

MUSIC PREFERENCE AND DISCRIMINATION IN
THREE SUMATRAN ORANGUTANS (*PONGO ABELII*)

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ABSTRACT

This investigation assessed musical preference and discriminative ability in three Sumatran orangutans. In Study 1, preferences for music vs. silence were examined in three phases. In Phase I, subjects made choices via touchscreen to replay a previously sounded music exemplar or listen to silence instead. In Phase II, subjects could “shuffle” between music exemplars and/or silence exemplars through touchscreen contact. In Phase III, subjects could produce musical notes by touching the keys on a virtual piano. In Study 2, subjects’ ability to discriminate ‘music’ from ‘scrambled music’ was tested using a touchscreen-delivered delayed matching-to-sample task. Results indicate subjects preferred silence to music (or were indifferent) and that they could not discriminate ‘music’ from ‘scrambled music’, suggesting orangutans do not find music reinforcing and/or do not perceive music the way humans do. Consequently, the use of music as environmental enrichment in captive primate facilities appears unfounded and may be aversive rather than enriching.

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Introduction

The production and appreciation of art and its aesthetic correlates have long been considered uniquely human aptitudes, evidence of particularly complex cognitive abilities (Rogers & Kaplan, 2007). Because of the entrenched assumption among the scientific community that nonhuman animals do not share the ability to create and enjoy art, and the inherent difficulty of measuring the appreciation of art, very little is known about the characteristics of such abilities in animals (Rogers & Kaplan, 2007). Although evidence of nonhuman simulation of artistic activity has been documented (e.g. chimpanzees, bottlenose dolphins and Indian elephants that paint on canvases), an aesthetic capacity in non-human animals has yet to be scientifically established (Rogers & Kaplan, 2007). It has been argued that whereas human art is produced and consumed for pleasure, non-human animals do not appreciate art for its own sake, and instead, simulate artistic activity, motivated by positive reinforcement (e.g., food rewards and/or positive affect conveyed by human caregivers) (Dutton, 2008; Lenain, 1997; Peron, 2012; Rogers & Kaplan, 2007). Despite such phenomena as rhythmic responses in parrots percussively synchronized to musical recordings (Patel, Iversen, Bregman & Shulz, 2009), the appreciation of music for its aesthetic qualities has been understood as an exclusively human capacity (Lenain, 1997). Although music is recognized cross-culturally as gratifying to humans of all ages, and has been successfully utilized in this capacity therapeutically, these same qualities and effects have not been confirmed in nonhuman animals (Hayes, Buffum, Lanier, Rodahl & Sasso, 2003; Hinds et al., 2007). At present, music, defined by the Merriam-Webster Dictionary as “the science or art of ordering tones or sounds in succession, in combination, and in temporal relationships to produce a

composition having unity and continuity”, (Music, 2013) remains understood as a universal and uniquely human cultural capacity (Patel et al., 2009).

Despite the fact that music has played an important role in human beings’ private and social lives for at least 35,000 years, its purpose has yet to be fully understood, leading evolutionary biologists to question why it developed at all (Patel et al., 2009). Darwin (1901) considered the musical faculty as one of the most mysterious abilities humans exhibit. Currently, music’s evolutionary role in human development remains undetermined and actively debated in the scientific community (d’Errico et al., 2003; Schafer & Sedlmeier, 2010). Some argue that music lacks an adaptive function, and that music may have emerged accidentally without evolutionary benefit. For example, music may be an irrelevant derivative of other adaptive behaviours (i.e., the rhythm of natural body movements, the intonation and inflection of speech, and the ability of the human brain to decipher many sounds at once) (Masataka, 2009). Others argue that music’s universality, specifically exemplified by the musical abilities of human infants, indicates that music has been hardwired into the human brain as a result of the evolutionary purpose(s) that it serves (Conrad, Walsh, Allen & Tsang, 2011; Homae, Watanabe, Nakano & Taga, 2012; Masataka, 2009).

One proposed function of music is that it may have displayed biological fitness. If a human could afford to take time away from activities necessary for survival (i.e., hunting, gathering, conflict, etc.) to make or to listen to music, they had to be an unusually healthy, productive and thriving individual to do so (Schafer & Sedlmeier, 2010). If music production and appreciation were perceived this way, these qualities

would have become naturally selected for and consequently would have evolved to become more sophisticated (Schafer & Sedlmeier, 2010).

Another proposed function of music is that it served as a social catalyst and instrument of communication. Music may have facilitated the synchronization of group activities, emotions and physiological arousal, the development and strengthening of social bonds, and the transport and dissemination of information (Schafer & Sedlmeier, 2010). Examples of music functioning in these ways in present-day human life can be seen in the biopsychosocial effects of national anthems, war songs, lullabies, campfire songs, and love songs. Musical sound between human mothers and infants has been scientifically documented as a critical factor in parent-child bonding and can quantitatively affect infant arousal (Falk 2004a; Falk 2004b; Shenfield, Trehub, & Nakata, 2003; Trehub, 2003). Chills, a form of physiological arousal that can be evoked through music, are believed to be a special physio-emotional response that guides behaviour (e.g. reunion behaviour) and affects social bonding (Bicknell, 2007; Panksepp, 1995; Panksepp & Bernatzky, 2002). Panksepp and Bernatzky (2002) suggest that for social, arboreal creatures, such as our ancestors, sound was an effective means of communicating and that there may have been a categorical benefit in being able to communicate emotion through the prosody (rhythmic, melodic quality) of vocalizations.

Interestingly, language, another human universal, and arguably a similar faculty, is widely agreed to have developed by means of natural selection; more precise and more detailed communication is assumed to have facilitated human survival and reproduction. In the same vein, Darwin (1901) proposed that music's evolutionary role is associated with language (Masataka, 2009). He hypothesized that music and language share an

evolutionary history, pointing to the fact that both music and language involve phrase structure, and necessitate learning and cultural transmission (Darwin, 1901; Masataka, 2009; Patel et al., 2009). Darwin proposed a theory of language development, described by some as the musilanguage model of music development, that involved a pre-linguistic stage in human evolutionary history in which communication was achieved via a prosodic protolanguage, more comparable to music than present-day language (Botha, 2009; Patel et al., 2009; Wallin, Merker, & Brown, 1999). Prosody refers to a means of acoustic expression conveyed through intonation, loudness, and tempo (e.g. poetry and rap music rely heavily on prosody) (Mitchell, Elliott, Barry, Cruttenden & Woodruff, 2003). Darwin (1901) believed this prosodic pre-linguistic system would have functioned as a precursor to both modern language and music (Patel et al., 2009; Wallin et al., 1999).

If music and language share an evolutionary history, it follows that musical capacity may be related to language capacity. At the very least, advancement of a theory of the evolution of music may have implications for the evolution of language, and vice versa. Ongoing cognitive research indicates that human and nonhuman primates (NHPs) share certain substructures of language and music, while other substrates appear to be exclusively human (Masataka, 2009). Nonetheless, although innate musical predispositions have been found in human infants (Masataka, 2007; Trehub, 2001; Zentner & Eerola, 2010), whether the same can be said of NHPs remains to be discovered (Masataka, 2009). Thus, as a means of determining which components of musical facility were present in the common ancestor of extant human and NHPs, examination of cognitive musical capacities in NHPs is of primary importance.

Research to date

Despite the need for research in this area, musical ability in NHPs remains relatively unexamined. Preliminary study of nonhuman primate music preferences (defined as a more frequent choice of one alternative over others) indicates that similar to human infants, a juvenile, human-raised chimpanzee (*Pan troglodytes*) preferred consonant-patterned music to dissonant-patterned music (consonance, defined as “static and evoking of a pleasant feeling” and dissonance, defined as “dynamic and intense, and that which gives rise to an unpleasant feeling”) (Sugimoto et al., p. 7, 2009). These findings appear to support the results of neurophysiological studies that have found distinct neural correlates of the perception of consonant and dissonant music in human adults that are associated with pleasant and unpleasant emotional states, respectively (Sugimoto et al., 2009). On the other hand, captive New World monkeys have been shown not to have a significant preference for consonant over dissonant sounds (McDermott & Hauser, 2004). While cotton-top tamarins (*Saguinus Oedipus*) and common marmosets (*Callithrix jacchus*) were observed by McDermott & Hauser (2007) to prefer slow tempo music over fast tempo music, they also appeared to prefer silence over music, as determined by subjects’ self-directed choice of positioning themselves in one of two branches of a dichotomous v-shaped maze. Each branch of the v-shaped maze contained a single auditory stimulus, such that monkeys chose exposure to one auditory stimulus over the other (e.g. silence over music) by positioning themselves in the corresponding maze-branch.

Investigations into the physiological effects of music on NHPs have yielded contradictory results. In one study of four singly housed baboons (three *Papio hamadryas* and one *Papio hamadryas-Anubis* hybrid), radio music made available to half of the

subjects was found to significantly lower heart rate, but had no observable effect on behaviour or blood pressure (Brent & Weaver, 1996). However, in another study on the effects of recorded harp music on the physiology of nine African green monkeys (*Chlorocebus sabaues*), music did not significantly affect subjects' heart rate, blood pressure, respiratory rate, or body-temperature before, during, or after exposure (Hinds, Raimond, & Purcell, 2007). Although these are interesting findings, in combination, they are too fragmented to constitute any conclusive evidence of NHP musical preference, preference for specific musical genres in NHPs, or for the beneficial physiological effects of music on NHPs.

Music and Captive Primate Care

Lack of confirmation of any beneficial effects of music on primates proves particularly problematic as, in primate facilities worldwide, music is used as auditory enrichment (as a means of distracting, relaxing and comforting captive primates) (Hinds et al., 2007; Lutz & Novak, 2005). Music has been assumed to be enriching for NHPs largely due to its confirmed positive effects in humans, which include lowered heart rate, pulse, blood pressure, increased respiratory oxygenation, reduction of agitation, stress and anxiety, increased endorphin levels and speedier recovery in post-surgical procedures (Hinds et al., 2007; Lutz & Novak, 2005). Because of the lack of research regarding the musical preferences of NHP's, the selection of music-type in primate care facilities is, for the most part, based on the preferences of human facilitators. However, even if it is determined that NHPs prefer music over silence, there is little reason to assume that human and NHP music preferences would be similar or even comparable (Lutz & Novak, 2005).

Some studies indicate that when given the opportunity, chimpanzees will initiate musical sounds, and according to qualitative observation, music appears to decrease aggressive behaviours and increase affiliative ones in chimpanzees (Howell, Schwandt, Fritz, Roeder & Nelson, 2003; Lutz & Novak, 2005; Videan, Fritz, Howell & Murphy, 2007). Nonetheless, the few studies that have investigated the reactions of NHPs to musical stimuli, have, for the most part, not allowed subjects to control music type, or have not explored music genre preferences (Howell et al., 2003; Line, Clarke, Markowitz & Ellman, 1990; Lutz & Novak, 2005; Markowitz & Line, 1989; Videan et al., 2007). Thus, the topic remains largely unresolved and in need of further investigation.

Assessing Preference

Given human infants' and most nonhuman animals' inability to directly communicate internal subjective desires through verbal or gestural communication, the study of human infant and nonhuman animal preference remains a challenging endeavor. An important question concerns how a subject's preference can be assessed, if they cannot directly communicate their likes or dislikes. A review of the preference literature involving non-communicative human infants and nonhuman animals indicates three main approaches:

Behavioural observation during stimulus exposure.

Observation of subjects' behaviour during stimulus exposure and has been particularly favored in the study of human infant preference. Since Robert Fantz (1961) introduced infant looking behaviour studies, eye-fixation paradigms have been used to test various aspects of infant detection, discrimination, preference, categorization, learning, and expectations of stimuli (Aslin, 2007). Infant visual, olfactory and auditory

preferences are often assessed via looking direction, looking time, fixation duration and the frequency of look-switching between simultaneously visible objects during exposure to experimental stimuli (Aslin, 2007; Conrad et al., 2011; Spears, 1964; Turati, Valenza, Leo & Simon, 2005; Wada et al., 2012). However, despite their popularity, behavioural preference measures, especially those involving auditory preference, are vulnerable to a variety of criticisms.

First, the use of behaviour as a measure of preference most often requires some (albeit operationally defined), subjective interpretation and/or classification by the experimenter. Even in the case of the frequently used looking-time paradigm in infants, Aslin (2007) warned that caution should be exercised in regards to the conclusions that can be drawn from these types of data. Despite the fact that sophisticated methods are used for measuring looking direction and point of visual fixation, this approach to measurement is vulnerable to error. For example, Slater and Findlay (1975) have detected potential sources of error inherent in the corneal reflection technique, widely used for measuring eye fixation position. Further, at a fundamental level, Aslin (2007) called into question the validity of the assumptions that looking behaviour is a measure of cognitive processing. He described duration of looking as a “many-to-one mapping problem: many potential ‘hidden’ variables contribute to a single dependent measure” (Aslin, 2007, p. 48). Aslin (2007) voiced particular concern about using looking behaviour to make inferences about the processing of auditory stimuli because the neural mechanisms that mediate looking behaviour in relation to auditory stimuli are more complex than those that mediate looking behaviour in relation to visual stimuli. Whereas with visual stimuli there is a linking hypothesis between gaze and visual processing (i.e. that gaze serves a

useful purpose for visual processing), with auditory stimuli the linking hypothesis is less direct (Aslin, 2007). The use of looking time in the study of nonhuman animal cognition is further complicated by the difficulties and/or limitations of placing and restraining nonhuman subjects (particularly in zoos and aquariums) in physical positions that allow optimal eye movement observation by experimenters.

The use of approach/avoidance as an indicator of preference in nonhuman animal research appears to avoid these difficulties. In this paradigm, stimuli are presented to subjects and preference is measured by the number and/or degree of approaches (movement of the body towards the stimulus) vs. non-occurrences (absence of response within a predetermined amount of time) (Fernandez, Dorey & Rosales-Ruiz, 2004). However, given the tendency for many species to approach any stimulus (regardless of whether or not the stimulus is reinforcing), the utility and accuracy of this paradigm is limited.

The least-aversive or most-desired choice paradigm.

The second approach, used to assess nonhuman animal auditory preference, involves a least-aversive choice paradigm in which the subject is forced to choose between two stimuli. For example, in primate auditory preference studies by McDermott and Hauser (2007), tests were conducted using a V-shaped maze, with each branch of the maze paired with a different auditory stimulus. Subjects were placed at the entrance to the maze and forced to choose between one auditory stimulus (in one branch of the maze) or another auditory stimulus (in the other branch of the maze). Here, the subject's choice of one of the two available branches of the maze is interpreted as an indicator of 'preference' for the chosen branch's accompanying auditory stimulus. However, because

the paradigm predetermines total exposure to one of the two stimuli, it is impossible to know if the subject is being forced to make a 'least aversive choice' or is expressing a most desired choice (Lamont, 2005). Consequently, preference in this paradigm could be interpreted as the least disliked of two stimuli *or* the most desired. Furthermore, this paradigm does not allow measurement of how motivated subjects are to listen to either of the stimuli.

Participant-controlled procedures.

Participant-controlled procedures appear to be the most appropriate and accurate approach to studying preference based on "liking" in non-communicative subjects (Lamont, 2005). Lamont (2005) argues that this approach allows greater confidence in concluding that subjects 'like' one stimulus *more than* another stimulus, as opposed to concluding that they 'dislike' one stimulus *less than* they dislike another stimulus. A participant-controlled procedure allows subjects to choose the duration, and in some cases, the type of stimulus during testing. For example, in a visual preference study using a sensory reinforcement procedure by Tanaka (2002), chimpanzees touched a button to view a stimulus. Slides were continuously presented as long as the subject continued to touch the button and if the button was touched within 10s of the previous touch, the same visual stimulus was presented again; food reward was often delivered irrespective of stimulus choice.

Another common participant-controlled procedure is a free-choice task with single-paired or multiple-stimulus methods in which subjects choose between concurrently presented pairs of stimuli (Fernandez et al., 2004). In these paradigms, preference is defined as choosing one stimulus more frequently than the other. When

subjects have made a choice between every combination of stimuli, the stimuli are ranked based on the percentage of times they were selected. If the stimuli themselves are not reinforcing enough to motivate participation, food reward may be delivered, irrespective of stimulus choice. This approach differs from a “least aversive” choice paradigm in that subjects are not forcibly subjected to the stimuli (as is the case of the V-shaped maze), but rather can choose to terminate participation, thereby limiting exposure to stimuli at any time.

Given the disadvantages of several of the aforementioned approaches to the study of preference in nonhuman animals, particularly in the assessment of acoustic preference, combined with the limitations of subject control in a zoo setting, several free-choice paradigms with varying degree of participant-control were employed in the present study.

Rationale

Species of Investigation

As great apes, orangutans are both phylogenetically and physiologically close to humans. Likely having diverged from the human lineage approximately 12-15 million years ago, orangutans share 97.4% of human DNA (Locke et al., 2011). Like all apes, orangutans mature slowly, are long-lived, and have long inter-birth intervals in comparison to other primates (Locke et al., 2011; Van Schaik, 2004). This extended period of physiological and mental development makes orangutans ideal for comparative study of life stages (i.e. infancy, juvenility, adolescence, and adulthood). Furthermore, orangutans have proven capable of colour vision and motivated to participate in computer-delivered, human-directed empirical investigation, making them ideal subjects for nonhuman primate research (Anderson, 2012; Tigges, 1963; Vonk, 2003).

Orangutans are considered the most solitary of all apes, the only ape species that do not typically live in large social groups, with the exception of mother-offspring pairs (Shumaker, 2007). Although adult orangutans do, on occasion, meet one another in the wild (e.g. when attracted to the same food), their social interaction is often limited to reserved visual contact (i.e. glances at one another from a safe distance) and little more (Van Schaik, 2004). Consequently, orangutans tend to be less vocal than other, more gregarious apes (i.e. gorillas, chimpanzees, bonobos, and gibbons) (Van Schaik, 2004). However, this is not to say that they are silent.

Considering their relatively solitary lifestyle, orangutans have a surprisingly varied vocal repertoire, the most distinctive and renowned of which is the long call. The long call is a vocalization composed of a series of groans and bellows that consists of an

introduction, a climax, and a tail-off. (Ross & Geissmann, 2007). The long call, emitted only by mature, flanged males, lasts between 15s and 4 min and can be heard by conspecifics as far as a kilometer away (Ross & Geissmann, 2007).

The long call is believed to function as a mating strategy and ‘spacing tool’, regulating interactions and relationships in overlapping home ranges (Delgado, 2006; Utami Atmoko, Singleton, van Noordwijk, van Schaik, & Mitra Setia, 2009). Flanged (fully adult) males emit the long call to make their presence known within a vicinity, prompting other males to respond in accordance with their relative dominance status (dominant males are more likely to approach lower ranked calls, while lower ranked males are more likely to move away from dominant ranked calls) (Delgado, 2006; Utami Atmoko et al., 2009). Similarly, female orangutans will adjust their range to remain within earshot of the long calls of dominant flanged males (for mating purposes), indicating that the identity and status of flanged males can be determined via long calls by other orangutans of both sexes (Delgado, 2006; Utami Atmoko et al., 2009).

More than 30 other types of orangutan vocalizations have been documented (Hardus et al., 2008), the large majority of which are made by manipulating the exhalation and inhalation of air through pursed lips (e.g. the ‘kiss-squeak’, used to communicate annoyance by rapidly sucking air in between pursed lips, the ‘raspberry’, etc.) and/or consist of grumbles, barks, screams, squeals, grunts, and the like. Because vocalizations are generally less common in orangutans than in other apes, and because their vocalizations bear little resemblance to music, there appears to be no reason to expect, from an ecological standpoint, that orangutans will be interested in, or appreciate music.

Orangutan auditory acuity.

