerus grypus*):
An experimental approach**

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Abstract

This thesis presents a series of training experiments on three captive grey seal (*Halichoerus grypus*) pups in an effort to demonstrate vocal learning, the modifying of vocalisations in form due to experiences with those of other individuals. One pup was non-vocal but participated in four experiments in which her responses to centre and off-centre pointing gestures and directional cues to laterally- and centrally-placed objects were investigated. She oriented successfully only towards laterally-positioned objects indicated by centre and off-centre pointing, pointing and head turning, and upper body turning. These results and her failure to follow pointing gestures towards an object located centrally behind her suggested she simply advanced in the direction of movement of the experimenter, stopping once she located an object. The other two pups were trained to vocalise when presented with a light and to remain silent otherwise and subsequently to match a total of nine moan and growl playbacks with vocalisations of the same type. Twelve novel moan and growl playback stimuli were then used, but these primarily elicited growls as responses. The animals failed to generalise the matching of vocal category, revealing they had been trained only to respond correctly and specifically to the nine original playbacks. These results demonstrated a capacity for contextual learning in which experience with the training procedure caused the pups to pair their production of particular vocalisations with new contexts (i.e. a light and specific playback stimuli). Lastly, one of these pups was trained to produce moans that had fundamental frequencies below 250 Hz. A comparison before and after the training protocol demonstrated that his responses had become both significantly lower and longer. Maturation was not responsible for this result since this pup continued to produce higher-pitched moans in non-experimental contexts. His control over the vocal apparatus to make these frequency and temporal adjustments represents an initial step in establishing whether grey seals are capable of vocal learning. Further studies are required to determine whether additional control over vocal production is possible in this and other pinniped species.

Declarations

- (i) I, Ari Shapiro, hereby certify that this thesis, which is approximately 34,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date: 1 May 2003

Signature of candidate

- (ii) I was admitted as a research student in September 2001 and as a candidate for the degree of M. Phil. in September 2001; the higher study for which this is a record was carried out in the University of St. Andrews between 2001 and 2002.

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- (iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of M. Phil. in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Chapter 1

A comparative look at vocal learning

A framework for understanding animal learning

Animals rarely live in a world of stability. Rather, they are engaged by environments defined by their fluctuating ecological and social domains. Life becomes unpredictable and the more variable the habitat, the greater a capacity to modulate behaviour is at a premium. The social milieu is a formidable domain to engage because it is reactive (Whiten & Byrne 1988). Whiten & Byrne (1988) argue that the intensely social quality of primate life played a formative role in selecting for intelligence. The selective pressures of social complexity on non-primate species have naturally placed similar demands on their cognitive capabilities, reconstituting their brains to take advantage of socially interactive environments (e.g. Bshary & Würth 2001; King et al. 2002). The spatial and temporal arrangements of social partners and competitors are in a constant state of flux. An individual continuously updates the aims of these parties through the conflation of their immediate behaviour and their past actions.

Behavioural and cognitive flexibility become precious commodities in navigating this interactive, reactive and variable social landscape. In these situations, natural selection has often rewarded learning, the altering of behaviour based on experience with particular circumstances (Mackintosh 1983), because it allows its owner to assess a novel scenario, compare a potential response against the relative success previous efforts have secured and act accordingly. This chapter is broadly concerned with social learning in which learning behaviour is shaped by information made accessible only by monitoring and probing the behaviour of other individuals (Janik & Slater 2000). This form of learning encompasses all communication signals and behaviours. Social learning within the realm of communication can be further subdivided into contextual learning and production learning.

Contextual learning pairs existing signals with novel contexts due to experiences with either the usage or comprehension of these signals produced by other individuals. It can occur by shuffling the units already present within the communication repertoire and assigning novel meanings to these new arrangements (Janik & Slater 2000). Production learning results when the acoustic properties of the signals themselves are modified because of experiences with the signals of other individuals (Janik & Slater 1997, 2000). This demands control over the communication apparatus itself. The remainder of this chapter will address production learning in the vocal domain, called vocal learning, which is regulated by the respiratory, phonatory and/or filter systems (Janik & Slater 2000; see Byrne 2002 for a recent application of this distinction to motoric imitation).

The range of influence of vocal learning on animal behaviour and communication is vast (see below). Clearly a slackening of genetic control was responsible for the transition from hard-wired motor skills regulating vocal communication to a scenario in which auditory experience and the acoustic environment could shape vocal behaviour considerably (Nottebohm 1970, 1972). Nottebohm (1972) enumerates the proximate factors requiring modification to achieve such an evolutionary shift, including the plasticity of neural circuitry, vocal apparatus anatomy and physiology and motivational limitations. Costs of supporting vocal learning in a population include the investment of additional time and energy in mastering the vocal repertoire, the reduced recognition of conspecifics due to their potential mimicking and adoption of heterospecific acoustic signals and the necessity of finding tutors from which to learn the appropriate vocal repertoire (Lachlan & Slater 1999). Despite such complications, examples of vocal learning have been found in a variety of taxa, including humans and numerous passerine, psittacid, hummingbird, bat and cetacean species (reviews in Nottebohm 1972; Baylis 1982; Janik & Slater 1997). This scattered occurrence of vocal learning among different branches of the phylogenetic tree is difficult to reconcile with a

single hypothesis (reviewed more broadly by Hauser et al. 2002). Rather, multiple selective pressures likely explain its evolutionary origins and how it maintains itself in current populations (Harcus 1977; Baylis 1982; Slater 1983, 1989).

Because vocal learning is a social phenomenon, its elucidation yields a deeper, more meaningful understanding of how nurture comes to dominate nature in vocal development and how conspecific acoustic interactions influence the behaviour of an individual and the community structure of a population. Vocal learning requires complex cognitive manoeuvring to discern the pertinent ambient acoustic signals worth mimicking, the appropriate social and behavioural context in which to broadcast them and the level of manipulation required to preserve or eschew the acoustic details of the original signal. The various hypotheses proposed to explain the origins and maintenance of vocal learning are now examined.

Ecology entertained

All communication involves a sender using signals to convey information through its environment to a receiver who must decide how to respond (Bradbury & Vehrencamp 1998). Fluctuations in a vocal signal's transmission quality and acoustic features may alert the receiver to particular aspects of their shared physical environment (Tyack 2000). The selective attenuation and distortion by reverberation of weaker components by the environment results in copying of the more penetrating, better propagating components of a signal (Hansen 1979). This is thought to optimise the learnt vocal repertoire for effective sound transmission in a specific environment (e.g. Robinson 1974; Slater 1989; Connor et al. 1998). Such habitat matching has been offered as a hypothesis for vocal learning (Slater et al. 2000), especially for species living in one or more habitats of changing transmission properties (Janik & Slater 1997).

A slight variation on this argument was offered by Falls et al. (1982) based on a study of the great tit (*Parus major*). (All bird species discussed in this chapter are oscines, or songbirds.) These birds copy similar songs precisely and most frequently and unfamiliar songs less accurately and less frequently (Falls et al. 1982). Since, they asserted, the precise details of song structure are only transmitted effectively at close range mimicking accuracy reflects proximity between singers. Because birdsong is relatively inexpensive energetically (e.g. Oberweger & Goller 2001), honest song matching among neighbours is a metabolically more efficient means of communicating spatial location within a territory than flying about to monitor conspecifics visually in adjacent territories. Less attention is paid to the detail of unfamiliar song because a stranger usually sings from far away, a distance over which these finer elements degrade. The environmental influence on the structural stability of birdsong can lead to a complex vocal matching dynamic dependent on proximity and familiarity.

Often the environment influences other life history characteristics of a species, which subsequently impact vocal learning and development. Marsh wren (*Cistothorus palustris*) populations, for example, are usually resident with the rare migrant bird subsequently remaining faithful to a single new area whereas the nomadic sedge wrens (*C. platensis*) settle unpredictably (Kroodsma 1996). Habitat stability likely explains this difference: marsh wrens settle in permanent marshes while sedge wrens utilise the more ephemeral wet meadows. Male marsh wrens accrue their song repertoire through imitation, an advantage for residents who can reliably mimic the songs of their permanent neighbours (Kroodsma 1996). By contrast, the songs of male sedge wrens are highly improvisational, allowing individuals to interact with and match conspecifics regardless of where they eventually settle (Kroodsma et al. 1999). Similar arguments have been made for the song learning behaviour of white-crowned sparrows (*Zonotrichia leucophrys*) in which sedentary populations (*Z. l. nuttalli*) settle and imitate their neighbours while the migratory populations (*Z. l. gambelli*, *Z. l.*

oriantha, *Z. l. pugetensis*) imitate multiple tutors (Nelson et al. 2001). The *nutalli* population lives in a benign coastal habitat where permanent settling is possible. The *gambelli* and *pugetensis* populations live at higher latitudes and the *oriantha* population at altitudes where the environment is less hospitable and more conducive to migratory behaviour (Nelson 1995, pers comm).

By fixing the medium in which acoustic signals are sent and constraining elements of an animal's natural history that bear significantly upon vocal development, the physical environment determines an ecological scaffolding upon which vocal learning might take hold. The natural social environment of a species is also of importance in predicting and understanding the occurrence of communication and vocal learning (King & West 1984; Tyack 1999), an issue discussed first among birds.

Unravelling the avian social milieu

If vocal learning is to function intraspecifically, the mimic's selection of suitable acoustic models is crucial in maintaining species-specific recognition (Marler 1970; Baylis 1982; Lachlan & Slater 1999). Indeed, limitations on song learning in birds often facilitate conspecific recognition (Slater 1983). Species identity can be encoded in the simultaneous use of multiple signal modalities (e.g. lark vocalisations paired with distinctive looping flights), the unique temporal arrangement of appropriated elements, the inclusion of conspecific elements that flank mimicked vocalisations or other species-specific vocal mannerisms (Nottebohm 1972; Baylis 1982). Nightingales (*Luscinia megarhynchos*), for instance, acquire relevant species-specific serial information from exposure to conspecific song (Hultsch & Todt 1992). Social bonds and interactions frequently serve to teach mimics the identity of potent and relevant acoustic models meriting incorporation into the vocal repertoire (Payne 1981).

Slater (1983) contends learning is necessary to provide an individual with a suite of vocalisations best suited for its unique habitat, life history and social interactions. This is dramatically evident in some of the most versatile vocal mimics. The marsh warbler (*Acrocephalus palustris*) is a Palaearctic migrant, summering in Europe and flying through southern Russia to Zambia, Africa for the winter to breed (Dowsett-Lemaire 1979). Their mimicking abilities are extraordinary with traces of the vocalisations of 212 (doubtless an underestimate) European and African bird species having been detected among the songs of different individuals! The learning period of the marsh warbler ends after 10-11 months, coinciding with the arrival of a bird at its breeding grounds with singing declining considerably once a female arrives in the territory of an unmated male (Dowsett-Lemaire 1979). These birds seem to copy acoustic features of their environment to communicate information that may be pertinent to mate selection and pair formation. Perhaps the vocal repertoire of a marsh warbler acts as an acoustic narrative of its travel history with the vocalisations of endemic bird species revealing its birthplace and migration route.

The studies of West & Stroud (1983) and West & King (1990) have revealed similar vocal virtuosity among European starlings (*Sturnus vulgaris*). Starlings raised in interactive human homes mimicked household sounds (e.g. a creaking door and ringing alarm), animal vocalisations (e.g. cats and dogs) and human greetings and phrases. Recombination of these acoustic fragments and the copying of intonation and cadence patterns of human speech were frequent. The mimicry was selective, generally restricted to scenarios in which an acoustic model was produced during or just before social interaction. Starlings appear to “bounce sounds off the animate environment, using behavioural reverberations to gauge the effects of their vocal efforts” (West & King 1990: 113). Perhaps they learn best when alert, but an acoustic narrative is again possible where starlings record socially engaging features of their environment to convey these interactions to conspecifics at a later time. Vocal interaction

allows adaptation to the local social landscape.

The importance of social interaction in the acquisition of allospecific vocalisations by African grey parrots (*Psittacus erithacus*) has been documented from slight modifications of Todt's (1975) live-tutoring system. In one study a subject learned nine object nouns, three colour adjectives, two shape phrases and the functional use of the word "no," allowing him to identify, request and reject object classes (Pepperberg 1981). Subjects only produced and understood allospecific code and vocal labels when this tutoring was referential, contextually appropriate and interactive (Pepperberg 1994).

Timing plays a relevant role in vocal learning as well (e.g. Nordby et al. 2002). Although all Northern cardinals (*Cardinalis cardinalis*) sing, it takes males three times as long to acquire 1.5 times as many songs as females (Yamaguchi 2001). This difference in timing allows males to imitate the songs of their neighbours when moving between new populations. Females, however, retain their natal dialect because of the shorter sensitive phase for learning new song. Some non-avian species described later retain vocal learning abilities well into adulthood. Learning is sustained as long as it remains ecologically and/or socially relevant.

Used aggressively, vocal matching often defends the right of the matcher to resources, territory or a mate (Baylis 1982; Janik & Slater 1997). A mimic can boldly address threats to a specific individual by matching this individual's vocal repertoire (Zahavi & Zahavai 1997). Indigo buntings (*Passerina cyanea*) who mimic the song of an adult neighbour are more likely to retain a patch of territory than those who mimic a juvenile or those who fail to mimic (Payne 1983). Counter-singing, the alternate singing of two males in close proximity in adjacent territories, seems to be an aggressive behaviour that occurs between a territorial male and a song-matching male. The more proficient the song copying ability of a chorister robin (*Cossypha dichroa*), the more effective and threatening his copied songs become

(Harcus 1977). Chorister robin vocal matching is also likely to serve the probable functions of co-ordinating song and preserving territorial stability.

Vocal matching can direct aggression interspecifically as well (Baylis 1982).

Broadcasting conspecific and heterospecific vocalisations might serve a territorial purpose by deceiving receivers acoustically that a higher density of potential rivals and/or predators is present within an area (Rechten, 1977 but see Slater 1981). Red-winged blackbirds (*Agelaius phoeniceus*) respond indentially and aggressively to blackbird song both when produced by conspecifics and when imitated by mockingbirds (*Mimus polyglottos*, Brenowitz 1982). Mockingbirds are generalist feeders and frequently mimic the songs of competing avian heterospecifics in the wild, including the sympatric red-winged blackbird. A mockingbird's mockery is thought to be advantageous by distracting potential competitors away from overlapping nutritional and territorial resources.

Birdsong is either arrested at frequent intervals or produced without interruption. Slater (1981) proposed that discontinuous song allows time for aggressive male counter-singers to await responses from competitors while continuous song functions intersexually and is produced by a male not expecting the female to reply. Intersexual selection is frequently offered as a hypothesis for vocal learning whereby more complicated and less monotonous male vocal repertoires enhance female stimulation (Nottebohm 1972; Janik & Slater 1997) and copied acoustic elements function in species or individual identification to facilitate pair bond formation (Rechten 1977; Dobkin 1979; Baylis 1982). Yearling indigo bunting males who imitated the song of neighbouring adult males significantly enhanced their territory tenure and their mating, nesting and fledging success relative to those who failed to mimic (Payne 1982). Plumage coloration was also relevant with bluer males experiencing higher levels of reproductive success than browner males. Blue matching males were most successful, brown non-matching males were least successful and blue non-matching and

brown matching males experienced intermediate success (Payne 1982). Mimicking abilities represent a significant factor in female indigo bunting mate selection that even overcome visual preferences.

Examples of the affiliative use of vocal learning abound, often stabilised at the level of social interaction within a population.

Socially stable, vocally labile

Whether vocal mimicry serves uniquely social or communicative functions or some blend of the two (Robinson 1991), it often manifests itself in stable community interactions (Kroodsma 1996). Cetacean species with individual-, group- or population-specific vocal signals are often structured around reliable individual bonds, steady group composition or fluid social relationships, respectively (Tyack 1997), a principle of broader taxonomic relevance as well. Group size is primarily regulated by the ecological constraint of the availability and abundance of food resources (Tyack 1986a).

Individual recognition maintained by acoustic signature signals is possible with vocal learning (Rechten, 1977 but see Nottebohm 1972), a particularly useful ability in environments with high levels of background noise (Janik & Slater 1997; Slater et al. 2000). By rejecting the acoustic models presented by conspecifics, vocal learning can generate and differentiate these species-specific, individually distinctive vocal signals (Janik & Slater 1997, 2000). Instead of converging on signals or certain features of signals to convey membership within a group, differentiation would allow an individual to generate a distinctive vocal repertoire. Individual recognition in such a system requires the very learning (Tyack & Sayigh 1997) that makes the scenario possible at the outset. The selective pressures of colonial living among cliff swallows (*Hirundo pyrrhonota*), for instance, have led chicks to maximise individual call variation and adults to distinguish between these

signals (Loesche et al. 1991). In contrast, non-colonial barn swallows (*H. rustica*) display less inter-individual differences among their calls and possess weaker discrimination capabilities. The individually distinctive flight call of the male American goldfinch (*Carduelis tristis*) facilitates female recognition of her partner (Mundinger 1970). Pair bonds are further cemented once the female begins mimicking her partner's flight call.

Vocal recognition is often favoured in social species that are longer-lived and capable of long-distance communication relative to their body size (McComb et al. 2000).

Preliminary experiments suggest signature vocalisations may play an important role in mother-calf interactions among Amazonian manatees (*Trichechus inunguis*, Sousa-Lima et al. 2002). Among cetaceans, the ontogeny and social functions of bottlenose dolphin (hereafter called dolphin) signature whistles have been studied extensively. Dolphins live in fission-fusion societies in which highly fluid associations of multiple animals are constantly reforming (Wells 1991). Signature whistles seem to play a role in reuniting mothers and calves after separation (Smolker et al. 1993), maintaining group cohesion (Janik & Slater 1998) and acoustically discriminating between individuals (Sayigh et al. 1999). Calves develop their signature whistles between one and seventeen months of age and these remain stable for the rest of their lives (reviewed in Tyack & Sayigh 1997; Tyack 1997, 1999). Female calves develop unique signature whistles, while male calves tend to develop whistles similar to their mothers (Sayigh et al. 1995). A selective pressure might exist among females to produce distinctive whistles to enable recognition among their calves. Because males disperse from their mothers, their mimicking of maternal whistles may facilitate kin recognition and inbreeding avoidance (Sayigh et al. 1990, 1995). Or perhaps this difference in whistle ontogeny represents a more fundamental difference between how females and males process and assign relevance to acoustic information. Regardless, vocal learning appears to be responsible for whistle acquisition.

Dolphins retain their mimicking abilities throughout their lives. Richards et al. (1984) trained a subadult female to produce highly accurate imitations of computer-generated model sounds. After establishing the training procedure, mimicry became spontaneous with acoustic features being copied by the subject that were not specifically reinforced. Reiss & McCowan (1993) designed an underwater keyboard with shapes that produced unique whistles when pressed, each associated with a particular object or activity. Two one-year-old male dolphins quickly and spontaneously mimicked these synthetic whistles, successively improving the frequency and temporal parameters of their copies. This free-choice system allowed the dolphins to select the components of the acoustic models most relevant for mimicry (Reiss & McCowan 1993).

Other studies have examined how dolphins might utilise these mimicking capabilities in the wild. In a study on two captive adults (one male and one female), both animals produced their own signature whistle most frequently. The second most common whistle produced was the signature whistle of the other individual (Tyack 1986b). Janik (2000) described matching whistle interactions by dolphins in the Moray Firth, Scotland in which the whistle produced by one individual was mimicked by a conspecific. These studies suggest that bottlenose dolphins use signature whistles in the wild as vocal labels to encode individual identity and address each other. Captive studies support this conclusion, which have demonstrated that whistles can serve as vocal labels for synthetic objects (Richards et al. 1984) and function in the construction and comprehension of acoustic “sentences” relating an action to an object (Herman et al. 1984). African grey parrots (Pepperberg 1981) and killer whales (*Orcinus orca*, van Heel et al. 1982) have also shown evidence of vocal labelling, but whether they exploit such abilities in the wild remains unknown. The individually distinctive signature whistles of bottlenose dolphins appear to be quite useful in maintaining strong and reliable interactive relationships despite considerable social fluidity among individuals.

Signature vocalisations also permit antiphonal dueting, the rapid exchange of acoustic signals between two individuals. Found frequently in tropical bird species, antiphonal dueting seems to facilitate mate recognition in dense foliage, establish and strengthen pair bonds and supplement sexual displays (Thorpe & North 1965; Thorpe & North 1966). Each tropical Bou-bou shrike (*Laniarius aethiopicus*) pair produces numerous uniquely timed and patterned duet sequences (Thorpe & North 1966). The male and female are capable of singing the entire sequence when its mate is absent, which usually hastens its return. African forest weavers (*Symplectes bicolor*) form pair bonds strengthened by antiphonal dueting with increasing synchronisation as the performance progresses (Wickler & Seibt 1980). The live-tutoring system (Todt 1975) used with African grey parrots was based on an antiphonal dueting model. The subjects completed phrases once the initial segment was presented by the experimenter and appeared nervous when the introductory portion remained unanswered (Todt 1975). Long bouts of antiphonal dueting even take place between mother and infant lesser spear-nosed bats (*Phyllostomus discolor*), displaying positive phonotaxis in response to one another's directive and isolation calls, respectively (Esser & Schmidt 1989). The mother's directive call is likely a signature signal, which apparently serves as an acoustic model for the isolation call of the pup. Antiphonal duets are complex interactions, requiring two individuals to achieve vocal synchrony with one or both initially or continuously learning the vocal signals necessary to complete the duet appropriately (Wickler & Seibt 1980).

