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Cocaine's effects on the perception of socially significant vocalizations in baboons

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Abstract

The effects of cocaine on the ability of baboons to discriminate among their natural affiliative 'grunt' vocalizations were examined to determine whether cocaine would produce discrimination impairments similar to those observed previously with acoustically-similar human vowel sounds [Hienz, R.D. Spear, D.J. Pyle, D.A. Brady, J.V. 1995. Cocaine's effects on speech sound discriminations and reaction times in baboons. Psychopharmacology, 122 (2) 147–157], or whether differences in cocaine's effects might occur associated with the social significance of the calls. The task employed digitized calls of actual vocalizations recorded in the wild [Rendall, D. Owren, M.J. Weerts, E.M. Heinz, R.D. 2004. Sex differences in the acoustic structure of vowel like grunt vocalizations in baboons and their perceptual discrimination by baboon listeners. Journal of the Acoustical Society of America, 115 (1) 411–421]. Baboons pressed a lever to produce a repeating 'standard' grunt, and released the lever only when one of four other 'target' grunts was selected to occur in place of the standard grunt. Cocaine (0.01–.56 mg/kg, i.m.) impaired call perception, and these impairments were more pronounced than those observed previously for acoustically-similar human vowel sounds. Cocaine also elevated reaction times as a function of dose. The results demonstrate that cocaine impairs perceptual discriminations of the natural grunt vocalizations of baboons, and suggest that cocaine may have more pronounced effects on the perception of biologically-relevant as opposed to non-relevant communication signals.

Keywords: Cocaine; Baboon vocalizations; Auditory perception; Discrimination; Baboon; Lever release

1. Introduction

The large number of reports in the literature on cocaine's cognitive/behavioral effects in a variety of organisms attests to the fact that cocaine can influence a wide range of biological and behavioral processes in both positive and negative ways. In rats, cocaine can enhance performance accuracy in a vigilance task (Grilly and Grogan, 1990; Grilly and Nocjar, 1990), shorten response latencies (Grilly, 1992), and enhance the rewarding effects of brain stimulation (Kornetsky and Esposito, 1981); but cocaine can also impair discriminative motor control in rats (Falk and Lau, 1991), elevate thresholds for detecting brain stimulation in rats (Kornetsky and Esposito, 1981), and decrease the accuracy of completing complex response sequences in monkeys (Branch and Sizemore, 1988). Cocaine's effects in humans also varies across tasks, with cocaine improving digit symbol substitution performance accuracy (Higgins et al., 1990), speeding up visual reaction times (Stillman et al., 1993), reversing sleep deprivation-induced decrements in reaction times (Fischman and Schuster, 1980), but also impairing repeated acquisition task accuracy (Fischman, 1984).

Research from this laboratory has also shown that cocaine can both improve and impair differing aspects of perceptual discrimination performances in baboons. Thus cocaine can improve (i.e., shorten) reaction time—a measure of motor function—when subjects are either detecting the presence of an auditory stimulus (Hienz et al., 1994, 1993, 1995), or discriminating a *difference*

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between successively-presented stimuli (Hienz et al., 1995, 1996b). At the same time, however, cocaine can impair performance accuracy—a measure of perceptual function—when baboons are discriminating among different speech sounds (Hienz et al., 1995) and tone pitches (Hienz et al., 2002), but not when detecting a tone's presence (Hienz et al., 1994, 1993). Additionally the type of impairment observed can depend upon the type of stimuli employed (tones vs. speech sounds), and the type of procedure employed (discrimination vs. identification, Hienz et al., 2003).

The finding that cocaine impairs the perception of human vowel sounds in baboons (Hienz et al., 1995, 2001a, 1996b), but does not affect auditory detection thresholds for simple tones (Hienz et al., 1994, 1993), suggests that cocaine disrupts mechanisms involved in the processing of spectral cues, or "pitch", as opposed to intensity cues, or "loudness" (Hienz et al., 1995, 2001a). Further, cocaine impairs vowel discriminability more so when the discrimination is between vowels that are more similar to one another in terms of their spectral structure (Hienz et al., 1995), a result that also suggests drug influences on those CNS mechanisms related to the processing of spectral cues. Other evidence suggesting cocaine's effects on auditory CNS function include the fact that cocaine users often experience hallucinations, with auditory hallucinations being most prominent (Brady et al., 1991; Siegel, 1978), and that children exposed to cocaine in utero have impaired verbal comprehension (Nulman et al., 1994). Direct effects of cocaine on the auditory system have also been shown in that cocaine decreases both auditory nerve response amplitudes and cochlear blood flow in guinea pigs (Shivapuja et al., 1993), reduces the amplitude and latency of human auditory event-related potentials (Herning et al., 1985; Robledo et al., 1993), and has been shown to interfere with mechanisms of auditory stimulus processing (Boutros et al., 1994; Herning et al., 1994).

The goal of the present research was to extend this prior work on the effects of cocaine on perceptual function in baboons to cocaine's effects on the perception of baboon vocal communication sounds. One straightforward reason for such an extension is to determine how the above-mentioned differing effects of cocaine on tones versus speech sounds might apply to the discrimination of an organism's own species-specific calls. In this regard, baboon calls are acoustically highly similar to human vowel sounds (described below), and based upon this physical similarity one might predict that cocaine's effects on these call discriminations would be highly similar to those described previously for vowel sounds. Importantly, however, baboon calls are highly socially-significant for baboons, whereas human vowel sounds have no such social significance in normal baboon social behavior. This in turn suggests that any differences in cocaine's effects on the discrimination of grunts versus vowels might indicate an effect of cocaine related to this functional difference between baboon grunts and human vowels. Thus an examination of cocaine's effects on the discrimination of natural calls may begin to provide insight into drug effects on the perception of species-specific calls of high social significance, and by extension to the effects of drugs on the perception of calls associated with differing motivational and/or social contexts (e.g., affiliation, dominance, subordinance, aggression, submission).

