Dissociation of Cortisol and Behavioral Indicators of Stress in an Orangutan (*Pongo pygmaeus*) During a Computerized Task

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ABSTRACT. Computerized testing can induce behavioral signs of frustration in apes. Three variations of a computer task were used to investigate the effects of inter-trial intervals and rate of cursor movement on frustrative behavior and cortisol in an orangutan. Behaviors were recorded during test sessions, and saliva was collected immediately after test sessions for cortisol assay. Behavioral results indicated that extended (20 sec) periods of delay between trials induced signs of frustration in the subject, including forceful manual manipulation of objects and self-scratching. However, cortisol results indicated that Hypothalamic-Pituitary-Adrenal (HPA) axis activity was not induced by task performance. Rather, cortisol levels were reduced during performance of computer tasks compared to baseline levels. Findings from this study suggest that behavioral and cortisol responses to stress induced by performance of computer testing can become dissociated. This study validates salivary cortisol as a measure of HPA activity in apes and demonstrates a normal circadian rhythm of cortisol release in an orangutan.

Key Words: Cortisol; Behavior; Stress; Computer; Primate; Orangutan.

INTRODUCTION

Stress responses produce a diversity of changes in the activity of endocrine and neural systems. These responses appear to be nonspecific to the types of stressors inducing them. Psychological stress has been demonstrated to influence the activation of the Hypothalamic-Pituitary-Adrenal (HPA) axis. In certain settings, for instance, stress responses may be induced in the absence of any external physical stressor. Situations involving low predictability, low controllability, and novelty can produce a rise in the levels of corticotropin-releasing hormone (CRH) from the hypothalamus and adrenocorticotropic hormone (ACTH) from the anterior pituitary gland followed by a subsequent increase in cortisol release from the adrenal cortex. These stress responses appear to provide adaptive advantages to the organism by mobilizing energy reserves that can be used to cope with the stressful situation (SAPOLSKY, 1992).

The development of noninvasive techniques for the assessment of stress in laboratory and free-ranging animals is a continual goal of researchers. Collection of urine, fecal, and saliva samples for the measurement of cortisol has become useful in studies with primates and domesticated animals (BEERDA et al., 1996; BOYCE et al., 1995; CZEKALA et al., 1994; ROBBINS & CZEKALA, 1997; SMITH & FRENCH, 1997; WHITEN et al., 1998). Saliva cortisol assessment provides a valid reflection of the unbound hormone in blood. In addition, saliva cortisol measurement reduces sampling stress compared to blood collection techniques. Research has been conducted examining salivary cortisol as a valid assessment of stress responses in humans (KIRSCHBAUM & HELLHAMMER, 1994). In nonhuman primates, factors such as food availability, group formation, social separation, and environmental novelty are capable of inducing physiological stress responses, including the release of cortisol (CHAMPOUX et al., 1993; HENNESSY et

al., 1995; HOFFMAN et al., 1995; LYONS et al., 1998). To our knowledge, no prior studies have utilized salivary cortisol as a measurement of stress induced during performance of a computer task in apes.

Many species of primates exhibit increased locomotor activity and self-directed behaviors during and after social or psychological stress exposure (AURELI & VAN SCHAIK, 1991; CASTLES & WHITEN, 1998; DUNN & BERRIDGE, 1990; ITAKURA, 1993; MAESTRIPIERI et al., 1992). During performance of computer tasks, apes will display behavioral signs of frustration. In orangutans, signs of frustration include self-scratching, forceful manipulation and biting of cage structures, and vocalizing. Features of computer tasks that might be expected to influence the frequency of such behaviors include (1) the amount of time and effort required to complete a trial, (2) the amount of time elapsed between food rewards, and (3) the extent to which the subject can work continuously on a task, without substantial delay between trials. During pilot testing with the subject of this study, behavioral responses to delay periods between computerized task trials were observed. Thus, three computerized tasks were developed which investigated the effects of effort, total time of task performance, and trial delays on the frequency of behavioral responses elicited.

The current study examines the extent to which features of computerized tasks affect the frequency of frustration-related behaviors produced and salivary cortisol levels during testing. The first goal of the study is to determine the effects of computerized task parameters on the frequency of behaviors indicative of emotional stress or frustration. The second goal is to determine the time course of salivary cortisol change subsequent to stimulation of the subject by computerized task performance. The final goal is to measure the correlation between behaviors produced and the level of cortisol, as measured in saliva samples.