Group dynamics

Strong bonds between individuals represent one kind of social dynamic. Vocal learning often enables communities stable at the family, group and population levels to acquire a shared acoustic repertoire as well (Tyack 1997), which may prevent inbreeding through the aural recognition of kin, favour co-operation between group members or facilitate

the recognition and exclusion of intruders (Nottebohm 1972; Janik & Slater 1997; Slater et al. 2000). Sperm whales (*Physeter macrocephalus*) communicate with codas, short patterns of clicks that are often exchanged between individuals. Several female sperm whales and their offspring constitute a stable coalescing of matrilineal family units and possess a group-specific coda dialect (Weilgart & Whitehead 1997). The limited transmission distance of the coda clicks seems to restrict their use to intra-group communication. These coda repertoires are likely achieved through vocal learning (Weilgart & Whitehead 1997).

One mechanism for achieving a shared vocal repertoire among group members is through the parallel modification of particular acoustic features of elements within this repertoire. When two unfamiliar groups of pygmy marmosets (*Cebuella pygmaea*) were housed together, all individuals experienced shifts in the peak frequency and bandwidth of their trills (Elowson & Snowdon 1994). The total duration and cycles per second remained constant, however, suggesting some features of the trill may fluctuate according to changing group composition while the more stable components might encode individual identity.

The dialects of resident killer whales in the coastal waters of British Columbia appear to be under similar social pressures. Pods consisting of multiple matrilines possess stable group-specific vocal repertoires of between 7 and 17 stereotyped calls (Ford 1989). Matriline members appear to produce the entire repertoire and engage in matched counter-calling, which may regulate group movement and behavioural synchrony (Miller et al. in press). Gradual and synchronous structural changes occur within the repertoire at varying rates among the different call types (Deecke et al. 2000). Cultural drift and horizontal transmission best explain these changes in resident killer whale vocal repertoires (Deecke et al. 2000; Miller & Bain 2000). Killer whales likely acquire their vocal repertoires via vocal learning. Evidence includes anecdotes of possible vocal imitation in the wild (Ford 1991), the training of a captive killer whale to mimic artificial sounds associated with objects and actions (van

Heel et al. 1982) and a study of the ontogeny of the maternally influenced call repertoire of a calf in captivity (Bowles et al. 1988).

The humpback whale (*Megaptera novaeangliae*) is a dramatic example of synchronous change in the vocal repertoire of a population. Themes, or collections of repeated units called phrases, did not seem to be preserved at intermediate levels, either appearing as a part of all songs at once or continuously increasing or decreasing in occurrence (Payne et al. 1984). The song changed constantly as it was sung without any re-incorporation of themes that had been dropped, indicating cultural and not cyclical development. An overall tendency existed for phrases of all themes to lengthen with time (Payne et al. 1984; Cerchio et al. 2001). Certain song variables underwent similar changes in populations from two geographical regions, suggesting song develops due to either cultural transmission or a genetic template (Cerchio et al. 2001). Humpback song was heard most frequently during the breeding season and was thought to be produced solely by males to broadcast species, sex and location information, their willingness to mate and their readiness to engage in antagonistic interactions with other males (Tyack 1981). These features and the vocal stability of song at the population level suggest its function in intrasexual and intersexual selection (Tyack 1999). Females may select males based on song quality, duration or intensity, features easily compared since all males sing the same song and change its structure in parallel.

Acoustic convergence through vocal learning may also serve an affiliative function by facilitating group cohesion (Tyack 1997). Group membership is thus achieved via the convergence of certain parameters of the vocalisations of black-capped chickadees (*Parus atricapillus*, Mammen & Nowicki 1981), males of the tropical songbird species *Cacicus c. cela* (Feekes 1982) and female colonial greater spear-nosed bats (*Phyllostomus hastatus*, Boughman 1998). When placed in social groupings of unfamiliar individuals, the contact

calls of male budgerigars (*Melopsittacus undulatus*) initially converged and subsequently underwent continuous and synchronous changes (Farabaugh et al. 1994). When a new recruit was added to a group of close social companions, a scenario apt to occur in the wild, the recruit's call converged on that of the group and no further changes were detected (Bartlett & Slater 1999). Convergence presumably integrates these new individuals into the social group, providing them with an acoustic badge of membership. Here vocal convergence represents a social imperative, increasing the selective pressure on vocal learning capabilities.

While vocal learning and convergence are questionable among most non-human primate species, chimpanzees (*Pan troglodytes*) may offer supportive evidence. Chimpanzees produce pant-hoots to respond to pant-hoots of conspecifics, upon securing prey or a rich food source, during aggressive interactions and as they rejoin their group (Mitani et al. 1992). A chorusing male chimpanzee pair utilised pant hoots more similar to each other than to those of other chorusing pairs (Mitani & Gros-Louis 1998). The higher-ranking individual within a pair tended to converge on the pant-hoot of his partner, possibly to reinforce social bonds. More recently Marshall et al. (1999) claimed that the temporal convergence of the pant-hoots within two captive populations of chimpanzees comprised of unrelated individuals demonstrated vocal learning. Genetic similarity was therefore not responsible for the temporal convergence of the pant-hoots within each population. The dissemination in the Florida population of a "Bronx cheer" sound produced by blowing air through pursed lips was offered as evidence for frequency-domain vocal learning (Marshall et al. 1999). Insufficient data were provided, however, to indicate conclusively that learning can modify the frequency parameters of this vocalisation. Some vocal accommodation might be present among chimpanzees but the question of vocal learning lingers ambiguously.

The pinniped possibility

Despite the insight into vocal learning gained by the broad taxonomic perspective considered above, its evolutionary origins and adaptive contributions remain blurry. The conclusive demonstration of vocal learning in additional taxa will help to supplement or withdraw evidence from the hypotheses entertained in this chapter.

The families of the suborder Pinnipedia, the Phocidae (true seals), Otariidae (fur seals and seal lions) and Odobenidae (walruses), are likely candidates for vocal learning based on their social and vocal behaviour. Spending the majority of their time at sea, pinnipeds haul out on shore to moult, whelp, lactate and mate. A synchronised postpartum oestrus and this clumping of females favour male strategies of defending territories near pupping sites (Boness & Bowen 1996). Lactation is faster and weaning more abrupt among phocids than otariids, reducing the time during which learning from the mother might occur (Caudron 1997). The dramatic increase in vocal activity of phocids during the breeding season may result from a sampling bias because of the difficulty of acquiring underwater acoustic recordings. Male Weddell seals (*Leptonychotes weddellii*) squabble aggressively and noisily over territory during the breeding season (Green & Burton 1988a; Green & Burton 1988b). In addition to territorial information, the song of the male bearded seal (*Erignathus barbatus*) may also broadcast his breeding condition to receptive females (Ray et al. 1969). The ephemeral ice floes upon which leopard seals (*Hydrurga leptonyx*) haul out considerably shorten their breeding season. The striking increase in calling in December and January by males and sexually receptive females in captivity is thought to coincide with their breeding season in the wild, allowing these solitary animals to locate mates acoustically (Rogers et al. 1996). The vocal behaviour of male harbour seals (*Phoca vitulina*) matches female distribution and density in space and time, which vary according to the topographical and tidal features of haul-out sites (Van Parijs et al. 1999).

Individual recognition based on acoustic discrimination varies among pinniped species. Elephant seal (*Mirounga angustirostris*) vocalisations are used by males in aggressive interactions by females to attract or defend their pups and by pups to indicate distress or a request to nurse (Bartholomew & Collias 1961). The calls of juvenile bulls are characterised by greater variability, fewer syllables and higher syllable rates than the stable vocal patterns of adult bulls (Shiple et al. 1986). While individual recognition may allow bulls to assess and confirm dominance without fighting (Shiple et al. 1986), it is probably absent from the mother and pup recognition calls that show little inter-individual variation (Insley 1992).

Northern fur seal (*Callorhinus ursinus*) mothers and pups may recognise each other acoustically because their unique calls are stereotyped, but considerably variable between individuals (Insley 1992). More conclusively, Galápagos fur seal (*Arctocephalus galapagoensis*) pups between ten days and two years of age preferred their mother's pup attraction call significantly (Trillmich 1981). An adult female harbour seal differentiated between pup calls produced by different pups, suggesting individual recognition of pups by mothers is possible (Renouf 1985). The individually distinctive acoustic repertoire of the pups may disappear after weaning when they lose their pup calls. California sea lion (*Zalophus californianus*) pups were capable of distinguishing their own mother's calls when they were two weeks old (Gisiner & Schusterman 1991). A mother's pup attraction call elicited the strongest calling response from her captive pup or yearling, which facilitated their reunion after separation (Trillmich 1981). These studies support the hypothesis that vocal learning may help produce individually recognisable calls among mothers and pups of certain pinniped species, which encourages successful weaning.

Minimal direct evidence exists for pinniped vocal learning. Each of three Antarctic Weddell seal populations separated by 20 km of ice produced unique vocalisations with slight

temporal and frequency differences among their shared vocal repertoires (Morrice et al. 1994). This implied microgeographic variation between potentially interbreeding, adjacent populations where new arrivals possibly learned the repertoire of the local population (Morrice et al. 1994). Geographic variation among male elephant seal threat vocalisations between populations of very recent origin on islands near the California and Baja California coasts might provide evidence for dialects (Le Boeuf & Peterson 1969). Two captive, sexually mature male harbour seals mimicked a few human phrases but slurred words together and lacked control over the higher frequencies of these signals (Ralls et al. 1985). A rigorous comparison of acoustic features between the human and seal vocalisations to determine similarity was sadly never conducted, but this anecdote is suggestive of natural mimicry and vocal learning abilities of pinnipeds in the wild.

Halichoerus grypus

The grey seal (*Halichoerus grypus*) shows promise for vocal learning. Three populations are found in the western Atlantic, the eastern Atlantic and the Baltic Sea (Davies 1957). Feeding opportunistically, grey seals consume energy-rich and locally abundant prey when available (Hammond et al. 1994). Fish are readily caught with a rapid swimming spurt, a forward thrust of the neck and a sudden clamping of the jaws (Anderson 1988). Grey seals of the North Sea occasionally travelled long distances to haul-out sites far away or repeatedly along local routes that include return trips to the same haul-out site (Thompson et al. 1991; McConnell et al. 1999). Individual variability was evident, revealing locomotive and behavioural specialisation. Immature animals spent more time near haul-out sites whilst adults travelled widely, particularly when food resources were abundant in other areas (Hammond et al. 1993).

The yearly breeding season is an especially dramatic time in the life cycle of a grey

seal. Females made a preliminary visit to a haul-out site one day to three weeks prior to whelping, remaining on land an entire day before giving birth (Burton et al. 1975; Anderson 1988). Most females on North Rona, Scotland demonstrated whelping and breeding site fidelity regardless of past pupping success (Pomeroy et al. 1994). The first females ashore generally congregated in areas with access to water, determining the locations of females arriving later and thus the overall distribution of the breeding colony (Pomeroy et al. 1994). After giving birth a mother grey seal immediately and repeatedly turned and sniffed her pup, presumably to record its olfactory identity and form a social bond (Burton et al. 1975). Pup begging was an honest vocal signal of hunger used when their mothers were not in the water (Smiseth & Lorensten 2001). Mothers smelled and touched their pups before allowing them to suckle, passively or violently rejecting the requests of non-filial pups (Fogden 1971). Maternal investment was unequal with females feeding and protecting sons for significantly more time than daughters (Anderson & Fedak 1987; Kovacs 1987). Because males experienced variable reproductive success that positively correlated with body size (Anderson & Fedak 1985; Kovacs & Lavigne 1986), higher maternal investment in sons made them more likely to secure better quality breeding areas and more copulations as they matured. Starvation, stillbirths, injuries from conspecifics, infection and misadventure often led to pup mortality (Coulson & Hickling 1964).

Grey seal bulls arriving first on the breeding ground were afforded the greatest opportunities to mate once females entered oestrus (Hewer 1960). Males who remained ashore for longer periods of time and in areas of higher female density experienced the greatest mating success (Boness & James 1979; Twiss et al. 1994). Facile distinctions between dominant and subordinate or tenured and transient males appear to oversimplify more complicated dominance patterns shaped by breeding site topography, female distribution and site fidelity (Twiss et al. 1998). Anomalies in pup relatedness and paternity

tests contradicted previous theories of mate fidelity (Amos et al. 1995). They rather suggested females were selecting genetically diverse partners with paternity arising through sperm competition and immunointolerance of sperm left by particular individuals (Amos et al. 2001). Females strongly rebuffed the attempts of bulls to mate (Cameron 1967), but late pupping mothers experienced greater difficulties repelling male advances (Boness et al. 1995). Virgin cows seemed to mate with younger bulls away from the breeding grounds (Hewer 1960). After four divisions the development of the fertilised egg is arrested, implanting four months later to coincide with the female moult (Anderson 1988). Because gestation only lasts seven months, this delayed implantation synchronises the onset of pupping each year.

Vocalisation rates and antagonistic interactions escalated as the breeding season progressed without significant differences in call production between day and night (Asselin et al. 1993). The vocal repertoire includes in-air (i.e. katara, gurgle, moan, growl, yodel and pup call) and underwater (i.e. rup, trot, rupe, moan, growl and five unnamed others) vocalisations (McCulloch et al. 1999). Schusterman et al. (1970) suggested a social function for these calls. Maximum signal strength, number of harmonics and fundamental frequency could be used to distinguish individual pup calls (Caudron et al. 1998). Mothers on the Isle of May, Scotland did not respond preferentially to the calls of their own pups, which led to numerous bouts of allo-suckling (McCulloch et al. 1999). On Sable Island, Nova Scotia, however, mothers rarely allo-suckled and made significantly more head and body movements towards playbacks of calls from their own pups (McCulloch & Boness 2000). Different selective pressures may have unevenly influenced the vocal behaviour and recognition in these two populations. Vocal recognition on Sable Island might have resulted either from their ice-breeding ancestry in which any mechanism to reduce deadly separations would have been favoured or from less crowded conditions allowing an acoustic bond between mothers

and pups to form (McCulloch & Boness 2000). In very uncrowded conditions, however, vocal recognition might have been unnecessary because visual and olfactory identification have become easier. Differences in experimental procedures, female selection criteria and sample sizes between the Isle of May and Sable Island studies might have contributed to these differences as well (McCulloch 1999).

Scope

The goal of this thesis was to assess whether the highly vocal and social grey seal is capable of vocal learning. Pinniped training has been successful in earlier studies (e.g. California sea lion: Schusterman & Feinstein 1965) and similar techniques were used in the studies explained in the subsequent chapters to train one male and two female grey seal pups. The initial training of these animals served as a foundation for the more complicated performance tasks required subsequently and is introduced in Chapter 2. This chapter also provides a description of the captive seals, the research facility and the other experiments conducted concurrently with the vocal learning project.

Before vocal behaviour was specifically reinforced, the pups were trained to follow the pointing commands of an experimenter to move left or right. Chapter 3 presents a separate study on the responses of one of the female grey seal pups to centre and off-centre pointing gestures and directional cues. Similar studies involving other species have argued that their subjects have understood the referential properties of these gestures and consequently may have possessed a theory of mind. These claims were not supported by the more parsimonious explanation of the performance of the grey seal pup presented in Chapter 3. She likely oriented herself in the direction of movement of the experimenter and advanced until she intercepted one of the objects that she had been trained to touch. Her failure to move towards an object placed directly behind her cast further doubt on her comprehension

of the referential quality of the pointing gesture.

Chapter 4 demonstrates that a male and female grey seal pup were capable of contextual learning in the vocal domain. They were trained to vocalise only when shown a bike light and to remain silent otherwise. With enough training, both pups were also capable of responding to moan and growl playbacks with vocalisations of the same type. The pups tended to respond to novel playbacks of these same vocal categories by growling, suggesting they had been trained to respond in kind to the *individual* playbacks without developing a generalised mechanism to match vocalisation type. The vocal control required to vocalise when exposed to a particular stimulus and to match vocal categories already present within the repertoire is possible only with contextual learning. These results are congruent with the cognitive performance of pinnipeds in other domains.

Lastly, the early stages of a vocal learning study are described in Chapter 5. The male grey seal pup was rewarded for producing moans with lower fundamental frequencies in response to a playback of a moan that had been lowered by slowing its playing speed. Initial shaping of the frequency parameters reduced the acoustic variability of his responses, suggesting he possessed some control over the pitch and duration of his vocalisations. Further studies examining the ability of the grey seal to mimic the frequency structure of novel, artificial playbacks are required to determine the extent to which vocal learning is possible and the acoustic range over which it can be flexibly controlled.

Conclusion

Vocal learning is thought to arise on the biological landscape when particular ecological, acoustic and social variables interface. Acoustic repertoires are shaped by the physical properties of their environments to improve communication efficiency between senders and receivers. Vocal learning demonstrates that its owner possesses the necessary

cognitive machinery to process acoustic stimuli and the appropriate physiological equipment to reproduce these stimuli exactly, partially, or not at all. It implies a level of sociality that might encompass the vocal recognition, labelling and addressing of conspecifics or the affiliative or antagonistic relationships rendered explicit through vocal distinctiveness or convergence. A rubric predicting vocal learning based on the ecological, social, reproductive and vocal characteristics of a species, however, is apt to remain elusive. Nevertheless, vocal learning operates within a realm where cognitive and social plasticity fuse unpredictably, transforming the very stuff of behaviour and communication into an intensely interactive milieu.

Chapter 2

General materials and methods

Facility

The captive research facility for grey seals at the Sea Mammal Research Unit in St. Andrews consisted of a main rectangular pool (42 m x 6 m and 2.5 m deep) and two smaller circular pools (3 and 5 m in diameter and 2 m in depth). Doors could be opened and secured with belts or bungee cords to allow the seals to move between the pools and into the dry areas for hauling out. The main pool was covered by removable panels that lay just beneath the water's surface and all pools were separated from one another and the neighbouring dry areas by metal fencing (Figure 2.1). Visual access was blocked by weaving opaque, white corrugated plastic between the rungs of these fences. A large underwater gate connecting the small pool to the main pool was opened only to facilitate moving the animals.

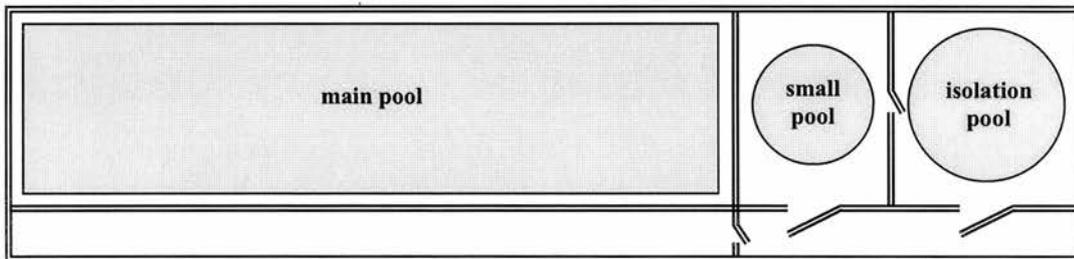


Figure 2.1: Schematic of pool facility. Grey areas correspond to water, the double lines indicate the walls and fences of the facility and doors are depicted as diagonal breaks.

Keycard access to the pool area was restricted to authorised staff and students. Frozen fish was stored, defrosted and cut in an indoor food preparation room where iron and multivitamin supplements, focus objects and clickers were also stored. An indoor garage was generally used for weighing animals, taking blood, skin and blubber samples and for some of the training procedures. Despite filtering mechanisms, the pools still accumulated algal

growth and faecal matter steadily. All pools were cleaned every 2-4 weeks by hand with brushes or a pressure washer.

The maintenance of the facility, the capturing and care of the animals and the experimental procedures were regulated according to the guidelines established by the Home Office Animals (Scientific Procedures) Act 1986 under project license # 60/2589.

Animals

Two adult females (Lola and Molly) and their female pups (Kylie and Nora, respectively) were transported from the Isle of May in the Firth of Forth, Scotland (56°10'N, 2°35'W) to the facility on 12 December 2002. Oscar, a male pup, was taken from the Isle of May on 10 January 2002 near the end of his post-weaning fast. Numerous grey seals use the Isle of May as a haul-out site to give birth, wean, lactate and mate. Because Molly failed to cooperate in respirometry experiments, she was released on 25 March 2002. An adult female, Polly, was caught at a haul-out site east of Tenstmuir Sands off the north-east coast of Fife, Scotland on 17 April 2002.

Lola, Molly and Polly were fed 5 kg of whole Atlantic herring (*Clupea harengus*) each day with single iron and double multivitamin supplements. Initially the pups were fed 1 kg of herring chopped into thirds daily, but this amount was gradually increased so they were gaining weight at a rate similar to that of wild grey seal pups. Oscar and Nora were both consuming 2 kg of herring and Kylie 2.5 kg each day by the end of July 2002. All pups were able to feed on whole fish by the end of June 2002 but Oscar and Kylie were fed halved herring to increase the number of trials during training sessions. The pups received a single iron and multivitamin supplement with each feeding. Occasionally new species of fish were added to the diet of the animals for particular experiments. Lesser and greater sandeels (*Ammodytes tobianus* and *Hyperoplus lanceolatus*, respectively) were fed to the animals for

the diving and respirometry studies. These sandeel species, plaice (*Pleuronectes platessa*), haddock (*Melanogrammus aeglefinus*) and Atlantic salmon smolts (*Salmo salar*) were used in the digestion studies mentioned below.