There is a close similarity between many human speech sounds and nonhuman primate vocalizations; the acoustic properties of baboon *grunt* calls in particular are so extremely vowel-like that they have been referred to as "prototypical human vowel sounds" (Owren et al., 1997). This great similarity exists in part because the vocalizations of humans and monkeys are similarly produced via vocal fold movements that are "filtered" by the resonance properties of the vocal tract cavity, which results in prominent spectral peaks ("formant" peaks) in the frequency spectrum of the vocalizations (Rendall et al., 1998). Fig. 1 is a schematic of the first 2 formant peaks (F_1 vs. F_2) for a number of human vowels and baboon grunts, and demonstrates the remarkable similarity in the acoustic properties of baboon *grunt* calls to human vowel sounds (adapted from Rendall et al., 2004). Further, the slight variations in the acoustic formants of baboon *grunts* are strongly related to caller identity, a finding consistent with the general view that the cueing of individual and sexual identity is a major function of this type of call in baboons (Rendall, 2003) as well as of coo calls in macaques (Rendall et al., 1998, 1996). Similarly, the vowel sounds of modern speech also contain slight formant variations that play a prominent role in cueing individual identity among humans (Bachorowski and Owren, 1997, 1999). These pronounced similarities between the structure and function of both human vowel sounds and baboon grunt calls suggests baboons as good models for the study of the effects of drugs on basic vocal perception in humans. Based solely on these

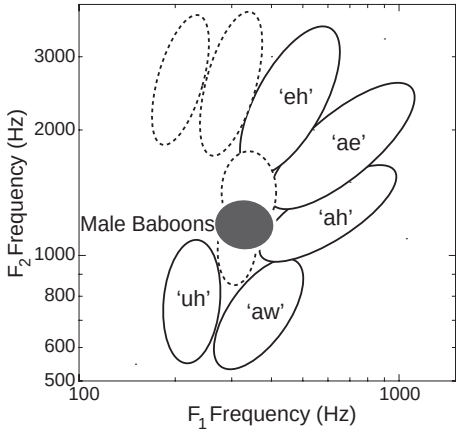

Fig. 1. A human vowel "formant plane"; each oval shows the range of the two main formants (F_1, F_2) for a number of vowels. Superimposed on the formant plane is the range of F_1 and F_2 formant peaks of 216 baboon grunt calls (dark circle). Adapted from Rendall et al. (2004).

acoustic similarities between human vowels and baboon grunts, one would expect that cocaine should impair the discrimination of baboon grunt calls in a fashion similar to what has already been demonstrated for human vowel discriminations.

On the other hand, it has also been well established that non-human primate vocalizations transmit information that is of high motivational and social significance to other members of the social group, that these vocalizations result in predictable behavioral responses from the listeners, and that the successful perception of appropriate social signals in nonhuman primates is particularly important for maintaining social relationships and preventing severe injury during social conflicts (Andrew, 1976; Byrne, 1981; Cheney et al., 1995; Hall and De Vore, 1965). The importance of accurate perception of vocal signals in natural settings has developed into the notion that many species are "specialized" in the recognition and CNS processing of their species-specific calls, an idea that has been attested to in numerous behavioral, lesion, and metabolic studies suggesting that monkeys, like humans, use the left hemisphere preferentially to process vocalizations (Ghazanfar and Hauser, 1999; Heffner and Heffner, 1984; Petersen, 1982; Petersen et al., 1978; Poremba et al., 2004). Given the social importance these vocalizations and the likely specialized CNS processing involved in their recognition, one might also equally predict the discrimination of these calls to be resistant to disruption via the administration of drugs such as cocaine.

The present experiment examined the effects of cocaine on the perception of affiliative baboon grunt calls, and compared these effects with those found in previous studies on cocaine's effects on the discrimination of human vowel sounds in order to assess cocaine's effects on the perception of species-specific, socially-significant vocalizations vs. non-species specific, non-socially significant sounds (i.e., human vowels) that possess a highly similar acoustic structure. It was expected that, if cocaine impaired the perception of baboon grunt calls in a fashion similar to that observed previously for human vowels, then these effects of cocaine would indicate a generalized effect of the drug on the processing of general auditory spectral information. On the other hand, if cocaine produced a different effect on the perception of baboon grunt calls, such results would be consistent with a selectivity of cocaine's effects related to the biological/social significance of the calls.

2. Method

2.1. Subjects

Four adult male baboons (*Papio anubis*) weighing between 25 and 33 kg served as subjects. Each baboon was housed separately in a large-primate cage ($170 \times 90 \times 127$ cm) equipped with a seating bench. All animals had auditory and visual contact with other baboons housed in the same colony room, and were maintained on a 22-h restricted feeding schedule with water continuously available in the home cage. Supplemental monkey chow and two pieces of fresh fruit were provided daily after each experimental session. The baboons were maintained on a daily 12-h light/dark cycle (6 a.m./6 p.m.). Animal care was in accordance with current NIH guidelines on "Principles of laboratory animal care".