Before any conclusions can be drawn regarding subjects' auditory preferences or abilities, it is of primary importance to identify their hearing range (auditory acuity). Auditory acuity research in non-communicative subjects (including human infants) predominantly employs behavioural conditioning tests and/or nonvolitional-nonbehavioural assessment procedures based on auditory evoked potentials (i.e. auditory brainstem response, otoacoustic emissions, auditory steady-state response, etc.) (Coleman, 2009; Rance et al., 2005). These procedures are employed to determine subjects' auditory thresholds (the lowest detectable auditory level), generally regarded as the most fundamental measure of hearing performance (Coleman, 2009). Resulting audiograms plot subjects' hearing sensitivity (i.e. differences in absolute thresholds of the tone) over a range of frequencies (Coleman, 2009; Harris, 1943).

Investigation of NHP auditory acuity dates back to the work of Elder (1934) and Wendt (1934), more than 70 years ago. Superfamilies of primates (a taxonomic category that ranks above family and below order) appear to exhibit distinctive patterns of hearing sensitivity, particularly at lower-range frequencies (Coleman, 2009). Generally, apes as compared to other NHPs, tend to be among the most sensitive to low-frequency acoustics and the least sensitive to high-frequency acoustics (Coleman, 2009). At the time of literature review, no orangutan auditory acuity assessments could be located, however, audiograms of close relatives of the orangutan were available for review.

A comparison of four audiograms of chimpanzees by Coleman (2009), reported the average chimpanzee's lower frequency limit as 125 Hz at 40 dB and the average upper limit as 32000 Hz at 80 dB. Coleman's (2009) average of audiograms for the

rhesus macaque (*Macaca malatta*) a species farther removed from orangutans than chimpanzees by several degrees, indicate that this old world monkey species' lower frequency limit falls around 63 Hz at 41dB and their upper frequency limit falls around 32000 Hz at 30dB. Comparatively, humans tested in the same labs under the same conditions appear to have a lower frequency limit that hovers on average at around 63 Hz at 40 dB and an upper frequency limit that falls at around 16000 Hz at 43 dB (Coleman, 2009). Thus, it would appear that humans share a similar lower frequency threshold to rhesus macaques and are more sensitive to lower frequency ranges than chimpanzees. However, humans also appear to be less sensitive to higher frequencies than both chimpanzees and rhesus macaques, which share relatively similar high frequency thresholds. Because orangutans are more closely related to chimpanzees and rhesus macaques than humans, we would expect orangutan auditory acuity to be most comparable to these two species. However, because orangutan audiograms could not be located in the literature, a broad assessment of subjects' auditory acuity was performed in this study.

Purpose of Investigation

The purpose of this series of investigations was first, to explore orangutans' preferences for music vs. silence, and second, to determine if orangutans could discriminate music from scrambled music. In the first study, preference for music vs. silence was explored in three phases. In the first phase, following exposure to a short sample of music belonging to one of seven musical genres, subjects were given the choice to continue to listen to the music sample previously played or to listen to silence instead. In the second phase of Study 1, subjects expressed preference for music or

silence via spontaneous and voluntary action. Through a mechanism similar to the “shuffle” function on an iPod, subjects were given the opportunity to *change* the current stimulus to another stimulus (from music to silence, silence to music, or from one genre of music to another) through touchscreen contact. In the third phase of Study 1, subjects were given the opportunity to independently and spontaneously produce musical notes through a virtual piano keyboard displayed on the touchscreen. Touching the keys displayed on the screen resulted in the corresponding note being played for as long as contact was maintained. In Study 2, Phase I, subjects’ ability to discriminate music from scrambled music was assessed via a standard delayed matching-to-sample (DMTS) task, in which subjects were rewarded for correct classification of stimuli as ‘music’ or ‘scrambled music’. In Study 2, Phase II, subjects’ ability to discriminate a female zookeeper’s voice from a male zookeeper’s voice was assessed to determine if subjects could discriminate between two categories of familiar auditory stimuli. Again, this auditory discrimination was assessed via a standard DMTS task in which subjects were rewarded for correct classification of stimuli as ‘male’ or ‘female’.

Method

These studies were reviewed and approved by the York University Animal Care Committee, Toronto, ON.

Subjects

Three Sumatran orangutans (*Pongo abelli*) housed at the Toronto Zoo, Toronto, Ontario participated in both studies. Subjects included two females: Sekali (21 years of age at time of testing) and Ramai (28 years of age at time of testing), and one male: Budi (6 years of age at time of testing). All subjects were born at the Toronto Zoo and had been regularly exposed to radio music as a method of environmental enrichment. Subjects had been previously trained to use a wooden dowel to operate a touch screen computer for prior studies investigating visual preference and discrimination. Participation in the study was voluntary and functioned as a form of enrichment. None of the subjects was food or water deprived at any time during testing.

Design

Experiments were implemented in orangutan holding areas accessible only to zookeepers and the experimenters. Ramai and Sekali were tested off-exhibit and Budi was tested both on- and off-exhibit. Although experimental subjects were physically separated from one another: (a) experimental subjects had some visual and auditory contact between enclosures during experimental sessions; and (b) subjects were not separated from other non-experimental conspecifics (Budi was housed with his mother, Ramai was housed with her daughter, and Sekali was housed with her son). Testing sessions lasted 30 - 60 minutes depending on subjects' motivation to participate. Experimental participation was voluntary. Subjects had free access to adjoining

enclosures, and could leave the testing area at any time. Absence from the testing area for 10 min or more resulted in the termination of that session. Each participant completed 1 session per day, 3-4 days per week. Test trials were administered and recorded using a 2.5 GHz dual-core Mac mini and a 21" colour PC computer monitor with a Keytec Magic Touch touchscreen unit attached. The computer hardware was stored in a mobile wooden housing that allowed the entire unit to be rolled to the front of each participant's enclosure during test sessions (see Figure 1).

Six of seven music genres employed were selected based on historically conventional and popular North American genres that test subjects would be relatively familiar with (as a result of the use of radio music as a form of enrichment at the Toronto Zoo). A seventh genre, Tuva throat singing, was selected because both the music and the way in which it is produced resemble orangutan long calls. Tuva throat singing is a type of overtone singing practiced by Tuva people in Southern Siberia. It is produced deep within the throat through the manipulation of resonances created as air travels past the vocal chords (Behar, Kumar & Kunov, 2001). The vocal chords, false chords, arytenoid cartilages, aryepiglottic folds, and epiglottic root are vibrated to generate sounds (Behar et al., 2001). Similarly, orangutan long calls are achieved through a series of powerful exhalations aided by the inflation of a large throat sac (Van Schaik, 2004). Given these similarities, it was theorized that this genre of music might serve as a more ecologically valid stimulus than the other genres employed.

Music exemplars were selected based on human preference indicated by the greatest number of purchases on iTunes, a popular application for downloading music (Apple Inc., 2013). Exemplars for each genre were selected from the iTunes Store's lists

of “top albums” (e.g. “top classical albums”, “top rock albums”, etc.) organized according to the “bestseller” filter. While not an exhaustive totality of selections, the total sum was intended to be a critical mass of selections highly preferable to a large sample of humans who have expressed preference through purchasing behaviour. A software program, written using Java, generated and delivered the experimental stimuli.

Auditory acuity assessment.

A broad assessment of Ramai’s and Sekali’s auditory acuity was performed in a single experimental session to confirm that subjects could hear the experimental stimuli and to ensure that they did not suffer from an unusual hearing deficit that would make them unrepresentative of the general orangutan population. Budi could not be tested because of a significant aversive reaction by his roommate (his mother) to the experimental stimuli.

Because of limited physical access to orangutan subjects as well as ethical and safety concerns, assessment procedures based on auditory evoked potentials were not feasible. Consequently, the Behavioural Observation Audiometry (BOA) test was employed to measure subjects’ auditory acuity. The BOA is a variation of the conditioned head turn test developed by Dix and Hallpike (1947) and Suzuki and Ogiba (1960) to assess auditory acuity in children (Werker, Polka & Pegg, 1997). Because the conditioned head turn procedure has proven an effective tool for audiological assessment across the human lifespan and provides data on subjects’ individual hearing differences, variations of the conditioned head turn response procedure have been adapted to assess nonhuman animals’ auditory thresholds (Werker et al., 1997). In the conditioned head turn procedure, the subject is positively reinforced for turning his/her head in the

direction of a sound whenever a change in the auditory stimulus is detected (Werker et al., 1997). According to a meta-analysis of all known primate behavioural audiograms by Coleman (2009), the use of either aversive (negative reinforcement procedures) or appetitive (positive reinforcement procedures) yields comparable absolute auditory thresholds (threshold values are similar in the middle frequencies, and only slightly differ in the highest and lowest frequencies).

During the BOA test administration, competing auditory, visual and tactile distractions were kept to a minimum whenever possible. Pure tones of various frequencies were delivered at 100.3 dB via an iPhone 5 speaker at close range (1.5m) 1m to the left or right of midline using the iPhone app 'High Frequency Noise' (Purple Innovation, LLC, 2010). Auditory tones of varying frequencies were delivered via speaker rather than headphones, due to limited physical access to subjects.¹

Control trials of silence in which a stimulus was not presented were intermixed with stimulus trials to assess the subjects' guess-rate. Any response judged to be a result of detection of the stimulus tone (i.e. eye or head re-orientation, body movement, etc.) was accepted and reinforced with a food-item (Hicks, Tharpe & Ashmead, 2000). Reinforcement of response behaviours has been found to enhance auditory acuity test conditions (Olsho, Kock, Carter et al., 1988; Olsho, Koch, Halpin et al., 1987). Upon establishing the subject's response to (i.e., detection of) the tone stimulus, the frequency of the tone was varied systematically (from 300 Hz to 14000 Hz by 100-1000 Hz

¹ According to Coleman's (2009) meta-analysis this results in thresholds that are lower in the frequency range than those obtained by headphones (average difference of 6dB in audiograms obtained via loudspeaker vs. via headphones). For the most part, open field audiograms (via speaker) and closed field audiograms (via headphones) share similar middle and high frequencies; however open field audiograms show slightly lower thresholds at frequencies less than 1kHz (Coleman, 2009). Nevertheless, Coleman (2009) notes that these differences do not appear significant at any of the frequencies reviewed in his meta-analysis.

increments) for a total of 18 separate stimuli that were each administered twice for a grand total of 36 trials per subject (see Table 1 for frequencies tested). A trial consisted of the subject targeting the forehead at midline followed by presentation of either a 10s tone or a 10s no-tone (i.e. silent) interval. Trials were separated by a 5-15s inter-trial interval (ITI). ITI's were systematically varied so that the subject could not anticipate trial initiation and feign an orientation behaviour in order to receive a food reward. Trials were blocked so that every 12 trials contained all of the frequency stimuli presented in order from highest frequency to lowest frequency.

The stimulus presentation and detection task was performed with two experimenters present; one who presented the tones and another who observed the test subject and made a determination as to whether an orienting response had been made. An observer-based scoring method was used in which the observing experimenter, blind to trial type (wearing soundproof headphones), seated face-to-face in front of the test subject, decided, for each trial, whether a tone or no-tone trial had occurred based on any of the subject's behaviours. A tap on the observing experimenter's shoulder by the experimenter delivering the tones indicated to the observer that a trial was completed, but the observer did not know whether a tone or no-tone trial had been presented. To aid the observing experimenter in setting a moderate criterion to qualify the stimulus as "detected" by the subject, the observer received trial-by-trial feedback of the correctness of her judgments (i.e. if a tone had been presented during that trial or not) (Morrongiello et al., 1990). Because subjects tend to habituate quickly during BOA tests, the test session did not exceed 36 trials (behavioural reinforcement also tends to decrease behavioural habituation) (Morrongiello, Fenwick & Chance, 1990). Frequencies were evaluated as

perceivable by each subject if judged “detected by the subject” by the trial observer 50% of the time or more (Coleman, 2009).

Because orangutan auditory acuity assessments could not be located in the literature, a pilot study of two human subjects (one male, one female), using the same methodology as those employed with Ramai and Sekali was executed. The results of the human pilot study were compared with published human auditory acuity assessments to better assess the accuracy of the methodology in *this study* (i.e., the degree of similarity vs. difference).

Study 1: Musical preferences.

Phase I: Music preferences vs. silence.

Seven libraries representative of seven musical genres, respectively (classical, jazz, rock, pop, children’s music, country and tuva throat singing), were assembled. Each library included 30 exemplars (a 30s musical segment) of its respective genre (see Appendices A-G for complete lists). Testing sessions (i.e., a testing occasion) lasted 30 - 60 minutes, depending on subjects’ motivation to participate. Each testing session consisted of the number of trials executed in the allotted time period (4-73 trials/session). Because the genres of music were randomized and counterbalanced, the number of trials conducted with each single genre of music was approximately equal.

At the beginning of a test session, the experimenter wheeled the experimental apparatus to the front of the subject’s enclosure (i.e., his/her daily holding area). Test sessions were voluntary, and subjects indicated their intention to participate by spontaneously approaching the experimenter and the experimental apparatus (this usually took less than 2 minutes). Once the subject chose to participate (with the touchscreen

facing away from the subject) the experimenter initiated the first test trial by turning on the touchscreen program, which immediately resulted in the playing of a 30s musical clip. While the clip was playing, its corresponding genre colour appeared full-screen on the monitor (see Table 2 for genre colours). After activating the first trial, the experimenter turned the touchscreen toward the subject and offered the subject the wooden dowel used to contact the touchscreen. Upon conclusion of the first clip, the screen subdivided into two halves, one of which displayed the genre-colour of the musical exemplar genre that had just played, and the other half displayed a grey screen. If the coloured half of the touch-screen was contacted with the wooden dowel, the previous 30s musical clip replayed. If however, the grey side of the touch-screen was contacted, 30s of silence ensued. The subject made a preferred choice for re-play or silence by touching the appropriate side of the screen with a wooden dowel (see Figure 2 for visual representation of trials). If neither side of the screen was contacted, the monitor display remained subdivided (i.e. one half grey, one half genre colour) indefinitely. To motivate participation (i.e., a choice one way or the other), a food reward (a standardized-sized slice of banana) was offered to the participant following each selection, regardless of which choice was made. Following each trial, a new 30s musical exemplar began to play automatically. The order of exemplars from each musical genre as well as the side of the screen on which either grey/silence or colour/genre appeared were randomized and counterbalanced to avoid participant and order effects. Subject behaviour during test sessions was closely observed and recorded.

Data analysis.

Preference for musical genre was assessed by a chi square analysis of the total number of times each subject chose to replay each genre (which in turn, was a sum of the total number of times the exemplars of that genre were replayed). Preference for music vs. silence was assessed by a chi square analysis of the total number of times each subject chose to replay a music exemplar versus the total number of times each subject chose silence instead. Group and individual preferences were compared. The potentially confounding contribution of side preference (recurrent choice of one side of the screen over the other) was evaluated by determining if the number of selections made via right-side selections vs. left-side selections was significantly different according to a chi square analysis. Results were analyzed per individual. Chi square statistical analyses were conducted using IBM SPSS Statistics version 21.0.

Phase II: Music-silence shuffle.

A program written using Java generated and delivered the experimental stimuli for Phase II. Stimuli consisted of the same seven genre libraries as those used in Phase I, with the exception that an eighth genre, silence, was also included. The silence exemplar library consisted of 30, 30s 'silent' exemplars. Upon activating the program, a randomly selected and genre-counterbalanced music or silence exemplar played. Following a 10s forced-listening period, touching the screen resulted in a "shuffle" (termination of play of the current exemplar, and activation of play of another randomly selected and genre-counterbalanced exemplar.) Alternatively, if the screen was not touched after the 10s forced-listening period, the exemplar continued to play indefinitely (musical exemplars were looped to allow indefinite continuous play). During experimental sessions the entire touchscreen displayed a monochromatic shade of pink (that was not used in Phase I) for

the duration of the session, regardless of the genre of music being played. A shuffle activated through touchscreen contact did not result in any visual changes on the touchscreen. Subjects were *only* positively reinforced with a slice of banana *before* and *after* each experimental session to motivate participation. During sessions, no food reinforcement was utilized in order to ensure that choices regarding exemplar play were not motivated by reward. Testing sessions lasted 30 - 60 minutes depending on subjects' motivation to participate. Subject behaviour during test sessions was closely observed and recorded.

Data analysis.

Group and individual preferences were compared. If quantitative data were deemed suitable for statistical analyses, preference for music vs. silence was assessed by a Wilcoxon signed-rank test analysis of the difference in the total time (in seconds) each subject chose to listen to music versus the total time (in seconds) the subject chose to listen to silence instead. Preference for musical genre was assessed by a Friedman's ANOVA analysis of the differences in the total times (in seconds) each subject chose to listen to one musical genre versus another (seven genres in all).

Phase III: Musical note production.

A program written using Java generated and delivered the experimental stimuli. Stimuli for Phase III consisted of 7 musical notes (C, D, E, F, G, A & B). Upon activating the program a set of 7 monochromatic vertical bars were displayed on the touch screen (resembling piano keys). Touching any of these 7 bars resulted in the playing of one of the 7 corresponding musical notes for as long as contact was maintained (see Figure 3). Once contact was terminated, the corresponding musical note ceased to play. Subjects

were only positively reinforced with a food item before and after experimental sessions to motivate participation. However, during trials, no food reinforcement was utilized. Consequently, choices regarding music note play were not motivated by food reward. Subject behaviour during test sessions was closely observed and recorded.

Data analysis.

If quantitative data were deemed suitable for statistical analyses, preference for generating musical notes over not generating musical notes was assessed by a Wilcoxon signed-rank test analysis of the difference in the total time (in seconds) subjects were observed playing on the virtual piano versus the total in (in seconds) subjects were observed engaging in any other activity. Group and individual preferences were compared.

Study 2: Auditory discrimination.

Phase I: Music vs. scrambled music.

The purpose of this study was to investigate whether orangutans could learn to discriminate between music and scrambled non-music samples, using a standard DMTS task.

A program written using Java generated and delivered the experimental stimuli. The experimental task for Study 2 consisted of a DMTS task in which subjects demonstrated their ability to differentiate music from scrambled music by identifying whether the stimulus was a musical clip, or a scrambled clip of the same musical selection via responses on a touchscreen computer. Stimuli included 5 musical clips and 5 scrambled clips (see Appendix H for list of music exemplars). Scrambled auditory stimuli (i.e. scrambled music exemplars) were constructed using Audacity (a free online audio

editor) by dividing each music sample into 0.5s segments, randomly re-ordering these segments, and playing the randomly re-ordered segments in reverse order. Trials were initiated by subjects touching an orienting stimulus at the centre of the touchscreen with a wooden dowel. This was followed by a 5s forced-listening period after which the image on the computer screen divided into two, one half displaying a green screen, the other half displaying a red screen. Touches to the green half of the screen were reinforced during presentation of the music sample, and touches to the red half of the screen were reinforced during presentation of the scrambled music sample. Comparison colour was counterbalanced across subjects. Reinforcement following a correct choice consisted of an acoustic chime delivered by the computer followed by a preferred food item delivered by the experimenter. The sounding of a horn (without reinforcement) followed incorrect responses. Following the 5s forced listening period, subjects were required to contact the touchscreen within 10s (auditory stimuli continued to play for the total 15s duration). Touchscreen contact (i.e. a choice) immediately terminated the playing stimulus, darkened the screen, triggered the sounding of a chime or horn (dependent on correct or incorrect response), and resulted in reinforcement or no reinforcement (dependent on correct or incorrect response). If no touchscreen contact occurred after the 10s interval, the stimulus was terminated, the screen darkened, and the subject was not rewarded (these trials were labeled as “incomplete trials”) (See Figure 4 for visual depiction of a trial). Data consisting of the number of correct and incorrect responses was collected following a training period consisting of numerous exposures to the experimental paradigm. An inter-trial interval (ITI) of 10s separated each trial from the next and

musical and scrambled clips appeared randomly in a session with equal frequency.

Subject behaviour during test sessions was closely observed and recorded.

Data analysis.