One of the female grey seals was generally placed in the main pool during the work week for respirometry experiments while the remaining animals were allowed to move freely between the small and isolation pools and the adjacent dry areas. The three pups entered the main pool on most weekends and some evenings.

Experiments

In addition to the training exercises described in this thesis, these grey seals were involved in several additional experiments. Respirometry studies were conducted in the main pool by lowering a series of panels over the surface of the water. A clear, Perspex box in one corner of the pool provided the only location where an animal could surface to breathe. The partial pressure of oxygen gas within this breathing box was monitored constantly and measurements were taken from a time-depth recorder (TDR) attached to the head of the study animal. These devices provided data on the amount of oxygen used for each dive, resting and diving metabolic rates and the quantitative variation in diving behaviour, which were used to generate a model of metabolic activity. An electronic feeder dispensed fish and could mimic changes in prey density and quality by varying the quantity, size and species of fish lowered into the water per unit time.

Two feeding experiments were conducted as well. The pups were fed a supplement in their diet each day for four weeks that contained trace levels of a harmless contaminant (decabromobiphenyl) dissolved in cod liver oil. Blood, blubber and faecal samples were taken every ten days for four weeks before, during and following the introduction of these supplements to glean information on how grey seals metabolise these contaminants and store

them in their fat reserves. A second feeding experiment focused on deriving species- and size-specific digestion coefficients of grey seals when consuming fish by feeding captive animals herring as a carrier species containing the otoliths from other target species and these target species whole. The partially or completely digested otoliths were filtered from the water and faeces to calculate these digestion coefficients.

General training procedures

The experimenter always wore an orange raincoat and a green glove on his right hand. During all training procedures food rewards were dispensed after depressing a clicker. This served as an acoustic bridge to reinforce the behaviour that had occurred immediately prior to the sound of the clicker. The first few feeding sessions involved merely clicking before throwing the fish to cause the animals to associate the sound with the imminent arrival of food. Incorrect responses to training commands caused the experimenter to say “No” firmly and withdraw from the training area for 15-20 seconds.

Each animal was trained to rest his/her head on a unique object at the end of a black PVC rod, a procedure called stationing. Oscar stationed on a black circle, Kylie on a grey triangle, Nora on a white square, Lola on a white ball and Molly and Polly on a yellow ball. This stationing training facilitated moving the animals within the facility and offered them stimulation in addition to their daily feedings.

Acoustic equipment

The training sessions described in Chapters 4 and 5 were recorded onto TDK ® SA90 High Position IECII/Type II audio tapes with a Sennheiser K6 microphone and a Marantz CP430 tape recorder. All vocalisations were subsequently digitised with Cool Edit Pro © at a sampling rate of 44100 Hz and 16-bit resolution using the Yamaha sound card OPL3-SAx of

a Toshiba Satellite 320CDT ®. A Teac PowerMax-500/B 3-way-subwoofer system (with a frequency response from 40 – 150 Hz for the subwoofer and from 150 Hz – 18 kHz for the two satellite speakers) broadcast the playback sounds to the pups. All training sessions presented in Experiment 2 of Chapter 4 and in Chapter 5 were monitored acoustically in the Real Time Spectrogram mode of Avisoft-SAS Lab Pro ©. Signal 3.1 © was used to trace the fundamental frequency contours and examine the acoustic parameters of the calls recorded for Chapter 5.

Chapter 3

The response of a grey seal pup to experimenter-given pointing and directional cues*

Abstract

A grey seal (*Halichoerus grypus*) pup was trained to use pointing signals given by an experimenter to determine whether to move left or right to a target object. While she responded significantly above chance to pointing gestures, pointing and head turning and upper body turns, she was unable to use head turns and eye movements alone to select the appropriate object. Pointing alone and with corresponding head turns administered from an off-centre position produced significant results whereas head turns alone from the same location were ineffective. The subject responded significantly to brief pointing gestures given by both ipsilateral and contralateral hands of an experimenter standing centrally and laterally. She did not select an object placed centrally behind her when slightly exaggerated pointing gestures were directed at this target. These findings are consistent with the hypothesis that this grey seal pup did not possess an understanding of the referential character of these pointing gestures. It is most likely that she proceeded in the direction of the movement of the signalling experimenter, stopping once she located an object. These results are discussed in terms of the cognitive vs. non-cognitive explanations of the success or failure of other species in similar studies.

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Introduction

Whether inconspicuous or obvious, shifts in body alignment, pointing gesture orientation, head alignment and gazing direction (eyes alone) can alter the focus of attention in human social interactions. Most conspicuously, manual pointing, the making of deictic gestures, can transfer an individual's attention to an object, location, or event by locating it in space with the gesturing arm (de Waal 2001). The pointing gesture is a referential signal that can be used universally to refer to any physical entity in the environment. This makes the real world context crucial for the appropriate usage and comprehension of pointing (Anderson & Keenan 1985) and requires this context to be understood by both the pointer and the observer for communication to occur. Motivation and internal state of the signaller are irrelevant in comprehending the pointing gesture because it directs attention to a feature of the external environment.

An important distinction has been made between gaze following, the capacity of an individual merely to track the gaze of another individual to an arbitrary point in space and joint visual attention, in which this gaze is tracked to the precise object on which the attention of this second individual is fixated (Emery et al. 1997). The implications of an ability to adjust one's attention according to these cues have been extended to visual perspective taking (Povinelli et al. 1990), self-awareness (Povinelli et al. 1990; Povinelli & deBlois 1992) and theory of mind (Povinelli et al. 1999). Of course appropriate responses to pointing gestures and gazing cues do not necessitate self-awareness or theory of mind but the complexity and flexibility of the usage and representation of these signals would be greatly enhanced if these phenomena were present.

Pointing as a social and communicative gesture emerges early in human development. Half of the infants in one study were pointing by roughly 12.5 months, often vocalising and looking at their mothers simultaneously (Leung & Rheingold 1981). The ability of infants to

use pointing cues to guide their visual attention is present before they begin to point themselves, but improves with age and with their own use of the gesture. By age 2, toddlers were capable of spontaneously using the direction provided by a pointing cue to find hidden objects (Povinelli et al. 1997). Children between 2.5 and 3 years of age used pointing, the placement of a marker on a target object and the viewing of a replica of this target object to select it among three possibilities at levels above chance (Tomasello et al. 1997). Despite their success in these studies, 3-year-old children were surprisingly unable to articulate why they selected the cup indicated by a pointing gesture (Povinelli & deBlois 1992). The majority of 4-year-old children, however, provided answers revealing they understood that their knowledge of the correct cup arose from observing the direction of the pointing gesture. A developmental decoupling seems to exist in humans between the appearance of appropriate responses to pointing behaviour and the corresponding comprehension of how this visual information produces knowledge.

As infants grew older, their ability to use the head orientation of an experimenter to shift their attention in the same direction matured (Scaife & Bruner 1975), but difficulties in localising objects outside their visual fields lingered until between 12 and 18 months of age (Butterworth & Jarrett 1991). Using changes in head orientation to locate targets was most accurate when the correct choice lay first along an infant's visual scanning path with 18-month-olds searching behind them once their visual field had been cleared of all other targets (Butterworth & Jarrett 1991). Three-year-old children correctly selected a target object when an experimenter's gaze was directed at the object but not above it (Povinelli et al. 1999).

These extensive data on humans raise the question of whether non-human animals possess an analogous ability to develop an understanding of deictic gestures. Correct responses to human pointing commands have been observed in domesticated dogs (*Canis familiaris*: Miklósi et al. 1998; Hare & Tomasello 1999; Soproni et al. 2001), capuchin

monkeys (*Cebus apella*: Anderson et al. 1995), orangutans (*Pongo pygmaeus*: Call & Tomasello 1994; Itakura & Tanaka 1998), gorillas (*Gorilla gorilla*: Peignot & Anderson 1999), chimpanzees (*Pan troglodytes*: Itakura & Tanaka 1998) and bottlenose dolphins (*Tursiops truncatus*: Herman et al. 1999; Tschudin et al. 2001). Because the ability to engage in and respond to pointing and gaze following offers a window on cognitive complexity and mental representation, the performance of numerous taxa in these kinds of studies might refine interpretations of what success and failure truly signify. Indeed, Anderson et al. (1995) and Hare & Tomasello (1999) charged others to replicate variations of these studies on other species to develop a broader and better understanding of mammalian cognition. Since debate even exists over whether the emergence of pointing behaviour in human infants corresponds to the development of a theory of mind (Butterworth & Jarrett 1991 vs. Leung & Rheingold 1981), demonstrating pointing comprehension among other taxa will provide insight into which cognitive mechanisms may be simultaneously at work to generate this understanding.

The success of the animals in these studies has encouraged a range of explanations from those firmly grounded in mentalistic interpretations to others assuming minimal higher level cognitive functioning. Gaze following and monitoring contain stronger evidence for theory of mind since they may implicate an understanding of the visual perspective of others and of how visual access to the environment imports this information into the brain. Visual co-orientation, turning the head and gazing in the parallel direction of another individual, has been demonstrated in numerous primate species by examining their response when they observe humans alter their gaze. Positive results have been obtained with chimpanzees (Povinelli & Eddy 1997; Call et al. 1998) and stump-tailed macaques but not black lemurs (*Eulemur macaco*: Anderson & Mitchell 1999). In the slightly unnatural scenario in which the attention of an individual was attracted by waving an orange above its head from a tower, five primate species (chimpanzees, sooty mangabeys (*Cercocebus atys torquatus*), rhesus

macaques (*Macaca mulatta*), stump-tailed macaques and pigtail macaques (*Macaca nemestrina*) followed this individual's gaze upwards to investigate the source of the distraction (Tomasello et al. 1998). Finally, rhesus macaques examined an object receiving the visual attention of a video taped conspecific for significantly more time than a symmetrically-placed distracting object (Emery et al. 1997).

This paper presents four experiments in which the ability of a young grey seal (*Halichoerus grypus*) pup to respond to human pointing and directional cues in several configurations was investigated. The central aim was to determine whether generalisation from operant conditioning might account for the performance observed in pointing tasks. Instrumental conditioning or visual discrimination between symmetrical movements of the experimenter may provide the necessary cues for a subject to perform at above chance levels. Such an explanation would suggest that a successful performance in such tests does not require comprehending the referential property of directional gestures. The results of this study call into question whether speculation in previous similar studies about the presence of mental complexity and theory of mind has been justified. Indeed, introducing other species to the experiments presented here might yield considerably different, more cautious interpretations of the cognitive mechanisms responsible for their performance when exposed to experimenter-given directional cues.

Two hypotheses therefore might account for the successful performance of an animal in pointing tasks: simple association or referential understanding. The association hypothesis predicts that responses to pointing stimuli are based solely on experience with prior training tasks. The subject is likely to respond by moving in the correct direction until intercepting an object, rather than identifying the general area indicated by the pointing gesture before initiating movement. Performance through association suggests that the subject will respond to poorly shaped pointing gestures rather than waiting for a signal that clearly reveals which

object has been chosen. These predictions suppose that the subject is responding according to localised motion without any understanding of the meaning behind the pointing gestures. Detection of any movement is therefore likely to trigger a response. One would also expect that a subject, once trained in a general two-choice pointing task, might generalise its response to other similar signals but would not respond correctly if pointing was used to refer to novel objects in its environment.

Referential understanding, however, suggests that the subject has the ability to generalise its performance to locate selected objects that have never been introduced before and/or that are located outside of its visual range. The subject comprehends that the selected object may appear anywhere along the relevant line path created by a pointing gesture. A capacity to comprehend spontaneously the meaning of pointing gestures originating from novel, visible locations on the experimenter's body (e.g., a leg or the head) also suggests referential understanding. Finally, the pointing gesture should override potentially more salient cues including the physical proximity of the pointer to the object and the presence of an alluring or distracting stimulus.

It is possible to distinguish between these two hypotheses experimentally after an animal has been trained to respond correctly to basic pointing gestures (i.e., lateralised hand and arm points). Referential understanding likely explains a subject's appropriate and spontaneous performance with respect to modified pointing cues (i.e., different regions of the experimenter's body, the position of the experimenter relative to the object, and the degree of completion of the gesture) and target object identity and arrangement. A poorer spontaneous understanding of how these variables influence the intention of the pointing gesture and the outcome of novel trials favours the simple association hypothesis. The experiments described below attempt to discern upon which hypothesis the performance of a grey seal (and potentially other animals) is based. This study arose opportunistically from the

preliminary pointing exercises required by the contextual and vocal learning studies (see chapters 4 and 5). Because the subject of this paper did not vocalise, the pointing experiments were designed to take advantage of her motivation and presence within the facility. In addition, her responses to pointing commands investigated learning behaviour from a unique sensory modality and experimental context. This permitted a more comprehensive understanding of the presence and absence of certain learning patterns in the young grey seal.

Experiment 1: Pointing with directional, postural gestures

This experiment addressed the salience of different pointing cues to direct a grey seal to an appropriate target object.

Materials and Methods

Subject and background.

Nora, a female grey seal pup between 5 and 6 months of age was used for all experiments in this study. Before these experiments commenced, Nora had been trained to station on a white, wooden square attached to a black PVC pole to facilitate moving her within the facility. She was also trained to respond correctly (nearly 100% accuracy) to pointing gestures issued by the right hand of an experimenter to a target white square on the left and right (considered here and for the remainder of this paper from the perspective of the experimenter). Note that this was purely a conditional response since no understanding of pointing as a referential gesture was required. Spontaneously correct responses to upper body turns to the left and right (see below) were observed in the days immediately prior to these experiments.

Apparatus and stimuli.

All sessions were tape recorded to monitor the outcome of each trial and any unique

behavioural observations. A 2.5 m metal gate at one end of a rectangular dry area prevented Nora from approaching the experimenter and food bucket. A plastic Tupperware container was suspended 30 cm off the ground in the centre of this gate. It served as Nora's starting position and as a reference point for the experimenter to position himself centrally in each trial. Two white, wooden squares (with a side length of 15 cm) were secured to either end of the gate at ground level. The one connected to the PVC pipe was laid in place while the other was cable tied to one of the metal bars. The squares were swapped after half of the sessions to control for any reaction differences arising from discrepancies in stimulus quality. The stool upon which the fish bucket sat in Experiment 1 was moved similarly to balance any unintentional spatial asymmetries.

Procedure.

Six sessions of 30 trials each were conducted over 6 days (during 10-18 April 2002). The experimenter wore an orange raincoat and green glove on the right hand while standing 1.3 m away from the centre of the gate. Each trial began by rapidly raising the (ungloved) left hand, stating the subject's name and slowly lowering the hand to the side. Nora stationed on the Tupperware container until a subsequent signal was administered.

Five directional commands to the left or right were possible: pointing (P), pointing and head turning (P+H), upper body turning (UB), head turning (H) and gazing (E). P trials required the experimenter to lower his head to his chest and use his right, gloved arm to point to the appropriate square with his hand and index finger extended. The P+H trials were identical except the head and eyes were directed towards the focus object as well. The body from the waist up was rotated during UB trials to the left or right. The head alone turned left or right with eyes focused on the appropriate target object in H trials. During E trials the eyes were moved left or right to look at one of the squares (Figure 3.1).

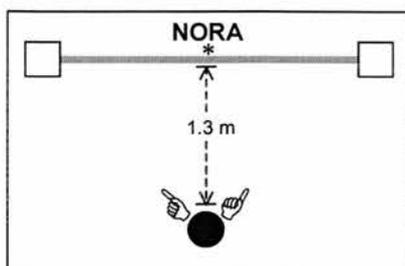


Figure 3.1: Overhead view of experimental set-up 1. Nora stationed behind the gate (grey line) on the central Tupperware container (*) until the experimenter (●) gestured to the left or right squares (□), generically indicated by the two pointing hands.

A “probe trial technique” (Soproni et al. 2001) was used in which every series of five trials consisted of three P trials and two other directional cues. The order was randomly assigned but with half of the correct responses in the session to the left and half to the right. Each novel directional command was tested three times during each session but no attempt was made to balance indicating left and right within command type. Since the gestures of the experimenter uniquely revealed in a random order the appropriate square to select, Nora could not have been informed by other cues (e.g., odour from a laterally placed reward or habituation to a pattern in the pointing sequence).

Once the command was issued, it was maintained until Nora moved towards and touched one of the squares with her nose, which qualified as her decision. When she chose correctly in both non-probe and probe trials, a training clicker was pressed and a piece of herring immediately dispensed. Selection of the incorrect square in any trial caused the experimenter to say “No” firmly, turn his back on the subject and walk away for 15-20 seconds.

Results and Discussion

Nora responded perfectly and spontaneously when upper body turns to the left and right were introduced in sessions preceding these experiments. Significance was determined by using a chi-square test to compare Nora’s actual performance results to those expected if she were choosing randomly between left and right with a 50% success rate (Figure 3.2). P

trials resulted in a performance significantly better than chance levels ($\chi^2 = 102.2, N = 110, df = 1, p < 0.001$). Nora performed perfectly and thus significantly better than expected by chance on P+H ($\chi^2 = 18.0, N = 18, df = 1, p < 0.001$) and UB trials ($\chi^2 = 18.0, N = 18, df = 1, p < 0.001$). She moved immediately to the correct square when these signals were administered and responded appropriately during the first P+H and UB trials to the left and right.

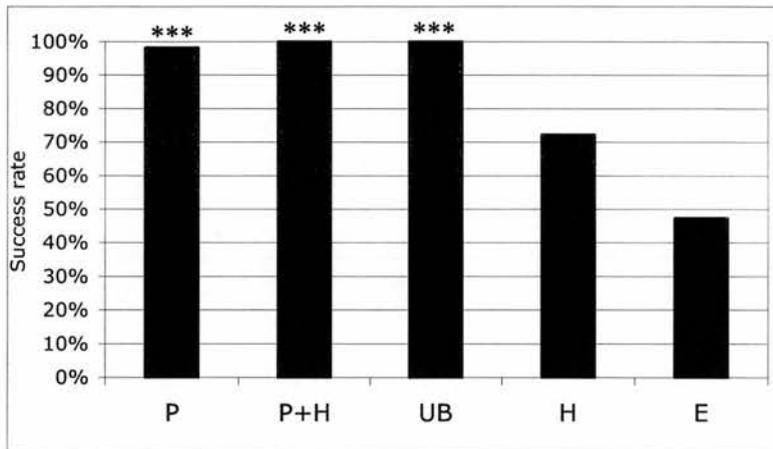


Figure 3.2: Results of Experiment 1 for pointing (P), pointing and head turning (P+H), upper body turning (UB), head turning (H) and gazing (E) trials. *** $p < 0.001$

No deviation from chance was detected for H ($\chi^2 = 3.6, N = 18, df = 1, p = 0.06$) or E trials ($\chi^2 = 0.1, N = 19, df = 1, p = 0.82$). Nora moved to the right on all H and E trials with the exception of a single E trial in which she moved left. She therefore responded correctly during the first H and E trials to the right but incorrectly during the first H and E trials to the left. She did not seem to detect these signals since her responses often lagged behind their execution, suggesting her movement to the right served as a default response. Thirteen of the eighteen H trials involved turning the head towards the right square, making her default decision seem correct more frequently (72%) than might be expected.

The clearly significant results from the P, P+H and UB trials suggest that Nora used obvious directional information and the general body posture of the experimenter to

determine which square to touch. The salient cue in the P+H trials was likely the pointing gesture since her correct movement to the left and right in these trials was abandoned in H trials to moving only right as described above. No referential comprehension of the pointing gesture is required to explain these results. It is more parsimoniously accounted for by a rule in which Nora moved to the square closest to the green glove or in the direction of movement of this glove. Perhaps Nora biased her movements in this way because this gloved, right hand always dispensed her food reward. Her success in UB trials revealed an attention to overall body posture absent from the more subtle H and E cues.

Experiment 2: Centre and off-centre pointing cues

Pointing studies on other species have revealed significant performance biases resulting from differences in the location of the experimenter relative to the target objects (e.g., chimpanzees: Povinelli et al. 1997). A comparable study was conducted here to determine whether Nora was similarly influenced.

Materials and Methods: Procedure

The apparatus and stimuli were identical to those presented in Experiment 1. Six 30-trial sessions were completed during 19-25 April 2002. A new probe trial pattern was used in which every five trials consisted of three centrally-administered P trials as above and a combination of two off-centre P, P+H, or H trials. The experimenter conducted these off-centre trials when standing 1.3 m behind one of the white squares on the left or right, separating him from the distal object by 2.8 m (Figure 3.3). This location allowed the gloved hand in off-centre trials to be closer to the ipsilateral square even when pointing to the contralateral square. Correct performance on these trials would thus refute a decision-making rule in which Nora selected the square closest to the glove.

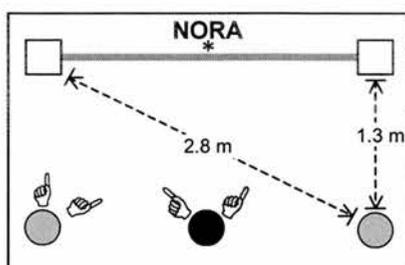


Figure 3.3: Overhead view of experimental set-up 2. Symbols as described in Figure 3.1. Commands issued from centre (●) or off-centre (○) with relevant distances labelled. Hands not depicted for off-centre right to clarify illustration.