2.2. Apparatus

Each baboon was tested in a modified baboon squeeze cage ($142 \times 74 \times 69$ cm) fitted within a double-walled sound-attenuating chamber (IAC Inc., model 1201A). An intelligence panel (76×97 cm) was attached to one side of the cage and contained a primate lever (BRS/LVE model PRL-003), a red light-emitting diode used as a cue light, and a pellet hopper for delivery of pellets via a mechanical feeder. With the animal positioned facing the panel, the cue light was at eye level, the pellet hopper was at chest level, and the response lever was at waist level in front of the right arm. Auditory stimuli were delivered through a wide-range speaker suspended above the test cage, vertically in line with the animal's normal head position, approximately 20 cm above ear level. Baboons were "shuttled" into the experimental apparatus for testing via a metal transfer cage.

2.3. Stimuli

The stimuli employed were digital versions of the individual grunt calls of five different adult male baboons recorded in the wild by Dr. D.A. Rendall, who collected and analyzed a large database of recordings from baboons in two populations in Botswana and South Africa (Rendall et al., 2000, 2004, 1999). The vocalizations were collected under specific observational protocols in which observers noted the positions and identities of callers, apparent receivers, and any salient behaviors and/or events before and after a call. Because the baboons were fully habituated to the presence of human observers, high quality recordings could be made at close range under natural ecological and social conditions. Recordings of calls in the wild can contain acoustic artifacts (e.g., background noises, random differences in call loudness and/or duration) that may compromise their use in laboratory experiments. However, due to the previously noted similarities in vocal-tract size and structure between baboons and humans (Owren et al., 1997), natural-sounding grunt calls can also be readily recreated using articulatory synthesis software designed to mimic the human vocal production process itself (e.g., the Klatt (1980) synthesis as implemented in CSRE® acoustic production software), given that all necessary acoustic parameters are specified. For the present experiments five adult male baboon grunts were generated via this method. Vocalizations generated from the spectral parameters of human vowels and natural baboon calls sound completely

"natural" (e.g., they do not sound like the synthetic speech produced by personal computers that "speak" text files via the concatenation of preprogrammed sounds). Digital re-creations of natural vocalizations also offer the distinct advantages of being excellent exemplars of individual calls, of being free of background acoustical noise, and more easily controllable for variations in stimulus duration and loudness. Studies have also shown that monkeys respond similarly to both natural calls and their digital versions (Norcross et al., 1994; Owren, 1990).

In human vowel perception, listeners can recognize most of the "back" vowels (e.g., 'aw', 'uh') based on F_1 alone, while listeners can recognize all vowels based on the first 2 formants alone (Borden and Harris, 1984). The higher formants contribute relatively little to the perception of these sounds due to their low audibility (i.e., the amplitudes of the formant peaks progressively decrease at successively higher formants due to the filtering of the vocal tract cavity—see Fig. 2), and is evidenced further by the fact that only the first three formants are typically reported for vowels in most speech production work. Accordingly, each of the five different adult male grunt calls was created by entering the amplitude and frequency of the fundamental pitch (F_0) as well as the amplitudes, frequencies, and bandwidths of the first 3 formants (F_1, F_2, F_3) into the acoustic production software. Additionally, natural intonation patterns (i.e., changes in F_0 over time) were also reproduced with the software. All parameters were taken from an analysis of 35–40 individual calls from each of 5 different adult male baboons provided by Dr. Rendall. One of the 35–40 calls from each of the 5 adult males was selected for digitizing. Care was taken to select a call from each individual that was "representative" of that individual in the sense that the major acoustic parameters (F_0, F_1, F_2, F_3) of the selected call fell near the midrange of those parameters for all calls available from that particular individual. A similar acoustic production technique was also employed to reproduce the vowel sounds of our previous studies (Hienz and Brady, 1988, 1989; Hienz et al., 1995, 2001a, 1996b); that is, the vowels were created as based upon the F_0 and F_1–F_3 values of the vowels /ç/, ('aw' as in 'caught'), /ɛ/ ('eh' as in 'let'), /a/ ('ah' as in 'lot'), /æ/ ('ae' as in 'cat'), and /u/ ('uh' as in 'book'), as taken from the classic human vowel formant analysis results of Peterson and Barney (1952).

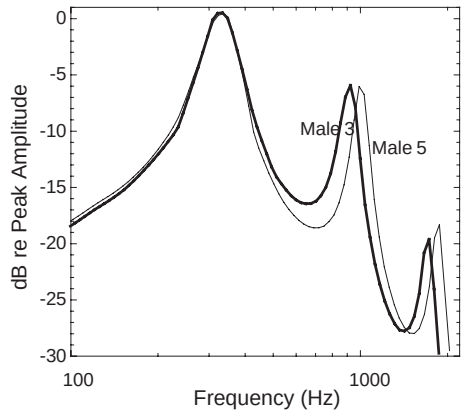

Fig. 2. The spectra of two male baboon grunts (relative amplitude in dB plotted as a function of frequency), depicting the differing formant structures of the grunts in terms of the locations of the first 3 formant peaks and their relative amplitudes, or loudnesses.

All grunt stimuli were presented via computer-controlled digital audio equipment from Tucker/Davis Technologies. All stimuli were 120 ms in duration and digitally shaped (20 ms rise/fall) to avoid onset and offset transients. Signals were passed through a programmable attenuator, an amplifier, and then to the wide-range speaker in each test chamber and presented at an average level of approximately 75 dBA, as calibrated with a sound level meter and condenser microphone (GenRad® 1981B sound level meter) placed at ear level. To prevent subjects from responding to possible loudness differences among stimuli, amplitude levels of all stimuli were varied by randomly selecting an intensity prior to each stimulus presentation. Stimulus intensity was varied over a range that encompassed the range of average intensity differences among all stimuli being tested (e.g., ±3 dB, in 1-dB steps). Stimulus presentation, behavioral contingencies, and data recording were carried out automatically by computer.