Discrimination of the music stimulus from the scrambled music stimulus was measured by a chi square analysis of correct vs. incorrect responses in the discrimination task. The ability to discriminate some music or scrambled exemplars better than others was assessed via a chi square analysis of the total number of correct discriminations per exemplar. Group and individual differences were compared. Statistical analyses were conducted using IBM SPSS Statistics version 21.0.

Phase II: Male vs. female voices.

The purpose of this study was to act as a control for Study 2, Phase I by investigating whether orangutans could learn to discriminate between two more familiar categories of sounds, via the same standard DMTS task employed in Study 2, Phase I.

The experimental task for Study 2, Phase II was identical to that of Study 2, Phase I with the exception that the stimuli consisted of two different categories of sound and two different screen colours than those employed in Study 2, Phase I (see Figure 5 for depiction of a trial). Categories of auditory stimulus were chosen based on their familiarity to the research subjects, who are exposed to these sounds on a daily basis. Recordings of two of the subjects' handlers' voices (1 male, 1 female) were employed as stimuli. So as to change as little as possible from Study 2, Phase I, the handlers were recorded with an iPhone 4 reading the lyrics of the songs used as stimuli in Study 2, Phase I. The two auditory categories were defined as a male handler's voice recordings vs. a female handler's voice recordings (each category consisting of 5 exemplars) (see

Appendix I for lyrics employed). Subjects were tested for their ability to differentiate their female handler's voice recording from their male handler's voice recording via touchscreen contact using the same procedure as that employed in Study 2, Phase I. Subject behaviour during test sessions was closely observed and recorded.

Data analysis.

Discrimination of the target stimulus from the distractor was measured by a chi square analysis of correct vs. incorrect responses in the discrimination task. The ability to discriminate some male-keeper or female-keeper exemplars better than others was assessed via a chi square analysis of the total number of correct discriminations per exemplar. Group and individual differences were compared. Statistical analyses were conducted using IBM SPSS Statistics version 21.0.

Results

Results will be discussed for each phase of each study separately. Results were analyzed per individual, however subject trends were also examined. An alpha level of 0.05 was used for all statistical analyses.

Auditory Acuity Assessment

Ramai and Sekali demonstrated similar auditory acuity. Ramai detected tones at frequencies between 800-8000Hz at 100.3 dB. Sekali detected tones at frequencies between 800-7000 Hz at 100.3 dB (see Table 3 for number of detections for each frequency tested).

The male and female human subjects demonstrated similar auditory acuity. The male detected tones at frequencies between 200-8000Hz at 100.3 dB. The female detected tones at frequencies between 200-10,000Hz at 100.3 dB (see Table 4 for number of detections for each frequency tested).

Study 1: Musical Preferences

Phase I: Music preferences vs. silence.

Quantitative analyses.

All test trials were included in analyses for a total of 39 sessions and 1416 trials for Budi, 37 sessions and 1258 trials for Ramai and 40 sessions and 1157 trials for Sekali. The number of trials conducted with each genre of music was approximately equal (see Table 5 for music genre exposure frequency, per subject).

When given the choice to replay a 30s music exemplar or listen to 30s of silence, Budi selected silence significantly more often than music $\chi^2 (1) = 93.57, p < .001$ and Sekali selected silence significantly more often than music $\chi^2 (1) = 814.90, p < .001$.

Although Ramai also made more silence selections than music selections, the difference was not statistically significant $\chi^2 (1) = 1.83, p < .176$ (see Tables 6-8 for frequency of music replay and silence selections per session, per subject).

Further, when subjects chose to replay the previous musical exemplar, they did not choose to replay any one musical genre of music more than any another musical genre ($\chi^2 (6) = 11.22, p < .082$ for Budi; $\chi^2 (6) = 2.67, p < .85$ for Sekali; and $\chi^2 (6) = 12.19, p < .058$ for Ramai) (Tables 9-11 show the frequency of music replay and silence selections for each genre for Budi, Ramai, and Sekali, respectively).

Budi displayed a significant side preference (i.e. significantly more selections made via right-side selections vs. left-side selections or vice versa) $\chi^2 (1) = 5.22, p < .05$. Ramai also displayed a significant side preference $\chi^2 (1) = 65.02, p < .001$, while Sekali did not display a significant side preference $\chi^2 (1) = 0.19, p < .659$ (See Table 12 for frequency of side selections per subject).

A plot of silence selection vs. music selections was used to assess the degree to which familiarity with, or exposure to, the grey touchscreen/silence pairing may have influenced preference (see Figure 6). The lack of a visual positive correlation between session date (i.e. the number of sessions following the first session) and number of grey/silence choices in Ramai's plots appears to indicate that familiarity was, not, in her case, associated with increasing preference for grey/silence (i.e. she did not appear to make more silence selections as she became more familiar with the test paradigm). However, Sekali's and Budi's data show a steady increase in silence selections from the beginning of testing in May (30% and 39% silence selections respectively) to mid-June (100% and 86% silence selections respectively). This visually identified trend may

indicate that Sekali's and Budi's demonstrated silence preferences were indeed influenced by familiarity.

Qualitative Analyses.

Despite consistent, continuous and voluntary participation throughout the experiment, all three subjects periodically displayed behaviours associated with orangutan distress during test sessions (Kaplan & Rogers, 2000; MacKinnon, 1974; Payne & Prudente, 2008; Rogers & Kaplan, 2000). These behaviours included posturing with raised hair, exaggerated and repetitive scratching of the torso, sputtering, blowing raspberries, spitting, banging the wooden dowel used for touchscreen contact on the ground, breaking the wooden dowel and using the wooden dowel to push the experimental apparatus away. Although these antagonistic behaviours (ABs) were most prevalent early on in the experiment and decreased as test sessions continued, they persisted to varying degrees throughout the duration of Study 1, Phase I. Sekali, in particular, appeared acutely distressed during test sessions, displaying the greatest number and most energetic ABs, as well as persisting in them longest. In comparison, Budi, the juvenile, displayed fewer ABs during testing and they reduced in frequency more quickly, and to a greater degree than in both Ramai and Sekali. Ramai also displayed fewer ABs and they extinguished more quickly than in Sekali.

Both Ramai and Budi made indiscriminate choices on multiple occasions during testing by either (a) leaving the wooden dowel in contact with the screen indefinitely, thereby making a choice before it was visually clear what that choice was, (b) by touching the center of the screen (straddling the two half screen choices) thereby making a "random" choice, or (c) by dragging the wooden dowel across the screen

indiscriminately without looking. Similar to the aggressive behaviour described above, this indiscriminate choice behaviour subsided over time, but did re-occur occasionally throughout the experiment. Ramai displayed appreciably more indiscriminate choice behaviour than the other subjects tested while Sekali displayed the least amount. Throughout testing, Budi often chose to take self-imposed breaks from testing (on average, 20-30min into testing) for 5-10 min, or to quit sessions entirely. This was not true of Ramai or Sekali. Unlike Sekali, Ramai occasionally allowed her roommate (her daughter) to steal the wooden dowel used for session participation, resulting in 5-10 min breaks as well. Interestingly, during times of stress, injury, excessive noise and/or commotion in, and around the orangutan enclosure (e.g. during construction, when keepers were heard speaking or approaching, or when strangers were present), all subjects tended to choose silence more than average (i.e. to repeatedly choose silence over music until the event was over) and/or to quit test sessions entirely. For example, during a test session after Budi had sustained a significant injury to his hand, he chose silence 79% of the time, in contrast to choosing silence 63% of the time across all test sessions.

Phase II: Music-silence shuffle.

Quantitative analyses.

As a result of irregular, inconsistent and discontinuous participation in this phase of Study 1, the quantitative data collected were not suitable or sufficient for statistical analyses.

Qualitative analyses.

All test sessions were included in behavioural analyses for a total of 22 sessions for Budi, 22 sessions for Ramai and 23 sessions for Sekali. From the onset and throughout the duration of Study 1, Phase II, subjects displayed an aversion to participation as well as significant ABs (more frequent, vigorous and persistent ABs than those observed in Study 1, Phase I). ABs include those described in Study 1, Phase I, with the addition of facing away from the experimenter, spitting saliva and/or water on the experimenter, leaving the test enclosure (with or without the wooden dowel), hitting and/or poking the experimenter with the wooden dowel, throwing the wooden dowel and other objects within or outside of the orangutan enclosure, scratching the experimenter, urinating on the experimenter, using objects to cover their heads and/or bodies, lying in or under buckets, as well as grabbing, scratching and biting conspecifics. These behaviours increased in number and intensity over the duration of testing. Consistent, uninterrupted, participation in Study 1, Phase 2 was never achieved. In early test sessions, subjects tended to initiate several rapid initial shuffles (between 1 and 20 shuffles) via contact with the touchscreen (including contact intended to push the apparatus away from the enclosure) before taking a long break or quitting the session entirely. A typical break (1-10 min) was normally followed by 1 to 10 shuffles and either another break or termination of participation. Even the limited participation described waned quickly over several testing sessions, becoming nearly nonexistent by the 5th to 10th session. Following the 13th session, subjects participated only briefly at the beginning of a session and/or irregularly, if at all. Subjects often prematurely ended test sessions by repeatedly returning the wooden dowel (used for touch screen choices) to the experimenter, or by repeatedly allowing a conspecific to steal the dowel and remove it from the testing area.

As early as the third testing session, subjects also began to display a new “rejection” behaviour in which, when handed the wooden dowel used to make touch screen choices, subjects deliberately blocked the dowel from entering their enclosure (often with an open palm, the back of a hand, or a shoulder). If the experimenter persisted in attempting to hand the dowel to the subject, the subject grew increasingly violent in their blocking and/or returning behaviours.

Phase III: Musical note production.

Quantitative analyses.

As a result of a significant antagonistic behavioural reaction to participation by all three subjects subsequent testing was terminated. Consequently, Phase III consisted of only a single test session. Because of irregular, inconsistent and discontinuous participation in this phase of Study 1, the quantitative data collected were not suitable or sufficient for statistical analyses.

Qualitative analyses.

Following a minimal degree of preliminary exploration of the new software program at the beginning of the first test session (i.e. a few initial touches to the touchscreen), all three subjects displayed the same ABs observed in Study 1, Phase II and subsequently no interest in participation. As a result of these behavioural observations and the effects of this type of behaviour on valid data collection, as well as ethical considerations, subsequent test sessions were cancelled, and Study 1, Phase III was terminated prematurely.

Study 2: Auditory Discrimination

The purpose of Study 2, Phase I was to investigate whether orangutans could discriminate music from scrambled music. Phase 2 was implemented as a control condition to determine if the same subjects could discriminate between familiar, nonmusical auditory stimuli (male vs. female zookeepers' voices).

Phase I: Music vs. scrambled music.

Quantitative analyses.

All test trials were included in analyses for a total of 28 sessions and 4122 trials for Budi, 28 sessions and 4170 trials for Ramai and 31 sessions and 5083 trials for Sekali. Budi did not make significantly more correct auditory discriminations of 'music' from 'scrambled music' stimuli than incorrect discriminations $\chi^2 (1) = 0.248, p < .618$, nor did Sekali, $\chi^2 (1) = 0.472, p < .492$ or Ramai, $\chi^2 (1) = 0.035, p < .853$ (see Table 13-15 for frequency of correct selections, incorrect selections and mistrials per session, per subject). However, Budi did make significantly more correct discriminations of some music/non-music exemplars more than others, $\chi^2 (9) = 358.376, p < .001$. Ramai, $\chi^2 (9) = 934.952, p < .001$ and Sekali, $\chi^2 (9) = 284.303, p < .001$ displayed the same pattern (see Figure 7). Furthermore, Budi displayed a significant side preference (making choices on one half of the screen significantly more often than choices the other half of the screen), $\chi^2 (1) = 209.825, p < .001$ as did Sekali, $\chi^2 (1) = 12.293, p < .001$. and Ramai, $\chi^2 (1) = 2464.853, p < .001$ (see Table 16 for frequency of left and right side selections, per subject).

Qualitative analyses.

Although all three subjects displayed some of the ABs observed in Study 1, II and III at the onset of Study 2, Phase I, these behaviours were less frequent and less vigorous

than those observed in Study 1, Phase II and III and decreased quickly over the first several test sessions. These behaviours included, but were not limited to, intermittent participation, abandoning sessions prematurely, sputtering, allowing the wooden dowel used for participation to be stolen by conspecifics, pushing the apparatus away from the subjects' enclosure, hitting the apparatus with the wooden dowel, banging the wooden dowel on the ground, throwing the wooden dowel and/or other found objects across the subject's enclosure, biting conspecifics, breaking the dowels, running and/or somersaulting away from the testing area, banging on walls and poking the experimenter with the dowel. By the 8th - 10th session, such ABs had significantly decreased, and were exhibited only in response to the subject making several incorrect choices in a row. Budi, the juvenile, displayed the most ABs in response to incorrect choices, while Sekali displayed a moderate amount, and Ramai, nearly none at all. Budi, however, displayed another notable behaviour in response to a series of incorrect choices, in which, on several occasions, he retrieved a tarp or blanket from the enclosure and hung it over his head while seated in front of the apparatus, thereby creating a "tent" that isolated him and the touchscreen from external visual and auditory stimuli. Another unusual behaviour of note was subjects' initiation of a new trial (by touching the orienting stimulus) before the experimenter had time to reward the subject for a correct choice on the previous trial. While this behaviour was observed on occasion in all three subjects, Sekali markedly displayed this behaviour much more frequently than the two other orangutans.

Initially Budi experienced difficulty in orienting to initiate a trial (by touching the orienting stimulus on the screen). This is likely a result of his young age and relative lack of experience with touchscreen paradigms relative to the two other subjects. However,

after receiving guidance over several test sessions, he ultimately reached competence comparable to Ramai and Sekali. By the 8th – 10th test sessions, all three subjects were participating immediately, consistently and energetically. This stood in stark contrast to the amount and quality of participation observed in Study 1, Phase II and III. However similarly to Study 1, Phase I, all three subjects occasionally appeared to make indiscriminate choices during testing by: (a) leaving the wooden dowel in contact with the screen indefinitely, thereby making a choice before it was visually clear what that choice was, (b) touching the center of the screen (straddling both half screen choices), thereby making a ‘random’ choice, or (c) dragging the wooden dowel across the screen indiscriminately without looking. This type of behaviour was nearly non-existent during initial testing sessions and increased as sessions continued. Ramai displayed appreciably more indiscriminate choice behaviour than the other subjects. Overall, however, Sekali showed the highest increase of this type of behaviour when initial test sessions were compared with later test sessions. Interestingly, similar to Study 1, during times of alarm, excessive noise or commotion (e.g. during construction, when keepers were heard speaking or approaching, or when strangers were present), subjects were likely to suspend participation or to quit test sessions entirely.

Phase II: Male vs. female voices.

Quantitative analyses.

All test trials were included in analyses for a total of 24 sessions and 5078 trials for Budi, 25 sessions and 6330 trials for Ramai and 24 sessions and 6445 trials for Sekali. Budi did not make significantly more correct auditory discriminations of ‘male keeper’ from ‘female keeper’ stimuli than incorrect discriminations $\chi^2 (1) = 0.492, p < .483$, nor

did Sekali, $\chi^2 (1) = 0.075, p < .784$. However, Ramai did make significantly more correct auditory discriminations of ‘male keeper’ from ‘female keeper’ stimuli than incorrect discriminations, $\chi^2 (1) = 5.438, p < .05$ (see Table 17-19 for frequency of correct selections, incorrect selections and mistrials per session, per subject).

Budi did not make significantly more correct discriminations for some exemplars more than others, $\chi^2 (9) = 2.062, p < .990$. However, Ramai made significantly more correct discriminations for some exemplars more than others $\chi^2 (9) = 631.246, p < .001$ and Sekali, $\chi^2 (9) = 1194.319, p < .001$ showed the same pattern (see Figure 8 for frequencies of correct selections per exemplar, per subject).

Budi did not display a significant side preference (making choices on one half of the screen significantly more often than choices the other half of the screen), $\chi^2 (1) = 0.709, p < .400$. Ramai however did display a significant side preference, $\chi^2 (1) = 1944.086, p < .001$, as did Sekali, $\chi^2 (1) = 1452.622, p < .001$ (see Table 20 for frequency of left and right side selections per subject).

Qualitative analyses.

Behaviour observed in Phase II was very similar to behaviour observed in Phase I. Although all three subjects displayed some ABs during initial training sessions, as was observed in Phase I, these behaviours more quickly became limited to circumstances in which the subject made several successive incorrect choices. As in Phase I, Budi displayed the most ABs in responses to incorrect touchscreen choices. Budi also continued to infrequently display his “tent-behaviour” during Phase II testing. Both Sekali and Ramai continued to occasionally initiate new trials before being rewarded for the previous correct trial response. In contrast to Phase I, subjects displayed the

“indiscriminant choice behaviour” earlier in Phase II than in Phase I. Similarly to Phase I, Ramai and Sekali exhibited this behaviour more frequently than Budi. However Ramai displayed the largest decrease in this behaviour over time. Also as was observed in Phase I, during times of stress, noise or commotion, subjects were prone to suspend or terminate participation.

Discussion

This investigation was designed to assess musical preference and discriminative ability in three Sumatran orangutans. Results indicate that subjects preferred silence to music (or were indifferent), that they did not discriminate 'music' from 'scrambled music', and that only Ramai discriminated between a 'male zookeeper's' and a 'female zookeeper's' voices. In the pages that follow, findings from the auditory acuity assessment and each phase of the two studies employed are discussed. This is followed by a general discussion, the limitations of the present findings and a conclusion section.

Auditory Acuity Assessment

As expected, Ramai and Sekali exhibited behavioural responses similar to those observed in infants tested using the same procedure (i.e. eye shifting, eye widening, head/body orientation) (Hicks et al., 2000). This indicates a valid application of the behavioural assessment process. On average, Ramai and Sekali detected frequencies between 800 Hz and 7500 Hz at 100.3dB. Although this is a much smaller range than those reported by Coleman (2009) for chimpanzees (125 Hz at 40dB - 32,000 Hz at 80dB) and humans (63Hz at 40dB – 16,000 Hz at 43 dB), they were comparable to the ranges obtained from a pilot study of 2 human subjects using the same methodology as that employed with Ramai and Sekali (see Table 4 for human auditory acuity results). Therefore, these differences are most likely a result of the inaccuracy of the methodology employed to assess auditory acuity range rather than any hearing deficits on the part of the subjects. The fact that Ramai and Sekali detected similar frequencies to one another supports this conclusion as it is unlikely that both subjects (who are biologically unrelated) would suffer from the same type or degree of hearing deficiency.

Study 1: Musical Preferences

Phase I: Music preferences vs. silence.

Results of Study 1, Phase I suggest that Budi and Sekali preferred silence to music, while Ramai, demonstrated no significant preference. Quantitative results further suggest that when all three subjects chose to replay music exemplars, they did not demonstrate particular genre preferences. Because subjects were rewarded for every selection regardless of whether music-replay or silence was chosen (and therefore had no reason to expect more versus less reward for any particular selection), and because the sides of the screen coupled with music and silence choices were randomly assigned and counterbalanced across trials, Budi's and Ramai's significant side preference (i.e. selecting one screen-side significantly more than the other) suggests indifference regarding preference for music or silence. In other words, Budi and Ramai appeared not sufficiently concerned with the results of their touchscreen choice (music or silence) to motivate them to reliably move their dowels from one half of the screen to the other. Sekali's lack of a significant side preference, on the other hand, supports the conclusion that she categorically preferred silence to music. In other words, Sekali chose silence so often that she did not (i.e., could not) choose one side of the screen significantly more often than the other (see Table 8 for frequency of Sekali's music and silence selections). Although these results suggest orangutans do not prefer music over silence, they also suggest individual differences with respect to the degree of such preferences. Behavioural observations support the quantitative findings in that all three orangutans displayed ABs in reaction to participation often associated with orangutan aggression/annoyance (Kaplan & Rogers, 2000; MacKinnon, 1974; Payne & Prudente, 2008; Rogers & Kaplan,

2000). The fact that Sekali appeared to be the most distressed during test sessions, exhibiting the greatest number and most energetic ABs, suggests a dislike of the musical stimuli employed in test trials and supports the quantitative results that she particularly preferred silence to music more than the other two subjects. Furthermore, both Budi and Ramai exhibited the “indiscriminate choice” behaviour and Sekali did not. These behavioural observations also support the hypothesis that Budi and Ramai may have been less concerned about the result of their choices, indicating a lesser preference for silence over music than Sekali.