The pointing sequence was pseudo-randomised with half of the correct directions for every gesture category (i.e., centre P, off-centre P, off-centre P+H, off-centre H) indicating the left square and half the right square. In all sessions, four of the twelve probe trials were reserved for each of the three off-centre commands. The pointing commands were maintained until Nora touched one of the squares with her nose. The reactions of the experimenter to correct and incorrect responses were identical to those described for Experiment 1.

Results and Discussion

The chi-square test was used again to assess Nora's performance (Figure 3.4). She performed significantly better than random in the centre P trials ($\chi^2 = 109.0, N = 109, df = 1, p < 0.001$), the off-centre P trials ($\chi^2 = 20.2, N = 24, df = 1, p < 0.001$) and the off-centre P+H trials ($\chi^2 = 20.2, N = 24, df = 1, p < 0.001$). The results of the off-centre H trials did not differ significantly from chance levels ($\chi^2 = 1.1, N = 23, df = 1, p = 0.30$). Nora reacted correctly in the first off-centre P and P+H trials but moved incorrectly in the first off-centre H trial.

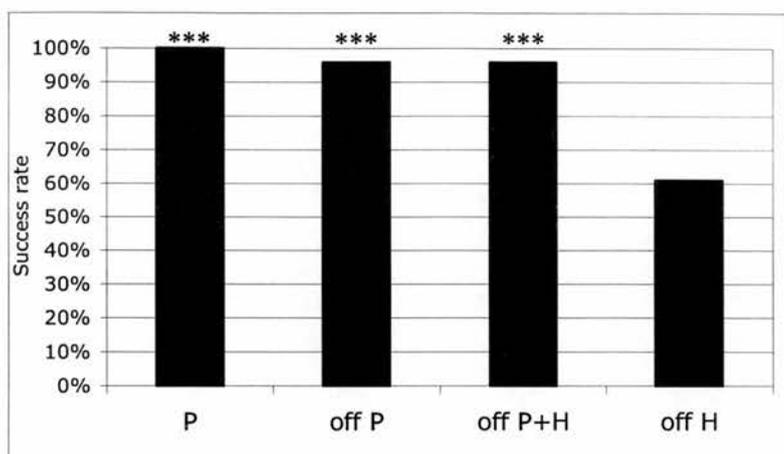


Figure 3.4: Results of Experiment 2 for centre pointing trials (P), off-centre pointing trials (off P), off-centre pointing and head turning trials (off P+H) and off-centre head turning trials (off H). *** $p < 0.001$

With the exception of one trial in which she moved left, all of Nora's errors during the H trials were made because she moved right regardless of the actual direction of the head turn. Occasionally before an off-centre trial was initiated or during the stationing phase of one of these trials, Nora would move to the square in front of where the experimenter was standing. Although each trial would only commence once she returned to the central Tupperware container, she did seem to be partially influenced by the asymmetrical position of the experimenter. This was not reflected in her actual selection of the appropriate square, however.

A referential understanding of the pointing gesture is again not required to explain these results. When off centre, the gloved hand was either extended straight ahead towards the ipsilateral square or horizontally towards the contralateral square. Simple visual discrimination between these distinctive pointing gestures might have contributed to Nora's success. The spontaneously correct response to the off-centre position of the experimenter, however, does suggest a somewhat more sophisticated understanding of the pointing gesture.

Experiment 3: Examining signal duration and ipsilateral and contralateral hand usage

Herman et al. (1999) suggested pointing gestures of a shorter duration produced by

both left and right hands were most appropriate for these kinds of studies. Leaving the hand suspended in the direction of the correct target object in Experiments 1 and 2 might have allowed Nora to visually consult the signal repeatedly, updating her orientation accordingly as she moved towards one of the squares. The introduction in this experiment of pointing with the left hand assessed how sensitive Nora's reactions were to the specific region of the experimenter's body dispensing the signal.

Materials and Methods: Procedure

No changes were made to the apparatus or stimuli specified in Experiment 1. Each of six sessions conducted between 27 April and 9 May 2002 contained 30 P trials. The experimenter stood centrally in ten trials, off-centre to the left in ten and off-centre to the right in the remaining ten in the same positions described in Experiment 2. The left and right green gloved hands each introduced half of the trials. The correct response was to the left in fifteen of these trials and to the right in the other fifteen. The order of these last two variables (i.e., left or right hand, left or right square) was randomised to balance the relative quantities of each option for the three possible positions of the experimenter. After the name of the subject was called and she stationed at the Tupperware container, all pointing signals were brief (< 1 s) and were terminated by an immediate return of the gesturing arm to the side of the experimenter (Figure 3.5). Nora's decision was taken to be the first white square she touched with her nose. The experimenter responded to Nora's correct and incorrect decisions as in Experiment 1.

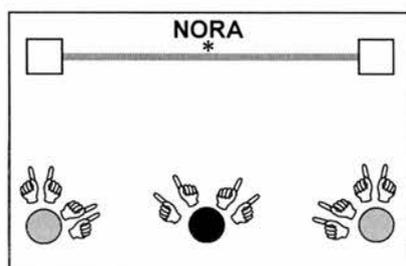


Figure 3.5: Overhead view of experimental set-up 3. Symbols as described in Figures 3.1 and 3.3. Both left and right hands were used to point at ipsilateral and contralateral targets from all three positions.

The resulting command sequence produced five categories suitable for analysis. The first two concerned the centrally located experimenter signalling the square by pointing with his ipsilateral arm (abbreviated sC) or contralateral arm (xC), requiring his arm to move across the front of his chest. Off-centre points with either hand to the target object directly in front of the experimenter constituted the third category (s/x same). Points to the square on the side opposite the off-centre experimenter were either made with the ipsilateral arm (s off) or the contralateral arm (x off), again causing the arm to pass in front of the chest.

Results and Discussion

A chi-square test revealed the results from all analysis categories were significantly above the values expected from random guessing (Figure 3.6): sC ($\chi^2 = 22.2, N = 26, df = 1, p < 0.001$); xC ($\chi^2 = 33.0, N = 33, df = 1, p < 0.001$); s/x same ($\chi^2 = 52.3, N = 60, df = 1, p < 0.001$); s off ($\chi^2 = 27.0, N = 38, df = 1, p < 0.001$); x off ($\chi^2 = 14.7, N = 22, df = 1, p < 0.001$). All pointing conditions produced a correct response in the first trial except for the first centre and off-centre ipsilateral points to the left square. No errors were made on the second of such trials, however.

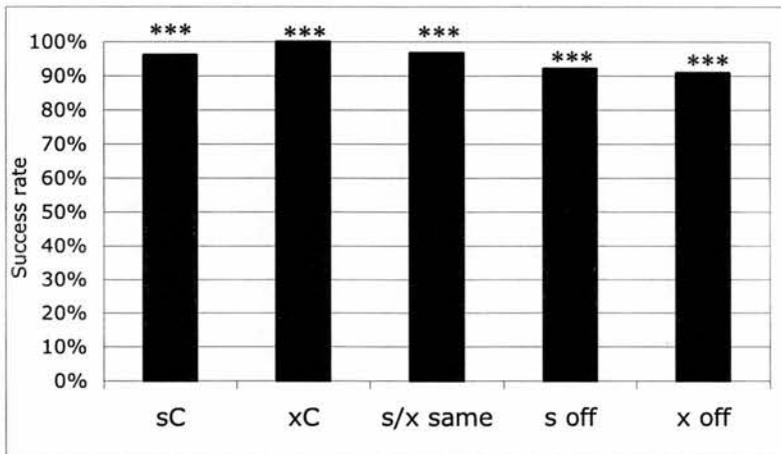


Figure 3.6: Results of Experiment 3 for centrally administered points to the square with the ipsilateral (sC) or contralateral (xC) arm, off-centre points with either hand to the square in front of the experimenter (s/x same) and off-centre points to the opposite square with the ipsilateral (s off) or contralateral (x off) arm. *** $p < 0.001$

All 9 mistakes in this experiment were again made because Nora incorrectly selected the right square. Curiously, 7 of these errors occurred when the left arm gave the command. Nora moved erroneously the first two times the left arm was used in the first session and in the first trial of the second session that began almost a week later. This suggests she rapidly transferred her movement associations with the right arm to those of the left arm within only a few trials. Nora's default decision to move right seemed on occasion to override the dramatic pointing gestures to the left. In some trials she began to orient and move to the right immediately before or just as the pointing motion was performed. She may have waited for an obvious signal for a finite period of time, after which she decided to move to the right even though she had not perceived any directional cue. This would also explain her infrequent behaviour to move to the right during the stationing phase of the trial.

Because the position of the pointing arm was maintained only momentarily before being withdrawn, Nora's correct decisions were not made by continuously consulting the direction of the pointing arm as she moved. It was more likely that the pointing gesture oriented Nora, causing her to move in that direction until she reached a white square. Since a green glove was worn on both hands, she probably selected the right as her default movement because she was concentrating on the arm delivering the fish. No referential understanding is necessary to explain her success here.

Experiment 4: Probing Nora's comprehension of the pointing gesture

It is possible in the previous experiments that Nora simply followed the direction of movement of the pointing signal, stopping upon finding a target object. This experiment introduced a third object and moved all three objects behind Nora to investigate how well she responded to pointing gestures requiring her to swim beyond the target objects closest to her. The overall design is similar to Experiment 1 in Herman et al. (1999).

Materials and Methods

Apparatus and stimuli.

This experiment was conducted in the larger of the two circular pools (5 m diameter). The Tupperware container was suspended 0.2 m above the surface of the pool and 0.8 m from the edge. Three cubes (side length of 15 cm) made from white corrugated plastic were placed in the water and tied along the edge of the pool behind and to the left (again from the perspective of the experimenter) of the Tupperware container, directly behind the Tupperware container and behind and to the right of the Tupperware container (Figure 3.7).

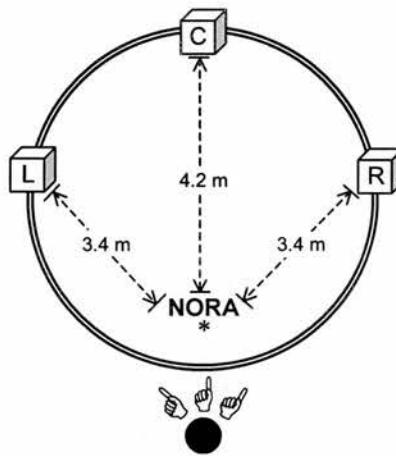


Figure 3.7: Overhead view of experimental set-up 4. Symbols as described in Figures 3.1, 3.3 and 3.5. Three cubes labelled left (L), centre (C) and right (R).

Procedure.

In a single day Nora was trained to station on the Tupperware container in the pool by treading water beneath it. Six sessions of thirty trials each were conducted from 11-16 May 2002. The experimenter stood on land in front of the Tupperware container. Each trial began with the experimenter articulating the subject's name and slowly lowering his head to his chest. The experimenter pointed with his right, gloved arm (index finger extended) to the cube determined by a randomised sequence of ten points to the left, ten to the centre and ten to the right. Each point was accompanied by the experimenter lifting and turning his head in

the direction of the pointing arm and focusing his eyes on the appropriate target. The experimenter exaggerated the central points a bit by leaning slightly forwards. Since the cubes were located behind Nora's stationing position, she could not visualise these targets until she turned in response to the pointing commands.

The first trial was a point to the central cube but Nora swam incorrectly to the left cube. Several points to the left cube were required in the second trial before she swam away from the Tupperware container in the correct direction. This delayed response probably resulted from the new experimental set-up, Nora not knowing she had to touch her nose to one of the cubes and her incorrect decision on the first trial. For all remaining trials, the experimenter pointed at the correct cube with his arm and oriented his head and eyes similarly until Nora touched one of the cubes with her nose. Herring rewards were tossed into the water for correct responses. The experimenter said, "No," as he turned and walked away from the pool for 15-20 seconds after an incorrect response, carrying the fish bucket with him to prevent Nora from helping herself to its contents!

Results and Discussion

All results were significantly different than expected from a random selection model in which Nora would choose indiscriminately among the cubes, selecting each one third of the time on average. A chi-square test (Figure 3.8) indicated that although Nora chose correctly more often than expected when the experimenter pointed to the left ($\chi^2 = 270.0, N = 60, df = 1, p < 0.001$) and right ($\chi^2 = 246.6, N = 60, df = 1, p < 0.001$) cubes, she chose incorrectly more frequently than expected when the central cube was indicated ($\chi^2 = 84.2, N = 60, df = 1, p < 0.001$). Nora moved correctly in response to the first point to the left cube but incorrectly to the first points to the centre and right cubes. The second point to the right cube did produce the correct movement.

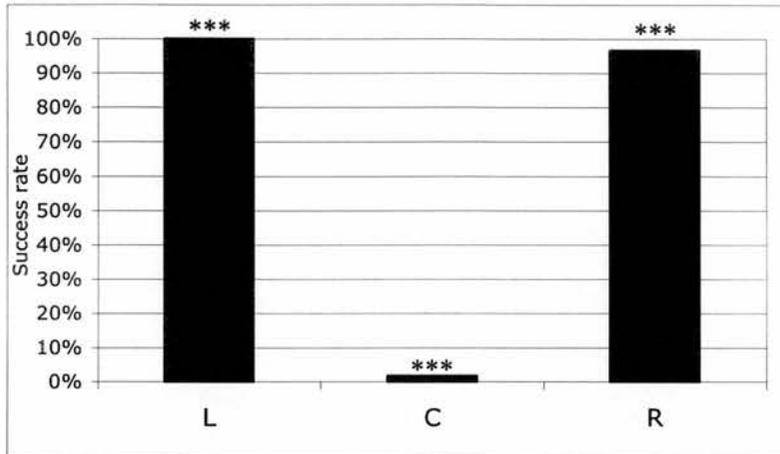


Figure 3.8: Results of Experiment 4 for points to the left (L), central (C) and right (R) cubes.

Nearly all of Nora’s mistakes (59 out of 61) occurred when the pointing gesture was directed at the central cube. She only selected the central cube correctly on one of the first few trials in the first session. When the experimenter pointed at the central cube, Nora most frequently swam to the left ($N = 45$). The experimenter twice extended his arm just right of centre when indicating this central cube, which led Nora to select the right cube in these trials. A consistent return on central trials to the lateral cube most recently indicated was not evident. Nora preferentially selected the left and right targets, ignoring the central cube behind her.

Nora quickly transferred her understanding of how to respond to left and right pointing commands on land to this new set-up in the pool. No spontaneous or consistent movement to the central cube, however, was observed during any of the trials in which the central cube was indicated. These results strongly discourage the hypothesis that Nora grasped the referential meaning of the pointing gesture. It seems Nora moved in the general direction of the extended arm until she intercepted a target object, which she touched immediately.

General Discussion

Nora, a 5- to 6-month old grey seal pup, significantly and successfully discriminated between moving to touch a square on the left or right in response to pointing gestures, pointing and head turning together and upper body turning administered from a central position. Her performance dropped to chance levels when the correct square was indicated solely by head turning or gazing. Nora performed significantly above chance when pointing gestures alone and with corresponding gaze were issued from off-centre locations. Off-centre head turning trials witnessed a return to chance levels. These results are strikingly better than those of similar experiments attempted with chimpanzees which apparently based their selection on the proximity of the gesturing experimenter to the object (Povinelli et al. 1997). In off-centre trials, the head turn seemed to help the chimpanzees select the correct object more than the pointing cues, a finding opposite to that found with Nora. Such differences may have arisen, however, from subtle discrepancies in the training procedure and therefore do not necessarily indicate variation among species.

Nora discriminated between pointing gestures made rapidly and with both ipsilateral and contralateral arms to select the left or right square appropriately. The displacement of the cubes outside of Nora's visual field and the introduction of a third cube directly behind the stationing target produced mixed results. She touched the left and right cubes significantly above chance levels but only once selected the central cube out of 60 trials.

On land Nora's mistakes were most frequently made because she moved to the right when she should have touched the left square (15/17 errors in Experiment 1, 10/11 in Experiment 2 and 9/9 in Experiment 3). On head turning and gazing trials she nearly always moved to the right, suggesting she was unable to discern these more subtle signals and selected the right square as her default option. In the water, however, Nora selected the left cube in 45 of the 60 trials in which the central cube was the correct choice. She seemed

sensitive to minimal changes in the placement of this central pointing gesture with slight displacements to the right occasionally leading her to select the right cube. The last two sessions contained several central cube trials in which Nora started swimming to one of the laterally placed cubes but returned to the Tupperware container before dashing off to the opposite cube. Her indecision about where to proceed on these trials was evident, suggesting that her poor performance did not result from an inability to resolve the direction of the pointing arm but rather from not understanding the referential association of a central point with the central cube.

Nora likely determined early in the experimental procedure that when a signal was administered she either needed to move left or right to receive a reward. The results of the four experiments revealed that Nora was capable of discerning conspicuous signals to laterally placed objects. She failed to respond to more subtle cues (i.e., head turning and gazing) and points directed to an object immediately behind her. Yet she performed spontaneously and significantly above chance levels when upper body turns and off-centre pointing trials were first introduced. Taken together, these observations indicate that salient, laterally-directed movements of the experimenter provided Nora with the information necessary to orient left or right and move accordingly. The pointing gesture, however brief, was more meaningful to Nora in this decision-making process than the position of the experimenter relative to centre. Nora's performance can be explained as a result of simple discriminative learning without invoking any referential understanding of the pointing commands. Her failure in the trials requiring her to select the central cube was particularly striking in this regard since she was probably still attempting to categorise this central point as a lateral gesture.

The results of this experiment therefore align most closely with the cognitively less demanding, association hypothesis since her correct performance is based largely on tasks on

which she had been specifically trained. Nora's responses failed to indicate an understanding that pointing gestures flexibly denote any object within any region of space. Although visually apparent pointing cues prompted Nora to move immediately and her performance was not influenced by the position of the experimenter, she was unable to link the specific direction indicated by each gesture with the unique placement of a target object. Rather, these cues seemed to indicate more generally for her the side along which she should move until intercepting the object. This explains her poor performance when new objects lay outside of her visual range and when pointing commands were directed towards novel locations. Referential understanding expects relatively consistent spontaneous transfer of successful response behaviour to new pointing tasks, a phenomenon that was not observed in these experiments.

It is compelling that a grey seal pup was capable of responding to human directional gestures at all. Pinnipeds have not been reported to point with their flippers or other regions of their bodies. The extent to which grey seals forage and travel in groups in the water remains unknown but the similar movement patterns and activity budgets within grey seal age groupings (Hammond et al. 1993) suggest that certain species of pinnipeds may engage in following and imitative social behaviour. It is possible in these contexts that seals use the body orientation and posture of conspecifics to determine their own swimming direction. Nora's correct reaction to movements involving the displacement or rotation of a large and conspicuous region of the experimenter's body (i.e., pointing, pointing and head turning and upper body turns) might have emerged as a by-product of this ability to attend to the gross alignment of the bodies of conspecifics. Alternatively, simple conditioning could also explain the results presented here.

The body of literature on pointing experiments represents a blend of opinions. Some researchers argue for referential comprehension and possible implications for theory of mind.

Others offer a more cautious explanation of why certain species lacking a rich cognitive understanding of the mental states and perspectives involved might still perform successfully on these tasks. Conflict exists even about whether or not human infants possess theory of mind as these abilities develop. Some have stressed its inevitability (Leung & Rheingold 1981) and others have emphasised its absence (Butterworth & Jarrett 1991). The evidence gathered from this study suggests the cautious approach might be a more appropriate view from which to regard most of these studies.

Several experimenters have claimed that bottlenose dolphins (Tschudin et al. 2001) and domesticated dogs (Miklósi et al. 1998, 2000; Soproni et al. 2001) have employed interspecific communication with human beings to perform successfully on pointing tasks. Tschudin et al. (2001) presented findings that out of six captive bottlenose dolphins, three performed above chance during a set of initial pointing trials, two during head turning trials and none during replica trials in which a model of the appropriate target was presented to the subject. Further testing led to more successful results. Soproni et al. (2001) suggested that dogs used a referential component and attentional cue to select the correct object when an experimenter turned her head and looked at this target. They performed poorly when the experimenter gazed above the object, possibly because the referential element had been withdrawn from the signals. Finally, Miklósi et al. (1998) introduced different lateral gestures in increasingly subtle cueing trials along a continuum of pointing, bowing, nodding, head turning and gazing. Given enough time the subjects performed significantly above chance for all cues.

The performance of the dolphins and dogs in these studies resulted from their successful discrimination between two symmetrical (albeit subtle at times) cues to determine whether a movement to the left or right would secure a reward. A consistent and spontaneous correct performance was absent in these studies when the novel, increasingly subtle cues

were introduced. It was likely that no interspecific communication was present beyond the usual information conveyed by discriminative conditioning. An ability of these animals to follow a central pointing gesture to an object directly behind their fields of view would more strongly implicate referential comprehension (e.g., Herman et al. 1999).