2.4. Procedure

A discrete-trial procedure was employed in which an animal was presented with a constantly repeating standard stimulus (e.g., A, A, A, A, A, etc.) into which was occasionally inserted a stimulus change (e.g., B). In the present instance, baboons were trained to hold down a lever to produce a series of repeating pulses of a standard grunt, and to release the lever only when a different, or 'target' grunt was inserted in an alternating sequence with the standard grunt (e.g., A, A, A, A, A, B, A, B; see Fig. 3). Specific details of the procedure are as follows: a flashing red cue light (5/s) signaled the start of each trial. Once the lever was pressed, the cue light became steady, and the train of standard stimulus pulses (2/s) began. One of the four target stimuli was randomly selected to alternate with the standard stimulus on each trial. This stimulus change between the standard and the selected target began at a random time of between 1 and 7 s following the initial lever press. Two presentations of the target stimulus alternated with the standard stimulus, resulting in a stimulus alternation interval 1.5 s in duration, as measured from the onset of the first target stimulus. Release of the lever at any time within this 1.5-s interval was considered a correct report, or "hit", of the stimulus change, and was reinforced with a 500-mg banana-flavored pellet, following which all stimuli were terminated. A 4-s inter-trial interval (ITI) followed, and any lever responses during the ITI re-initiated the ITI. Lever releases in the absence of stimulus changes produced an 11-to 15-s timeout from the contingencies, signaled by terminating the cue light. Failure to detect the stimulus

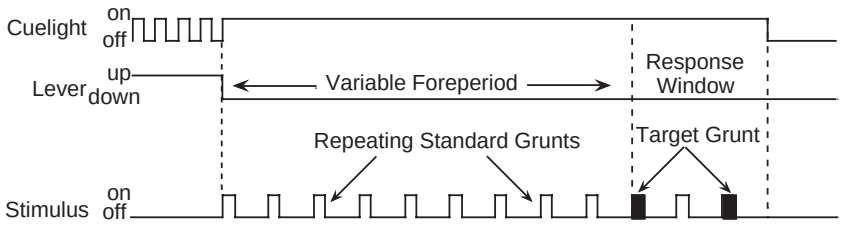

Fig. 3. A schematic diagram of a trial in the behavioral discrimination procedure illustrating how a lever press produces a constantly repeating standard stimulus, and how a correct lever release in the presence of a stimulus change results in reinforcement.

change, as indicated by holding the lever through the 1.5 s of the alternation period, resulted in the termination of all stimuli; the light remained off until the lever was released, following which the next ITI was initiated. Randomly on 20% of the trials, "catch" trials were presented to measure false-alarm rates; during each catch trial only the standard stimulus was presented throughout the trial. Lever releases during catch trials also produced a timeout of 11 to 15 s. In the present study, the grunt of Male 5 was employed as the standard stimulus, and the grunts of Male 1, Male 2, Male 3, and Male 4 served as the target stimuli.

2.5. Drug administration

Cocaine and saline were administered intramuscularly in the gluteal region. Injections were given at approximately the same time each day, immediately before the session started. The actual injection site was varied from day to day to avoid tissue damage from frequent injections. Cocaine doses were administered once or twice weekly, typically on Tuesdays and/or Fridays. On all other days, 0.5 ml NaCl vehicle was injected. All drug volumes were adjusted to be about 0.5 ml, with concentrations derived by dissolving drug in 0.9% sterile saline. Cocaine doses administered were 0.032, 0.1, 0,18, 0.32, and 0.56 mg/kg; this dose range included doses that did not alter performances as well as doses that produced cessation of responding. Each dose was administered at least twice and in a mixed order such that the lower doses were given randomly and the highest doses were given later. This regimen allowed the baboons to become familiar with the drug prior to receiving high doses that might produce sensitization. After 2 exposures were obtained at each dose, additional doses were administered if there were large differences between first and second exposures at any given dose.

2.6. Data collection and analysis

Sessions were 100 min in duration and occurred five days a week at approximately the same time each day. Each session was divided into blocks of 100 trials each. During this time baboons typically performed 5 full blocks of trials, i.e., 500 discrimination trials. For each target stimulus, the percent correct score for each block of trials was defined as the number of releases within the 1.5-s alternation interval divided by the total number of trials presented for each target stimulus within the block, multiplied by 100. False alarm rates were defined as the number of releases within the 1.5-s alternation interval when no stimulus change occurred, divided by the total number of catch trials presented within the block, multiplied by 100. Reaction times to each target stimulus were timed from the onset of the first presentation of a target stimulus to the release of the lever. Median reaction times for correct releases to each target stimulus were computed for each block of trials; medians of the reaction times were calculated because the physiological limits on reaction times can skew reaction time distributions. Baseline performances were defined as stable when the following conditions were met: 1) the percentage of correct responses to all target stimuli were 80% or greater during all blocks in a session; 2) false-alarm rates were less than 30% for all blocks of trials in a session; and 3) there were no systematic changes in the time course of these measures across blocks within a session or across sessions.