Phase II: Music-silence shuffle.

The observed aversion to participate in Study 1, Phase II suggests three possibilities: (a) subjects were indifferent as to whether a music stimulus was playing or not, (b) subjects preferred music to silence but did not have enough of a preference for genre or song to motivate shuffling the playing exemplar, (c) subjects found the music aversive and demonstrated their preference for silence through a refusal to participate in test sessions and by distancing themselves from the aversive stimulus, or (d) subjects negatively reacted to experimental manipulations (e.g., were frustrated by not being rewarded per trial). However, the number, degree, and severity of ABs in combination with the aversion to participate suggest that music was not perceived as a rewarding stimulus in and of itself, and that music, may have been perceived as an aversive stimulus. In other words, if subjects preferred music to silence but did not have a preference for genre or song, it is unlikely that they would exhibit such negative behavioural reactions to test sessions. Although in theory, subjects had the option to listen to silence as opposed to music by repeatedly shuffling the exemplar in-progress

until the software program randomly selected a silence exemplar, subjects did not participate consistently enough to learn to control the program in that way. Instead, subjects expressed distress through ABs not typically observed in these subjects during similar test sessions of prior studies investigating visual preferences (L. Adams & S. MacDonald, personal communication, September 5, 2012). The “rejection” behaviour observed in Study 1, Phase II had also never been observed during any prior experimental sessions with this group of subjects before. Experimental participation provides mental stimulation and entertainment for these captive animals and such a deliberate refusal to participate in test sessions is unprecedented. The fact that subjects were averse to participating in Phase II (in which subjects were not provided food reward for participation during sessions) but were willing to consistently participate in Phase I (in which subjects were rewarded with food for each music or silence selection), again suggests that music did not serve as a reinforcing stimulus in and of itself, and that instead, food reward was necessary to motivate participation in activities that involve music. In contrast, in prior comparable studies at the same location using the same touchscreen to investigate visual preferences (where no food reward was offered as motivation), these same subjects voluntarily participated on a consistent basis (L. Adams & S. MacDonald, personal communication, September 5, 2012).

Phase III: Musical note production.

In Study 1, Phase III, again, the number, degree and severity of ABs observed, in combination with the aversion to participate, appear to indicate that subjects were not independently motivated to generate musical notes and that musical notes were not rewarding stimuli, in and of themselves. These results indicate the same preference for

silence over musical stimuli observed in Study 1, Phase I and II, suggesting that the preferences for silence observed in Phase I and II are not associated with a lack of personal control over the presentation of musical stimuli.

Study 2: Auditory discrimination

Phase I: Music vs. scrambled music.

The statistical results of Study 2, Phase I indicate that none of the three subjects could discriminate 'music' exemplars from their 'scrambled' counterparts. Subjects were, however, more accurate in correctly discriminating some exemplars more than others. When we examine the number of correct discriminations made for each exemplar (see Figure 7), all three subjects correctly classified 'music' as 'music' more often than they correctly classified 'scrambled music' as 'scrambled music'. While this could indicate a superior capacity to identify music as 'music' (in contrast to detecting scrambled music as 'scrambled music'), these results are more likely explained as a result of the subjects' significant side preferences.

Phase II: Male vs. female voices.

The quantitative results of Study 2, Phase II, indicate that while Budi and Sekali did not discriminate a familiar male orangutan keeper's voice from a familiar female orangutan keeper's voice, Ramai was able to do so. As in Study 2, Phase I, Ramai and Sekali were more accurate in correctly categorizing some exemplars more than others, but Budi was not. When we examine the number of correct discriminations made for each exemplar, Ramai and Sekali, by and large, correctly classified either 'female keeper' exemplars as 'female keeper' more often than they correctly classified 'male keeper' exemplars as 'male keeper' or vice versa (see Figure 8). Interestingly, however, both

Ramai and Sekali displayed a significant side preference, whereas Budi did not.

Therefore, as described above, Ramai and Sekali's significant side preferences most likely account for the observed differences in accuracy at making correct 'female keeper' discriminations vs. making correct 'male keeper' discriminations. However, in Ramai's case, she deviated enough from her side preference so as to achieve apparent overall correct discrimination of 'male' vs. 'female' voices.

Ramai's apparent ability to discriminate between a familiar 'male keeper's voice' and a familiar 'female keeper's voice', suggests that orangutans may be capable of discriminating and/or categorizing auditory stimuli and communicating those discriminations through the experimental paradigm employed. Furthermore, these results coupled with Ramai's demonstrated inability to discriminate between 'music' and 'scrambled music' in Phase I suggests that Ramai may not perceive 'music' the same way humans do (i.e., she does not perceive 'music' as discriminable from or qualitatively different than 'scrambled music' the same way she perceives a 'male keeper's voice' as discriminable or qualitatively different than a 'female keeper's voice').

Budi and Sekali's inability to discriminate between the voices of a male and female zookeeper whom they have interacted with and listened to on a daily basis for most of their lives suggests the discrimination and/or categorization of auditory stimuli may be a more difficult and complicated task for orangutans than would have been assumed given the typical human capacity with the same task. Because both Budi and Sekali are younger than Ramai, these findings also suggest that auditory discrimination and/or categorization aptitudes in orangutans could be associated with age and/or experience (i.e., ability increases with age and experience). A review of the primate

cognition literature revealed a surprising lack of investigation of auditory cognitive ability in apes (i.e., auditory discrimination and categorization, long- and short-term memory for auditory stimuli, etc.). However, investigations of Japanese monkeys' (*Macaca fuscata*) and rhesus macaques' (*Macaca mulatta*) auditory encoding and memory functions have revealed that auditory stimuli are markedly "fragile as discriminative stimuli" in these species (Kojima, 1985, p. 1; Ng, 2012; Ng, Plakke, & Poremba, 2009). Using a go/no-go auditory DMTS task, Kojima (1985) found that due to difficulties in encoding and rehearsal, auditory stimuli could not be transferred to long-term memory. Using an auditory DMTS task, Ng (2012) and Ng et al. (2009) found that rhesus macaques had difficulty determining if two sounds were the same or different, suggesting poor short-term memory for auditory stimuli. Auditory discrimination performance in this experiment was found to be significantly better with primate vocalization sound types than with non-vocalization sound types (Ng et al., 2012). This improved performance on vocalization sound types may be a result of familiar, biologically significant conspecific sounds or it may be related to the functioning of auditory neural substrates and the organization of the neural networks in the primate auditory system (Ng et al., 2012). These results of orangutans' close relatives combined with the results of Study 2 warrant future investigations into the auditory encoding and memory abilities of orangutans and other primates.

Phase I & II.

The decrease in ABs and increase in consistent participation observed in Study 2, Phase I and II in contrast to Study 1, Phase II and III, support the hypothesis that food rewards may be necessary to motivate orangutans to participate in activities that involve

music. Further, the fact that the orangutan displayed ABs primarily when they had made several incorrect choices in succession suggests that: (a) the types of antagonistic behaviour observed are indicative of annoyance and/or frustration and that (b) these subjects were highly motivated to achieve correct responses (resulting in a food reward). Budi's "tent behaviour" in response to a series of incorrect choices might have been an attempt to improve his performance on the task by enhancing the auditory stimulus and dampening extraneous noise. Because these subjects appeared to be highly motivated to achieve correct discriminations, Sekali's significant side preferences may indicate a lack of understanding of 'how to' achieve a correct answer to the question posed (i.e. does this auditory stimulus belong to category a or b?) rather than indifference. In other words, if Sekali did not know the correct answer, she may have resigned herself to choosing one side of the screen on a consistent basis in order to score correctly at least half of the time and thereby earn a minimum of half of the possible food rewards. However, the fact that Ramai also displayed a significant side preference, but demonstrated an understanding of how to answer the question posed, suggests that Sekali's side preference does not necessarily indicate that she did not understand the experimental paradigm.

The unusual observed behaviour of initiating new trials before the experimenter had time to reward subjects for the previous correct choice, may have been associated with observed side preferences as well, in that, because subjects could only earn a maximum of half of the available number of food rewards using a side preference approach, initiating the maximum number of trials possible became more important than if subjects were capable of receiving a food reward for every trial by correctly discriminating 'category a stimuli' from 'category b stimuli'. The fact that Sekali

demonstrated this behaviour more often than Ramai supports this hypothesis. However the fact that Budi displayed this behaviour less often than Ramai, does not. In other words, because Ramai was correctly discriminating between the ‘male zookeeper’s’ and ‘female zookeeper’s’ voices, she was receiving more than half of the available food items (i.e., she was answering correctly more often than she would have on a side preference-only based strategy and more often than Sekali and Budi). Therefore, based on the hypothesis described above, we would expect that Ramai would demonstrate the ‘new trial before reward’ behavior less often than both Sekali and Budi (who did not correctly discriminate between ‘male’ and ‘female’ voices).

General Discussion

The results of Study 1 strongly suggest that orangutans prefer silence to music or are indifferent to either and that they are *not* independently motivated to listen to particular musical genres, nor to any of the types of music employed in Study 1. These results support McDermott and Hauser’s (2007) findings that cotton-top tamarins (*Saguinus oedipus*), also preferred silence to music when provided a choice. The results of Study 1 also suggest that when given the opportunity, orangutans are not independently motivated to produce or to explore the perceptual qualities of musical notes. These results, combined with the behavioural observations recorded in Study 1, stand in direct opposition to other music-related primate investigations that indicate that, when given the opportunity, chimpanzees independently initiate musical sounds and furthermore, that music-broadcast tends to decrease aggressive behaviours in chimpanzees and increase affiliative ones (Howell et al., 2003; Lutz & Novak, 2005; Videan et al., 2007).

Thus, the question arises: why do humans, even human infants, universally share a predisposition for the enjoyment of music that such close relatives (i.e. orangutans) appear not to share? Are these differences related to perceptual ability? Do orangutans perceive music as we do? Given the tendency of subjects to choose silence, suspend test participation, or quit sessions entirely during times of alarm, excessive noise and/or commotion, it is possible that the observed preference for silence over music may relate to the potential for music to mask other auditory stimuli that provide valuable information, (e.g. keepers are preparing food, a stranger is approaching, or conspecifics are fighting). Consequently, future investigations of preference for other types of noise vs. silence in primates are warranted. However, the results of Study 2 imply a more profound explanation, mainly that orangutans may not perceive music the same way we do. In particular, Study 2 results suggest that human-defined music exemplars and scrambled versions of the same exemplars are not perceived as qualitatively different by orangutans. This finding could explain why orangutans do not appear to find the music employed in this Study 1 particularly appealing. Whereas humans perceive music as a united, stable, rhythmic and harmonious stimulus, this may not be the case for orangutans and other NHPs. Perhaps orangutans do not perceive human-defined music as qualitatively different from other auditory stimuli, or perceive music as more similar to indiscriminate noise. The antagonistic behavioural observations observed in Study 1, Phase II and III (e.g. pushing the apparatus broadcasting music away from the orangutan enclosure, body scratching and vocalizations typical of aggressions/annoyance, breaking the wooden dowel used for participation, and the “rejection behaviour”) suggest that human-defined music is most likely perceived as a mild-to-moderate aversive stimulus.

This could explain why music is perceived as unappealing and/or aggravating to orangutans.

The results of Study 1 and 2 do not provide evidence for an aesthetic musical sense, music appreciation or musical faculty in NHPs, nor do they demonstrate more complex cognitive abilities than previously assumed in animals. Although the perception and appreciation of music may not be a uniquely human faculty, orangutans, one of our closest relatives, do not appear to share: (a) music appreciation as demonstrated by preference for the music employed in this study rather than silence, and/or preference for producing musical notes over not doing so, or (b) equivalent musical perceptual capacity demonstrated by the ability to discriminate between 'music' and 'non music' stimuli. To the degree that Ramai's ability to discriminate between male and female voices demonstrates superior auditory discrimination ability (compared to Budi and Sekali), this does not appear to be associated with more preference for music over silence or for specific music genres. Nonetheless, it is worth noting that Ramai did not significantly prefer silence to music as both Budi and Sekali did. Therefore, it's possible that Ramai's apparent superior auditory discrimination abilities were associated with music being less aversive for her than it was for Budi and Sekali.

Results suggest that music (as typified by the exemplars selected for inclusion based on human preference) is not gratifying for orangutans and that, although not confirmed directly in this study, the positive therapeutic effects of these types of music on humans are unlikely to be applicable to orangutans as well. These conclusions are supported by Hinds et al.'s (2007) findings that recorded harp music did not significantly

affect the heart rate, blood pressure, respiratory rate, or body-temperature of nine African green monkeys (*Chlorocebus aethiops*).

Importantly, these results, particularly the behavioural observations, suggest that the common practice of using Western, human-defined music as an enrichment tool in primate care facilities is unfounded, misguided, and may even result in effects opposite to those intended. Although it could be argued that perceptual abilities related to music appreciation are shaped by experience and that preference for music, although not innate, could be developed through experience, the subjects' prior experience with music (regularly used as auditory enrichment tool at the Toronto Zoo) combined with their apparent preference for silence over music or indifference appears to refute this hypothesis (Lamont, 2005).

The implications of the results of Study 1 and 2 on music's evolutionary role in human development are more complicated. Particularly, in reference to Darwin's musilanguage model of music development, results appear to point to one of three possible conclusions: (a) music and language do not share an evolutionary history and there was likely no prosodic protolanguage that preceded language as we understand it today, (b) music and language share an evolutionary history but the development of Darwin's proposed prosodic protolanguage occurred after humans significantly diverged from the lineage shared with orangutans or (c) that music and language share an evolutionary history and the development of Darwin's prosodic protolanguage occurred before humans diverged from the lineage shared with orangutans, but, the human-centric music used to investigate orangutan music capacity is inappropriate.

Music exemplars for Study 1 were selected based on human-preference as indicated by the greatest iTunes purchases, intended to be a critical mass of selections preferable to a large number of humans who expressed preference through purchasing behaviour. However, given the research findings on auditory acuity in primates, there is reason to believe that primates may perceive sound and more specifically music, differently than humans. Chimpanzees, a close phylogenetic relative of orangutans, appear more sensitive to higher frequencies of auditory stimuli than humans (Coleman, 2009). Because we cannot perceive a proportion of these higher frequencies, it is possible that some or all of the music highly preferred by humans contains high frequency tones that might be perceived as aversive to the high-frequency-competent listener (e.g. orangutans). This could explain why subjects, (even if they do indeed share a musical capacity with humans) do not prefer the music employed in this study to silence and/or do not appear capable of discriminating it from scrambled 'non-music'. In other words, maybe modern day human-defined 'music' has diverged so far from what Darwin's prosodic protolanguage sounded like to constitute an inappropriate stimulus in investigations concerning music evolution, primate music preference and discrimination. An investigation of the degree and quality of the higher frequencies found within the music exemplars employed in this study would have been warranted and informative. Future studies concerning primate music capacity would benefit from these types of analyses. Furthermore, future studies investigating primate musical capacity might benefit from approaching the selection of music exemplars from a less human-centric perspective and from a more primate-centric one. This would involve the selection of music exemplars that: (a) are limited with respect to higher frequencies, (b) that focus on

lower frequencies, and (c) that more closely resemble primate vocalizations (i.e. less variability with respect to pitch and more variability with respect to rhythm, given that the majority of orangutan vocalizations are made via the exhalation of air through the throat/lips or consist of grumbles, barks, squeals and grunts). It is important to note, that in this vein, Tuva throat singing was employed as a genre in Study 1 because it shares some resemblance to orangutan long calls. However it was also not preferred over silence, nor was it preferred over other genres of music.

Nevertheless, orangutan long calls serve as an interesting example of a vocalization that appears to serve a direct evolutionary and adaptive purpose. The long call, emitted by male orangutans, is observed to function as both a mate-attraction tool and a territorial spacing tool, regulating dominant male spacing and relationships in overlapping home ranges (Delgado, 2006; Utami Atmoko et al., 2009). Because female orangutans will adjust their positioning to remain within earshot of the long calls of dominant males, it is possible that this vocalization elicits an erotic response in female orangutans that inspires approach behaviour (Delgado, 2006; Utami Atmoko et al., 2009). In this way, the long call's function is remarkably similar to several hypothesized evolutionary functions of music (e.g. displaying biological fitness, eliciting physiological arousal, developing/strengthening social bonds, transporting information, etc.) (Schafer & Sedlmeier, 2010). Therefore it could be argued that the long call functions as a type of prosodic protolanguage itself and its existence may support Darwin's (1901) musilanguage model of music development.

In reference to the species tested in this investigation, it is important to note that as far as primates are concerned, orangutans possess some qualities (atypical of the

primates order) that make them unlikely candidates for demonstrating musical capacity when compared to other closely-related primate species. Because orangutans typically do not live in large social groups like chimpanzees, gorillas and bonobos, they are consequently less gregarious and less vocal than other apes (Shumaker, 2007; Van Schaik, 2004). Furthermore, because orangutans are categorically arboreal, spending the majority of their time in trees, they are less vulnerable to ground-dwelling predators. Consequently, it is reasonable to hypothesize that orangutans, in comparison to ground-dwelling apes, may require less detailed or expressive communication to warn other conspecifics of impending predatorial danger. Orangutans' predisposition towards an arboreal, solitary lifestyle, coupled with their lack of vocality, means that sociality and vocal communication is of lesser importance and under less selective pressure in orangutans than in other closely related primate species. As discussed earlier, several of the proposed evolutionary functions of the human music faculty are related to sociality and communication (Schafer & Sedlmeier, 2010). Therefore, it is reasonable to hypothesize that despite their phylogenetic closeness to humans, orangutans may be among the least likely ape species to possess a musical faculty. Consequently, future investigations exploring primate music preference and discrimination may be well served in seeking out a more social and vocal ape for investigation. Chimpanzees (*Pan troglodytes*) and Western gorillas (*Gorilla beringei*) are examples of such experimental candidates in that they are more closely related to humans than orangutans, live in large social groups, and are less arboreal and more vocal than orangutans (De Waal, 2005). Sugimoto et al.'s (2009) finding that similarly to human infants, a juvenile human-raised chimpanzee preferred consonant-patterned music to dissonant-patterned music, suggests

some type of musical discrimination ability in chimpanzees. Furthermore, a recent analysis of the Western gorilla's genome sequence (human's closest living relatives after chimpanzees), found that in 30% of the genome, gorillas are closer to humans, than chimpanzees are to humans (Sally et al., 2012). Sally et al (2012), found approximately 500 genes showing parallel accelerated rates of evolution in the gorilla, human and chimpanzee lineages, particularly genes involved in sensory perception, brain development and hearing. Genes involved in hearing were found to be most strongly enriched in parallel accelerations of Gorillas and humans (Sally et al., 2012). These findings indicate that gorillas and chimpanzees, particularly gorillas, like humans, may have evolved more sophisticated hearing and listening abilities than other primate species. Consequently, investigation of the music preferences and discrimination capacity of these species could significantly contribute to debates over the evolution of music and language in humans.

