Published in final edited form as:

Behav Neurosci. 1998 February ; 112(1): 83–88.

Lateralized Changes in Tympanic Membrane Temperature in Relation to Different Cognitive Tasks in Chimpanzees (*Pan troglodytes*)

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Abstract

Lateralized changes in tympanic membrane (TM) temperature were assessed in chimpanzees. Subjects were engaged in 1 of 3 different cognitive tasks, including matching-to-sample, visual-spatial discrimination, and a motor task. During execution of each task, TM temperatures were taken from each ear over a 20-min time period. The TM temperatures at each time interval were subtracted from a baseline measure to assess relative change in blood flow. For the matching-to-sample and visual-spatial discrimination tasks, significant lateralized changes in TM temperature were found, with left-ear temperature increasing and right-ear temperature decreasing. No laterality effects were found for the motor or control tasks. These data provide the first evidence of laterality in physiological functioning in chimpanzees and suggest that transient asymmetries in cognitive functions are associated with changes in cerebral blood flow as assessed by TM temperature change.

There has been a resurgence of interest in the study of hemispheric specialization in animals. Recent studies indicate the presence of perceptual, cognitive, motor, and neuroanatomical asymmetries in a wide range of species (see reviews by Bradshaw & Rogers, 1993; Denenberg, 1988; Fagot & Vaclair, 1991; Hopkins, 1996; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Nottebohm, 1979; Ward & Hopkins, 1993). These cumulative results clearly challenge the long-held belief that hemispheric specialization represents a hallmark of human evolution.

The extent to which functional asymmetries in animals are analogous or homologous to asymmetries in humans remains a topic of considerable debate (Bradshaw & Rogers, 1993; Corballis, 1991; Ettlinger, 1988). A majority of the studies on laterality of function in animals have focused on purely behavioral measures, particularly in research involving nonhuman primate subjects. At present, very little is known about the anatomical or physiological mechanisms that underlie the expression of behavioral asymmetries in nonhuman primates. This stands in strong contrast to studies in humans where there is considerable validity between behavioral asymmetries and physiological asymmetries as assessed by a wide range of measures such as electrophysiology, positron emission tomography (PET), or cerebral blood flow (Sergent, 1994; Wood, Flowers, & Naylor, 1991). To foster the interpretation of findings in nonhuman primates as compared to humans, it is critical that the level of analysis move beyond a purely behavioral dimension. Ideally, the use of neural imaging techniques in conjunction with behavioral performance would be a beneficial comparative

approach. However, the procedural and pragmatic constraints placed upon subjects in PET or electrophysiological studies precludes their widespread use in nonhuman primates. It would be desirable to validate behavioral evidence of asymmetries with physiological changes without the need for invasive techniques.

In this study, data are presented on the use of a temperature gauge to assess changes in cerebral blood flow as reflected by changes in the tympanic membrane (TM) temperature. The TM is warmed by the brain and cooled by branches extending from the carotid artery (Webb, 1973). The TM also shares blood vessels with the hypothalamus, and TM temperature is highly correlated with the temperature of the hypothalamus (Benzinger, 1969; Dickey, Ahlgren, & Stephen, 1970; Rawson & Hammell, 1963). Two studies in humans have attempted to measure lateralized changes in cerebral temperature in relation to cognitive challenge. Meiners and Dabbs (1977) reported decreased temperature in the right ear (right hemisphere) for a spatial task compared to the left ear (left hemisphere). No differences in the reduction of ear temperature were evident for a verbal task. Swift (1991) similarly examined lateralized changes in TM temperature for verbal and spatial cognition tasks but did not find overall lateralized changes in TM temperature. The inconsistencies between these studies could be due in part to procedural and task differences. For example, Swift required participants to depress a key in response to different demands of the tasks but made no attempt to account for the effects of this motor response on temperature change. This is particularly significant because all participants were required to use their right hand to respond, which may have induced an asymmetry in temperature unrelated to the cognitive demands of the task. More recently, asymmetries in TM temperature have been found to be associated with stress behavior in human children and rhesus monkeys (Boyce, Higley, Jemerin, Champoux, & Suomi, 1996). Left-right differences in TM temperature were positively correlated with locomotion during social separation in monkeys and negatively correlated with measures of cortisol at 4 months of age.