The "maximal effects" of cocaine on percent correct scores were calculated by selecting the lowest percent correct score from among the 4–5 blocks of trials of each drug session, and subtracting the average percent correct score from the immediately-preceding day's saline vehicle session. For comparison, estimates of percent correct scores following vehicle injections were calculated in an identical manner. Because cocaine lengthened reaction times, the maximal effects of cocaine on reaction-time values were calculated by selecting the longest median reaction time from among the 4–5 blocks of trials of each drug session, and subtracting the median reaction time value at the corresponding time from the preceding day's saline session. For comparison, estimates for reaction times following sessions during which vehicle was injected were calculated in an identical manner. The statistical significance of changes at the $p = .05$ level was assessed by determining whether each performance measure following drug fell outside of the 95% confidence interval ($\pm 1.96 \times$ s.d.) for the different baseline performance measures.

As previous studies found linear correlations between the size of cocaine's discrimination performance impairments and physical similarities among vowels (Hienz and Brady, 1988; Hienz et al., 1995, 2001a), a similar analysis was conducted here. This analysis examined correlations

between the discrimination performance changes following cocaine and the changes in the grunts in terms of F_1 and F_2, since discrimination of vowel sounds by both humans and animals has been shown to depend predominantly on changes in these first 2 formants (Hienz et al., 1996a; Kewley-Port and Watson, 1994; Sinnott and Kreiter, 1991; Sommers et al., 1992). Discriminability following cocaine was examined as a function of changes between the target and standard grunts for the first formant (ΔF_1), the second formant (ΔF_2), and additionally for changes in the absolute sum of the changes in F_1 and F_2 (ΔF_{SUM}) and for changes in the fundamental pitch (ΔF_0). These measures were chosen to examine whether animals were focusing on either first or second formants exclusively (the ΔF_1 and ΔF_2 measures), a combination of changes in F_1 and F_2 (the ΔF_{SUM} measure), or changes in the fundamental pitch (the ΔF_0 measure). For all measures, formant differences for each target grunt were expressed in terms of a Weber fraction (i.e., $[F_T - F_S]/F_S$), with F_T being the target grunt formant frequency, and F_S being the standard grunt's formant frequency. In this manner, all formant changes could be plotted on the same x-axis. For the analysis one cocaine dose was chosen that represented a maximal drug effect for each baboon, and linear regression functions were fitted to each measure for each animal. The doses selected for this analysis were 0.18 mg/kg for baboon DR, 0.32 mg/kg for baboons AC and ST, and 0.56 mg/kg for baboon CA.

3. Results

In general, all baboons performed the grunt discriminations at the 80% correct level within 5–10 sessions; this rate of acquisition of the discriminations is nearly identical to that observed previously for the acquisition of human vowel discriminations (Hienz and Brady, 1988). Additionally, the discriminability of baboon grunts did not differ from the discriminability observed previously for human vowels, with performances under non-drug conditions being at the 95–100% level for both types of stimuli (data not shown).

Fig. 4 shows the dose-related effects of cocaine on the discrimination of baboon grunt calls for all baboons (left). For comparison purposes, the average dose-related effects of cocaine on the discrimination of human vowel sounds in three baboons is shown to the right, as adapted from Hienz et al. (1995). In both graphs, the error bars represent 95% confidence limits about the saline average points, with points outside of these limits being significant at the $p = .05$ level. Following cocaine, much greater deficits were observed in the discrimination of the baboon grunt calls, compared to deficits in the discrimination of human vowels. Since identical behavioral procedures were employed under both instances, these more pronounced effects are likely a function of stimulus-related differences between baboon grunts and human vowels.

Possible stimulus-related differences in discriminability for the baboon grunt and human vowel stimuli are illustrated in Fig. 5, which shows the relative changes in the first 2 formants of the grunts and vowels, expressed as a proportional difference from the respective standard grunt or vowel employed in each case; that is, $(F_{T1} - F_{S1})/F_{S1} \times 100$, where $F_{T1} = F_1$ for the target stimulus, and $F_{S1} = F_1$ for the standard stimulus. This change measure is the same as a Weber fraction, and allows all formant changes for both grunts and vowels to be plotted on the same axes. Fig. 5 shows that 3 of the 4 target grunts (Male 2, Male 3, Male 4) had much smaller changes in F_2 relative to the standard grunt, compared to the target vowels. One of the grunts (Male 4) also had a much smaller change in F_1, compared to the vowels. The formant changes for grunt Male 1, on the other hand, were comparable to the vowels. Based on these

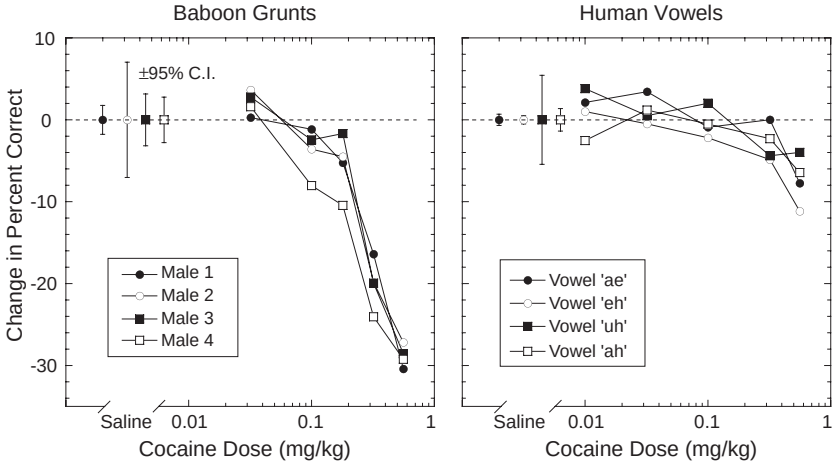

Fig. 4. The average dose-related effects of cocaine on the discrimination of baboon grunt calls (left), and human vowel sounds (right) as adapted from Hienz et al. (1995). Each point represents the difference between the peak effect on a drug day, as compared to the previous non-drug (saline) day. Error bars represent 95% confidence limits ($p = .05$) about the saline average points.