Limitations

As is often the case in captive animals investigations, the present study was limited with respect to sample size. As a means of experimental replication, repeated observations of three subjects were carried out in an effort to obtain a large sample of behaviour. Replication requires that an experimental group contain a sufficient number of individuals to offer a complete and accurate assessment of behaviour. Replication provides two crucial advantages. First, it provides an average of outcomes based on multiple independent observations, as opposed to a single and possibly atypical one. This affords *more* information and *more reliable* information, making it less likely that conclusions are based on unusual and uncommon cases. Second, it increases validity because it allows estimations of error (calculated by looking at the variation between several estimates of the same effect) (Field, 2009). Thus, the chance of detecting a real effect in an experiment is intrinsically related to sample size (Field, 2009; Hurlbert, 2009). In collecting repeated observations of three subjects, large samples of *behaviour* were obtained rather than behaviour from a large sample of *individuals* (Machlis et al., 1985). When such methods are employed: (a) it is less likely that the small sample is a reliable representative of the population parameters we wish to estimate and (b) the probability of rejecting the null hypothesis is often greater than the reported alpha level, resulting in increased chances of Type I error. Consequently, inferences about a population of individuals (i.e. orangutan species) based on the results obtained are less valid than if more individuals had been tested (Field, 2009).

Another limitation of experiments involving captive animals, as opposed to human subjects, is less control of the experimental environment and experimental

subjects. These experiments were implemented at the Toronto Zoo. Although experimental subjects were physically separated from one another, there were some compromises that were unavoidable: (a) experimental subjects had some visual and auditory contact between enclosures during experimental sessions, and (b) subjects were not separated from other non-experimental conspecifics (Budi was housed with his mother, Ramai with her daughter, and Sekali with her son). Considering there has been repeated scientific confirmation of social learning in both captive and wild orangutans, visual and auditory contact during experimental sessions, could have resulted in more similar experimental behaviour between subjects in Study 1 than would have been expected if subjects were isolated during testing (Jaeggi et al., 2010; Merrill, 2005; Stoinski & Whiten, 2003). For example, subjects who saw conspecifics choosing silence and/or reacting negatively to musical stimuli, may have replicated these behaviours themselves. Furthermore, subjects' roommates served as a potential distraction during testing and in rare cases a physical obstacle from full participation (e.g. stealing a subject's dowel, blocking the screen, breastfeeding, etc.). It should be noted however, that although roommates had physical access to experimental subjects, they were successfully lured into adjoining enclosures with food for the majority of testing.

Furthermore, although the testing area was accessible only to zookeepers and experimenters, experimenters had little control over other extraneous stimuli. For example, a zookeeper could enter the testing area in mid-trial carrying food, or a construction vehicle could be parked outside the orangutan pavilion for the duration of a testing session. Generally speaking, auditory, tactile and visual stimuli competed for subjects' attention to varying degrees throughout testing and in ways that were not

measurable, and therefore could not be controlled for when analyzing the results. Despite attempts to counteract this potential confound by executing a large number of trials, this lack of experimental control inevitably and unavoidably affected the behavioural and quantitative results to some degree.

Finally, it is important to note that although in every phase of this investigation, preference was assessed through free-choice participant-controlled paradigms, Study 1, Phase I and II were less participant-controlled than in Study 1, Phase III. In other words, in Study 1, Phase I and II, although subjects had access to adjoining enclosures by which they could avoid the stimuli being tested or could terminate a test session (by not participating for 10 min or more), during participation, they were required to listen to music exemplars and/or to make choices between music-replay and silence. This was particularly true in Study 1, Phase II in which no touchscreen selection resulted in continuous play of the current stimulus. Conversely, in Study 1, Phase III, subjects had more control over stimulus-activation in that they *initiated* musical notes themselves by touching the screen. If subjects did not touch the screen, stimuli were not sounded. Therefore ‘preference’ as assessed in Study 1, Phase I and II may be more vulnerable than ‘preference’ as assessed in Study 1, Phase III to being interpreted as a ‘least-aversive preference’ as opposed to a preference based on desire or ‘liking the most’. This returns focus to the definition of preference in terms of either ‘least aversive’ or ‘most desirable’. Whether the two perspectives in this experimental context can be exclusively distinguished is questionable, as what is ‘least aversive’ can be perceived as ‘most desirable’, and what is ‘most desirable’ can be perceived as ‘least aversive’ (i.e. “I don’t like music, therefore I prefer silence” or “I like silence, so I prefer not to listen to

music”). For example, in Study 1, Phase III, even if subjects had demonstrated preference for generating musical notes through touchscreen contact, one could argue that this also constituted a least aversive choice, in that boredom, or silence could be aversive and musical notes, in comparison, could be relatively entertaining or distracting. Nonetheless it would appear that although not absolute, Study 1, Phase III represents more of a measure of desirability than in Study 1, Phase I and II, in which subjects were subjected to musical stimulus and had to take action to avoid further stimulus exposure. This is of particular relevance in this investigation, in which the combined results of Study 1 suggest music may be aversive and silence may be less aversive, if not desired.

Finally, subjects’ choice of “silence” cannot be interpreted as a choice of true categorical silence per se, in that the silence condition was relatively uncontrolled and only characterized by a lack of experimental auditory stimuli. Therefore the “silence” condition in this context was filled with various ambient zoo-noises. The effect of ‘true silence’ through the use of a sound chamber or other means of soundproofing on the results of this type of paradigm would be an interesting area of inquiry for future investigations.

Auditory Acuity Assessment

Because of limited physical access to subjects’ as well as ethical and safety concerns, assessment procedures based on auditory evoked potentials were not feasible. Consequently, behavioural conditioning and observational procedures were employed to measure subjects’ auditory acuity. Hicks et al. (2000) found that the difference between electrophysiological measures of acuity and behavioural measures of acuity is larger in auditory acuity research than in visual acuity research (Hicks et al., 2000). This could be

interpreted as an indication that the BOA does not provide an acutely accurate measure of auditory acuity. However, this testing limitation should not significantly affect results as Rance et al. (2005), found that hearing thresholds in infants obtained via auditory steady-state response (ASSR) are highly correlated with thresholds obtained via behavioural methods (visual response audiometry). Furthermore, some argue that behavioural conditioning procedures more readily function as an index of functional hearing than auditory evoked potentials procedures based on electrophysiological responses that do not necessarily equate with functional hearing (Werker et al., 1997). Although ideally the auditory acuity testing setting would have been more strenuously controlled with regards to extraneous noise and vibration (i.e. testing in a double-walled sound attenuating chamber), due to limited access to and control of subjects, this was not feasible and therefore, it is possible that ambient noise and/or vibrations resulted in less accurate audible frequency values (Coleman, 2009).

Furthermore, the methodology employed assessed subjects' auditory acuity at a single threshold of 100.3 dB. This stands in contrast to the more systematic method of auditory acuity assessment in which tone amplitude is varied to find subjects' auditory thresholds (the *lowest* detectable auditory level) at various frequencies. Because the absolute thresholds of the tones used in testing were not varied, the resulting auditory acuity assessment is not as precise as it might have been had tone amplitude been varied for the frequencies tested. Furthermore, the auditory acuity assessment did not employ a large number of trials. Testing was completed in a single session of 24 trials per subject in an environment where extraneous noise could not be controlled. Furthermore, ITI length was not formally randomized, nor was the order of the delivery of the frequency

stimuli (i.e., frequency stimuli were presented from highest to lowest frequency).

Consequently, the results of this assessment are less accurate and/or durable than if more trials had been employed for each subject in a quieter testing environment, and both ITI length and frequency-delivery order had been formally randomized. In the context of this investigation, auditory acuity assessments were only executed to ensure that test subjects could hear the experimental stimuli (i.e., they did not suffer from unusual hearing deficits). Therefore the levels of precision offered by a larger sample of behaviour and the variation of tone amplitude were not deemed necessary. However, given the lack of literature addressing auditory acuity in orangutans, combined with the differences in the auditory acuity ranges obtained in this study and Coleman's (2009) meta-analysis, future studies that more directly and precisely assess orangutan auditory thresholds are warranted and could have implications for the interpretations of results from the current series of investigations.

Finally, due to a significant negative behavioural reaction by Budi's roommate (his mother) to the stimuli used in the auditory acuity investigation, Budi's hearing could not be reliably tested. Although it is unlikely that Budi suffers from an acute hearing deficit (there is no behavioural evidence to support that conclusion), this possibility cannot be ruled out.

Study 1: Musical Preferences

Phase I: Music preferences vs. silence.

The potential confounding contribution of subject choices based on perceived "choice-*correctness*" (i.e. a subject's belief that one genre/colour is the "correct" choice) rather than *preference* cannot be conclusively ruled out via the methodology employed.

However, it is important to note that the observed deviance from 100% selection of a specific colour and its representative genre, suggests that a specific screen colour/genre was not perceived by subjects as the “correct” choice, or a behaviour that would be exclusively reinforced (because alternative choices were made by the subjects and reinforced). A further potential limitation related to the use of colours to represent music genres is that it is possible subjects preferred one colour to another and that colour preference thus confounded their music vs. silence selections. However, the lack of a demonstrated genre preference by any of the test subjects (or a colour preference), suggests the absence of such a confound.

Additionally, according to the preference-feedback hypothesis, there remains the possibility that music vs. silence choices may have become influenced by familiarity (Ellington, 2001). According to research on the preference-feedback hypothesis, liking can increase as a function of familiarity (Ellington, 2001). Because grey, representing silence appeared 7 times as often as any other colour (representing the other 7 genres) during testing, it is possible that over several trials, grey/silence became more familiar and accordingly more preferred. A plot of grey/silence selection vs. colour/music selections was used to assess the degree to which familiarity may have influenced preference for grey/silence (see Figure 6). The lack of a visual positive correlation between session date (i.e., the number of sessions following the first session) and number of grey/silence choices in Ramai’s plots appears to indicate that familiarity was, not, in her case, associated with increasing preference for grey/silence (i.e., she did not appear to make more silence selections as she became more familiar with the test paradigm). However, Sekali’s and Budi’s data show a steady increase in silence selections from the

beginning of testing in May (30% and 39% silence selections respectively) to mid-June (100% and 86% silence selections respectively). This visually identified trend may indicate that Sekali's and Budi's demonstrated silence preferences were influenced by familiarity. On the other hand, the behavioural observations in Study 1, Phases II and III, both of which employ different methodologies not subject to this confound, confirm the results of Study 1, Phase I. Consequently, the likelihood of familiarity being responsible for the results found in Study 1, Phase I is reduced. However, in retrospect, representing all of the musical genres with a single colour would have decreased the potential confounding effects of this variable and would be recommended for future studies.

Phase II: Music-silence shuffle.

Although in theory subjects had the option to listen to silence as opposed to music (by repeatedly shuffling the exemplar in-progress until silence was randomly selected by the software program), subjects did not participate consistently enough to control the program to this degree. Subjects' aversion to participation and/or irregular, inconsistent participation in this phase of Study 1 compromised both the sufficiency and the meaningfulness of data collected. In other words, when the experimenter activated a trial, a randomly selected exemplar would play indefinitely until the subject initiated a stimulus shuffle through touchscreen contact. In this regard, preference would be measured by total time each exemplar played (indicating preference). However, refusal to participate and/or inconsistent participation resulted in limited stimuli shuffles and consequently, continuous play of the current music exemplar. Therefore, although the data would indicate "preference" for the stimulus that played for the session's duration, in reality, it is highly questionable whether this number signified "preference" or aversion to

participate. Consequently, because the data collected were not suitable or sufficient for statistical analyses, conclusions about this phase of Study 1 relied wholly on subjective qualitative behavioural observations. Although such qualitative research methods are a useful, informative and arguably crucial component of empirical investigation, ideally the analysis of objective, quantitative numerical data would have been employed to identify statistical relationships and support the behavioural results. A consequence of this limitation is that the validity, reliability and generalizability of quantitative findings are reduced.

Phase III: Musical note production.

As a result of significant ABs, aversion to participation, as well as ethical considerations, Study 1, Phase III was terminated prematurely. Consequently Phase III suffered from a lack of sufficient and suitable quantitative data and relied wholly on qualitative behavioural observations. Accordingly, Phase III suffered from the same limitations as Phase II with respect to validity, reliability and generalizability. However, it should be noted that aversion-to-participation in this phase could be more categorically interpreted as a preference for silence to musical notes, as the stimuli were not activated (i.e. did not sound) unless a subject actively participated in the trial by touching the keyboard displayed on the touchscreen. However in contrast to Phase II, Phase III consisted of only a single experimental session and therefore conclusions drawn from relatively limited behavioural observations are less conclusive.

Phase II and III

In comparing Study 1, Phase II and III to Study1, Phase I and Study 2, Phase I and II, it is important to note that there were differences in the use of food reinforcements

(i.e. in Study 1, Phase I and Study 2, food reinforcements were used to motivate participation, whereas in in Study 2, Phase II and III, no food reinforcement were employed). This makes interpretation of the behavioural results observed in Study 1, Phase II and III more difficult. Although it has been inferred here that the aversion to participate and ABs observed in Study 1, Phase II and III were a result of the stimulus employed (i.e. music and musical tones), it is possible that because the subjects had been rewarded with food for participation in Study 1, Phase I, that the ABs observed in Study 1, Phase II and III were instead, a reaction to the withdrawal of food reinforcement (i.e. an orangutan strike). However, subjects' consistent participation and lack of ABs during a similar study that investigated visual preferences (without food reinforcement), makes this interpretation of the behavioural results unlikely (L. Adams & S. MacDonald, personal communication, September 5, 2012). Rather, it appears that, unlike visual stimuli that are intrinsically rewarding (i.e. interesting and stimulating enough to motivate participation without supplementary reinforcement), musical auditory stimuli are not.

Study 2: Auditory discrimination

Phase I: Music vs. scrambled music.

A potential limitation of Study 2, Phase I is that the 'scrambling' method employed to create 'scrambled music' exemplars may not have been sufficient to result in 'scrambled music' exemplars that were categorically discriminable from music exemplars. Although an unofficial pilot of the discriminability of these exemplars was undertaken with human subjects, and was confirmed to be satisfactory in that regard, it is possible that these two groups of stimuli were simply not sufficiently dissimilar for

orangutans. Other methods of ‘scrambling’ musical stimuli could be employed in future research to determine if this is the case.

Phase I and II.

The use of two different colours (as discrimination choice tools) in Phase II than those used in Phase I could serve as a confound if subjects were less able to discriminate between the two colours used in Phase I than the two colours used in Phase II, or vice versa. However, there is no reason to believe that red and green are less discriminable to orangutans than yellow and blue. Furthermore, the comparable results of Phase I and II for Budi and Sekali suggest that the colours used as a discrimination choice tool did not affect their results. On the other hand, this similarity does not rule out a possible colour discrimination confound.

It should also be noted that because Phase II was employed directly after Phase I, the observed improvement in Ramai’s discrimination abilities in Phase I vs. Phase II could be explained by learning or practice. In other words, Ramai may have proved able to discriminate the auditory stimuli employed in Phase II because, when she began testing in Phase II, she had accumulated experience with the experimental paradigm (via Phase I) and consequently was more skilled at expressing discriminations in Phase II than in Phase I. In other words, if Phase II had been implemented before Phase I, Ramai may have demonstrated a similar learning curve and a consequent ability to discriminate ‘music’ from ‘scrambled music’.

Furthermore, because Budi and Sekali failed to discriminate between two categories of familiar stimuli in Phase II of Study 2 (the control condition), it’s possible that the lack of significant findings in Phase I and II represent these subjects’ inability to

master the software program employed, rather than an inability to discriminate between stimuli categories. However, orangutans have repeatedly demonstrated the ability to master touchscreen delivered DMTS tasks in experiments concerning visual stimuli, first- and second-order relations, and social relationships (Vonk, 2002; Vonk, 2003). Consequently, it is unlikely that inability to master the experimental paradigm is responsible for the quantitative results obtained. Furthermore, Ramai's success at discriminating between categories of auditory stimuli in Phase II appears to demonstrate that an orangutan is capable of mastering the experimental paradigm employed. However, ideally, an additional visual, touchscreen-delivered DMTS task would have been employed to act as a control for Phase I and II, as means of validating the experimental paradigm employed.

Conclusions

The most striking finding of this series of investigations is that orangutans did not find music reinforcing. They were not independently motivated to listen to the music exemplars employed, nor to produce musical notes, either preferring silence to music or, alternatively, demonstrating indifference. Furthermore, the results of Study 2 suggest that this finding may be linked to how orangutans perceive music and discriminate music from other auditory stimuli. Orangutans were unable to discriminate human-defined music exemplars from scrambled versions of the same exemplars. While humans generally perceive music as a united, stable, rhythmic, harmonious and gratifying stimulus, this did not seem to be the case for these orangutans. It is possible that orangutans do not experience human-defined music as qualitatively different from other auditory stimuli (i.e. indiscriminate noise) and/or find musical sounds aversive. In either case, results suggest that the music employed in these investigations was not rewarding for them. Consequently, the use of these genres of music as environmental enrichment in captive primate facilities appears unfounded and may in fact be aversive, resulting in negative behavioural and/or psychological effects.

Although the implications of the findings of these investigations on music's evolutionary role in human development are more complex, these findings contribute to current debates about the evolution of music and language in humans and to approximations of when music production and appreciation developed in human history. Finally, the investigative findings focus scientific attention on how the appreciation and perception of music and other auditory stimuli differ for human and nonhuman animals

and suggest a more primate-centric approach to future studies on enriching sounds for non-human primates.

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Appendix A

Study 1, Phase I and II Classical Music Genre Exemplars

Name	Time	Album	Artist
1 La campanella in G-Sharp Minor fr...	4:47	Liszt - My Piano Hero (Deluxe Edit...	Lang Lang
2 Carmen: Act I: Habanera: L'amour...	3:31	Lord, Marie-Josée: Gershwin, Ber...	Marie-Josée Lord, Metropolitan Or...
3 Etudes Opus 125, No. 1, A Major (...)	2:36	The Piano Poet	Frédéric Chopin
4 Keyboard Concerto in F Minor, B...	3:34	J.S. Bach: Piano Concertos BWV...	Bernard Labadie, Les Violons du...
5 Symphony No. 9 in D Minor "Chor...	13:01	Beethoven: 9th Symphony - Huma...	Orchestre Symphonique De Montr...
6 Etude in F Minor, Op. posth. " Mét...	1:57	Mozart: Piano Concerti Nos. 19 & 23	Hélène Grimaud
7 Concerto in G Minor, RV 416: II. A...	3:09	Vivaldi: Cello Concertos	Jean-Guihen Queyras, Akademie f...
8 O Holy Night	5:57	The Colors of Christmas	The Bach Choir, Royal Philharmoni...
9 String Quartet No. 19 in C Major,...	8:14	Mozart String Quartets	Quatuor Ébène
10 Symphony No. 6 in F Major, Op. 6...	11:41	Beethoven: Le souffle du temps (I...	Kent Nagano & Orchestre Symp...
11 Partita II BWV 1004 in D minor, I...	5:36	Bach: Sonatas & Partitas for solo...	Isabelle Faust
12 Symphony in D Minor, M. 48: II. All...	11:12	Schmitt: La tragédie de Salome - ...	Yannick Nezet-Seguín & Metropoli...
13 La bohème, Act 3: "Donde lieta usci"	3:29	Anna Netrebko - Live At the Metro...	Anna Netrebko, Metropolitan Oper...
14 Salve virgo regia - Ave gloriosa m...	2:59	Secret Voices - Chant & Polyphon...	Anonymous 4
15 String Quartet, K. 589: Larghetto	6:27	Mozart: Prussian Quartets	Emerson String Quartet
16 Lincolnshire Posy (Arr. T. Higgins f...	2:22	CSO Resound - Chicago Sympho...	Chicago Symphony Orchestra, br...
17 Borrowed By Ives: Traditional Mel...	3:26	Charles Ives: Four Sonatas	Hilary Hahn & Valentina Lisitsa
18 Symphony No. 4 in F Minor, Op. 3...	10:51	Tchaikovsky: Symphony No. 4	Valery Gergiev & Mariinsky Orche...
19 Concerto for Violoncello and Orch...	4:13	Il Progetto Vivaldi 2	Sol Gabetta, Andrés Gabetta & Ca...
20 Piano Concerto No. 3 in D Minor,...	16:56	Rachmaninoff: Piano Concerto No...	Garrick Ohlsson, Atlanta Symphon...
21 Piano Sonata No. 3 in C, Op. 2, N...	10:51	Alice Sara Ott Plays Beethoven	Alice Sara Ott
22 Die Walküre, Act III: Der Augen le...	5:56	Wagner	René Pape, Staatskapelle Berlin...
23 Cuatro Piezas Españolas: II. Cuba...	4:21	Manuel De Falla: Noches en los J...	Javier Penabaz
24 Symphony No. 9 in C Major, D. 94...	16:41	Beethoven: Eroica Symphony - Sc...	Berliner Philharmoniker & Wilhelm...
25 O gloriosa Domina (Gregorian)	0:36	Hispania & Japan - Dialogues	Hesperion XXI, La Capella Reial...
26 Symphony No. 7 in E Major: I. Alle...	20:10	Bruckner: Symphony No. 7 in E M...	Kent Nagano & Bayerisches Staat...
27 Chasse-neige	5:50	Liszt: Piano Works	Nikolai Lugansky
28 Armida abbandonata, HWV 105: A...	4:50	Il caro Sassone - Handel in Italy	Lucy Crowe, The English Concert...
29 Cantata "Ich habe genug" BWV 8...	7:01	Andreas Scholl - Bach Cantatas	Andreas Scholl, Kammerorchester...
30 Symphony No. 6 in B Minor, Op. 5...	7:17	Shostakovich: Symphonies Nos. 6...	Royal Liverpool Philharmonic Orc...