Call & Tomasello (1994) have discussed how Chantek, an enculturated orangutan, better understood novel pointing scenarios and the attention-directing character of pointing than an orangutan named Puti raised in captivity with other orangutans. During his upbringing Chantek undoubtedly had been casually and intentionally exposed by his human caretakers to more situations in which pointing played a relevant social and interactive role than Puti, contributing to their differences in performance. While Call & Tomasello (1994) speculated that Chantek viewed humans as intentional beings whose attention can be controlled and exploited, the work of Povinelli & deBlois (1992) casts doubt on this interpretation. Three-year-old humans were unable to offer a rationale for why they looked under the cup pointed to by an experimenter whereas 70% of the 4-year-olds could state that they observed the experimenter “show,” “tell,” or “point” to the correct cup (Povinelli & deBlois 1992). Taken alone, it is possible to interpret the behaviour of the 3-year-olds as a result of simple conditioning. The 4-year-olds revealed that this understanding appears at a particular developmental stage, rendering the behaviour of the 3-year-olds more insightful. Thus, although Chantek behaved correctly, he might have lacked an understanding of why he chose appropriately and of the corresponding intentional stance of his human interlocutors. Nora may have been similarly enculturated as a result of her regular interactions with human beings during her first, formative months of life.

Chimpanzees rapidly learned to select the cup indicated by the “knower,” the experimenter they observed perform the baiting, over that of a “guesser” who entered the room after the baiting had taken place (Povinelli et al. 1990). No decrease in performance

was observed when this guesser remained in the room but placed a bag over his head during the baiting procedure. Povinelli et al. (1990) offered visual perspective taking as an explanation for the success of these chimpanzees. It is possible, however, that a rule in which the animals consistently responded to the experimenter who performed the baiting regardless of the behaviour of the guesser could have served as the basis for their mastery of the task. The inability of rhesus macaques to succeed in identical experiments suggested they arrived at an alternative means to attempt to solve the problem, one in which the identities of the experimenters were of primary relevance (Povinelli et al. 1991).

Other experiments testing the responses of primates to directional cues given by an experimenter have been more restrained in their interpretations of the successful results. A female rhesus macaque was trained to point to the one tray among three containing food to inform a naïve human experimenter. The macaque performed quite poorly when the roles were reversed and she was expected to respond to the pointing of the experimenter, suggesting her pointing behaviour was a conditioned response to the training (Hess et al. 1993). Itakura & Tanaka (1998) explained the correct usage of tapping, pointing, head turning and gazing cues by chimpanzees, orangutans and human infants between 18 and 27 months as a simple, non-cognitive association between head, eye and postural orientation and the appropriate object. Similar results in gorillas with the exception of the glancing cues were accounted for as a result of the spatial proximity of the cue to the object without any referential understanding (Peignot & Anderson 1999). Chimpanzees tracked the head orientation and gaze of an experimenter behind them but Povinelli & Eddy (1997) argued for an absence of a comprehension of intentionality, the tendency found in humans to assign motivations and goals to animate objects in the physical world. The neural resources of primates (and possibly other mammals) dedicated to these tasks of monitoring gaze and head orientation (e.g., Perrett et al. 1985; Kawashima et al. 1999) do not necessitate the

corresponding cognitive comprehension of their implications for perspective sharing and theory of mind. Instead, they may have arisen due to the selective benefit of being able to access visually relevant social and physical features of their environment (e.g., predators and conspecific allies and aggressors).

The experiments of Herman et al. (1999) were justified, however, in their claim that bottlenose dolphins might have understood the referential quality of the human pointing gesture. Indeed, one subject spontaneously and correctly touched an object located centrally behind her during 40% of the trials in a set-up similar to that described in Experiment 4. Her performance increased to 88% when exaggerated cueing to this central object was transiently introduced. She also comprehended commands that combined pointing gestures with symbolically communicated objects. This flexibility in performance was highly suggestive of a more generalised understanding of the referential property of pointing commands. Similarly, the findings of Hare et al. (2000) offered compelling evidence that chimpanzees possess a strong understanding of what conspecifics can and cannot see and how this presence or absence of visual information is relevant in competitive foraging scenarios. Their study is peppered with suggestive anecdotes, collectively arguing that the subordinate animals had a true understanding of what dominant individuals were and were not capable of seeing, how the unique possession of visual information provided a biased foraging opportunity in favour of the subordinate and the necessity to conceal this knowledge differential until the food was acquired.

The results of the experiments presented here and the majority of other pointing studies are most parsimoniously explained as the result of simple conditioning that does not infer a higher level of cognitive understanding of the tasks at hand. The pointing literature would benefit greatly from studies in which success is only possible through the very referential comprehension many are hoping to find and not through mere lateral

discrimination of physically symmetrical directional commands. An expansion of this work into other mammalian species will continue to refine how we categorise taxa according to their responses to and comprehension of obvious to subtle directional cues. The question endures whether the profound shaping of the social and communicative landscape through the frequent deployment of pointing, head turning and gazing cues remains uniquely human.

Chapter 4

Contextual learning in the vocal domain in grey seals*

Abstract

Two grey seal pups were trained to vocalise when a light was presented and to remain silent while performing other tasks in response to hand signals. Further work demonstrated that these animals could be trained to respond to playbacks of moans and growls with vocalisations of the same category. They appeared to be unable to generalise this response, however, since novel moan and growl playback stimuli tended to elicit growls. This, in addition to the long periods of training necessary to have these animals produce the appropriate categorical responses, cast doubt on the possibility of an automatic mechanism of matching vocalisation type. Together the results clearly demonstrated that grey seals could be trained to modify the usage of their calls in an operant conditioning procedure and are, therefore, capable of contextual learning in the vocal domain.

* After slight modification, this chapter will be submitted to *Animal Behaviour* with Vincent M. Janik and Peter J. B. Slater as co-authors.

Introduction

Contextual learning is a form of social learning that yokes signals already present within an individual's repertoire to novel contexts based on experiences with how other individuals deploy these signals (Nelson & Marler 1994; Janik & Slater 1997, 2000). Janik & Slater (2000) further decompress contextual learning into comprehension and usage learning. The former occurs when an individual acts as a receiver, using experiences with the signal usage of others to extract a novel meaning from a signal. Alternatively, usage learning occurs when this individual actually learns to *produce* a signal from its repertoire in a novel context. Contextual learning in the vocal realm can play a substantial role in vocal development and the emergence of an appropriate species-specific ability to interact vocally. An individual must simultaneously come to understand the situations in which it is suitable to vocalise and how to respond appropriately to the calls of others. Contextual learning in the vocal domain often represents an evolutionary compromise between an unlearned vocal repertoire deployed in broadly the correct circumstances for nearly immediate communication and one flexibly learned to account for unpredictable features of the environment that significantly impact vocal usage (Seyfarth & Cheney 1997). The demonstration of contextual learning offers persuasive evidence that individuals can learn to monitor and use variable social and ecological phenomena to release very precise behavioural responses.

Comprehension learning is widespread in the animal kingdom and is of particular relevance to the behaviour surrounding alarm calling since it requires understanding which features of the environment represent predatory threats and how best to respond to each of these dangers. In particular, Diana monkeys (*Cercopithecus diana*) produced alarm calls in response to playbacks of leopard (*Panthera pardus*) growls, predatory crowned hawk eagle (*Stephanoaetus coronatus*) shrieks, Campbell's monkey (*Cercopithecus campbelli*) leopard

alarm calls and chimpanzee (*Pan troglodytes*) leopard alarm calls, but not to chimpanzee social screams (Zuberbühler et al. 1997; Zuberbühler 2000, 2002). Diana monkeys have apparently developed a thorough understanding of the calling behaviour of both non-predatory and predatory sympatric heterospecifics. Their ability to differentiate between chimpanzee alarm and social calls suggests a striking attention to not only the vocalising species, but also to the class of vocalisation to determine their most appropriate vocal and behavioural response. Their behaviour is crucial for their survival and is likely to be a consequence of comprehension learning occurring early in life.

Leopards, crowned and martial (*Polemaetus bellicosus*) eagles and pythons (*Python sebae*) each provoke vervet monkeys (*Cercopithecus aethiops*) to produce an acoustically distinct alarm call (Struhsaker 1967; Seyfarth et al. 1980; Cheney & Seyfarth 1990). Although infants and juveniles alarm call at numerous predatory and non-predatory species alike, they mostly reserve leopard alarm calls for terrestrial mammals, eagle alarm calls for birds and snake alarm calls for snake-like objects (Seyfarth & Cheney 1980; Seyfarth & Cheney 1986). The responses of infants to these calls were more likely to be correct when they first looked at the responses of an older animal. These observations are consistent with the hypothesis that predispositions and both comprehension and usage learning mediate vocal development in vervet monkeys since these animals come to link their experiences with perceiving and producing alarm calls to their observations of concurrent adult behaviour (Seyfarth & Cheney 1997).

Brown-headed cowbirds (*Molothrus ater*) hatch and fledge in heterospecific nests. The acquisition of their species-specific song represents one of the most striking avian examples of intersexual usage learning (West & King 1988). During the breeding season male cowbirds sing relentlessly to females, manoeuvring through literally thousands of songs. Females selectively prune and mould male song by performing abrupt wing strokes in

response to certain components, a display that stimulates the males to sing these elements at a significantly elevated rate. Usage learning occurs rapidly under these circumstances, managed by a deadline imposed by reproductive necessity.

These primate and bird species exploit contextual learning in the vocal domain to navigate through socially and ecologically complex environments. Although studies in the wild broadly reveal the natural context in which learning is useful, research on captive animals offers more conclusive insight into their precise capabilities and behavioural flexibility. The demonstration of usage learning in animals can be divided into different stages requiring an increasingly complex and controlled vocal apparatus. The first step consists of showing that an animal can vocalise on command, reliably producing a call when exposed to a particular stimulus. While success with this initial stage is encouraging, it may represent a by-product of the animal entering a more excited motivational or physiological state in which the threshold for vocal activity has been lowered. The second stage therefore requires this subject both to vocalise and to remain silent on command by differentiating between two stimuli. A third, more complicated level of usage learning requires an animal to produce different call types in response to distinct commands. This requires an ability to differentiate among unique components of the vocal repertoire and produce them in particular contexts. This study is the first to investigate systematically these three levels of usage learning.

Most of the early experiments investigating contextual learning in the vocal sphere sought to bring vocal behaviour under operant control (Skinner 1953) by reinforcing vocal responses to unique stimuli and changes in vocalisation rates. Positive results demonstrated that subjects had at least some control over their vocal production and an ability to use their vocalisations in a novel context detached from social interactions (e.g. to avoid an electric shock stimulus or when viewing a coloured light or a target of a particular size). This early

experimental technique produced successful results with budgerigars (*Melopsittacus undulatus*: Ginsburg 1960), chickens (*Gallus gallus*: Lane 1960, 1961), guinea pigs (*Cavia porcellus*: Burnstein & Wolff 1967), rats (*Rattus rattus*: Lal 1967), dogs (*Canis familiaris*: Salzinger & Waller 1962), cats (*Felis catus*: Molliver 1963), *Cebus* monkeys (Myers et al. 1965; Leander et al. 1972), lemurs (*Lemur catta*: Wilson 1975), California sea lions (*Zalophus californianus*: Schusterman & Feinstein 1965) and human beings (Rheingold et al. 1959; see Krasner 1958 for review). Most of these studies conclusively demonstrated that their animals were capable of vocalising on command and vocalising and remaining silent on command, the first two steps of usage learning described above.

Similar studies to the kind just described but conducted on marine mammals have remained sparse, partly because of the difficulty in determining the underwater behavioural and social contexts in which these animals become vocally active. Since visual range is limited underwater, these animals rely strongly on acoustic communication, offering a compelling biological system in which to investigate learning behaviour in the vocal domain. Few experiments have been conducted on the vocal behaviour and control of pinnipeds. Schusterman & Feinstein (1965) trained a generally non-vocal captive California sea lion to produce clicks underwater. Originally rewarding any vocalisations, the experimenter gradually accepted only clicks produced in specific contexts. In particular, the subject was trained to click to have a target lowered into its pool that it could strike to receive food. Furthermore, this sea lion managed to respond successfully to a discrimination exercise in which it clicked or remained silent in the presence of a large or small circular target, respectively. A parallel reinforcement schedule with large and small triangles did not witness any drop in performance.

Two captive, adult male harbour seals (*Phoca vitulina*) imitated English words and phrases uttered frequently by one of their human trainers, suggesting that these animals may

naturally mimic conspecifics or salient acoustic features of their environment (Ralls et al. 1985). This vocal imitation emerged in the kind of strongly interactive (yet artificial) context shown to produce mimicry in some bird species (e.g. European starlings (*Sturnus vulgaris*) that had been hand-raised by humans: West & Stroud 1983; West & King 1990). The capacity of these harbour seals to use particular vocalisations in specific social contexts would have provided a demonstration of contextual learning, but no experimental investigation of this sort was conducted.

This study investigated whether two captive grey seal pups were able to use contextual learning to perform successfully in trained vocal tasks. Grey seals are sexually dimorphic phocids inhabiting the land and waters of the western Atlantic Ocean, eastern Atlantic Ocean and Baltic Sea (Davies 1957). Adults, juveniles and pups produce distinct tonal and guttural vocalisations in air during breeding and lactation and subsequently underwater (Asselin et al. 1993; McCulloch 1999). Although conflicting evidence has been reported regarding the ability of mothers to distinguish between the vocalisations of their pups (McCulloch et al. 1999; McCulloch & Boness 2000), these pup calls appeared to be stereotyped and individually distinctive (Caudron et al. 1998; McCulloch et al. 1999). This study investigated whether grey seals were capable of vocalising and remaining silent on command and differentially producing moans and growls after they had heard playbacks of the same call type. Asselin et al. (1993) and McCulloch (1999) provided spectrograms and acoustic descriptions of these two vocalisation categories among the underwater and in-air vocal repertoires of the grey seal. Underwater vocal activity fluctuated as the breeding season progressed with increased growling observed at its beginning and end (Asselin et al. 1993).

This contextual learning study was initiated in large part to explore more comprehensively the flexibility and usage of the grey seal vocal repertoire. The literature

lacks any discussion about the extent to which these animals possess control over their vocal output, both in terms of timing and the category of their vocalisations. Categorical vocal matching in grey seals has not been documented in the wild or in captivity. Experiments that test for contextual learning in the vocal domain broadly provide information on repertoire size, ontogeny and development, acoustic perception and resolution, and vocal control and flexibility. Insight into these areas helps direct future training, playback and recording efforts. The experiments discussed at length below investigate how grey seal pups might learn how to use visual and acoustic stimuli to control their vocal output. Although the command and reward training procedures did not resemble the phenomena that characterise a largely independent post-weaning existence (i.e., the dispensing of food according to an interactive vocal performance rather than an autonomous ability to hunt), the implications for how young grey seals learn to modify their behaviour according to external stimuli remain very real indeed.

Experiment 1: Vocalising on command

This first stage examined whether Oscar and Kylie were capable of vocalising only after observing a specific visual stimulus, withholding all vocal responses at other times.

Materials and Methods

Training began on 31 January 2002 with two grey seal pups (one male (Oscar) and one female (Kylie)) between two and three months of age at the time. The procedure for this experiment developed gradually between 31 January and 22 March 2002. Training sessions occurred once per day, five to seven times each week except for a gap from 10-18 March 2002. Testing occurred with each individual separately; the training was conducted on land with a gate separating the experimenter and animal (Figure 4.1). Initial sessions consisted of presenting a bicycle light and waiting for the pup to vocalise before rewarding it. They soon

started to call incessantly regardless of whether the light was present. To increase attentiveness to the signals of the experimenter, stationing trials were introduced in which Oscar and Kylie were required to touch their noses to a PVC-mounted wooden black circle and grey triangle, respectively, when it was placed in front of them. Any vocalising at this stage was considered an incorrect response. Two of these shapes were then cable tied at ground level to opposite sides of the gate. A PVC pipe was used to direct the animals to touch these shapes until the experimenter could merely point to the shape to elicit the appropriate movement and stationing response. A Tupperware container was suspended from the middle of the gate. The animals were rewarded for stationing on this container at the beginning of each trial before the experimenter pointed to one of the target shapes. Once the pups were performing successfully in these pointing trials, the bike light was reintroduced.

The eventual procedure consisted of isolating one individual, stating the subject's name and waiting several seconds while it stationed on the Tupperware container without vocalising. According to a predetermined randomised sequence that did not limit the maximum number of consecutive trials featuring the same command, the experimenter presented the bike light or pointed to the target object on the left or right. Since a fixed number of fish pieces were used for training, incorrect responses produced an increased number of trials in a particular session (Oscar: range of 19-44 with mean (\pm SD) of 25.9 ± 6.9 ; Kylie: range of 19-34 with mean (\pm SD) of 24.7 ± 4.8). The sound recording and digitising equipment is described in Chapter 2. Data sheets recording information on the task and success of each trial were completed by an assistant. Figure 4.1 illustrates this training procedure.

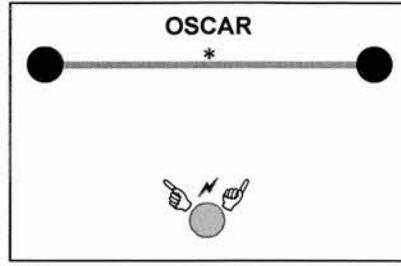


Figure 4.1: Overhead view of training schematic for Experiment 1. Oscar (or Kylie) stationed behind the gate (grey line) on the Tupperware container (*) at the beginning of each trial. The experimenter (○) then directed Oscar to station on the left or right circles (●) by pointing, represented by the two hands, or to vocalise by presenting the bike light (⚡).

Results

Training results are shown for Oscar and Kylie in Figures 4.2 and 4.3, respectively. These displays begin on 21 February 2002, the first day when both pointing and vocalising trials were introduced during the same training session, and conclude on 25 March 2002. The number of pointing and vocalisation trials varied between sessions according to the randomisation schedule and the success of the pups. The sessions with an overall success rate lower than that of the pointing and vocalisation trials alone contained additional incorrect trials in which the animal had vocalised during the Tupperware stationing phase.

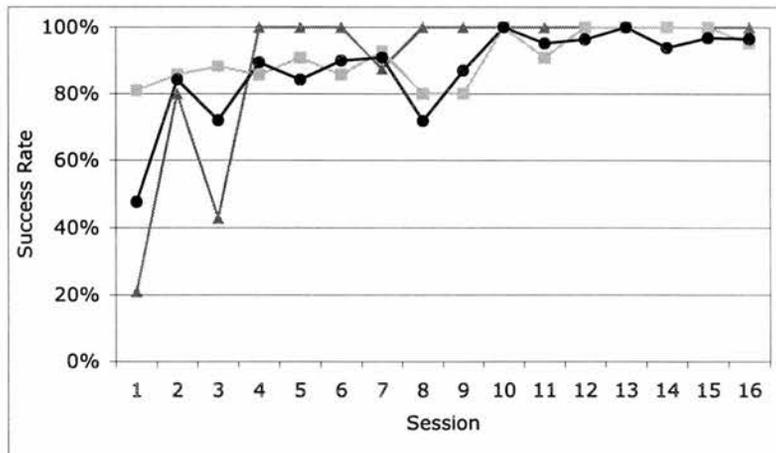


Figure 4.2: Oscar: vocalising on command performance results (21 February – 25 March 2002). Success rates are displayed for pointing trials alone (■), vocalisation trials alone (▲) and all trials together (●).

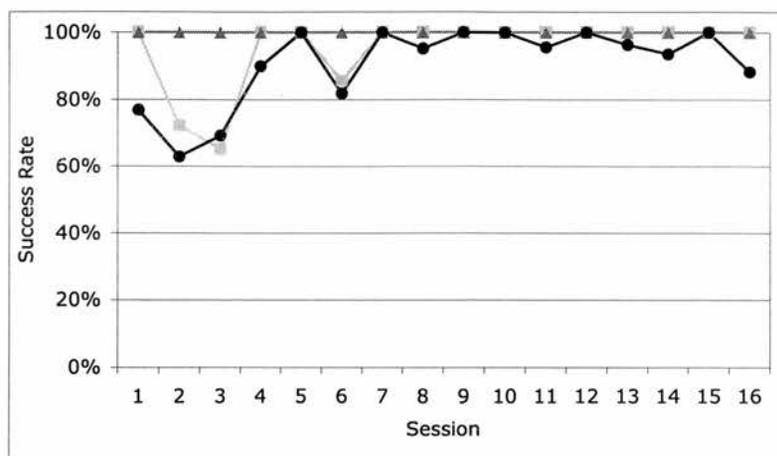


Figure 4.3: Kylie: vocalising on command performance results (21 February – 25 March 2002). Symbols are the same as those in Figure 4.2.

These figures demonstrate that Oscar and Kylie acquired proficiency in the tasks of vocalising and remaining silent on command. Pointing trials consistently elicited appropriate responses from both animals across training sessions, an expected result since the vocalisation task was only reintroduced after high success rates had been achieved on pointing trials alone. Oscar’s success rate in the vocalisation trials was considerably more variable than Kylie’s immediately perfect performance, partly because Oscar was arbitrarily held to a stricter training regimen at first. Movement to one of the shapes when the light was presented was considered an incorrect response for Oscar but was initially ignored for Kylie.

Most of the mistakes in the first few combined task sessions were movement related and occurred during vocalisation trials. The last dozen sessions witnessed a reversal, however, in which mistakes were most frequently made by vocalising on pointing trials. The time lag between the presentation of the light and the production of a vocalisation by the subjects fell to under 1 s on average in most sessions. In the first two trials of the first session after the break in training from 10-18 March 2002, this time lag increased to over 7 s for Oscar and over 4.5 s for Kylie. These times decreased to those preceding the training interruption by the end of this session and for all subsequent sessions.