The hypothesis tested by this study is that variation in the temporal distribution of work time induces variation in the frequency of frustration-related behaviors. Specifically, even brief periods of delay between trials might be expected to cause an increase in the frequency of frustration-related behaviors. A competing alternative to the hypothesis under study is that frustration-related behaviors are determined solely by the time between food deliveries. In this case, the frequency of frustration-related behaviors displayed during a computer test session is directly related to this inter-reward interval. For example, computerized tests that produced a constant temporal distribution of reward might be expected to elicit constant levels of frustration-related behaviors. Computerized tasks which allowed the subject to continuously work toward a goal may be less frustrating than a task in which the subject was not able to constantly work toward achieving a goal. Alternatively, testing conditions that required that the subject spend more time working toward a goal may elicit more frustration than tasks requiring a lesser amount of work time (ROSE et al., 1982). This study examines whether a modest delay between trials, irrespective of the amount of time and effort required to complete a trial or the inter-reward interval, is capable of inducing both behavioral signs of frustration and alterations in salivary cortisol levels in an orangutan.

METHODS

Madu, a female orangutan (*Pongo pygmaeus*), age 15 yr, was the subject in the current study. The subject was born in captivity at the Yerkes Regional Primate Research Center and had spent a majority of her life at the Language Research Center of Georgia State University in the company of another female orangutan. She had been housed singly for the past one year, including the current study.

The subject was housed in a home cage measuring 411 × 488 cm. The testing station was composed of a 51 × 81 cm clear plastic (lexan) window through which the subject could view a computer monitor. The station contained a port measuring 20 × 30 × 17 cm, through which the subject could manipulate a joystick. The port was located within the lexan window, 30 cm above a platform upon which the subject sat during testing.

The subject was tested using an IBM-compatible computer system. The monitor displaying the task was located approximately 80 cm above the seating platform on a computer cart outside of the testing cage. The front face of the monitor was positioned approximately 60 cm from the lexan of the test station. A Kraft model KC3 joystick was used for performance of the task. An automatic pellet dispenser allocated pellets after completion of correct trials. The dispensing tube from the automatic pellet dispenser fed into a PVC tube that delivered a 1-g food pellet at mouth level, 45 cm, above the seating platform.

Baseline saliva samples (taken on non-test days) were collected on four days throughout the experimental phase of the study (Fig. 3). Post-experiment baseline saliva samples were also collected on four successive days, beginning five days after the completion of computerized testing. On each collection day, samples were taken at 09:30, 12:00, 12:30, 12:45, 13:00, and 17:30. On test days, saliva was collected at the same times as on non-test days. Test sessions consisted of performance of one of three computerized foraging tasks, collection of saliva samples, and measurement of behaviors produced. Experimental testing began at 12:00 and ended at 12:30. Only one experimental task was performed each test day. During the experimental phase of the study, the three tasks were each presented an equal number of times ($N = 11$), in a balanced order. There were 33 test days over a total study period of 90 days. Test days were distributed approximately evenly over the entire study period.

The three computerized tasks used in the current study each required the subject to move a cursor on the monitor using the joystick. A trial was completed when the subject brought the cursor into contact with a target. The three computer tasks appeared visually similar but differed in cursor progression rate and period of delay between trials. In all three tasks, the monitor displayed a cursor in the shape of an oblong white dot, an open green field, and a target, the letter G. The letter G was located at the opposite side of the monitor screen from the cursor. The *Four-problem* task presented a cursor which traveled rapidly (10 jumps/sec) upon movement of the joystick and required that the subject work four problems per trial to receive a food reward. The subject was prohibited from correctly performing the first three out of every four problems per trial in this test condition. An invisible barrier was constructed into the program to prevent correct responding so that the trial ended when the subject moved the cursor within an approximately 1 cm radius of the target. On the fourth problem there was no such invisible barrier and the subject could contact the target to complete the problem and the trial. The total time for completion of four problems in each trial in this task was approximately 25 sec. This task was included to determine whether prohibiting the subject from responding correctly on a majority of the problems (75 %) induced behavioral signs of frustration and alterations in cortisol level. The task was expected to increase task effort demands, thereby allowing investigation of the effects of effort on behavioral and HPA axis stress responses. The *Slow-cursor* task presented a slowly progressing cursor (1 jump/sec) upon joystick movement and required the subject to work one problem per trial to receive a food reward. Each subsequent trial followed the previous trial without substantial delay in this task; however, the cursor moved at a rate allowing one trial to be completed every 25 sec. This task was used to examine the effects of extended working times on the alteration of salivary cortisol levels and behavior. The *Inserted-delay* task also presented a rapidly moving cursor (10 jumps/sec) upon joystick movement and required that the subject complete only one problem per trial to receive a food reward. However, a 20-sec delay