Appendix B

Study 1, Phase I and II Jazz Music Genre Exemplars

Name	Time	Album	Artist
1 What a Wonderful World (Single V...	2:20	Louis Armstrong's All-Time Greate...	Louis Armstrong
2 At Last	3:01	At Last!	Etta James
3 The Look of Love	4:41	The Look of Love	Diana Krall
4 Take Five	5:24	Dave Brubeck's Greatest Hits	Dave Brubeck
5 Oh My My	4:43	Chances	Jill Barber
6 La Vie en Rose	3:10	Greatest Hits	Edith Piaf
7 Ain't No Sunshine	3:26	Time After Time (International Ver...	Eva Cassidy
8 I'll Be Seeing You (1944 Single)	3:33	The Complete Commodore Recor...	Billie Holiday
9 Fever	3:22	Fever	Peggy Lee
10 Sing, Sing, Sing	8:40	The Essential Benny Goodman (R...	Benny Goodman
11 Dance Me to the End of Love	3:55	Careless Love	Madeleine Peyroux
12 New York, New York	3:42	New York, New York	Frank Sinatra
13 Somethin' Stupid	2:50	Swing When You're Winning	Robbie Williams
14 Forever In Love	4:59	Kenny G: Greatest Hits	Kenny G
15 Summertime	4:58	Porgy and Bess	Ella Fitzgerald & Louis Armstrong
16 Green Onions	2:54	The Best of Booker T & The MGs	Booker T. & The MG's
17 Soul Bossa Nova	2:44	Big Band Bossa Nova	Quincy Jones & Quincy Jones and...
18 Never Quit Loving You	2:58	Chances	Jill Barber
19 Besame Mucho	6:40	The Look of Love	Diana Krall
20 This Masquerade	8:04	Breezin'	George Benson
21 A Kiss to Build a Dream On (Singl...	3:04	Louis Armstrong's All-Time Greate...	Louis Armstrong
22 Going Home (Edit)	4:16	Kenny G: Greatest Hits	Kenny G
23 Chances	3:43	Chances	Jill Barber
24 In a Sentimental Mood	4:16	The Very Best of John Coltrane	John Coltrane & Duke Ellington
25 So What	9:22	Kind of Blue	Miles Davis
26 I Put a Spell on You	2:38	The Best of Nina Simone	Nina Simone
27 When You're Smiling (The Whole...	4:06	Louis Armstrong's All-Time Greate...	Louis Armstrong
28 Misty	2:49	The Original Misty	Erroll Garner
29 The Boy from Ipanema	4:52	Quiet Nights (Bonus Track Version)	Diana Krall
30 Blue In Green	5:37	Kind of Blue	Miles Davis

Appendix C

Study 1, Phase I and II Rock Music Genre Exemplars

Name	Time	Album	Artist
1 Don't Stop Believin'	4:09	Journey: Greatest Hits	Journey
2 Crawling Back to You	3:45	Break the Spell (Deluxe Version)	Daughtry
3 Sweet Home Alabama	4:45	20th Century Masters - The Millen...	Lynyrd Skynyrd
4 Under the Bridge	4:25	Red Hot Chili Peppers: Greatest Hits	Red Hot Chili Peppers
5 Losing My Religion	4:27	In Time - The Best of R.E.M. 1988...	R.E.M.
6 Bully	4:01	Bully - Single	Shinedown
7 Livin' On a Prayer	4:10	Bon Jovi Greatest Hits	Bon Jovi
8 The Sound of Winter	3:28	The Sea of Memories (Deluxe Edit...	Bush
9 Knockin' On Heaven's Door	5:36	Guns N' Roses: Greatest Hits	Guns N' Roses
10 Enter Sandman	5:31	Metallica	Metallica
11 Rock 'n Roll All Nite	2:48	Greatest Kiss	KISS
12 Hotel California	6:30	Hotel California	Eagles
13 Rock You Like a Hurricane	4:15	20th Century Masters - The Millen...	Scorpions
14 Rockin' In the Free World	4:41	Neil Young: Greatest Hits	Neil Young
15 Nothing Else Matters	6:28	Metallica	Metallica
16 New Orleans Is Sinking	4:18	Yer Favourites (International Versi...	The Tragically Hip
17 Albatross	4:14	Albatross - Single	Big Wreck
18 Eye of the Tiger	4:03	Eye of the Tiger (Remastered)	Survivor
19 Here Without You	3:58	Away from the Sun	3 Doors Down
20 How to Save a Life	4:22	How to Save a Life	The Fray
21 We Will Rock You	2:02	Queen: Greatest Hits	Queen
22 Sweet Child O' Mine	5:56	Appetite for Destruction	Guns N' Roses
23 Lips of an Angel	4:21	Extreme Behavior	Hinder
24 Kryptonite	3:53	The Better Life	3 Doors Down
25 Smoke On the Water	5:38	The Very Best of Deep Purple	Deep Purple
26 Hey Jude	7:09	1	The Beatles
27 Stairway to Heaven	8:02	Mothership (Remastered)	Led Zeppelin
28 Paradise City	6:46	Appetite for Destruction	Guns N' Roses
29 Livin' On a Prayer	4:10	Bon Jovi Greatest Hits - The Ultim...	Bon Jovi
30 Here Comes the Sun	3:05	Abbey Road	The Beatles

Appendix D

Study 1, Phase I and II Pop Music Genre Exemplars

Name	Time	Album	Artist
1 Call Me Maybe	3:13	Call Me Maybe - Single	Carly Rae Jepsen
2 Coming Home	3:58	Last Train to Paris (Deluxe Version)	Diddy - Dirty Money & Skylar Grey
3 Domino	3:51	Domino - Single	Jessie J
4 Give Me All Your Lovin' (feat. Nicki...)	3:22	Give Me All Your Lovin' (feat. Nicki...)	Madonna
5 Give Me Everything (feat. Ne-Yo,...)	4:12	Planet Pit (Deluxe Version)	Pitbull
6 Good Feeling	4:06	Good Feeling - Single	Flo Rida
7 Good Life	4:13	Waking Up (Deluxe Version)	OneRepublic
8 Hangover (feat. Flo Rida)	4:04	Hangover (feat. Flo Rida) - Single	Taio Cruz
9 Hey Ya! (Radio Mix/Club Mix)	3:55	Speakerboxxx / The Love Below	OutKast
10 Hit the Lights	3:14	When the Sun Goes Down	Selena Gomez & the Scene
11 Invincible	3:43	Stoms (Deluxe Edition)	Hedley
12 Like a Prayer	5:40	Like a Prayer	Madonna
13 Love You Like a Love Song	3:08	When the Sun Goes Down	Selena Gomez & the Scene
14 Marry the Night	4:24	Born This Way (Bonus Track Versi...	Lady GaGa
15 Marry You	3:50	Doo-Wops & Hooligans (Deluxe V...	Bruno Mars
16 Moves Like Jagger (The Voice Per...	3:21	Moves Like Jagger (The Voice Per...	Maroon 5
17 Mr. Know It All	3:52	Stronger (Deluxe Version)	Kelly Clarkson
18 Not Over You	3:38	Sweeter	Gavin DeGraw
19 The One That Got Away	3:47	Teenage Dream (Deluxe Edition)	Katy Perry
20 Party Rock Anthem (feat. Lauren...	4:22	Sorry for Party Rocking (Deluxe V...	LMFAO
21 Pump It	3:32	Monkey Business	The Black Eyed Peas
22 Right Round (feat. Ke\$ha)	3:27	Right Round (feat. Ke\$ha) - Single	Flo Rida
23 Shut Up and Dance	3:54	Shut Up and Dance - Single	Victoria Duffield
24 Stereo Hearts (feat. Adam Levine)	3:30	Stereo Hearts (feat. Adam Levine)...	Gym Class Heroes
25 Stronger (What Doesn't Kill You)	3:41	Stronger (Deluxe Version)	Kelly Clarkson
26 This Is How We Do It	4:37	This Is How We Do It	Montell Jordan
27 Till the World Ends	3:57	Femme Fatale (Deluxe Version)	Britney Spears
28 Tonight Tonight	3:20	Whatever	Hot Chelle Rae
29 Wavin' Flag	3:40	Troubadour	K'naan
30 We Found Love (feat. Calvin Harris)	3:35	We Found Love (feat. Calvin Harri...	Rihanna

Appendix E

Study 1, Phase I and II Children's Music Genre Exemplars

Name	Time	Album	Artist
1 Down By the Bay	2:11	Singable Songs for the Very Young	Raffi
2 The Wheels on the Bus Go Round...	1:27	30 Toddler Songs (for ages 2+)	Countdown Kids
3 Teddy Bears' Picnic	2:44	There's a Hippo In My Tub	Anne Murray
4 Des maisons	2:00	Génération Passe-Partout	Cœur de pirate
5 If You're Happy and You Know It	1:14	20th Century Masters / the Best of...	Raffi
6 We Love a Luau	1:30	Born to Play	The Backyardigans
7 Twinkle Twinkle Little Star	1:19	150 Fun Songs for Kids (Digital Ve...	Countdown Kids
8 Biscuits In the Oven	2:26	Baby Beluga	Raffi
9 Flute Sonata in E-Flat, BWV 1031,...	2:32	Baby Einstein: The Definitive 100	The Baby Einstein Music Box Orc...
10 Where Did We Go Wrong?	1:24	Phineas and Ferb Holiday Favorites	Cast - Phineas and Ferb
11 Skip to My Lou	1:41	You Are My Sunshine	Elizabeth Mitchell
12 Sesame Street Theme	1:48	Sesame Street: Platinum All-Time...	The Kids
13 The Duck Song	3:11	The Duck Song (The Duck and th...	Bryant Oden
14 Wonderwheel	3:21	For the Kids	Dan Zanes
15 She'll Be Comin' Round the Mount...	2:43	Great Big Hits, Vol. 1	Sharon, Lois & Bram
16 The Cat Came Back	3:34	The Cat Came Back	Fred Penner
17 Apples and Bananas	1:40	One Light, One Sun	Raffi
18 Jingle Bells	2:09	Christmas Album	Raffi
19 Daydream Land	3:09	Lullaby	Jewel
20 Part of Your World (Soundtrack)	3:14	Disney Princess: The Ultimate So...	Jodi Benson
21 The Bare Necessities (From "The...	4:50	Julie Andrews Selects Her Favorit...	Bruce Reitherman & Phil Harris
22 Rock-a-Bye Your Bear	1:24	Hot Potatoes! The Best of The Wi...	The Wiggles
23 Cluck, Cluck, Red Hen	1:34	The Corner Grocery Store	Raffi
24 Six Little Ducks	1:37	More Singable Songs	Raffi
25 Gordon	2:09	Thomas & Friends: All Star Tracks	Thomas & Friends
26 The Best Day Ever (feat. Spongeb...	3:00	SpongeBob's Greatest Hits (Origi...	SpongeBob SquarePants
27 Mary Had a Little Lamb	2:22	123 Favorite Kids Songs	Baby Genius
28 Do Your Ears Hang Low?	0:52	30 Toddler Songs, Vol. 2	Countdown Kids
29 If You're Happy Clap Your Hands	1:15	Children's 100 Classic Songs Coll...	Songs For Children
30 The Hampster Dance Song	3:32	Hampsterdance the Album	Hampton the Hampster

Appendix F

Study 1, Phase I and II Country Music Genre Exemplars

Name	Time	Album	Artist
1 All Your Life	3:51	The Band Perry	The Band Perry
2 Alone With You	3:30	Barefoot Blue Jean Night	Jake Owen
3 Are You Gonna Kiss Me or Not	3:04	Thompson Square	Thompson Square
4 Barefoot Blue Jean Night	2:47	Barefoot Blue Jean Night	Jake Owen
5 Better Than I Used to Be	3:21	Emotional Traffic	Tim McGraw
6 Country Girl (Shake It for Me)	3:45	Tailgates & Tanlines	Luke Bryan
7 Crazy (Single Version)	2:41	Patsy Cline's Greatest Hits (Rema...	Patsy Cline
8 Dancin' Away With My Heart	3:52	Own the Night	Lady Antebellum
9 Dirt Road Anthem	3:49	My Kinda Party	Jason Aldean
10 Drink In My Hand	3:11	Chief	Eric Church
11 Drink On It	3:31	Red River Blue (Deluxe Version)	Blake Shelton
12 God Gave Me You	3:49	Red River Blue (Deluxe Version)	Blake Shelton
13 Honey Bee	3:30	Red River Blue (Deluxe Version)	Blake Shelton
14 Hurt	3:36	American IV: Man Comes Around	Johnny Cash
15 I Don't Want This Night to End	3:39	Tailgates & Tanlines	Luke Bryan
16 I Walk the Line	2:41	Johnny Cash: 16 Biggest Hits	Johnny Cash
17 If I Die Young	3:42	The Band Perry	The Band Perry
18 Just a Kiss	3:38	Own the Night	Lady Antebellum
19 Mean	3:57	Speak Now	Taylor Swift
20 Need You Now	3:57	Need You Now	Lady Antebellum
21 Ours	3:57	Speak Now	Taylor Swift
22 Over You	4:13	Four the Record (Deluxe Edition)	Miranda Lambert
23 Red Solo Cup	3:46	Clancy's Tavern	Toby Keith
24 Ring of Fire	2:35	Johnny Cash: 16 Biggest Hits	Johnny Cash, June Carter & Merl...
25 Somebody Somewhere	3:29	Somebody Somewhere - Single	Dallas Smith
26 Springsteen	4:23	Chief	Eric Church
27 Stuck Like Glue	4:07	The Incredible Machine (Deluxe E...	Sugarland
28 Take a Back Road	3:29	Take a Back Road	Rodney Atkins
29 Tattoos On This Town	3:22	My Kinda Party	Jason Aldean
30 We Owned the Night	3:17	Own the Night	Lady Antebellum
31 A Woman Like You	3:29	A Woman Like You - Single	Lee Brice
32 You	2:44	Neon	Chris Young

Appendix G

Study 1, Phase I and II Tuva Throat Singing Music Genre Exemplars

Name	Time	Album	Artist
1 Artii-Sayir (Kargiraa Duet)	1:08	Tuva: Voices from the Center of Asia	Andrei Chuldum-ool & Tumat Kara...
2 Artii-Sayir (Kargiraa)	1:05	Tuva: Voices from the Center of Asia	Vasili Chazir
3 Atchamaining Ohi...	2:38	Music from Tuva	Igor Koshkendey
4 Borbannadir	1:26	Tuva: Voices from the Center of Asia	Anatolii Kuular
5 Borbannadir	0:54	Tuva: Voices from the Center of Asia	Mikhail Dopchun
6 Borbannadir	0:48	Tuva: Voices from the Center of Asia	Tumat Kara-ool
7 Cave Spirits	0:56	Tuva, Among the Spirits: Sound,...	Tuva, Among the Spirits: Sound,...
8 Ezengileer	1:22	Tuva: Voices from the Center of Asia	Marzhimal Ondar
9 Kara Durujaa	1:25	Music from Tuva	Igor Koshkendey
10 Kargiraa-Style Song	2:19	Tuva—Voices from the Land of th...	Tuva Ensemble
11 Khomuz Melodies (Performed by...	1:49	Tuva: Voices from the Center of Asia	Achymaa Targin Chandanmaa To...
12 Khoomei	0:34	Tuva: Voices from the Center of Asia	Fedor Tau
13 Khoomei	0:26	Tuva: Voices from the Center of Asia	Sundukai Mongush
14 Khoomin Uran Setgemj (5 Differen...	5:00	Gobi	Egshchiglen
15 Kozhamik (With Khoomei, Sigit, a...	2:00	Tuva: Voices from the Center of Asia	Tumat Kara-ool
16 Lullaby (With Khoomei)	1:08	Tuva: Voices from the Center of Asia	Bilchit-Maa Davaa
17 Medley of Various Throat-singing...	2:56	Tuva: Voices from the Center of Asia	Ensemble "Amirak"
18 Mungaral (Song of Sorrow)	6:24	Music from Tuva	Igor Koshkendey
19 Pesnya Khomeyzi (Song of Khoo...	2:33	Melodii Tuvi: Throat Songs and Fo...	M. Dakpay
20 Sigit "Alash"	1:38	Tuva: Voices from the Center of Asia	Mergen Mongush
21 Sigit (With Igit, a Bowed Instrument)	2:12	Tuva: Voices from the Center of Asia	Anatolii Kuular
22 Song of Oidupah	3:49	Music from Tuva	Igor Koshkendey
23 Steppe Kargiraa	1:20	Tuva: Voices from the Center of Asia	Fedor Tau
24 Sygyt, Khoomei, Kargyaa (Styles...	4:43	Voices of the Real World	Shu-De
25 Tespeng Khoomei	0:46	Tuva: Voices from the Center of Asia	Sundukai Mongush
26 Throat Singing Solo	3:46	Kongurei	Shu-De
27 Tongup Honar Boldum-Na Be	3:16	Music from Tuva	Igor Koshkendey
28 Touva/Tuva. Heupej Khöömii	4:05	Chants épiques et diphoniques. E...	Toumat
29 Tuva	7:03	Disappearing World	The Tuvians
30 U Miloy Sergi (My Beloved Girl's E...	3:04	Melodii Tuvi: Throat Songs and Fo...	Kara-sal Ak-ool

Appendix H

Study 2, Phase I Music Exemplars

Name	Time	Album	Artist
1 Baa Baa Black Sheep	0:15	Singable Songs for the Very Young	Raffi
2 Wagon Wheel	0:15	Single	Darius Rucker
3 Good Morning Heartache	0:15	Billie Holiday's Greatest Hits	Billie Holiday
4 You Shook Me All Night Long	0:15	Back in Black	AC/DC
5 Serenade No. 13 in G Major, K. 525	0:15	Mozart	Mozart

Appendix I

Study 2, Phase II Song Lyrics Recited by Orangutan Keepers

Baa, baa, black sheep

Baa, baa, white sheep, have you any wool? Yes sir, yes sir, three bags full. One for the master, one for the dame, and one for the little girl who lives down the lane. Baa, baa, white sheep, have you any wool? Yes sir, yes sir, three bags full.

Do your ears hang low?

Do your ears hang low? Do they wobble to and fro? Can you tie them in a knot? Can you tie them in a bow? Can you throw them over your shoulder like a continental soldier? Do your ears hang low? □Do your ears hang high?□Do they reach up to the sky?