In a series of experiments, Hopkins and colleagues have reported evidence of behavioral asymmetries in perceptual and cognitive functions in chimpanzees using a visual half-field paradigm (Hopkins, 1997; Hopkins & Morris, 1989; Hopkins, Washburn, & Rumbaugh, 1990). For example, pattern and visual-spatial discriminations have been shown to be better performed by the right in contrast to the left hemisphere in chimpanzees (Hopkins & Morris, 1989; Hopkins et al., 1990). In a preliminary study aimed at assessing circadian variation in core body temperature in chimpanzees, Fowler, Hyatt, and Hopkins (1996) found lateralized variations in TM temperature, particularly when the subjects were engaged in a cognitive task. The present study further examines the potential use of measuring TM temperatures in relation to different cognitive tasks to assess physiological changes in hemispheric specialization. On the basis of previous behavioral evidence of right hemisphere asymmetries in pattern and visual-spatial discriminations in chimpanzees (Hopkins & Morris, 1989; Hopkins et al., 1990), it was hypothesized that lateralized differences in TM temperature would be found for these cognitive tasks. Specifically, if blood flow cools the brain (Minard & Copman, 1963) and subsequently the TM, as suggested by Meiners and Dabbs (1977), then the right ear should exhibit reduced temperature compared to the left ear for tasks that selectively engage the right hemisphere.

Method

Subjects

Six adolescent chimpanzees (*Pan troglodytes*), 5 males (Carl, Winston, Scott, Lamar, and Jarred) and 1 female (Katrina), ranging from 8 to 10 years of age, served as subjects. All 6 chimpanzees were raised in captivity at the Yerkes Regional Primate Research Center (YRPRC) and raised in the YRPRC nursery following standard nursery protocol for great apes (see Bard, 1994, for description of nursery rearing practices).

Apparatus

The basic test system used was the Language Research Center Computerized Test System (LRC-CTS) and has been described in detail elsewhere (Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989). The test system consisted of a personal computer (386-compatible), a 13-in. color monitor, and an analog joystick. Tympanic membrane temperatures were assessed by use of a Thermoscan (Thermoscan, San Diego, CA) instant thermometer.

Tasks

During the course of this study, three behavioral tasks were administered to the chimpanzees. Below is a description of each task. Before the onset of testing, the chimpanzees were trained to reliably use the LRC-CTS using the training procedures described in previous studies (see Hopkins, Washburn, & Hyatt, 1996). Two of the tasks, matching-to-sample and spatial discrimination, have been previously demonstrated to elicit lateralized functioning in chimpanzees when presented within a divided visual field paradigm (Hopkins & Morris, 1989; Hopkins et al., 1990).

Matching-to-sample—Before the onset of this study, all subjects were trained to a high level of accuracy (>80% correct over a block of 200 trials) on an automated version of the matching-to-sample (MTS) task using procedures described elsewhere (Hopkins & Washburn, 1994; Rumbaugh et al., 1989; Washburn, Hopkins, & Rumbaugh, 1989). For the MTS task, on each trial a sample stimulus appeared in a random position on the computer monitor. The cursor, a white 9-mm × 9-mm plus sign (+), was also positioned randomly on the computer monitor. Subjects were required to manipulate the joystick to direct a collision between the cursor and the sample stimulus. If this condition was met, then the sample was erased from the screen and two comparison stimuli immediately appeared at random positions on the computer monitor. One comparison stimulus was identical in physical appearance to the sample stimulus. The second comparison stimulus, or foil, was physically different in appearance from the sample stimulus. Correct responses were recorded when subjects moved the cursor to the comparison stimulus that was identical to the sample stimulus. Incorrect responses were recorded when the subjects moved the cursor to the comparison stimulus that was different from the sample stimulus. The stimuli were random-color geometric patterns generated by the available computer graphics algorithms (see Washburn, 1990) and measured 5 cm × 3.5 cm in dimension. When moving on the monitor, the cursor moved at a speed of 6 cm/s. The dependent measure was the percentage of correct responses during the course of a given test session. Percentage correct was derived by dividing the number of correct responses by the total number of trials.