Experiment 2: Categorical imitation of specific moan and growl playbacks

The vocal control of these pups was further investigated by training them to respond to moan or growl playbacks with vocalisations of the same category. Although no published studies have formally correlated behaviour with particular vocalisations, observations suggested that Kylie and Oscar moaned before being fed and when they unsuccessfully tried to move to another area within the enclosure. Growls were used aggressively when another animal approached too closely.

Methods

Playback stimuli.

Playbacks were made from five moans and four growls produced by Oscar and four moans and five growls produced by Kylie during Experiment 1 and baseline vocal repertoire recording sessions made in non-experimental contexts. Each animal was only exposed to the moans and growls it had produced. These two categories of sounds were described by McCulloch (1999) and are easily distinguished by ear and with spectrograms (Figure 4.4). A set of more easily discernible moans and growls was subsequently selected for Kylie to replace the unintentionally ambiguous original signals to which she was responding poorly. Moans are tonal and consist of a strong fundamental frequency below 1.5 kHz with the most intense harmonics below 4 kHz and only weak sound energy above 5 kHz (Figures 4.4a, b). Growls, however, are characterised by more broadband sound energy lacking harmonic structure with a dynamic range extending as high as 15 or 20 kHz (Figures 4.4c, d). Most sound energy in the growls is below 2 kHz. Whilst moans were used most frequently by the animals when they begged for food and to move to other areas of the facility, growls were generally used in aggressive interactions between animals.

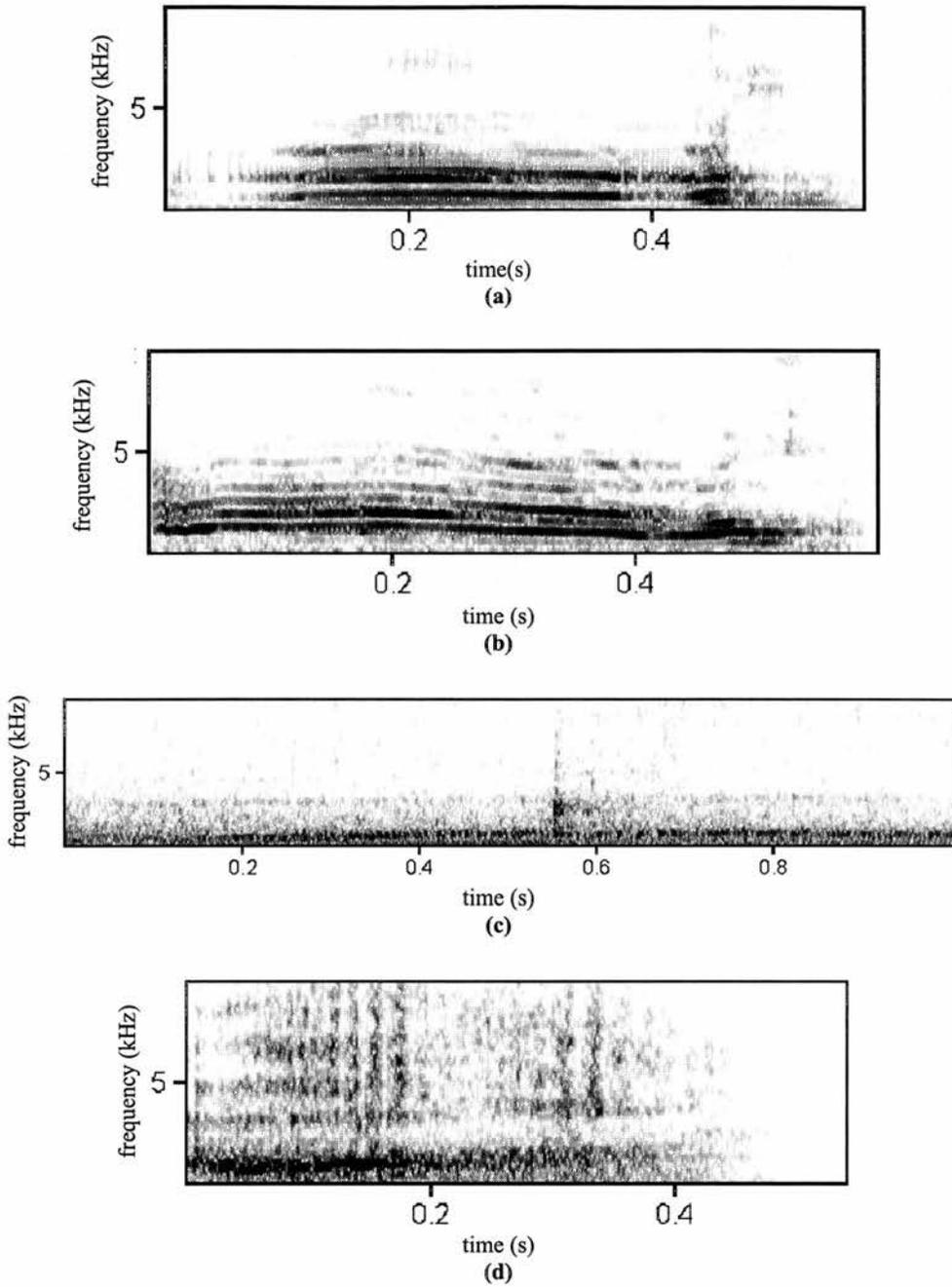
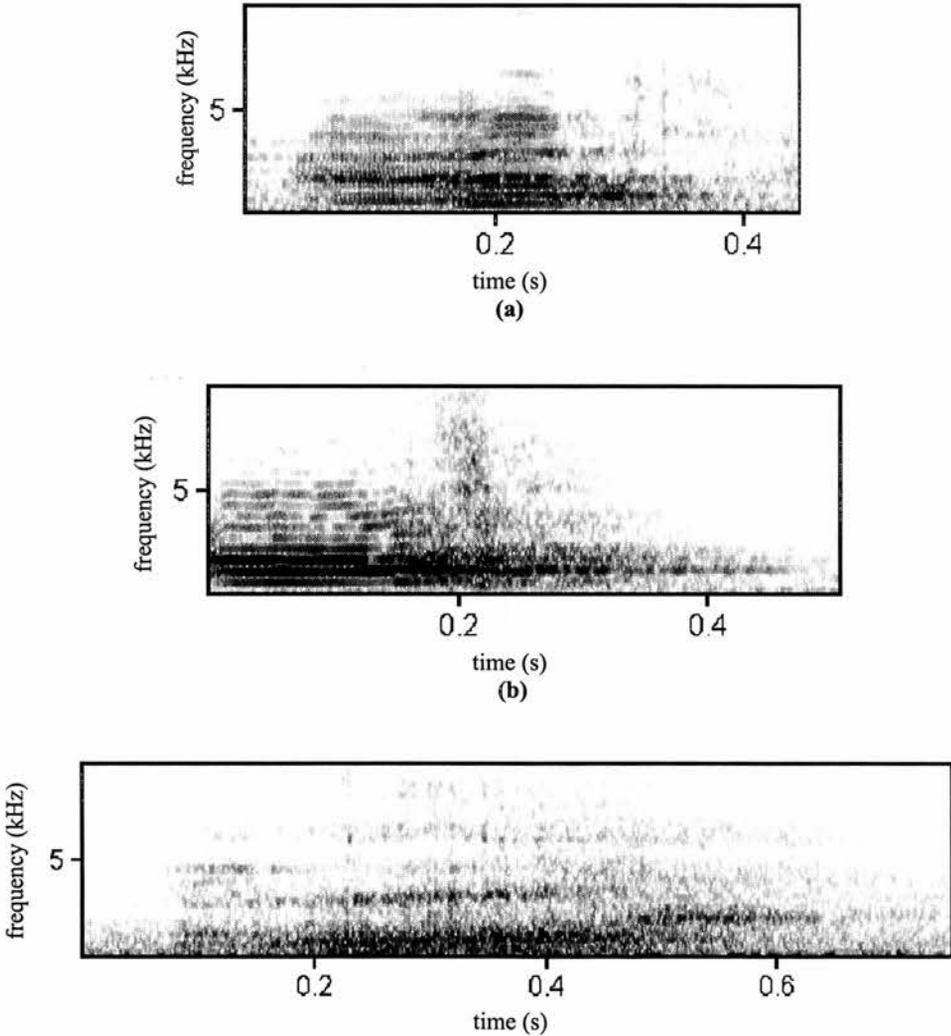


Figure 4.4: Sample spectrograms of playback stimuli: moan (a) and growl (c) from Oscar and moan (b) and growl (d) from Kylie. The x-axis corresponds to time (s) and the y-axis to frequency (kHz).

All playbacks were standardised in amplitude and burned onto a compact disc in a random order with each moan and growl appearing the same number of times. The sessions were monitored and recorded with the electronic equipment described in Chapter 2.

Examples of the novel moans and novel growls introduced subsequently in the experiment (see Procedure below) are depicted in Figure 4.5. These novel sounds were recorded as responses to the original playbacks and were selected for roughly similar duration (Table 5.1). Amplitude was again standardised and new compact discs were burned in which every fourth trial introduced one of these novel playback stimuli. The three intervening trials involved playing the same moans and growls between which the animals had been trained to differentiate. The order was randomised and two of these sequences of 48 playbacks were generated, each of which was used in alternate training sessions. Table 5.1 displays the quantity and average duration of all playback stimuli.



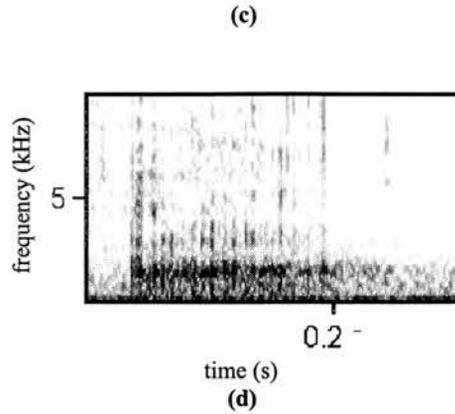


Figure 4.5: Examples of spectrograms of novel playback stimuli: moan (a) and growl (c) from Oscar and moan (b) and growl (d) from Kylie.

Table 4.1: Quantitative description of acoustic features of training and novel playback stimuli. Duration is expressed in s.

	Oscar	Kylie
Quantity: training moans	5	4
Average duration \pm standard deviation: training moans	1.5 ± 0.9	0.7 ± 0.2
Quantity: training growls	4	5
Average duration \pm standard deviation: training growls	2.6 ± 1.2	0.5 ± 0.2
Quantity: novel moans	6	6
Average duration \pm standard deviation: novel moans	0.4 ± 0.1	0.4 ± 0.0
Quantity: novel growls	6	6
Average duration \pm standard deviation: novel growls	0.7 ± 0.1	0.3 ± 0.1

Procedure.

This phase began on 26 March 2002 and was moved indoors to protect the electronic equipment from the elements and to reduce ambient noise. The generic set-up was similar to Experiment 1 (Figure 4.6). The experimenter stood centrally before the pup and a few pointing trials to the right during each session were maintained to compel the animals to pay close attention to the experimenter's signals. The first two weeks of the new set-up involved playing a sound, presenting the bike light and awaiting a vocal response from the animal. The light was gradually phased out as they were trained to vocalise after hearing the playback stimulus. The experimenter opportunistically rewarded categorical imitation of the playback with multiple clicks and multiple fish.

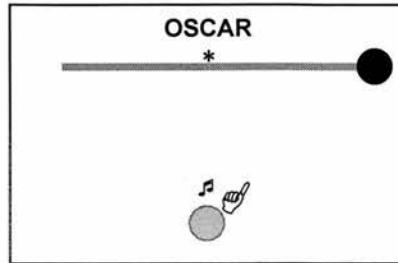


Figure 4.6: Overhead view of training schematic for Experiment 2. Symbols are the same as those described in Figure 4.1. Pointing gestures were only made to the right and vocalisations were elicited with playbacks (♪) instead of a bike light.

Pointing trials were still used to prevent the animals from vocalising constantly and to provide positive feedback in the event of a long string of incorrect vocal responses. Strict rewarding for categorical similarity began on 19 April 2002. The playback sequences containing the novel moans and growls described above were introduced on 14 May 2002 for Oscar and 19 June 2002 for Kylie. The two sequences were alternated five times each.

Results

The training procedure was dynamic with the evaluation criteria shifting gradually and logically to build from one stage to the next. An attempt to alternate playing three moans with three growls met with poor results because the animals clung to a single response category (moans for Oscar and growls for Kylie) and received food rewards frequently enough to make concentrating on the differences between the playbacks unnecessary. Oscar subsequently heard only growls and Kylie only moans until they reliably began producing this second category of sounds. After production of this unfavoured type stabilised, the number of moan and growl playbacks was again adjusted to be nearly equal. Eventually both categories of sounds were presented in an alternating fashion until the pups were responding successfully to a randomised sequence in which no more than three stimuli of the same category were played in a series. It was necessary to shape Oscar's growls by first accepting quick exhalations of air that gradually emerged more definitively as growls within the first

six sessions. Oscar achieved proficiency by session 23 whereas Kylie required a total of 47 sessions. The ten sessions involving the novel moan and growl stimuli were subsequently conducted.

Figures 4.7 and 4.8 present the performance results for Oscar and Kylie, respectively, only for the trained playback stimuli during the novel playback sessions. These figures show the trials judged to be correct and incorrect within each session. It is evident that both Oscar and Kylie were capable of matching the moans and growls on which they had been trained with vocalisations of the same type. Since Kylie was involved in other experiments unrelated to the ones presented here, she was occasionally fed the majority of her food in a different context. Occasionally the total number of successful trials decreased suddenly for several sessions in a row due to the reduced quantity of fish that remained for training purposes. Vocal responses to the novel playbacks used in the last ten sessions are shown in Figures 4.9 and 4.10. Oscar and Kylie responded to the first novel moan and the first novel growl playbacks by growling.

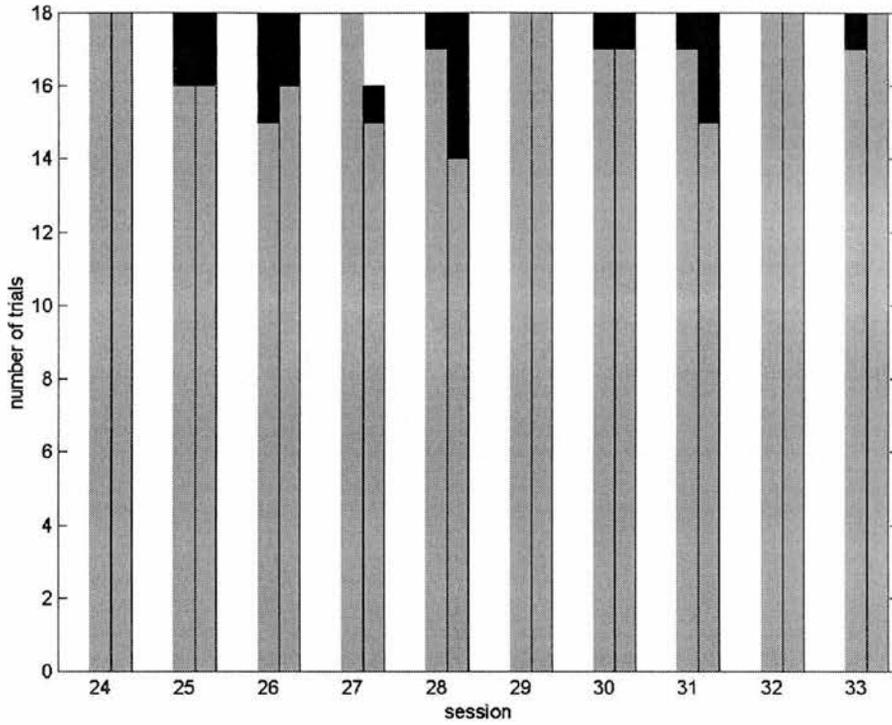


Figure 4.7: Oscar's performance results when in ten sessions involving novel playbacks among stimuli in which he had been trained to respond categorically to playbacks of moans and growls. Each set of double bars corresponds to a unique training session, beginning on 14 May and ending on 1 June 2002. The first bar of each pair reflects his success during moan playback trials and the second bar his success during growl playback trials. The light grey represents the number of trials in which Oscar responded correctly (i.e. matching the category of the playback vocalisation in his vocal response) whereas the dark grey represents the number of incorrect trials.

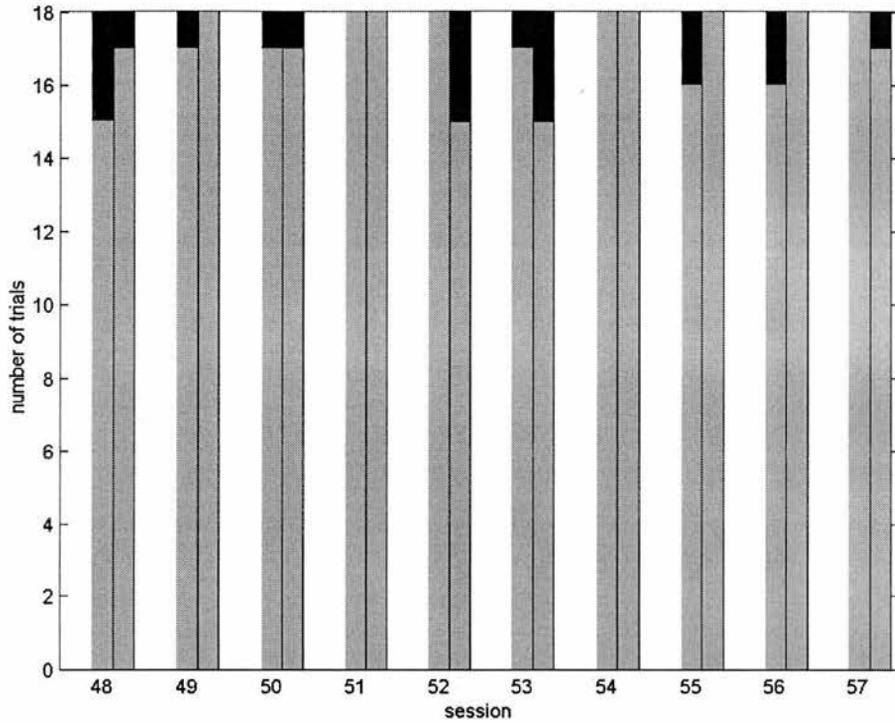


Figure 4.8: Kylie's performance results during ten sessions involving novel playbacks among stimuli on which Kylie had been trained. Sessions spanned from 19 June to 1 July 2002. See Figure 4.7 for a key to this figure.

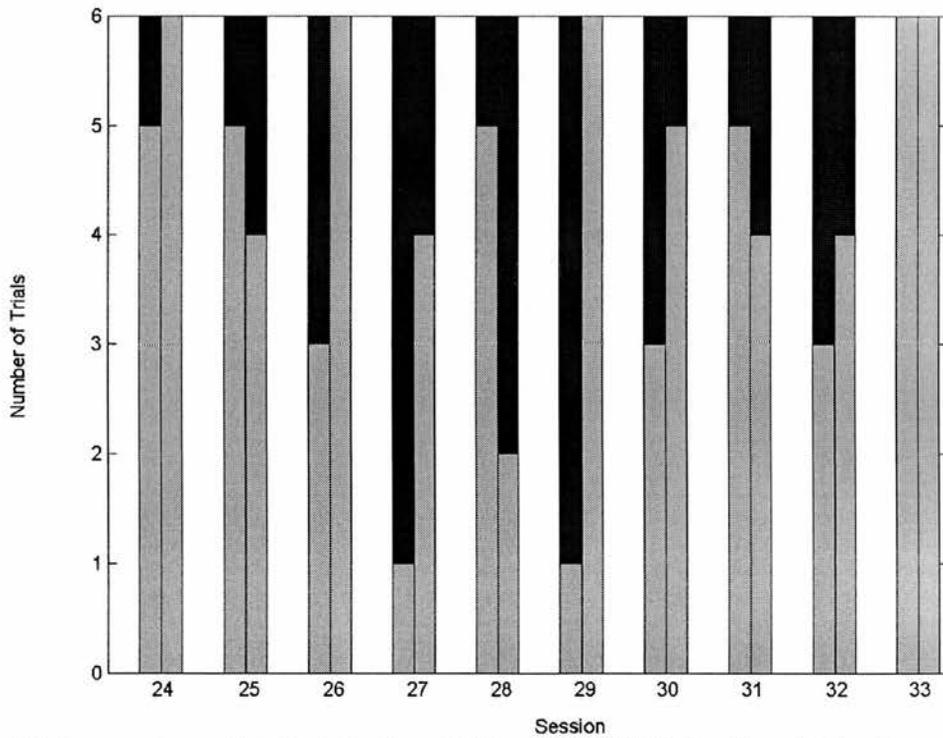


Figure 4.9: Responses to novel playbacks by Oscar: 14 May to 1 June 2002. See Figure 4.7 for a key to this figure.