relative changes in both F_1 and F_2, one might predict that the grunts of Male 4 and Male 1, respectively, should show the maximal and minimal drug-related deficits, assuming that the deficits are a function of these F_1 and/or F_2 differences. Differential effects of cocaine on the grunts of Male 4 and Male 1 are suggested in Fig. 3, although the differences are small. Further, given the relative similarity of the Male 1 grunt to the human vowels, it is noteworthy that cocaine's effects on the discriminability of the Male 1 grunt were still quite large, relative to cocaine's effects on discriminability of the four vowels shown in Fig. 4.

Grunt discriminability following the maximally-effective doses of cocaine was also examined as a function of the 4 measures of the physical similarities among grunts described previously to determine whether cocaine's effects may have been correlated with changes in F_0, F_1 or F_2, or to a combination of changes in F_1 and F_2, (the ΔF_0, ΔF_1, ΔF_2, and ΔF_{SUM} measures). When correlations were examined for each of these measures for each animal, none of the measures showed a statistically significant correlation at the $p=.05$ level; a high correlation ($r>.90$) was required for significance, given the small number of points involved. The highest correlation obtained was 0.54 (for the ΔF_1 measure for baboon DR). Thus there was no clear indication of cocaine's effects in reducing grunt discriminability being related to any obvious acoustic differences between target grunts and the standard grunt.

False alarm rates were also examined as a function of cocaine dose for all baboons, and were found to not differ significantly from vehicle control false alarm rates at the $p=.05$ level, nor did the false alarm rates change in any consistent manner as a function of drug dose. The time course of changes in percent correct scores across individual sessions were also examined for all baboons by calculating detection percentages over 10-min bins from the start of each session. For three of the four baboons tested, cocaine produced deficits in call discriminability that peaked within the first part of the session, followed by a gradual recovery over the remaining session time to pre-drug discrimination levels. Additionally, cocaine's effects on call discriminability lessened with repeated exposures to the same dose, suggesting the development of tolerance to these perceptual decrements.

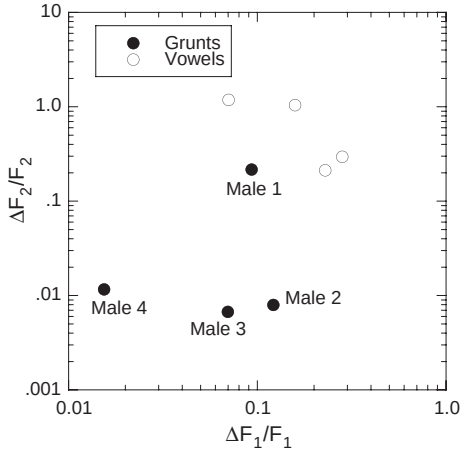

Fig. 5. Changes in the first 2 formants, F_1 and F_2, of the target baboon grunts and human vowels employed, expressed as a proportional difference relative to the standard grunt and vowel stimuli.

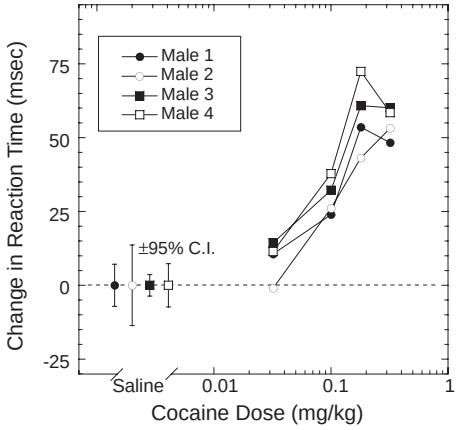

Fig. 6. Changes in median reaction times following cocaine, averaged across the 4 baboons. Shown are the differences between the maximum reaction time obtained on a drug day, and the average reaction time in the immediately preceding saline day, averaged across all replications for each grunt at each dose. Vehicle points represent identically derived data, with error bars representing 95% confidence limits ($p=.05$) about the saline averages.

Fig. 6 displays the observed changes in median reaction times following cocaine. Shown are the differences between the maximal median reaction time obtained on a drug day, and the average of the median reaction times of the immediately preceding saline day, averaged across all replications for each grunt at each dose. Vehicle points represent identically derived data, with error bars representing 95% confidence limits about the saline averages. Reaction times showed a general increasing trend as a function of drug dose. At the highest doses, two of the four baboons showed downturns in their individual dose-effect functions, reflecting the fact that these high doses produced prolonged pauses in the baboons' performances that resulted in data being obtained either early, late, or sometimes sporadically throughout the sessions. Thus the slight downturn at the high dose data points likely does not reflect a true maximum pharmacologic effect of the drug at these points.

4. Discussion

The present results show clearly that cocaine produces impairments in the perception of species-specific grunt calls in baboons, and that these perceptual decrements appear to be greater than those reported previously for the perception of similar human vowel sounds. As noted previously, baboon grunt calls are highly similar acoustically to human vowel sounds, but at the same time possess a social

significance for baboons that human vowel sounds do not have. These results thus suggest the intriguing possibility that cocaine may differentially affect the perception of biologically-relevant, socially-significant sounds, as opposed to acoustically similar but non-biologically relevant sounds. Such a conclusion needs to be considered carefully, since these differential effects of cocaine might also be a result of other factors.