period was inserted between trials in this condition. The *Inserted-delay* task was designed to determine whether modest delays between trials elicited behavioral signs of frustration and a corresponding alteration in cortisol levels. Food intake remained constant across task types given that the subject received one food pellet for each correct trial (e.g. one pellet was dispensed approximately every 25 sec regardless of the test condition being performed).

One audible tone was used on all three task types to indicate proper completion of trials. A second audible tone was used only on the *Four-problem* task to indicate a need to continue working to receive a food reward. The delivery of food was executed by the automatic pellet dispenser immediately following completion of each correct trial, with delivery occurring prior to delay onset during *Inserted-delay*.

Saliva for cortisol assay was collected immediately before starting the 30-min test session, immediately upon completion of the test session, and 15 and 30 min after completion of the test session. Following collection of the pre-test saliva sample, the computer apparatus was moved into the test station, the computer program was initiated, and the joystick and pellet dispenser were mounted. The test session began when the task appeared on the screen and the subject was provided access to the joystick. Following completion of the test session and collection of the post-test saliva sample, the computer apparatus and all other equipment were removed from the test station.

Saliva was collected using the following procedure. A feeding tube was placed in the subject's mouth along the pockets of the lower jaw. The tube was attached to a vacuum pump as well as to a 50-ml collection tube. Saliva was aspirated into the collection tube until four to ten drops of saliva were obtained. The saliva was then transferred into a 1-ml eppendorf tube using a disposable pipet. The samples were frozen at approximately −17°C for later assay.

Cortisol assays were performed using coated-tube radioimmunoassay kits (Diagnostic Products Corporation, Los Angeles) with procedures modified for the overall lower concentration of steroids in saliva as compared to blood. Intra- and inter-assay coefficients of variation were 13.88 and 16.06%, respectively. The least detectable dose was 0.72 nmol/L. Food items given to the subject as part of her regular diet or as food reward for performing computerized tasks contained no cortisol.

An ethogram was prepared based on pilot testing of the three tasks to correlate internal emotional frustration with overt behaviors. The behaviors were measured within each 25-sec trial, including inserted periods of delay. Each behavior was scored as either occurring or not occurring during an individual trial (1-0 sampling). Only behaviors that appeared to be produced with substantial force were recorded. Eight behaviors were recorded: manipulate free object, manipulate stationary object, manipulate joystick/port, self-scratch, self-slap, bite cage/object, vocalize, and spit/extend fingers. For statistical analysis, the eight behaviors measured were compiled into four categories (Table 1). The first behavioral category, "Manual manipulation," represents manipulation of free or stationary objects in the cage such as the joystick port or cage bolts. The behavioral category termed "Self-directed" refers to behaviors that are self-directed such as scratching or slapping. The third category, "Cage biting," includes behaviors such as biting cage wire. The final behavioral category, "Observer-directed," describes behaviors such as spitting at or extending the fingers through the cage wire toward the experimenter. Six 30-min behavioral

Table 1. Eight behaviors measured and their categorical affiliation.

Manual manipulation	Self-directed	Cage biting	Observer-directed
Manipulate free object Manipulate stationary object Manipulate joystick/port	Self-scratch Self-slap	Bite cage	Vocalize, Spit/extend fingers

baseline sessions were conducted during which behaviors were measured with no computer apparatus present. During behavioral baseline sessions, behaviors were recorded during 25-sec intervals. For purposes of statistical analysis, each 25-sec interval was considered to be one trial. These behavioral baseline sessions were run at the same time of day (12:30 to 13:00) as testing sessions. Two observers agreed on behaviors displayed during real time observation sessions on more than 90% of trials for each of the four behavioral categories.

Throughout the study period, the subject was fed the diet on which she had been maintained for more than one year prior to the experiment. Her diet, which consisted of vegetables, fruits, and chow, was distributed at the same time periods on each day throughout the experiment. Her overall food intake remained constant across both testing and baseline days throughout the entire study. On baseline behavioral and cortisol sampling days, the subject was given vegetables during the time period (12:00 to 12:30) in which she would have been performing a computer task and receiving food reward.