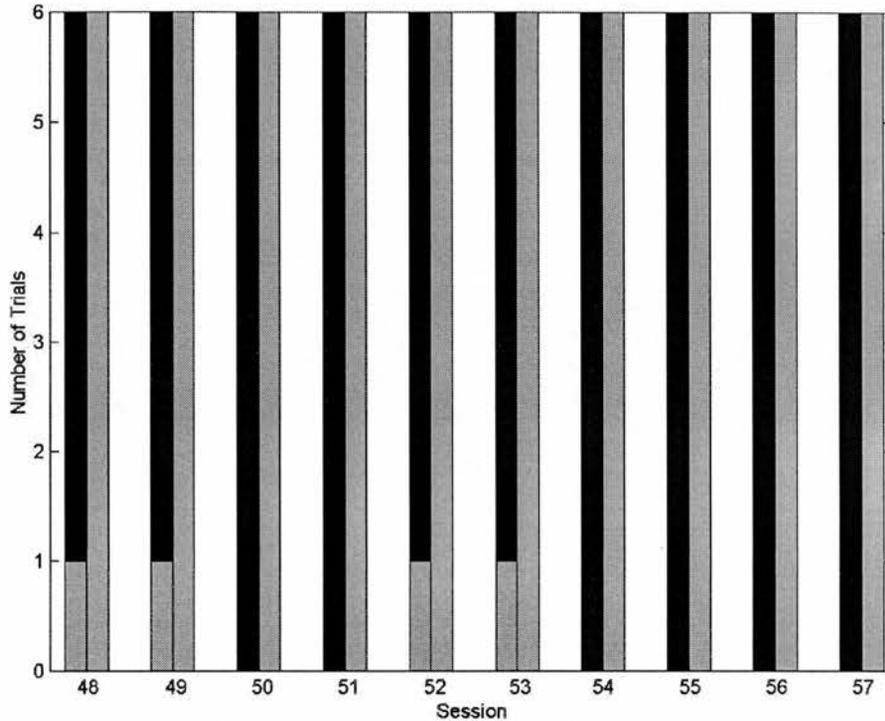


Figure 4.10: Responses to novel playbacks by Kylie: 19 June to 1 July 2002. See Figure 4.7 for a description of this figure.

In the last ten sessions Oscar performed significantly above chance in response to the training moan and growl playbacks combined (Figure 4.7: $\chi^2 = 275.4$, $N = 358$, $df = 1$, $p < 0.001$). Oscar responded to all novel playbacks in the first of these sessions significantly better than if he were moaning or growling randomly (Figure 4.9: $\chi^2 = 8.33$, $N = 12$, $df = 1$, $p < 0.01$). However, although his success in this and the last sessions was strikingly high, his performance oscillated over the interim. Kylie similarly responded during the novel playback sessions to the training stimuli at above chance levels for the moans and growls together (Figure 4.8: $\chi^2 = 288.0$, $N = 360$, $df = 1$, $p < 0.001$). She growled in response to the majority of the novel stimuli (Figure 4.10: 56 of 60 novel moan playbacks and 60 of 60 novel growl playbacks). Kylie's responses to the novel playbacks in the first of these ten sessions did not differ from random (Figure 4.10: $\chi^2 = 0.33$, $N = 12$, $df = 1$, $p = 0.57$). Because Oscar and Kylie were rewarded for responding correctly to novel stimuli, it would be misleading to compare their performance across all ten sessions to that expected if they were moaning and

growling randomly. Possible training and learning effects may therefore have influenced their ability to discern between these new playbacks over time.

Discussion

Two captive grey seal pups were trained in Experiment 1 to vocalise only when presented with a light and to remain silent and move in the direction of a glove point to laterally-positioned target objects. All categories of vocalisation were rewarded in response to the light in this first part of the experiment since the primary objective was to control the timing and context of vocal production in these animals. The vocal behaviour of the two seals was thus under operant control since it could be managed by a stimulus and released according to a schedule of differential reinforcement (Ginsburg 1960). These grey seals demonstrated usage learning because this training procedure required them to produce vocal signals already within their repertoire in a novel context (Janik & Slater 2000). The animals were operating in a cross-modal sensory paradigm, using visual stimuli to determine their appropriate locomotive or acoustic responses. They had achieved the first two stages of usage learning, namely vocalising on command and differentially responding to discrete stimuli by either vocalising or remaining silent.

Once these grey seals were responding successfully to a single visual cue, different signals were introduced to determine the sophistication of their ability to control their vocal production. In this second phase of the training procedure the pups learned to respond to nine playbacks of their own moans and growls by producing vocalisations of the same type. It was found necessary to use playbacks of a single vocalisation category during the majority of the early training sessions until proficiency with this type was reached. The alternative vocalisation type was then reintroduced and appropriate responses were reinforced. The experimenter ultimately switched between moans and growls for a decreasing number of trials according to the success of the animals. The seals did not need to attend to the specific

playback stimuli during these initial sessions to respond correctly since only a single vocal category was being played and rewarded. Once the frequency of alternation between moans and growls increased, however, a new response strategy was required that involved listening to the stimulus before vocalising. This transition emerged rapidly, accounting for the abrupt shift observed from mediocre to nearly flawless performance.

Four possibilities may have accounted for Kylie requiring nearly twice as many sessions as Oscar before achieving similar success levels in performance. First, Oscar may have distinguished between the moan and growl playbacks using slightly more variable acoustic features that had been standardised in the stimuli played to Kylie. Duration is one example of such a feature that was highly variable in Oscar's playbacks but more conserved in Kylie's (Table 5.1). This does not deny the possibility of contextual learning, but rather shifts the context to which Oscar was attending away from a categorical domain and into an alternative acoustic domain. If this interpretation is correct, it would have afforded him the ability to distinguish between moans and growls earlier in the training procedure.

Another explanation for the lag in Kylie's performance may have been that she received a reduced number of trials per day on average since she was involved in additional experiments. Her motivation may have abated after feeding in a different context, producing the lack of responsiveness occasionally observed. Thirdly, Kylie produced numerous moan and growl intermediates that were difficult to classify, leading to a slightly unsystematic set of rewarding criteria. The ambiguity of both Kylie's vocal responses and the experimenter's willingness to reward might have contributed to the longer time period Kylie needed to learn to distinguish moans from growls. Finally, individual variation in perceiving, learning and attending to the experimental tasks may have led to the difference in performance between the two seals.

Once the novel playbacks had been introduced, both animals continued to respond correctly to the moans and growls used as the original playback stimuli with only minor

fluctuations in performance. Oscar's reactions to the novel stimuli were highly variable. Figure 4.9 does not resemble a learning curve or reflect an immediate ability to assign these new playbacks to the appropriate vocal category. His initial success should be evaluated cautiously since it broke down dramatically in subsequent sessions, which suggests that his performance might have been due either to chance or an unknown training effect. Oscar's body posture suggested that moaning required more energy than growling since, in addition to simply vocalising, he often rotated to one side and moved his front flipper against the gate in both experimental and non-experimental contexts. He could have primarily growled in response to the novel playbacks on days when he was not as motivated to pay attention since it seemed to require less of an energetic investment. But he continued to respond successfully to the training stimuli (Figure 4.7), which would not be expected since motivation would have influenced his overall performance. Judging from Oscar's rapid learning of the nine training stimuli, it may be that he had been trained within only ten sessions to respond appropriately to the novel playbacks, accounting for his perfect performance in the final session (Figure 4.9).

The results presented in Figure 4.10 show that Kylie growled in response to most of the novel stimuli (116 out of 120). This is in direct contrast to her nearly flawless performance during the trained moan and growl playback trials of the final ten sessions (Figure 4.8). The selection of growls as a default response to novel stimuli may have stemmed from a motivational bias since Kylie seemed to use more energy to produce the loud and intense moans than the soft growls. The longer period of time required to train Kylie initially may also explain this discrepancy. She often responded to all playbacks in these early sessions by either only moaning or only growling until she learned to distinguish between the individual stimuli. The ten sessions with the novel stimuli may reveal an identical pattern, representing the early phase in a longer period of being able to discern between them. Finally, the novel playbacks used for Oscar might have been unintentionally

more similar to his original stimuli than those played for Kylie, explaining his more rapid progress in producing the appropriate vocal response.

The stimuli and responses in Experiment 2 were both acoustic, indicating that with training these grey seals were able to listen to the specific playback of nine sounds that they had produced, broadly assign them to one of two groups and respond with a vocalisation from the same vocal category. This behaviour did not result from an automatic physiological response to mimic the playback category for two reasons. First, 23 and 47 days were required to train Oscar and Kylie, respectively, to distinguish between and respond correctly to moans and growls, too long a period of time to infer automatic mimicry. Secondly, their performance in response to the novel playbacks remained unstable with a general inclination for Oscar and an overwhelming tendency for Kylie to produce growls when the playback stimulus was unfamiliar. These pups had been trained to respond specifically to the nine original stimuli by either moaning or growling but they both failed to generalise this response when novel playbacks of the same two vocal categories were introduced. These results strengthen the argument for contextual learning in the vocal domain because Oscar and Kylie learned to produce elements of their vocal repertoire in particular playback contexts due to experience with the training procedure. This demonstrated the third, more sophisticated level of usage learning.

The majority of the moans and growls used to train Oscar and Kylie were opportunistically recorded when the animals were interacting vocally in non-experimental contexts. Moans were often produced continuously by Oscar and Kylie, as they brushed a flipper against the gate when they were hungry before the first feeding session of the day, or when they unsuccessfully attempted to move into a different area of the facility. Seals whose movements brought them into close proximity with Oscar and Kylie often provoked antagonistic and aggressive interactions, causing them to growl. Both moans and growls therefore seemed to have been released in contexts associated with particular physiological

states and social interactions. The training results demonstrated that these same moans and growls could be evoked in a very different non-social, purely acoustic context. The vocal responses to the playbacks were divorced from the circumstances that typically generated them, revealing a striking ability of these two pups to learn novel contexts in which elements of their vocal repertoire were to be deployed.

The novel playbacks were recordings of responses to the original moan and growl stimuli made in the days just before the final ten sessions commenced (the preceding 3 and 11 days for Oscar and Kylie, respectively). Interestingly, although they had correctly produced these moans or growls in response to the original playback stimuli, they were largely unable to reassign these same responses to the identical categories when they heard them played as the novel signals days later. Further research is required to address whether a continued or altered training programme might facilitate a bridging of this striking disconnect between production and perception.

The neural circuitry exploited by these grey seals to distinguish calls is unknown, but a higher level cognitive mechanism that represents specific elements (such as particular vocalisations) as units distributed among discrete categorical groupings is consistent with other findings in pinnipeds. California sea lions have demonstrated an ability to form equivalence and functional classes, successfully clustering groups of symbols into one of two categories (Schusterman & Kastak 1993, 1998; Kastak et al. 2001). Schusterman et al. (2000) claimed that equivalence may help these sea lions classify conspecifics as friends or foes and heterospecifics as non-threatening or predators. The responses of the grey seal pups to the playbacks in this study by either moaning or growling suggests a similar process may have facilitated their separating of these stimuli into two discrete categories. Schusterman & Kastak (1998) provided evidence that equivalence might have emerged in their sea lions during training in conditional discrimination tasks functionally similar to those presented here. Experiments are therefore needed to determine whether grey seals are also capable of

representing equivalence and functional classes.

Grey seals possess a communication system whose development can be influenced by contextual learning in the vocal domain. While these animals would obviously not receive food in the wild for vocalising appropriately, some form of conspecific social compensation might reinforce the production of certain vocalisations in specific situations. This possibility is supported by the evidence that most vocal activity observed in grey seals seems to occur during social interactions (see Introduction). Since the underwater vocal activity of most pinnipeds has not been thoroughly investigated, it remains questionable whether they use contextual learning in the vocal domain in the wild and whether it at all parallels the learning and vocal development described in some species of birds, primates and cetaceans (e.g. West & King 1988; Seyfarth & Cheney 1986; Zuberbühler 2000; Richards et al. 1984).

The area of pinniped acoustics would benefit greatly both from longitudinal examinations of the natural vocal development of these animals to determine how their repertoire emerges and from studies exploring how they use their vocalisations in the wild. The evidence for contextual learning in the grey seal presented here suggests the possibility of a more elaborate usage and deployment of the vocal repertoire than previously thought. Future work might focus on which features grey seals use to distinguish between original moan and growl playbacks as used in this study. Additional inquiry into the extent to which subadult and adult pinnipeds are capable of similar tasks would reveal whether vocal contextual learning is possible at any age or is restricted to a particular phase of development. Nevertheless, this study demonstrates that grey seal pups were capable of contextual usage learning in which they flexibly paired vocalisations already within their repertoire with novel contexts.

Chapter 5

Production learning in the vocal domain in grey seals

Abstract

A male grey seal pup was rewarded for producing moans with a fundamental frequency below 250 Hz compared to those ranging between roughly 225 and 600 Hz before training. A comparison of his vocalisations before and after the training procedure revealed a significant shift in the production of moans to those that were both lower and longer. All measured features of the fundamental frequency were significantly lower once the training was completed including the initial, final, maximum, minimum and average frequencies. Since this study is only the first stage in the possible experimental demonstration of the presence of vocal learning in a pinniped species, future research projects are discussed that would build on the findings presented here.

Introduction

Production learning occurs when an animal modifies its own signals because of experiences with those of other individuals (Janik & Slater 1997, 2000). Vocal learning is a specific type of production learning in which the respiratory, phonatory or filter systems make the vocalisations themselves more or less similar to an acoustic model (see Chapter 1 for an extensive literature review on this topic). As a polyphyletic trait, vocal learning appears in human beings and some passerine, parrot, hummingbird, bat and cetacean species (surveys in Nottebohm 1972; Baylis 1982; Janik & Slater 1997). This sporadic phylogenetic appearance has generated numerous hypotheses about the functional significance of vocal learning including territorial defence, pair bond maintenance, mate attraction, habitat matching, rapid speciation, individual, group and kin recognition, and the notion that it may result from a “cultural trap” (Harcus 1977; Baylis 1982; Janik & Slater 1997; Slater et al. 2000). Although the origins of vocal learning remain difficult to ascertain, its consequences in the social arena are dramatic. The ability to mimic or eschew the acoustic features of one’s physical and social environment may allow an individual to address a conspecific through imitation, narrate its experiences acoustically by imitating salient elements from its daily or migratory journeys and label physical objects or conspecifics with unique vocalisations.

Demonstrating vocal learning is challenging since ideally an animal must show that it is able to imitate accurately acoustic signals not already present within its repertoire (Janik & Slater 2000). Close observations of vocal ontogeny and how it is influenced by social interactions in the wild (e.g. marsh warbler (*Acrocephalus palustris*): Dowsett-Lemaire 1979; greater horseshoe bat (*Rhinolophus ferrumequinum*): Jones & Ransome 1993) and under controlled conditions (e.g. indigo buntings (*Passerina cyanea*): Payne 1981; killer whales (*Orcinus orca*): Bowles et al. 1988; lesser spear-nosed bats (*Phyllostomus discolor*): Esser & Schmidt 1989) have often provided a reliable indication of whether vocal learning is present.

Other studies have experimentally examined vocal convergence in which either the vocal repertoire of an individual comes to match that of the group into which it has been introduced (e.g. greater spear-nosed bats (*Phyllostomus hastatus*): Boughman 1998; budgerigars (*Melopsittacus undulatus*): Bartlett & Slater 1999) or the vocalisations of the members of a newly formed group coalesce in acoustic space (e.g. budgerigars: Farabaugh et al. 1994; greater spear-nosed bats: Boughman 1998; chimpanzees (*Pan troglodytes*): Marshall et al. 1999). While vocal learning is often suggested as the most likely explanation for the performance of the subjects in these studies, it is possible that their vocal repertoire is largely inherited.

The most conclusive evidence for vocal learning has emerged when animals mimic an acoustic model previously absent from their vocal repertoire. Starlings (*Sturnus vulgaris*) are among the most striking vocal mimics, capable of imitating sounds that they had heard, most often produced in interactive contexts, including human speech, other animal vocalisations and some mechanical noises (West & Stroud 1983; West & King 1990). African grey parrots (*Psittacus erithacus*) have not only mimicked human speech but have also learned to vocalise nouns, colour and shape adjectives and to use the word “no” in functionally correct situations (Todt 1975; Pepperberg 1981). These parrots therefore seem capable of exploiting their vocal imitation abilities to assign vocal labels to entities and features within their environment. These results are indicative of the widespread incidence and flexibility of avian vocal learning.

Many marine mammals have demonstrated striking vocal learning capabilities, which may have been shaped over time by their unique species-specific social dynamics (Tyack & Sayigh 1997). The vocal convergence of humpback whale (*Megaptera novaeangliae*) song, for example, in which all males within a population incorporate, modify and eliminate elements synchronously, is likely to be a result of vocal learning operating well through

adulthood (Payne et al. 1984). A captive killer whale calf produced some of the calls within her mother's vocal repertoire by one year of age (Bowles et al. 1988) and a captive six-year-old female imitated artificial frequency-modulated tones that were used for particular objects when they were introduced into her pool (van Heel et al. 1982). These studies suggest that vocal learning may maintain the group-specific vocal repertoire of the stereotyped calls that are produced by some populations of killer whales (Ford 1989).

Vocal learning has been rigorously studied in bottlenose dolphins (*Tursiops truncatus*, hereafter referred to as dolphins). Richards et al. (1984) trained a captive dolphin to imitate computer-generated model sounds by successively rewarding: (1) any whistle in response to an acoustic signal (of 4 kHz and 0.25 s in duration); (2) whistles of roughly the same duration as model sounds introduced after this acoustic signal; (3) whistles approximating the fundamental frequency and harmonic structure of these model sounds. The experimenters gradually shaped the dolphin's vocal responses, causing the animal to imitate sine, square and triangle waves and constant-frequency tones successfully.

These findings have been replicated in part by Sigurdson (1993) who trained two dolphins to mimic down-ramp, up-ramp and U-shaped whistle models both when the same model sound was played in a series and when these stimuli were alternated. Spontaneous mimicry of a trainer's whistle (Caldwell & Caldwell 1972) and computer-generated whistles associated with particular objects and activities (Reiss & McCowan 1993) have been documented as well. These vocal mimicry and labelling abilities may be important in the ontogeny of individually-distinctive signature whistles (Sayigh et al. 1995), the use of these signature whistles to label and recognise conspecifics (Tyack 1986; Sayigh et al. 1999) and in matched whistle interactions that may have resulted from animals addressing one another (Janik 2000).

The evidence for vocal learning in pinnipeds is confined to a single promising study

in which two adult male harbour seals (*Phoca vitulina*) were found to mimic a few English phrases coarsely without the precise control over frequency modulation and sound separation (Ralls et al. 1985). The flexibility and scope of this imitative ability were not examined experimentally, but the results strongly support the hypothesis that vocal learning was responsible. Because vocal learning creates and regulates aspects of the social and vocal behaviour of the species described above, its demonstration in pinnipeds would suggest it has strongly influenced their natural history as well. The acoustic recognition of individually-distinctive pup calls by grey seal (*Halichoerus grypus*) mothers remains ambiguous (McCulloch et al. 1999; McCulloch & Boness 2000), but is precisely the kind of phenomenon that would be generated and facilitated by vocal learning. This study investigated whether vocal learning is present in grey seals, a phocid that vocalises in air and under water during all stages of development (e.g. Schneider 1974; Asselin et al. 1993; Caudron et al. 1998; McCulloch 1999), by attempting to train a male pup to produce moans with lower fundamental frequencies than before.

Materials and Methods

Subject and training.

Oscar, a male grey seal pup, participated in the vocal learning training from 2 June until 28 July 2002. The training set-up for this experiment was nearly identical to that presented in Experiment 2 of Chapter 4 (Figures 4.6 and 5.1).

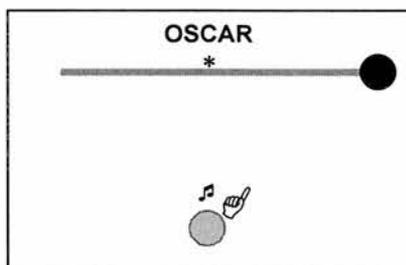


Figure 5.1: Aerial view of training procedure. Oscar stationed behind the gate (grey line) on the Tupperware container (*) at the beginning of each trial. Moans were elicited through playbacks (♫) with the experimenter (⊙) infrequently directing Oscar to station on the right circle (●) by pointing, represented by the hand.

The experimenter stood centrally to administer playbacks, occasionally pointing to the stationing object if Oscar experienced difficulty with the training task. Originally, five low and five high moans (the acoustic parameters of which are described in more detail in Chapter 4) that Oscar had produced in previous sessions were used as playbacks and he was rewarded for lower and higher responses, respectively. This task proved to be too complicated for the amount of time remaining for this study. A new playback stimulus was therefore generated by taking one of Oscar’s moans and slowing it down to 137.5% of its original duration to produce a lower pitched signal. The spectrograms of the original and modified stimuli are provided in Figure 5.2 and their acoustic parameters are given in Table 5.1.