Good morning heartache

Good morning, heartache, what's new? Stop haunting me now.
Can't shake you, no how. Just leave me alone, I've got those Monday blues. Straight through Sunday blues. Good morning, heartache, here we go again.

Wagon wheel

So rock me mama like a wagon wheel, rock me mama any way you feel. Hey mama rock me. Rock me mama like the wind and the rain, rock me mama like a south-bound train. Hey mama rock me.

You shook me all night long

And you shook me all night long. Yeah, you shook me all night long. You got me goin', shook me all night long. You had me shaking and you shook me all night long. Yeah, you shook me, baby, you took me. You shook me all night long. Yeah, you shook me all night long.

Table 1

Frequencies (Hz) employed in the auditory acuity assessment

Stimulus
14000 Hz
12000 Hz
11000 Hz
10000 Hz
9000 Hz
8000 Hz
7000 Hz
6000 Hz
5000 Hz
4000 Hz
3000 Hz
2000 Hz
1000 Hz
800 Hz
500 Hz
400 Hz
300 Hz
200 Hz

Table 2

Colours used to represent music genres in Study 1, Phase I

Genre	Colour
Classical	Turquoise
Jazz	Purple
Pop	Green
Rock	Black
Children's	Red
Tuva Throat Singing	Orange
Country	Yellow
Silence	Grey

Table 3

Auditory acuity assessment results for orangutan subjects

Stimulus (Tone Frequency)	Number of Detections	
	Ramai	Sekali
14000 Hz	0	0
12000 Hz	0	0
11000 Hz	0	0
10000 Hz	0	0
9000 Hz	0	0
8000 Hz	1	0
7000 Hz	2	1
6000 Hz	1	1
5000 Hz	1	1
4000 Hz	1	1
3000 Hz	1	1
2000 Hz	1	1
1000 Hz	2	1
800 Hz	1	1
500 Hz	2	2
400 Hz	0	0
300 Hz	0	0
200 Hz	0	0

Note. Number of tone detections by orangutan subjects for each frequency tested at 100.3 dB.

Table 4

Auditory acuity assessment results for human subjects

Stimulus (Tone Frequency)	Number of Detections	
	Male Human	Female Human
14000 Hz	0	0
12000 Hz	0	0
11000 Hz	0	0
10000 Hz	0	1
9000 Hz	0	2
8000 Hz	1	2
7000 Hz	2	2
6000 Hz	2	2
5000 Hz	2	2
4000 Hz	2	2
3000 Hz	2	2
2000 Hz	2	2
1000 Hz	2	2
800 Hz	2	2
500 Hz	2	2
400 Hz	2	2
300 Hz	2	2
200 Hz	2	2

Note. These results were obtained from an unofficial pilot study of auditory acuity in two human subjects using the same methodology as that employed with animal subjects. The table includes a list of the number of tone detections by subject for each frequency tested at 100.3 dB.

Table 5

Frequency of music genre exposure per subject in Study 1, Phase I

Genre	Frequency		
	Budi	Ramai	Sekali
Classical	207	180	177
Tuva	201	188	161
Hip Hop	207	197	173
Children's	202	203	154
Jazz	202	166	173
Country	197	160	154
Rock	200	164	165
Total	1416	1258	1157

Table 6

Frequency of Budi's music and silence selections, per session in Study 1, Phase I

Date	Music Selections	Silence Selections	Total
26-May-12	20	13	33
31-May-12	19	15	34
06-Jun-12	19	22	41
14-Jun-12	11	21	32
18-Jun-12	6	38	44
19-Jun-12	2	5	7
21-Jun-12	9	20	29
25-Jun-12	1	5	6
26-Jun-12	15	35	50
27-Jun-12	18	33	51
03-Jul-12	5	25	30
04-Jul-12	12	36	48
11-Jul-12	7	27	34
12-Jul-12	10	20	30
13-Jul-12	9	28	37
18-Jul-12	16	34	50
19-Jul-12	7	27	34
20-Jul-12	20	29	49
24-Jul-12	4	24	28
25-Jul-12	14	28	42
27-Jul-12	19	24	43
08-Aug-12	16	29	45
09-Aug-12	19	25	44
10-Aug-12	19	26	45
15-Aug-12	15	24	39
16-Aug-12	19	22	41
17-Aug-12	10	23	33
29-Aug-12	13	21	34
30-Aug-12	6	6	12
31-Aug-12	18	25	43
06-Sep-12	30	34	64
07-Sep-12	16	24	40
08-Sep-12	20	24	44
13-Sep-12	0	4	4
14-Sep-12	12	16	28
21-Sep-12	4	6	10
24-Sep-12	25	31	56

25-Sep-12	22	21	43
27-Sep-12	19	20	39
TOTAL	526	890	1416
Total trials		1416	

Table 7

Frequency of Ramai's music and silence selections, per session in Study 1, Phase I

Session Date	Music Selected	Silence Selected	Total
23-May-12	7	13	20
30-May-12	8	8	16
07-Jun-12	14	8	22
08-Jun-12	15	26	41
13-Jun-12	25	27	52
19-Jun-12	21	24	45
21-Jun-12	22	51	73
26-Jun-12	11	17	28
27-Jun-12	16	24	40
28-Jun-12	22	22	44
03-Jul-12	16	21	37
04-Jul-12	15	24	39
06-Jul-12	16	14	30
11-Jul-12	14	14	28
12-Jul-12	4	3	7
13-Jul-12	16	21	37
18-Jul-12	12	10	22
19-Jul-12	15	30	45
20-Jul-12	19	16	35
24-Jul-12	17	20	37
25-Jul-12	17	10	27
27-Jul-12	17	15	32
08-Aug-12	18	21	39
09-Aug-12	17	14	31
10-Aug-12	15	18	33
15-Aug-12	21	12	33
16-Aug-12	9	5	14
17-Aug-12	11	16	27
29-Aug-12	19	20	39
30-Aug-12	15	6	21
31-Aug-12	25	13	38
08-Sep-12	21	24	45
13-Sep-12	19	15	34
14-Sep-12	26	21	47
21-Sep-12	11	10	21
25-Sep-12	16	16	32
27-Sep-12	23	24	47

TOTAL	605	653	1258
Total Trials		1258	

Table 8

Frequency of Sekali's music and silence selections, per session in Study 1, Phase I

Session Date	Music Selected	Silence Selected	Total
24-May-12	14	6	20
30-May-12	17	16	33
31-May-12	4	6	10
7-Jun-12	13	20	33
11-Jun-12	9	35	44
13-Jun-12	4	56	60
14-Jun-12	0	8	8
18-Jun-12	4	22	26
19-Jun-12	1	35	36
21-Jun-12	3	26	29
26-Jun-12	0	13	13
27-Jun-12	0	38	38
28-Jun-12	0	10	10
3-Jul-12	1	29	30
4-Jul-12	1	18	19
11-Jul-12	0	33	33
12-Jul-12	4	19	23
13-Jul-12	2	25	27
18-Jul-12	0	31	31
19-Jul-12	0	34	34
20-Jul-12	2	27	29
24-Jul-12	0	35	35
25-Jul-12	2	25	27
27-Jul-12	0	31	31
8-Aug-12	0	26	26
9-Aug-12	0	29	29
10-Aug-12	1	33	34
15-Aug-12	0	27	27
16-Aug-12	3	23	26
17-Aug-12	1	22	23
29-Aug-12	1	26	27
30-Aug-12	0	18	18
31-Aug-12	2	32	34
6-Sep-12	0	26	26
7-Sep-12	0	31	31
8-Sep-12	1	40	41
14-Sep-12	1	22	23

24-Sep-12	0	38	38
25-Sep-12	0	30	30
27-Sep-12	2	43	45
TOTAL	93	1064	1157
Total Trials		1157	

Table 9

Frequency of Budi's music and silence selections per musical genre in Study 1, Phase I

Genre	Frequency of Music Replay Selections	Frequency of Silence Selections
Classical	95	112
Tuva	79	122
HipHop	83	124
Children's	72	130
Jazz	58	144
Country	71	126
Rock	68	132

Table 10

Frequency of Ramai's music and silence selections per musical genre in Study 1, Phase I

Genre	Frequency of Music Replay Selections	Frequency of Silence Selections
Classical	85	95
Tuva	104	84
HipHop	100	97
Children's	94	109
Jazz	76	90
Country	77	83
Rock	69	95

Table 11

Frequency of Sekali's music and silence selections per musical genre in Study 1, Phase I

Genre	Frequency of Music Replay Selections	Frequency of Silence Selections
Classical	11	166
Tuva	12	149
HipHop	12	161
Children's	12	142
Jazz	18	155
Country	13	141
Rock	15	150

Table 12

Frequency of touchscreen side selections per subject in Study 1, Phase I

Subject	Frequency of Right-Side Selections	Frequency of Left-Side Selections
Budi	751	665
Ramai	486	772
Sekali	571	586

Table 13

Frequency of Budi's correct selections, incorrect selections and mistrials per session in Study 2, Phase I

Session Date	Correct Selections	Incorrect Selections	Mistrials
26-Feb-13	2	1	0
28-Feb-13	9	9	5
4-Mar-13	20	26	12
5-Mar-13	20	12	4
6-Mar-13	5	9	2
11-Mar-13	45	62	3
12-Mar-13	82	64	2
14-Mar-13	118	123	2
15-Mar-13	95	100	1
18-Mar-13	73	95	1
19-Mar-13	99	101	0
20-Mar-13	108	113	4
22-Mar-13	103	100	4
26-Mar-13	97	105	0
28-Mar-13	90	79	5
29-Mar-13	123	117	1
3-Apr-13	79	79	4
9-Apr-13	83	94	3
11-Apr-13	54	69	3
12-Apr-13	112	115	2
15-Apr-13	105	81	4
17-Apr-13	104	102	1
19-Apr-13	72	62	1
22-Apr-13	89	83	1
24-Apr-13	88	96	2
26-Apr-13	76	96	3
2-May-13	37	20	3
3-May-13	57	64	3
Total	2045	2077	76
Total trials		4122	

Table 14

Frequency of Ramai's correct selections, incorrect selections and mistrials per session in Study 2, Phase I

Session Date	Correct Selections	Incorrect Selections	Mistrials
26-Feb-13	15	8	3
28-Feb-13	11	11	0
04-Mar-13	26	20	0
05-Mar-13	19	17	1
06-Mar-13	49	41	3
11-Mar-13	52	58	1
12-Mar-13	41	40	0
15-Mar-13	73	63	6
18-Mar-13	89	85	1
19-Mar-13	74	83	1
20-Mar-13	65	69	1
22-Mar-13	99	115	3
26-Mar-13	60	66	8
28-Mar-13	123	117	2
29-Mar-13	96	89	0
03-Apr-13	112	129	1
04-Apr-13	79	89	0
05-Apr-13	69	73	1
09-Apr-13	92	91	1
11-Apr-13	97	102	5
12-Apr-13	119	119	1
15-Apr-13	76	71	1
19-Apr-13	47	37	1
22-Apr-13	108	102	0
24-Apr-13	106	112	2
26-Apr-13	106	105	1
30-Apr-13	83	82	1
02-May-13	93	97	4
Total	2079	2091	49
Total trials		4170	

Table 15

Frequency of Sekali's correct selections, incorrect selections and mistrials per session in Study 2, Phase I

Session Date	Correct Selections	Incorrect Selections	Mistrials
2013-02-26	9	9	0
2013-02-28	32	40	0
2013-03-04	46	51	2
2013-03-05	24	30	0
2013-03-06	80	73	0
2013-03-11	49	47	0
2013-03-12	67	55	0
2013-03-14	69	71	1
2013-03-15	96	90	0
2013-03-18	126	143	1
2013-03-19	95	107	1
2013-03-20	117	101	1
2013-03-22	84	87	0
2013-03-26	129	118	0
2013-03-28	116	112	2
2013-03-29	97	119	1
2013-04-03	60	64	3
2013-04-04	88	93	0
2013-04-05	48	56	0
2013-04-09	58	56	0
2013-04-11	99	106	0
2013-04-12	82	79	0
2013-04-15	102	112	0
2013-04-19	75	84	0
2013-04-22	103	113	1
2013-04-24	109	105	2
2013-04-26	132	136	0
2013-04-30	85	90	2
2013-05-02	97	97	0
2013-05-03	65	60	1
2013-05-04	78	62	1
Total	2517	2566	19
Total trials		5083	

Table 16

Frequency of touchscreen side selections per subject in Study 2, Phase I

Side	Budi	Ramai	Sekali
Left	2526	3688	2417
Right	1596	482	2666
Total	4122	4170	5083

Table 17

Frequency of Budi's correct selections, incorrect selections and mistrials per session in Study 2, Phase II

Session Date	Correct Selections	Incorrect Selections	Mistrials
2013-05-06	61	59	2
2013-05-08	94	91	4
2013-05-10	135	150	3
2013-05-14	43	27	2
2013-05-16	93	81	7
2013-05-21	120	136	3
2013-05-23	100	108	2
2013-05-24	122	129	2
2013-05-25	100	101	3
2013-05-27	153	147	4
2013-05-29	100	98	8
2013-06-03	109	122	7
2013-06-04	121	121	2
2013-06-06	83	106	10
2013-06-10	109	100	2
2013-06-11	109	115	7
2013-06-12	106	108	7
2013-06-18	115	137	7
2013-06-20	75	80	18
2013-06-21	99	120	5
2013-06-26	71	45	9
2013-06-27	116	120	5
2013-06-28	140	121	3
2013-07-02	140	142	5
Total	2514	2564	127
Total trials	5078		

Table 18

Frequency of Ramai's correct selections, incorrect selections and mistrials per session in Study 2, Phase II

Session Date	Correct Selections	Incorrect Selections	Mistrials
2013-05-06	105	90	0
2013-05-08	181	138	4
2013-05-10	159	120	1
2013-05-14	122	78	1
2013-05-16	97	113	0
2013-05-17	156	155	1
2013-05-21	147	140	7
2013-05-23	174	176	2
2013-05-25	140	142	1
2013-05-27	87	99	6
2013-05-30	124	121	7
2013-06-03	85	95	1
2013-06-04	122	124	6
2013-06-06	102	123	6
2013-06-10	138	111	8
2013-06-11	173	152	2
2013-06-12	154	144	1
2013-06-18	166	151	1
2013-06-20	100	91	14
2013-06-21	95	84	2
2013-06-24	22	22	15
2013-06-26	168	157	3
2013-06-27	115	114	6
2013-06-28	157	169	3
2013-07-02	168	164	5
Total	3257	3073	103
Total trials	6330		

Table 19

Frequency of Sekali's correct selections, incorrect selections and mistrials per session in Study 2, Phase II

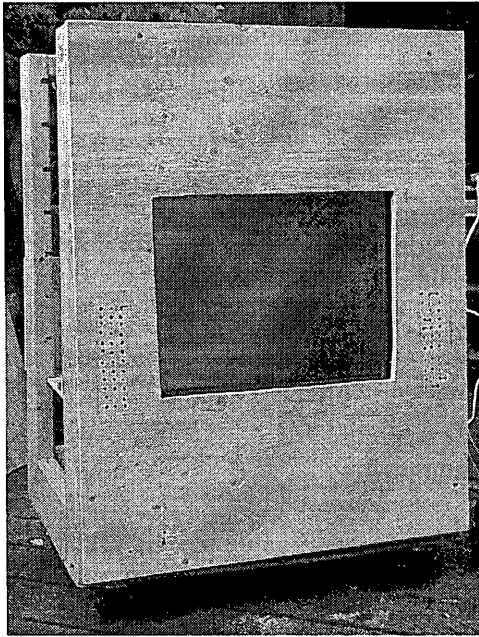
Session Date	Correct Selections	Incorrect Selections	Mistrials
2013-05-06	120	116	5
2013-05-08	168	161	2
2013-05-10	159	146	1
2013-05-14	70	87	3
2013-05-16	80	85	0
2013-05-17	103	91	1
2013-05-21	171	168	1
2013-05-23	171	158	2
2013-05-25	159	149	0
2013-05-27	153	149	2
2013-05-29	126	132	3
2013-06-03	86	92	0
2013-06-04	129	139	3
2013-06-06	139	143	3
2013-06-10	161	151	0
2013-06-11	74	69	1
2013-06-12	149	154	1
2013-06-18	119	129	2
2013-06-20	127	127	8
2013-06-21	108	91	1
2013-06-26	183	183	0
2013-06-27	128	117	1
2013-06-28	177	206	0
2013-07-02	174	168	2
Total	3234	3211	42
Total trials		6445	

Table 20

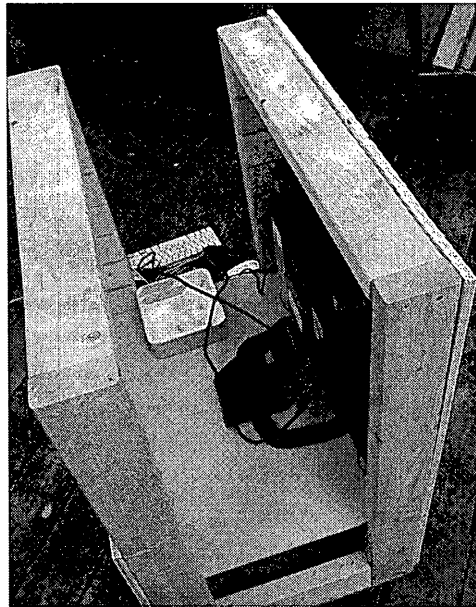
Frequency of touchscreen side selections per subject in Study 2, Phase II

Side	Budi	Ramai	Sekali
Left	2569	4919	4753
Right	2509	1411	1692
Total	5078	6330	6445

Figure 1a & 1b. Photographs of the mobile computer hardware housing unit.



a)



b)

Figure 2. A visual representation of trials from Study 1, Phase I. Rectangles represent sequential touchscreen screenshots. The blue arrows represent touches to the touchscreen. Scenario A depicts a trial in which the subject chooses silence over music replay. Scenario B depicts a trial in which the subject chooses music replay over silence.