RESULTS

The subject completed an average of 63 trials per test session. Table 2 displays the total number of trials completed in each test condition, the number of trials in which frustration behaviors occurred, and the percentage of total trials in which behaviors occurred. Frustration behaviors occurred more frequently in each behavioral category in the *Inserted-delay* task than in either of the other two tasks. The Friedman test (SIEGEL & CASTELLAN, 1988) was conducted to determine if the differences in frustration behavior among the three test conditions were reliable across test sessions. For Friedman analysis, test sessions (N=11) were treated as subjects. The total number of trials in which any behavior occurred differed significantly across the three test conditions (Friedman test, Chi Square = 17.1, $df = 2$, $p < .001$). As seen in Figures 1 and 2, the number of trials in which manipulation and self-directed behaviors occurred differed significantly across the three task types (Friedman test, Chi Square = 18.6, $df = 2$, $p < .001$, and Chi Square = 7.5, $df = 2$, $p < .05$, respectively). Specifically, the frequency of manual manipulation of objects and self-directed behaviors was higher in the *Inserted-delay* condition than in the *Four-problem* or *Slow-cursor* conditions. However, the number of trials in which behaviors occurred in the categories "Cage biting" and "Observer-directed" did not differ significantly across task types. During the six behavioral baseline sessions, the subject rarely engaged in frustrative behaviors. The subject showed manual manipulation of objects during four baseline trials out of 382 (1% of total trials) and self-directed scratching during three trials out of 382 (1% of total trials). No cage biting or observer-directed behaviors were observed during these baseline sessions.

Table 2. Total number of trials in which behaviors occurred in four behavioral categories for three test conditions.

Test condition	Manual manipulation	Self-directed	Cage biting	Observer-directed
Four-problem	27	31	26	1
$N = 693$	3.9% of trials	4.5%	3.8%	0.1%
Slow-cursor	7	38	29	2
$N = 695$	1.0%	5.5%	4.2%	0.3%
Inserted-delay	412	90	30	4
$N = 708$	58.2%	12.7%	4.2%	0.6%

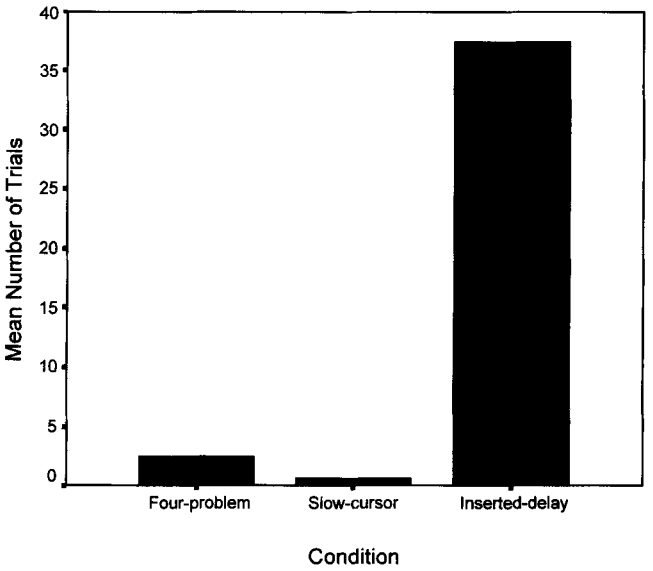

Fig. 1. Mean numbers of trials per session in which manual manipulation occurred.

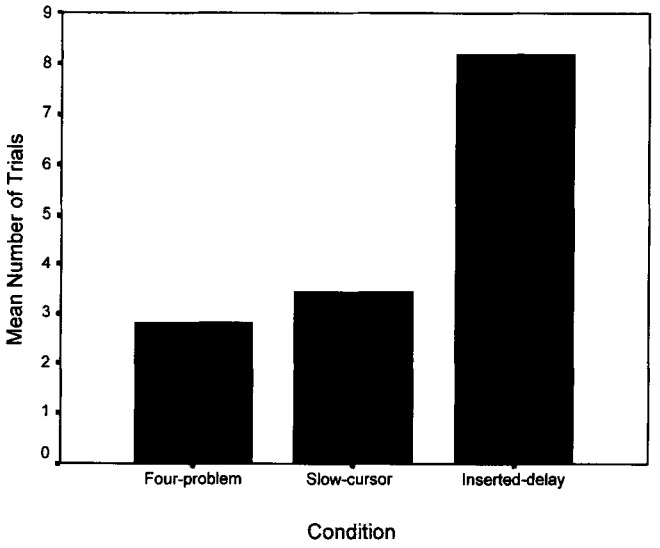

Fig. 2. Mean number of trials per session in which self-directed scratching or slapping occurred.