One such possible factor is the existence of differences in the relative discriminability of the two types of stimuli. The grunts, for example, may have been less discriminable among one another, compared to the vowel stimuli, making the grunt discriminations relatively more difficult and consequently more prone to impairment following cocaine. This possibility is suggested by the fact that for 3 of the 4 discriminated grunts, the relative F_1 and F_2 formant differences were smaller than those of the vowels, as was shown in Fig. 4. On the other hand, observations that argue against this interpretation include the facts that: 1) the grunt of Male 1 was quite similar to the vowels in terms of relative formant differences, but the cocaine-induced reductions for the Male 1 grunt were still much greater than those previously observed with human vowels; 2) the cocaine-induced reductions for the Male 1 grunt were observed across baboons; and 3) cocaine's impairments in the discriminability of the Male 1 grunt and the grunts of Males 2, 3, and 4 were all quite similar in magnitude, in spite of their acoustic formant differences.

A second possibility is that cocaine's effects on these discriminations is a generalized effect of the drug on overall behavioral performance. However, prior studies have documented the effects of a number of drugs of abuse, including cocaine, in threshold detection tasks, and have shown for example, that cocaine impairs visual thresholds but not auditory tone thresholds under identical behavioral procedures (Hienz et al., 1994, 1993). Thus the effects of cocaine can be quite modality-specific, which allows one to rule out an overall effect of cocaine on either motivation or on general performance under such conditions. In the present case, percent correct detections of the stimuli were lowered following cocaine, while reaction times were raised for some stimuli but lowered or not affected for others, and false alarm rates were not significantly affected. Such differential effects on aspects of these discrimination performances tend to rule out a generalized drug effect on overall performance. Prior studies have also shown such differential performance effects in that diazepam and Δ-9-THC (the main psychoactive ingredient in marijuana) impair the perception of vowel sounds, but reaction times to the stimuli are lengthened by diazepam and not affected by Δ-9-THC (Hienz and Brady, 1988, 1989, 1987; Hienz et al., 1995). Further, drug-induced changes in motivation in this type of discrete-trial, self-paced procedure are typically minimal since animals are required to make an "observing response" (e.g., depress and hold the lever) to initiate each discrimination trial. When performance disruptions occur (e.g., at extremely high drug doses), animals typically do not initiate trials at all. Consequently, when data are obtained, they are relatively free of possible motivational changes that might affect overall performance. Finally, since no significant changes were observed in false alarm rates following cocaine in the present study or in prior studies of cocaine's effects on vowel discriminations (e.g., Hienz et al., 1995), cocaine does not appear to bias responding in any systematic manner, but specifically affects stimulus discriminability under this type of discrimination procedure. On the other hand, prior work (Hienz et al., 1996b) has shown that cocaine can systematically elevate false alarm rates when animals are performing an "identification" procedure in which they are required to release to one type of stimulus (e.g., one vowel sound), but not release to another (e.g., a different vowel).

A third possibility is that baboons simply do not attend to or discriminate among baboon grunt calls and human vowel sounds in the same fashion. For example, they may attend to different pitch and/or intensity cues when performing the two types of discriminations, or they many not be as sensitive to the inherent acoustic differences among different baboon grunt calls, as compared to those that exist among human vowel sounds. However, it has already been demonstrated that baboons are comparable to humans and other animals when it comes to discriminating changes in the formant structures of complex signals such as those contained in baboon grunt calls and human vowel sounds. That is, baboons are like humans in that they discriminate among human vowels via the information contained in the formant structure of the vowels (Hienz and Brady, 1988), and also discriminate among baboon grunt calls via this same type of formant information (Hienz et al., 2004; Rendall et al., 2004). Additionally, signal detection thresholds for baboons detecting changes in vowel formants are comparable to those observed for humans, other monkeys, cats, and birds (Hienz et al., 2004). Further, signal detection thresholds for baboons detecting changes in the formant structures of their own grunts are approximately the same as their thresholds for detecting changes in comparable human vowels. For example, baboons can detect about a 35-Hz change in the second formant of a grunt, (Hienz et al., 2004), whereas the relative F_2 differences in the grunts discriminated in the present study ranged from 60–270 Hz. These observations indicate that baboons do not differ significantly from humans in their ability to discriminate among complex signals such as baboon grunts and human vowels, nor do they differ from humans in how they make these discriminations. Further, baboons are not unique in this regard, as others have also demonstrated that macaque monkeys have signal detection thresholds for discriminating changes in vowel formants that are similar to those measured in humans (Sinnott and Kreiter, 1991; Sommers et al., 1992).

A fourth possibility is that cocaine's differential effects on the discrimination of socially-significant grunt calls are

related to the fact that discriminations among baboon grunt calls and among human vowel sounds represent two different types of perceptual discriminations. Grunt discriminations may be more "natural" in the sense that they are more akin to the types of discriminations made in the natural ecological environment of baboons, and as a result may involve specialized (i.e., "hardwired", "innate", or "automatic") mechanisms that differ from more general perceptual discriminations. For many animals, including nonhuman primates, specialized mechanisms exist for the encoding and decoding of important perceptual information related to species survival, such as those concerning reproduction, predation, the maintenance of social cohesion, and the handling of social aggression. As noted in the Introduction, the vocalizations of baboons and other nonhuman primates do provide information that is of motivational and social significance to other members of the social group, and these vocalizations result in predictable behavioral responses from the listeners (Andrew, 1976; Byrne, 1981; Cheney et al., 1995; Hall and De Vore, 1965). It might not be surprising then to find a differential effect of how a drug might influence possibly "specialized" discriminations as opposed to other generally learned discriminations.