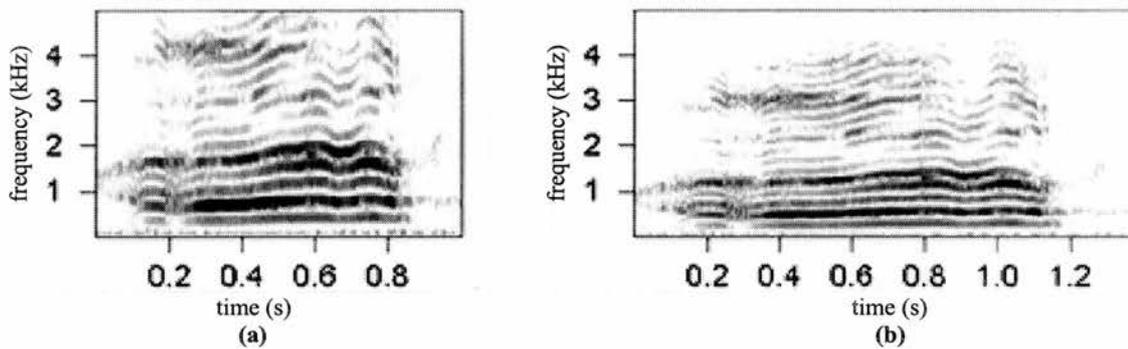


Figure 5.2: Spectrograms of original (a) and lowered (b) moans.
Table 5.1: Acoustic parameters of the high and low playback stimuli.

<i>Playback type</i>	Original	Low
<i>Duration (s)</i>	0.8	1.1
<i>Initial frequency of fundamental (Hz)</i>	256.9	171.3
<i>final frequency of fundamental (Hz)</i>	334.8	247.0
<i>average frequency of fundamental (Hz)</i>	345.9	248.0
<i>minimum frequency of fundamental (Hz)</i>	256.9	171.3
<i>maximum frequency of fundamental (Hz)</i>	422.0	299.7

Chapter 2 provides an inventory of the equipment used to record and monitor acoustically the sessions in real time. All sound energy below 2 kHz was displayed on a

computer screen for 35 s before refreshing. Early sessions consisted of solely playing this artificially lowered moan and rewarding for vocal responses whose average fundamental frequencies were below a cut-off frequency of 250 Hz. This value was chosen because it was closer to the average fundamental frequency of the lowered playback stimulus (Table 5.1) and was located in the lower region of Oscar's frequency range. Once Oscar began in general to produce moans with fundamental frequencies reliably below 250 Hz, which he did after seventeen training sessions, five testing sessions were conducted. In the first few trials of each of these sessions, the experimenter allowed Oscar to call in response to the playback until he produced a sufficiently low moan. In the final twelve trials, Oscar received a reward for his first response to the playback independent of its acoustic structure, to determine whether he was indeed producing reliably lower calls without specific reinforcement.

Analysis.

The last twelve moans of the five experimental sessions immediately preceding and just concluding the vocal learning training were analysed. This allowed a comparison between Oscar's vocal responses before and after specifically reinforcing lower pitched moans. Opportunistic recordings of moans produced in non-experimental contexts were made during the last five days of this study to determine whether Oscar's entire repertoire had experienced any uniform changes due to maturation or physiological development. Moans with additional background sounds (e.g. seagulls, the playback that had not elapsed completely) were excluded from analysis. Signal 3.1 was used to calculate the peak frequency and trace the fundamental frequency contours of each of these moans to determine their duration and beginning, ending, maximum, minimum and average frequency values. Tracing was possible until the fundamental frequency was lost in background noise both visually and by listening. Since parts of the fundamental frequencies of especially soft moans

were occasionally washed out, a straight line was drawn to connect the parts just before and after these sections. Time did not permit the tracing of the contours by a second experimenter who had remained unaware of whether they were generated from moans produced before or after the training protocol, though this would have been ideal. The Mann-Whitney U test was used to determine whether any significant differences existed between these parameters before and after the vocal learning training was conducted.

Results

Table 5.2 shows the acoustic features of nineteen of the highest moans recorded in non-experimental contexts at the time of the five testing sessions. Tables 5.3 and 5.4 provide data on moans recorded in experimental contexts before the training began for this study and on moans recorded from after this training had occurred, respectively.

Table 5.2: Acoustic parameters of high-pitched moans ($N = 19$) recorded in non-experimental contexts.

	Mean (\pm SD)	Maximum	Minimum
<i>duration (s)</i>	1.3 \pm 0.6	2.6	0.5
<i>initial frequency of fundamental (Hz)</i>	451.5 \pm 136.5	727.8	208.0
<i>final frequency of fundamental (Hz)</i>	451.4 \pm 111.0	708.9	324.2
<i>average frequency of fundamental (Hz)</i>	462.8 \pm 127.3	733.7	297.6
<i>minimum frequency of fundamental (Hz)</i>	387.2 \pm 134.0	685.0	159.0
<i>maximum frequency of fundamental (Hz)</i>	538.5 \pm 122.2	789.0	360.9

Table 5.3: Acoustic parameters of moans ($N = 59$) recorded in experimental context before the training of this experiment began.

	Mean (\pm SD)	Maximum	Minimum
<i>duration (s)</i>	0.3 \pm 0.1	0.5	0.1
<i>initial frequency of fundamental (Hz)</i>	370.1 \pm 75.7	587.2	177.4
<i>final frequency of fundamental (Hz)</i>	406.9 \pm 58.4	642.2	244.6
<i>average frequency of fundamental (Hz)</i>	402.1 \pm 55.8	610.4	231.6
<i>minimum frequency of fundamental (Hz)</i>	337.2 \pm 53.7	519.9	177.4
<i>maximum frequency of fundamental (Hz)</i>	452.2 \pm 57.2	666.7	250.8

Table 5.4: Acoustic parameters of growls ($N = 60$) after the vocal learning training had been completed.

	Mean (\pm SD)	Maximum	Minimum
<i>duration (s)</i>	1.1 \pm 0.4	2.6	0.3
<i>initial frequency of fundamental (Hz)</i>	335.9 \pm 80.1	550.5	177.4
<i>final frequency of fundamental (Hz)</i>	322.7 \pm 39.4	434.3	238.5
<i>average frequency of fundamental (Hz)</i>	321.3 \pm 38.0	422.1	230.4
<i>minimum frequency of fundamental (Hz)</i>	245.1 \pm 38.5	330.3	146.8
<i>maximum frequency of fundamental (Hz)</i>	421.9 \pm 76.6	685.0	287.5

All of the measured acoustic features experienced significant changes. The moans following the training were significantly longer in duration (Mann-Whitney test: $N_1 = 59$, $N_2 = 60$, $z = -9.123$, $p < 0.001$) and significantly lower in all of the frequency parameters of the fundamental frequency (initial: $N_1 = 59$, $N_2 = 60$, $z = 2.433$, $p < 0.001$; final: $N_1 = 59$, $N_2 = 60$, $z = 7.587$, $p < 0.001$; maximum: $N_1 = 59$, $N_2 = 60$, $z = 2.933$, $p < 0.001$; minimum: $N_1 = 59$, $N_2 = 60$, $z = 8.181$, $p < 0.001$; average: $N_1 = 59$, $N_2 = 60$, $z = 7.502$, $p < 0.001$). Figure 5.3 summarises the duration and average fundamental frequency data. It reveals that while the moans produced after the training were nearly all longer compared to those before, the change in the frequency distribution of the responses seems to represent a change towards producing moans in the pre-existing lower region of his frequency range (i.e. primarily below 400 Hz).

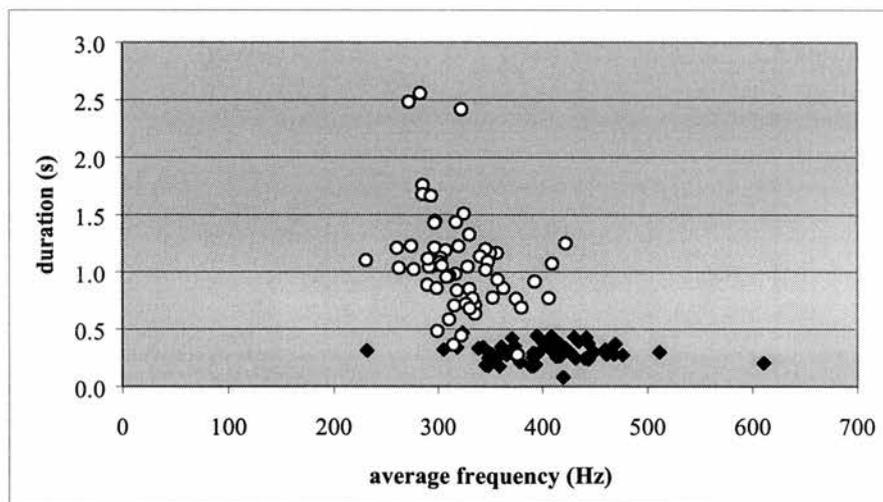


Figure 5.3: Average frequency vs. duration plot. The black diamonds represent moans produced before training and the white circles those moans produced after training.

Discussion

This study represented the first attempt to train a pinniped to control the acoustic features of its vocalisations and offers encouraging results that merit future work to investigate vocal learning in the grey seal. After being rewarded for moans in the lower region of his frequency range, Oscar produced significantly longer and lower moans in the training context when they were not specifically reinforced. The initial, final, maximum, minimum and average frequencies of the fundamental frequency of his responses were all significantly lower than before this training procedure began. Although these changes were consistent with the acoustic structure of the playback, mimicry was likely not responsible for his success because the frequency parameters of his responses were not rewarded for their similarity to the stimulus.

Since duration was not considered among the criteria necessary for correct performance, his lengthened moans may have been an artefact of the training or the result of an inverse physiological correlation between the duration and pitch of vocal production. Because Oscar was capable of producing higher-pitched moans of equal or longer duration than some of his lower-pitched moans (Table 5.2), the former hypothesis seems more probable. Depending on the complexity of the training task, an animal may pair the correct behaviour actually receiving the reward with other unnecessary responses that are performed simultaneously. Generally these irrelevant actions are lost as the animal determines the precise task that is required.

Maturation and developmental changes often alter the vocal apparatus, the filtering structures and resonance cavities of an organism, and these changes can have a dramatic influence on vocal production (see Janik & Slater 2000). These did not seem to contribute to the changes observed in Oscar's responses as the training progressed since he retained his ability to produce both higher and shorter moans (Table 5.2). This implies that Oscar may

have possessed the vocal control required to lower the pitch of his vocal responses. If production learning in the vocal domain was indeed responsible for Oscar's success in this study, he demonstrated control over his phonatory (i.e. larynx) and respiratory systems to account for the alterations in pitch and duration respectively (Janik & Slater 2000).

This experiment, however, unfortunately lacks the appropriate control of another individual exposed to the same rearing conditions as Oscar but who was not trained and rewarded to produce lower-pitched moans. Such a control would have offered a helpful means of comparison to determine whether the changes observed in vocal output and range occur independently of the training. It may be, for example, that developmental changes imposed a physical posture upon the animal at the training station that rendered the production of higher-pitched vocalisations more difficult. Physical effects at the acoustic source, possibly involving a maturing larynx or a directional trend in changing pulmonary pressure, could also be responsible for the vocal patterns presented above. Since a directional shift in vocal production (i.e., towards moans with lower frequencies) was sufficient for correct performance and more exacting control over the frequency range was not required, learning may not be the most appropriate explanation for these observations. It is possible, for instance, that Oscar may have simply habituated to the task of producing lower moans without learning why he was being rewarded or understanding more generally his ability to produce sounds of different pitches.

While this study has not conclusively demonstrated vocal learning in the grey seal, it suggests that, with additional training, Oscar might have been able to modify other acoustic elements of his vocalisations. Further research is required to probe more completely the extent of this vocal flexibility in the grey seal. A next step is to train grey seal subjects to produce sounds above and below a particular frequency threshold in response to discrete stimuli. The subsequent introduction of a random sequence of these stimuli would reveal

whether the animals were capable of controlling and moving within their frequency range to produce moans. Similar training procedures could be used to assess their control over other acoustic parameters such as duration, amplitude and the relative energy distributed among different harmonic frequencies.

Successively reinforcing better imitations of an artificially modified call from the grey seal vocal repertoire or a novel computer-generated sound would provide the most convincing evidence for vocal learning. Animals broadly mimicking playback stimuli would offer insight into the control they possess over their vocal apparatus. Stimuli might include sounds that are frequency-modulated, adjusted for increased or decreased amplitude or duration, have unique distributions of spectral energy or some combination of these parameters.

Richards et al. (1984) successfully conducted a similar study on bottlenose dolphins by rewarding increasingly improved attempts of an animal to imitate artificial whistles. The grey seal vocal repertoire would make this task slightly more difficult because they often produce broadband and atonal noises. It would first be necessary to reinforce the production of purely tonal vocalisations to investigate these issues properly. If vocal learning does prove to be present in the grey seal, investigation of its relevance in the wild in interactions with conspecifics and the environment will be of particular interest.

This study confirms that grey seals are capable of producing moans of longer duration and lower pitch, but leaves unanswered the question of whether they can actually perceive these acoustic differences. It provides preliminary evidence that these animals may be capable of vocal learning. Their performance suggests a scenario in which individuals may attend to one another as acoustic models to learn their appropriate species-specific vocal repertoire or be capable of fine scale recognition of individuals according to unique features of their vocalisations. Indeed, this last hypothesis is supported by data demonstrating that

some female grey seals responded preferentially (via head and body movements) to the calls of their own pups (McCulloch & Boness 2000, but see McCulloch et al. 1999), an acoustic recognition task that would be facilitated by vocal learning. Territorial defence has been offered as the possible origin of vocal learning in other species (Harcus 1977; Baylis 1982). Grey seal bulls who have been hauled out for longer amounts of time on the breeding ground in areas of high female density have been found to experience elevated mating success (Boness & James 1979; Twiss et al. 1994). Vocal learning could play a role in helping to maintain territory during the reproductive season in the form of antagonistic mimicry of other territory holders.

If grey seals are indeed capable of production learning in the vocal domain, it increases the complexity of their social and behavioural landscape. It would also require a reconsideration or expansion of the current hypotheses that entertain the possible evolutionary pressures which selected for vocal learning originally. The grey seal may therefore provide the next taxonomic glimpse into understanding the evolutionary, behavioural and vocal mechanisms which have produced one of the most complicated phenomena in animal communication.

Chapter 6

Conclusion

A few concluding points

All three pups learned rapidly to respond to experimenter-given pointing signals to laterally-placed shapes, suggesting that young grey seals (*Halichoerus grypus*) could control the timing and direction of their movements. Nora spontaneously and correctly reacted to upper body turns and central and off-centre ipsilateral and contralateral pointing and pointing and head turning gestures, movements that involved the rotation or reorientation of a conspicuous region of the body of the experimenter. In the trials in which the head or eyes were moved alone, Nora most often selected the right square, the shape nearest the gloved hand that dispensed her fish rewards. Nora performed better than chimpanzees (*Pan troglodytes*) in the off-centre pointing trials but worse in the head turning and gazing alone trials (Povinelli et al. 1997). She failed to move towards a centrally-located cube behind her in all but one trial, a task on which a bottlenose dolphin (*Tursiops truncatus*) had been trained successfully (Herman et al. 1999). As discussed at length in Chapter 3, Nora likely did not possess a referential comprehension of these pointing and directional gestures. Rather, her results indicated that she was merely discriminating between conspicuous movements of the experimenter to move left or right.

Previous research efforts have tended to exaggerate the implications that successful results have for the cognitive abilities of their subjects. More studies are required that use experiments similar to those presented here and elsewhere (e.g. Herman et al. 1999) to investigate more thoroughly whether animals truly understand the referential properties of pointing and other directional cues. The findings in Chapter 3 would benefit from further

research into whether grey seals or other animals that have been trained to use pointing gestures towards centrally- and laterally-located objects might then generalise their reaction when a novel pointing direction is introduced. Other studies that replicate the design of Povinelli et al. (1990) would further reveal whether grey seals, like chimpanzees, can discriminate between the gestures of two pointers, one of which possesses correct information about the location of a reward. Nora showed a basic ability to respond appropriately to pointing gestures but additional experimental work would help elucidate more precisely the mechanisms responsible for her success and failure.

Choral virtuosity

The vocalisation studies required Oscar and Kylie to display increasing control over their vocal apparatus. They were quickly trained to vocalise when presented with a bike light and to remain silent in response to other hand signals. This initial result demonstrated both that pups could regulate the timing of their vocal activity and that they could produce moans, growls and snorts of varying duration and frequency structure in response to a specific visual stimulus. Subsequently both animals successfully responded to training in which they matched the vocalisation category of nine specific moan and growl playbacks. Taken alone, these data would have suggested a superb ability of these animals to match moans and growls in kind. They failed to generalise this response, however, when exposed to novel moan and growl stimuli, with Oscar performing erratically and Kylie growling during the majority of these trials. This second phase of the experimental procedure revealed that both pups had been able to learn to listen to a set of nine specific stimuli, assign each to one of two categories and respond by producing a matching vocalisation type.

These studies illustrated that the two grey seals were capable of contextual and, more specifically, usage learning in the vocal domain, connecting particular situations with the

release of specific vocalisations already present within their repertoire. The possible benefits of these abilities in the wild are discussed in Chapter 4. Future research might focus on whether grey seals can be trained to associate different vocalisation categories with various objects, similar to the vocal labelling work of Richards et al. (1984) in which cross-modal contextual learning was exploited to use unique acoustic signals as labels for different objects. It is not clear which features of the original nine playbacks Oscar and Kylie used to distinguish moans from growls. A study examining how the animals responded to these same stimuli with slightly modified temporal and frequency parameters would offer insight into this issue. Further experiments could be conducted in a pool to investigate whether the control a grey seal has over its in-air vocalisations similarly exists for its underwater repertoire.

Chapter 5 presents the initial results of a study on vocal learning in the grey seal. Oscar was rewarded for producing moans with a fundamental frequency below 250 Hz in response to one of his recorded moans that had been artificially lengthened and lowered. Compared to the moans taken from his final sessions in the contextual learning experiment, the moans at the end of this vocal learning training procedure were significantly lower and longer, features that resembled the playback stimulus more closely. More time would have been needed to ascertain whether a higher pitched playback could be used to train Oscar to generate higher moans and whether he could differentially produce low and high moans in response to lower and higher stimuli, respectively.

This study is suggestive, but hardly conclusive about the degree of control Oscar has over his vocal production. The reduced variability in Oscar's moans by the end of the training indicates he was likely capable of manipulating the pitch of his vocalisations. Maturation and physiological development were not sources of his tendency to moan with lower pitch and longer duration. At the same time as the final stages of the training were

taking place, Oscar was still producing higher pitched vocalisations in non-experimental contexts. No effort was made in these experiments to reinforce the imitation of artificial, frequency-modulated computer-generated vocalisations based on actual calls that he had produced. A study examining whether grey seals possess such an ability to mimic accurately novel sounds not already present within the repertoire would determine whether they are capable of vocal learning, a likely possibility considering the decisive findings of Chapter 4 and the preliminary data of Chapter 5.

Training, conditioning and learning

While the training for this thesis had to be conducted nearly every day, the pups were very amenable to the procedures and generally responded rapidly and successfully to each new protocol that was introduced. Correct locomotive and vocal performance was contingent on attending to the visual signals presented by the experimenter or the playback stimuli and responding appropriately. All of the findings presented here can be explained as a result of conditioning. Overall the pups displayed no sudden or spontaneous flashes of insight into the training procedures and failed to generalise how they should respond when slight variations on familiar commands were introduced. Although Nora did react correctly to the trials in which upper body turns and ipsilateral and contralateral off-centre pointing were first introduced, she erred nearly every time the pointing arm was directed towards the central cube behind her. Oscar and Kylie did not match the novel moan and growl playbacks with vocalisations of the same type. While these animals did learn to perform correctly with a sufficient number of training sessions, their success was based on associating specific stimuli with particular responses rather than developing a general understanding of the broader task required.

The success of these experiments begs the question of which selective pressures arise in the early months of grey seal development to facilitate using the gestures of an experimenter to alter their direction of movement and to produce elements from the vocal repertoire in novel contexts. Grey seal mortality is especially high in their first year of life (Coulson & Hickling 1964), placing a premium on adapting behaviour to survive under highly variable environmental conditions. Indeed, while the tasks required for the training procedures presented here may have been modest compared with the challenges presented by their natural habitat, learning is essential in both scenarios. Conducting similar experiments on juvenile and adult grey seals would indicate whether learning in the locomotive and vocal realms remains possible or diminishes with age.

Chapter 3 discusses potential circumstances in the wild where attending to the physical movements of other entities in the environment might provide information on the presence of food, a haul-out site, or other conspecifics. It is possible, however, that, just as Nora might pursue a moving fish by swimming in the same direction, she oriented in parallel to a moving glove or region of the experimenter's body in the pointing study. The performance of Oscar and Kylie suggests a specific flexibility in the vocal domain to learn unique contexts in which different elements and features of their vocal repertoire should be produced and emphasised. The adaptive role that contextual, and potentially production, learning in the vocal domain serves in the wild will become clearer only when a more thorough understanding of the natural social and vocal development of these animals emerges. One exciting possibility is that grey seals might be capable of addressing and responding to particular individuals by broadly matching the vocal category and features of calls produced by conspecifics. Such a phenomenon has been offered as an explanation of the vocal behaviour observed in bottlenose dolphins (Tyack 1986; Janik 2000) and resident killer whales (*Orcinus orca*; Miller et al. in press).

Ultimately the results described in this thesis represent a glimpse into the possible influence learning can have on the actions and vocalisations of the grey seal. The behavioural complexity suggested by these findings compels parallel studies to be conducted in other mammalian species, helping to elucidate how contextual and production learning became an adaptive response to evolutionary pressure and biological necessity.

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