Large day-to-day variability was identified in the daily levels of cortisol in this subject (Fig. 3). However, as shown in Figure 4 (data derived from eight baseline days), the subject exhibited a circadian pattern of cortisol release that is normal for diurnal primates, with the peak of cortisol occurring in the early morning followed by a decline in cortisol levels throughout the day (CZEKALA et al., 1994; KRIEGER et al., 1971; PLANT, 1981; SMITH & NORMAN, 1987). The overall change across the six daily samples in the levels of cortisol was statistically significant

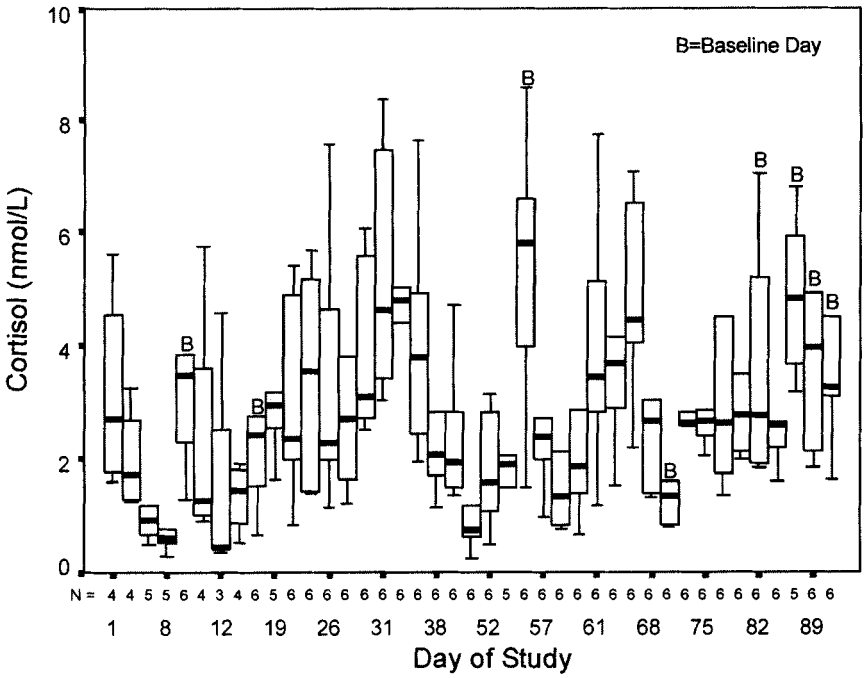

Fig. 3. Median daily cortisol levels throughout entire study. *N*: Number of samples; box: interquartile range; dark bar: median; T-bars: highest and lowest values excluding outliers (values exceeding 1.5 box lengths from box boundary).

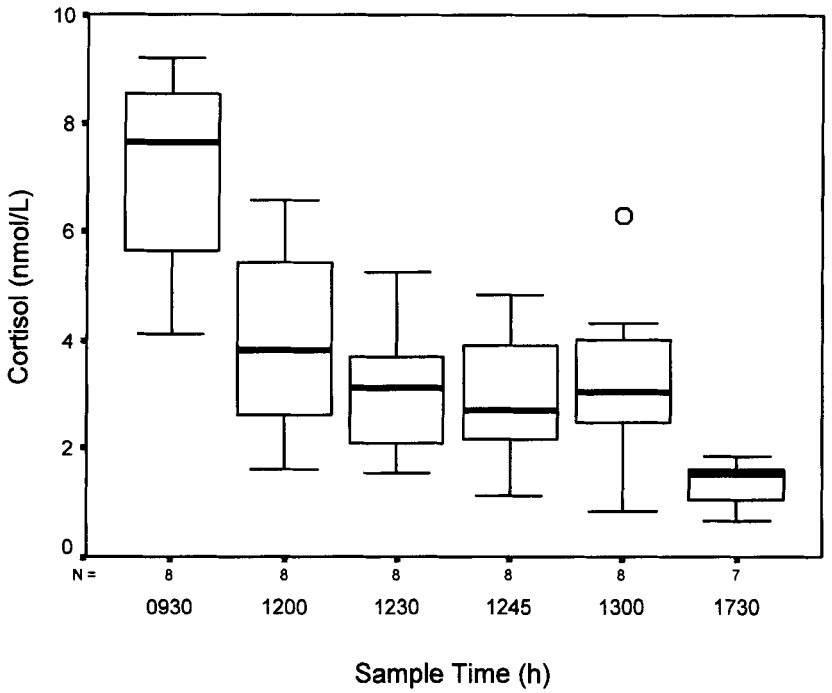

Fig. 4. Median cortisol level for six daily samples in baseline condition. O: Outlier.