While this last possibility does not provide an intuitively obvious explanation of why such discriminations might be subject to more disruption, rather than less, following cocaine, others have observed drug effects on motivational and social aspects of behavior. For example, drugs that exert effects via GABAergic and dopaminergic mechanisms have been shown to disrupt established social interactions in group-living primates (Miczek et al., 1984; Weerts et al., 1993; Winslow and Miczek, 1985). Further, these disruptions are dependent on social rank, and are thought to be due in part to alterations in the perception of social signals. Drug-treated dominant animals, for example, increase aggressive threats and vocalizations towards non-treated conspecifics; drug-treated subordinate animals initiate inappropriate behavioral responses and vocalizations, and receive more social and aggressive displays from non-treated conspecifics. In this regard, it is also noteworthy that cocaine has also been shown to have direct effects on the auditory system in that it decreases both auditory nerve response amplitudes and cochlear blood flow in guinea pigs (Shivapuja et al., 1993), reduces the amplitude and latency of human auditory event-related potentials (Herning et al., 1985; Robledo et al., 1993), interferes with mechanisms of auditory stimulus processing in humans (Boutros et al., 1994; Herning et al., 1994), and impairs verbal comprehension in children exposed to the drug in utero (Nulman et al., 1994).

Why might cocaine differentially affect perceptual discriminations of stimuli that are highly socially significant? As noted above, drugs that exert effects via GABAergic and dopaminergic mechanisms have been shown to disrupt established social interactions in group-living primates (Miczek et al., 1984; Weerts et al., 1993; Winslow and Miczek, 1985), and it may be that cocaine adversely affects the specialized mechanism(s) underlying aspects of these complex social processes. Alternatively, these differential effects may be related to the obvious functional role of grunts to baboons in terms of their social significance vis-à-vis the absence of any such function for tones and human vowel sounds. Prior work has already suggested that drugs of abuse may affect both the initiation of agonistic behaviors and the perception of social signals that communicate subordination or appeasement in primates (Haber et al., 1981; Schlemmer and Davis, 1981). Baboon vocalizations also include a number of call types that can be distinguished by their function (i.e., they only occur in certain situations) as well as by certain invariant acoustic features of the calls. Affiliative grunts, for example, are emitted in friendly greeting at a distance (female–infant, male–infant, adult–adult), during grooming, during feeding, in excited choruses when the grunts of one animal evoke grunts in others, and in a continuous chorus of grunts while moving through dense cover (Andrew, 1976; Cheney et al., 1995). The readiness with which grunts are answered suggests that they are used in social contact situations and, as noted previously, function to identify the calling individual. Baboons also grunt when approaching lower-ranking baboons, with the grunts appearing to have a mollifying effect on subordinates (Cheney et al., 1995). Other baboon call types include 'threats', which are typically associated with aversive social situations such as attacks or threats and are given by the aggressor(s), and 'screams' and 'fear-barks', which are most frequently associated with defensive reactions related to submission and fear (Byrne, 1981). Thus there is a vast repertoire of behaviors and associated vocal signals underlying nonhuman primate social organization that may be affected by drug action, and obviously drugs of differing mechanisms of action may differentially affect such functional systems.

The present results did not indicate that the reductions in discrimination accuracy following cocaine were correlated with the similarities between grunts. Correlations of greater drug effects with increasing similarities among vowel stimuli have been demonstrated following acute administration of cocaine, diazepam, morphine, and buprenorphine in baboons (Hienz and Brady, 1988, 1989; Hienz et al., 1995, 2001b), suggesting that the effects of cocaine on vowel discriminations result from disruptions in CNS mechanisms involved in the processing of the spectral cues related to pitch. The lack of such an effect in the present study was not expected, since baboon grunts and humans vowels are acoustically quite similar. On the other hand, this added difference in the way cocaine affects grunt discriminations versus vowel discriminations is consistent with the suggestion that the grunt discriminations may involve a different, more specialized underlying perceptual mechanism.

In sum, the present results show that cocaine impairs the perception of baboons' affiliative grunt calls, and that

the observed impairments are greater than those previously observed when baboons discriminated among acoustically-similar human vowel sounds. The larger cocaine-induced impairments observed with these natural call discriminations are not obviously related to 1) a general effect of cocaine on overall performance, 2) apparent differences in the acoustic structures of the two types of stimuli, 3) differences in the types of acoustic cues utilized by baboons to discriminate among the two types of stimuli, or 4) differences in the abilities of baboons to discriminate between the fine structural changes of the two types of stimuli. As baboon grunt calls are highly socially-significant for baboons, whereas human vowel sounds are not, the results are in agreement with the hypothesis that these differential effects may be related to the highly socially-significant role that these calls serve in baboon social behavior. If so, these results have implications for cocaine's potentially greater disruptive effects on the human perception of biologically relevant stimuli as well. Further work is needed, however, to more definitively support this hypothesis. In this regard, work in progress is exploring the effects of cocaine and other stimulant-like and sedative-like compounds on the perception of different call types (e.g., affiliative, aggressive, submissive) as well as natural functional signaling differences inherent in baboon calls (e.g., sexual identity, individual identity) to determine the effects of compounds on socially significant perceptual function as well as assess the utility of these species-specific call discriminations in providing a model of the effects of drugs on motivational and social processes.

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