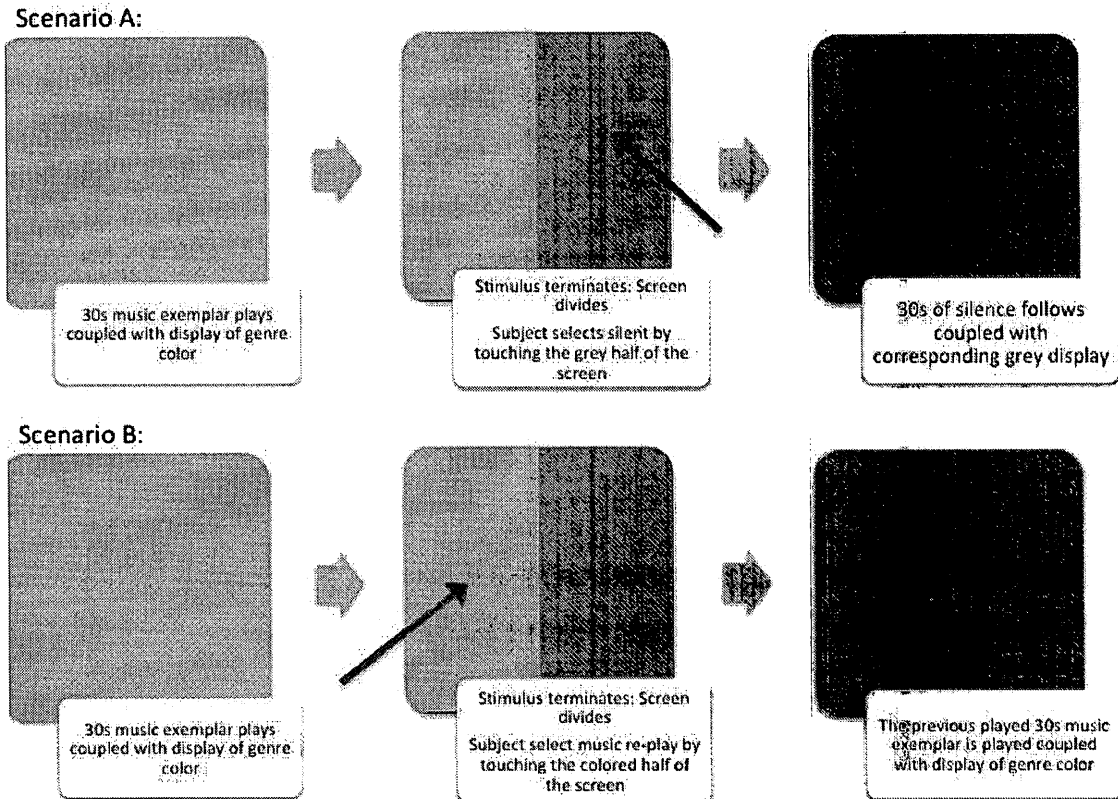


Figure 3a & 3b. A screenshot of the virtual monochromatic piano keyboard used in Study 1, Phase III. In (a) the keyboard is pictured as it appeared when no keys have been contacted. In (b) the keyboard is pictured as it appeared when the center key had been contacted

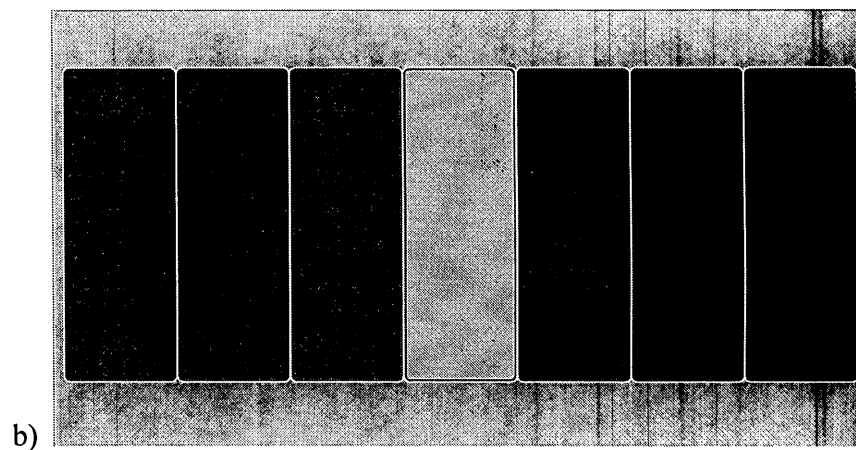
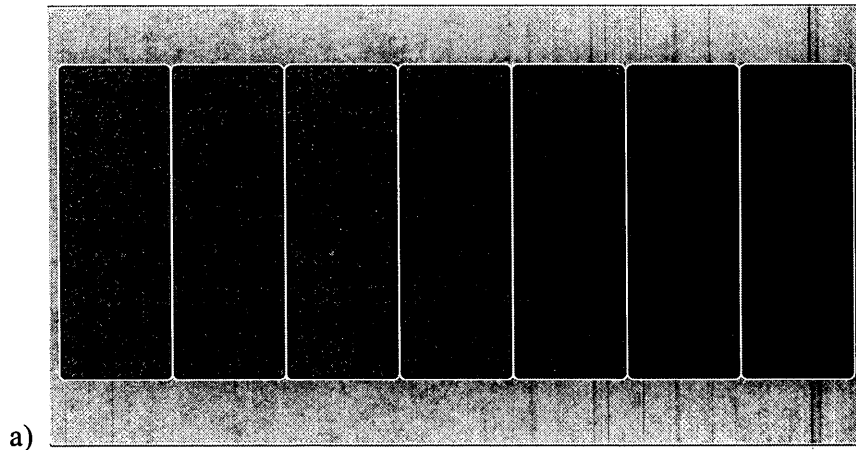


Figure 4. A visual representation of a trial from Study 2, Phase I. Rectangles represent sequential touchscreen screenshots.

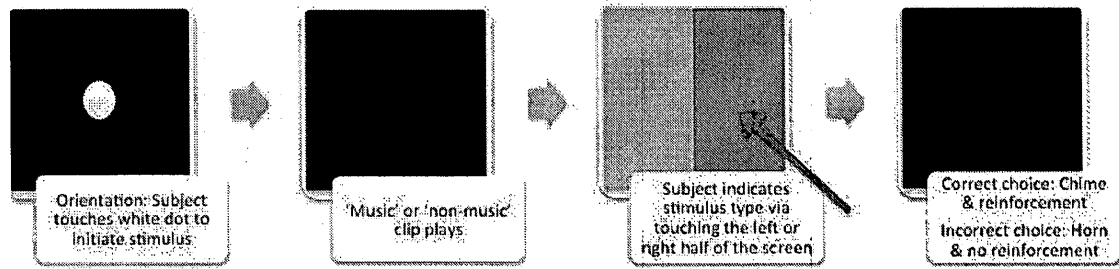


Figure 5. A visual representation of a trial from Study 2, Phase II. Rectangles represent sequential touchscreen screenshots.

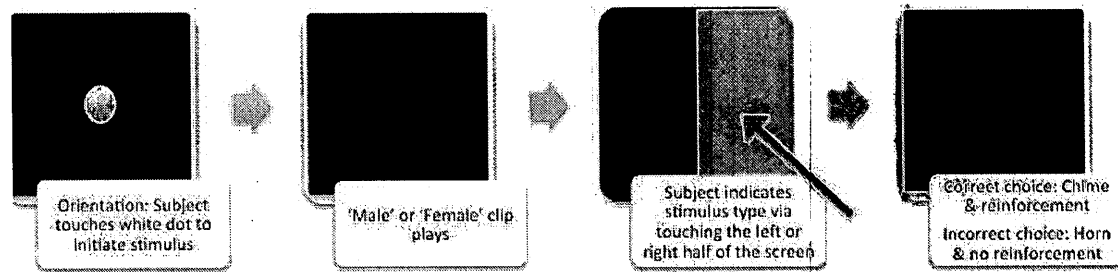
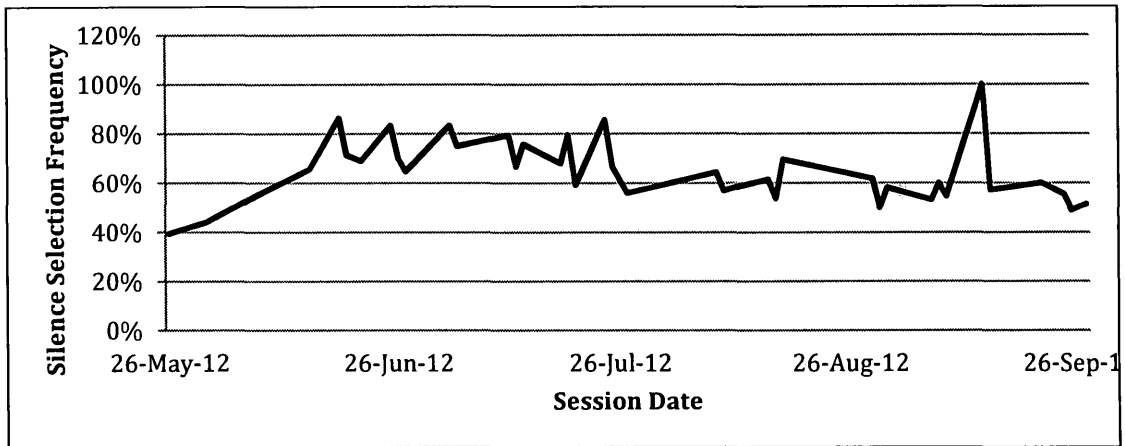
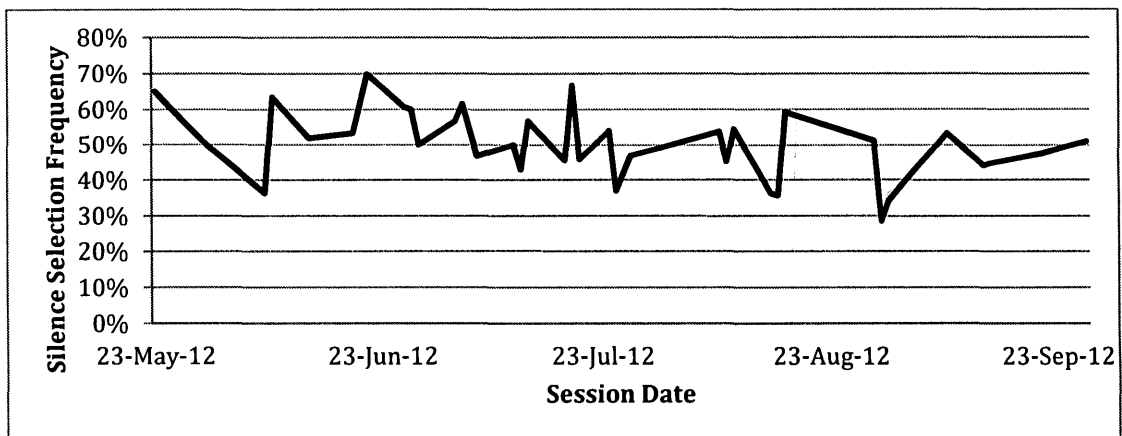


Figure 6a, 6b & 6c. Study 1, Phase 1 silence selection trend across time.

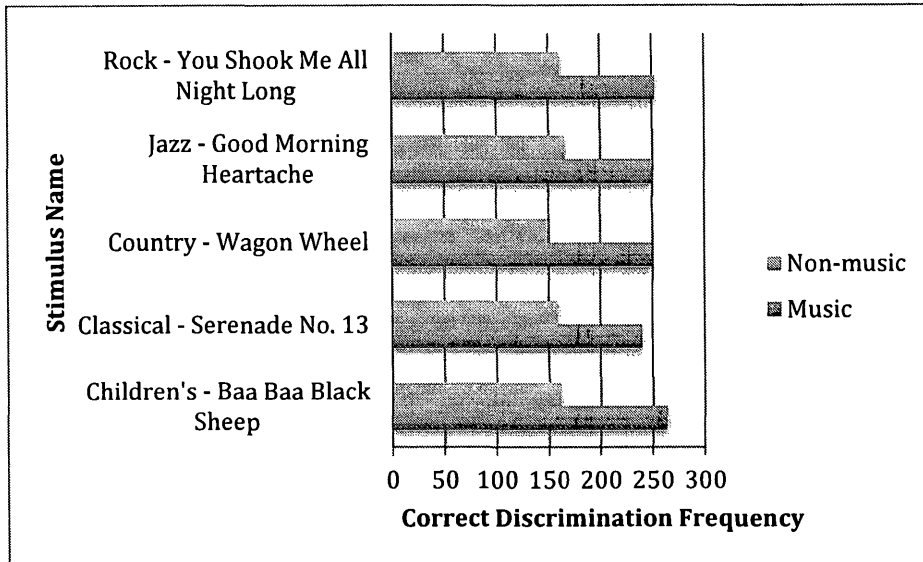


a) Budi

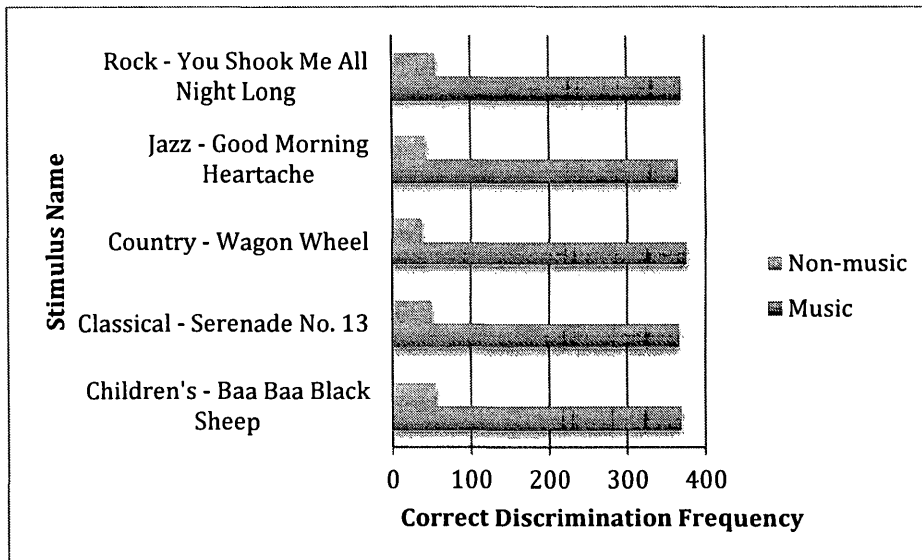


b) Ramai

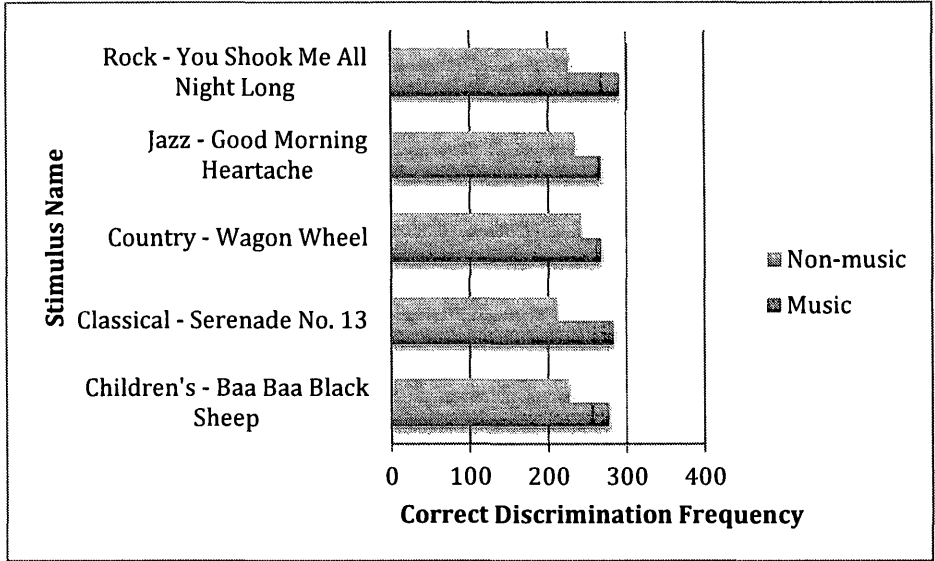
Figure 7a, 7b, & 7c. The number of correct 'music' vs. 'scrambled music' discriminations by exemplar in Study 2, Phase I.



a) Budi

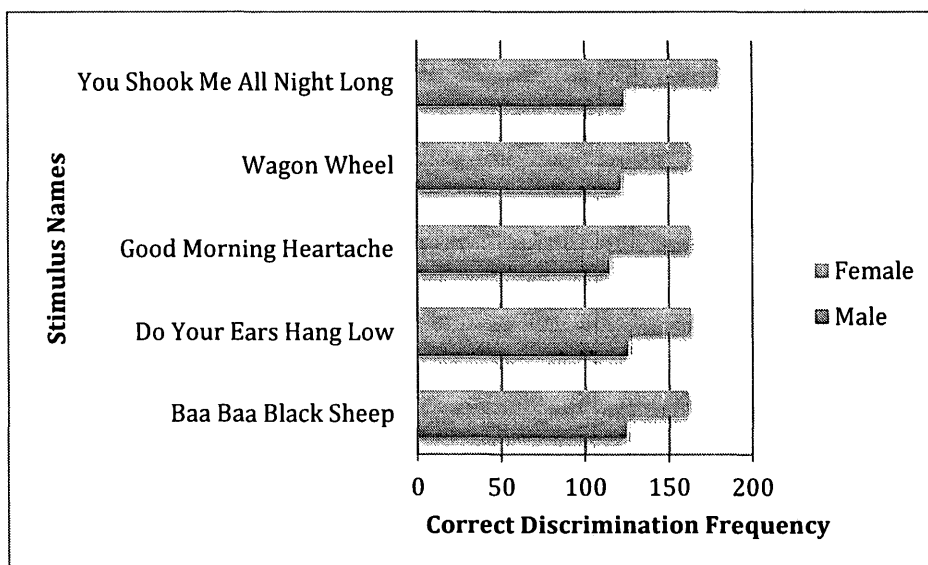


b) Ramai

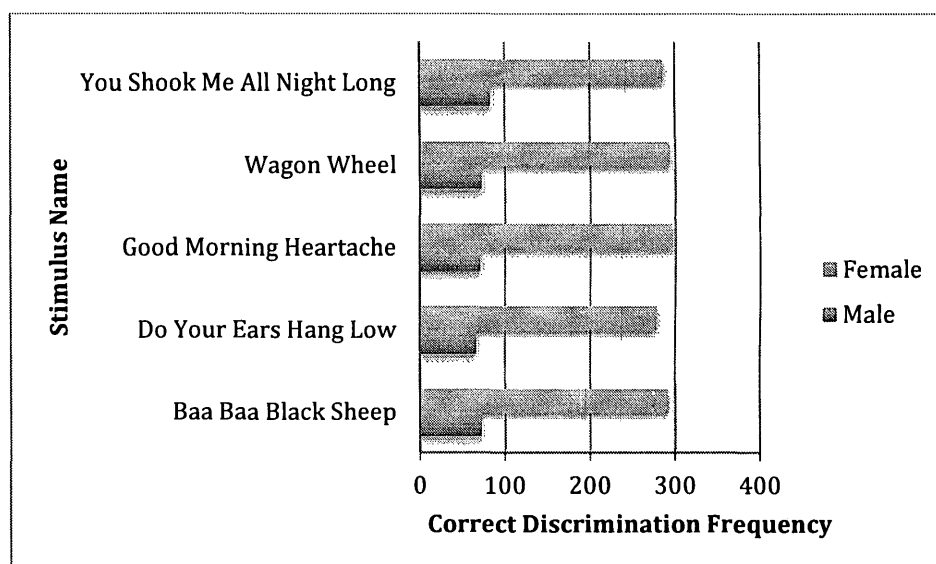


c) *Sekali*

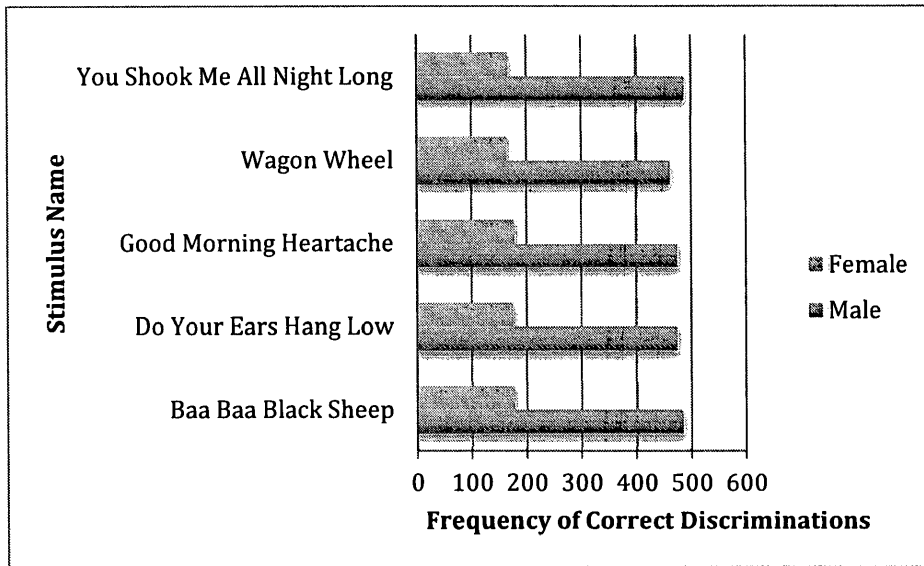
Figure 8a, 8b, & 8c. The number of correct 'male keeper's voice' vs. 'female keeper's voice' discriminations by exemplar in Study 2, Phase II.



a) Budi



b) Ramai



c) *Sekali*