[ANOVA: F (5, 41) = 13.42, $p < .001$]. There were no significant differences between baseline salivary cortisol samples taken during the experimental phase of the study (non-test days) and those obtained after completion of the experimental phase of the study (post-experiment baseline). In addition, there was no evidence for periodicity in the level of cortisol in baseline samples taken at the time during which experimental testing would have occurred. To measure the effects of computer task performance on cortisol release, the values for the three samples obtained following computerized testing (or at comparable times on baseline days) were combined and analyzed using a two-way ANOVA. The independent variables were condition and sample time. There was a statistically significant effect of condition. The levels of cortisol immediately following completion of testing and 15 and 30 min following testing completion (samples taken at 12:30, 12:45, and 13:00, respectively for both testing and baseline days) differed across the baseline, *Four-problem*, *Slow-cursor*, and *Inserted-delay* conditions [ANOVA: F (3, 106) = 2.92, $p < .05$]. Specifically, cortisol levels were lower for all three test conditions compared to samples taken at the same times on baseline days (Fig. 5). There was no main effect of sample time and no significant interaction between condition and sample time. In addition, the Pearson product-moment correlation between cortisol level (mean of three post-test samples) and the frequency of frustrative behavior during the same test session was not statistically significant ($r = 0.44$, $N = 11$). Post hoc tests using the Least Significant Difference method indicated that cortisol levels were significantly reduced for the *Slow-cursor* and *Inserted-delay* conditions compared to baseline (p's $< .05$).

DISCUSSION

The behavioral results indicate that imposed periods of delay between trials induced behav-

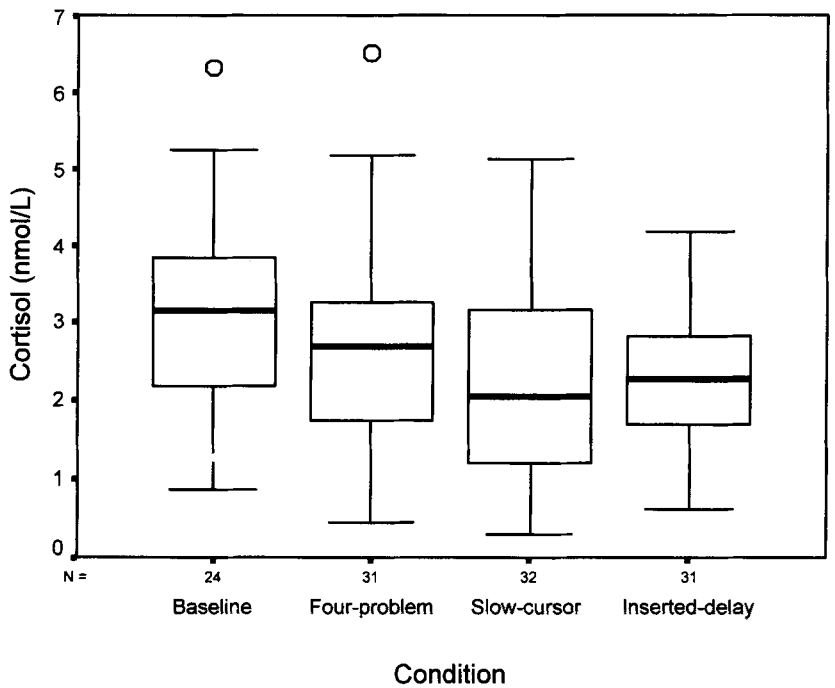

Fig. 5. Median cortisol levels of samples taken at 12:30, 12:45, and 13:00 for four conditions.

ioral signs of frustration in this subject. Manual manipulation occurred in 15 times as many trials in the *Inserted-delay* task than in the *Four-problem* or *Slow-cursor* tasks. Similarly, self-directed behaviors occurred in more than twice as many trials in the *Inserted-delay* task than in the *Four-problem* or *Slow-cursor* tasks. The sharp differentiation of conditions by the subject is notable, given that the time between food deliveries was held constant. This suggests that how work time and wait time are allocated in a computer task influences the emotional state of the subject. The *Slow-cursor* task induced less frustration-related behavior than *Inserted-delay*, suggesting that working one trial continuously for 25 sec, despite the slow rate of cursor movement, was less frustrating than quickly completing the trial in 5 sec and waiting 20 sec for another trial to begin. Furthermore, *Four-problem*, which required that the subject work four problems per trial for a single food reward, appeared less frustrating than *Inserted-delay*. This may seem counterintuitive if one assumes that an animal knows when it has responded incorrectly and attempts to perform trials correctly to receive a food reward. The immediate opportunity to perform another trial following incorrect responding in *Four-problem* may have alleviated the frustration potentially generated by incorrect responding. Furthermore, differential reward was eliminated as a mediating factor in the production of frustration-related behaviors in this experimental paradigm, given that total food received and the temporal distribution of food reward were equivalent for all three test conditions. The low level of behavioral responding observed during baseline sessions indicates that behaviors produced during performance of *Inserted-delay* were not due solely to free time available during periods of delay. Had this been the case, one might expect the subject to engage in manipulatory and self-directed behaviors while not performing computerized testing in her home cage.

Behavioral signs of frustration may have been induced in the subject during delays in computerized testing due to the presence of food that could not be obtained. When no computerized testing was occurring, the subject was not presented with an appetitive stimulus (food reward for performance of computer tasks) at close proximity and was not in one of the known situations that may induce signs of frustration. In this case, no frustration was induced when the subject was not engaged with a task. However, while testing, the subject was provided access to a computerized system that would dispense food as a reward for completing correct trials. During periods of delay between trials, the subject was unable to work toward receiving food reward. This lack of control may have induced behavioral signs of frustration. Research in humans has demonstrated that uncontrollability in experimental tasks can lead to an increase in cortisol release and autonomic nervous system activity (PETERS et al., 1998). In sum, it appeared that continually working on a task, whether correctly or incorrectly, was the most important factor in alleviating overt signs of frustration during performance of computer tasks in this subject. Behavioral indicators of frustration were induced when the subject was required to wait a short period between performance of correct trials.

Salivary cortisol results indicate that activity of the HPA axis did not increase with inserted periods of delay between trials, slow cursor movement, or requirement to work four problems per trial for one food reward in computer testing. In fact, it appears that performance of computerized tasks lowered the circulating levels of cortisol in this subject. The reward provided by performance of computer tasks may reduce physiological or psychological stress (i.e. hunger, boredom – states which may not regularly induce behavioral signs of frustration as evidenced by baseline behavioral recordings) normally experienced during similar time periods in this subject. Previous research using reinforcement extinction paradigms and shifts from variable to fixed reinforcement schedules demonstrated an increase in adrenocortical activity due to the experimental stressors (COE et al., 1983; COOVER et al., 1971). However, the current test involved presentation of only fixed interval reinforcement paradigms indicating that reinforcement schedule did not play a part in the development of the subject's behavior. In addition,

research with rhesus macaques suggests that these animals exhibit fewer frustration-related (self-scratching) and stereotypic behaviors, similar to those being scored in the current study, when presented with the opportunity to perform computerized tasks. Furthermore, these subjects preferred not to select a free food option if the computerized tasks were disabled for a period of 30 min or longer due to the selection of free food. This evidence suggests that factors other than receiving food reward alone can be motivating for the animals when performing various computerized tasks (WASHBURN & RUMBAUGH, 1992).

Collectively, results from the current study indicate that in this orangutan subject there was a dissociation between behavioral and HPA axis stress responses. Behavioral indicators of stress do not always correspond closely to measures of HPA axis activity. In a study of human newborns, researchers found that exposure to graded stressful stimulation resulted in increased behavioral responses to the stressor (GUNNAR et al., 1998). However, the differences in behavioral distress between conditions did not predict the levels of plasma cortisol induced by the stressor. Furthermore, the physiological stress response to the stressor was not reduced when behavioral distress was decreased by providing the newborn with an outlet for frustration (sucking on a pacifier). Previous research has also demonstrated that interindividual variation can exist such that infants may show high behavioral responses and low cortisol responses, or vice versa, on an individual basis (LEWIS et al., 1993). This raises the possibility that the subject in the current study is a highly reactive individual behaviorally but does not respond physiologically through the HPA axis based on the stressors presented in this study. Additionally, the duration of the stressors presented in this computerized task or the magnitude of frustration induced may not be great enough to induce cortisol release. In fact, the computerized tasks presented in this study are quite limited events during the course of the day and are relatively rare as compared to more global time scales.

In principle, it might be argued that frustration or stress induced by expectancy of performing computerized tasks on non-test days induced elevated cortisol levels in the subject on non-test days. However, the subject was given her normal diet of vegetables on non-test days during the time when she would otherwise have been working a computer task, so she was obviously not food deprived on non-test days. In addition, test days occurred approximately once every three day over the course of this study so that there was no consistent expectancy about performance of tasks for the subject. No behavioral indications of frustration were observed on non-test days during the period of 12:00 to 12:30, which corresponded to the period of computerized testing. Furthermore, analysis of baseline salivary cortisol levels indicated no difference between samples collected on non-test days during the experimental phase of the study and samples taken following completion of the experimental phase of the study.

Literature from the field of human emotion has distinguished between frustration and stress and there appears to be a biological basis for this distinction (HENRY, 1992). It is possible, therefore, that cortisol levels reflect physiological stress while self-directed behaviors reflect psychological frustration. Both of these phenomena are nevertheless rooted in biological systems that appear to be dissociated in the context of the computerized tasks being performed in this study.

There are at least two possible mechanisms by which behavioral and physiological stress responses could have become dissociated in the current study. First, behavioral responses to frustration induced by the task may have decreased the physiological response. The subject was not prevented from utilizing available outlets of frustration, such as self-scratching or manual manipulation of objects. Thus, by responding behaviorally, the subject may have prevented the increase in cortisol that usually follows a frustrating event. After preventing an initial increase in the HPA axis response through behavior modification, the levels of cortisol may be further

reduced below baseline levels by the food and nonfood rewards (WASHBURN & RUMBAUGH, 1992) obtained from working on computerized tasks. An alternative possibility is that the *Inserted-delay* condition stimulates brain regions not directly associated with, or that have minor influence on, the HPA axis. In this case, behavioral responses would not necessarily be correlated with cortisol levels. Increased activity of the autonomic nervous system might result in the irritation of epidermis, for example, that could cause the animal to exhibit self-directed scratching behavior. Indeed, administration of anxiogenic drugs in macaques results in autonomic nervous system activation and an increase in the expression of vigilance and scratching. Scratching is also elicited in macaques by electrical or pharmacological stimulation of the locus coeruleus, a noradrenergic brain center involved in anxiety (MAESTRIPIERI et al., 1992). Recently, LEAVENS et al. (2001) have provided evidence that, for chimpanzees, variation in computerized task difficulty may induce cognitive stress that results in the production of self-directed behaviors. It is possible that the types of stressors introduced to the current subject, while capable of inducing behavioral indications of cognitive stress, were not capable of inducing an HPA axis response. Future studies may address the impact of task difficulty on both behavioral and HPA axis stress responses. After reviewing the findings of the current study, we would not imply that a general case could be made for the orangutan as a species. Rather, we suggest that, as has been shown in humans, orangutans, and possibly apes in general, can display a dissociation of the behavioral and HPA axis responses to stressors. Nevertheless, it is unclear as to the exact mechanisms responsible for the dissociation of behavioral and cortisol responses to the frustration induced by computerized task performance in this orangutan.

There is a growing interest in the elucidation of behavioral (i.e. self-directed scratching) and physiological signs of frustration in social and experimental settings (CASTLES et al., 1999; PETERS et al., 1998; TROISI et al., 1991). The research presented here provides a new method for correlating behavioral and HPA axis indicators of frustration in apes. This study demonstrates a normal circadian rhythm of cortisol release in an orangutan and validates salivary cortisol as a measure of HPA axis activity in an orangutan. Future stress research with primates should examine the effectiveness of computerized testing in reducing circulating glucocorticoid levels and daily stress in laboratory-housed animals. Furthermore, the characterization of effects of manipulation of additional testing variables, such as task difficulty and controllability, on HPA axis activity and behavioral responses may provide information on the stimulus factors which modulate activation of the stress system in nonhuman primates (CROES et al., 1993; PETERS et al., 1998). The development of convenient and reliable methods for sampling cortisol and inducing physiological stress responses due to cognitive stimulation in nonhuman primates will allow researchers to further investigate the factors contributing to variation in stress responses.

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