Spatial discrimination (INSPECT)—The INSPECT task is designed to assess visual-spatial discrimination, and the animals were trained on this task following the procedures described by Hopkins and Morris (1989) before the onset of testing in this study. During testing, at the onset of each trial, the cursor was positioned randomly on the computer monitor. In addition, a white 1-cm diameter circle appeared in the center of the computer monitor (herein referred to as the fixation point). The subjects were required to manipulate the joystick to place the cursor directly in the center of the fixation point. If this condition was met, a stimulus was presented 4 cm laterally to either the left or right of the fixation point. The stimulus was presented for 300 ms and then erased from the screen. The stimulus was two parallel horizontal lines connected by a short vertical line (1.75 cm). One horizontal line was 4 cm in length and the other was 2 cm in length. After stimulus presentation, the subjects were required to move the cursor either upward or downward depending on the location of the short horizontal line. If the short line was above the long line, the subjects had to move the cursor upward in the direction of the top of the computer monitor. If the short line was below the long line, then subjects were required to move the cursor downward toward the bottom of the computer monitor. As with the MTS task, the dependent measure was percentage correct. Percentage

correct was defined as the number of correct responses divided by the total number of trials within a test session.

Motor task (SIDE)—This task has been described by Rumbaugh et al. (1989). A trial began with a computer-generated 1.5×3 -cm blue rectangle (referred to as the target) appearing on and in the center of an edge of the computer monitor. The cursor, a white 1-cm diameter circle, was presented in the middle of the screen. The subjects were required to move the cursor via joystick manipulation until contacting the target. The position of the target was randomly determined across trials and varied between the left, right, top, and bottom edge of the computer screen. The dependent measure was response time, recorded in 100ths of a second, which was defined as the time between the first movement of the cursor and the detection of a collision between the cursor and target.

Procedure

Subjects were tested in their home cages between 9:30 a.m. and 12:00 p.m. Although all subjects lived in social groups, they readily separated from their group for the purposes of joystick testing. At the onset of each test session, the experimenter arrived with the computer system placed on a cart. The cart was positioned approximately 40-50 cm from the front of the subject's home cage, with the computer monitor facing the subject. The joystick was affixed to the home cage by attaching it to a permanently mounted Lexan plate that had a small hole (3 cm in diameter) drilled in it that allowed the handle of the joystick to be inserted into the cage (through the cage mesh) but inhibited access to the remaining portion of the joystick (see Hopkins et al., 1996, for description). For the MTS and INSPECT tasks, all correct responses were followed by the delivery of a secondary reinforcer (a high-pitched tone, 1 s in duration) and food reinforcement (either a squirt of juice or a peanut given by the experimenter). Incorrect responses were followed by a low, raucous tone 1 s in duration and no food reinforcement. For the SIDE task, contact between the cursor and target resulted in the delivery of reinforcement. All trials for each task were separated by a 2-s intertrial interval during which time the computer monitor was blank. During the 20-min test session, the subjects completed between 52 and 104 trials, depending on the task and performance on a given day.

Before the onset of this study, all subjects had been trained to present each ear for temperature assessment using the Thermoscan device (see Fowler et al., 1996). Assessing changes in TM temperature in relation to cognitive functions was accomplished easily by taking temperatures at specified time intervals within a behavioral test session. In this study, at the onset of each test session and immediately before the beginning of behavioral testing, a measure of TM temperature was taken in both the left and right ears. A 20-min test session was then administered to the subjects. During the 20-min test session, four TM temperatures were collected for each ear at 5-min intervals. Thus, five temperatures were taken in each ear at 0-, 5-, 10-, 15- and 20-min time periods. During each temperature assessment, three measurements were taken and the highest temperature reading was recorded by the experimenter. Order of ear testing was randomized across subjects and within a test session.

The subjects were initially tested on either the MTS or INSPECT task. The order of task presentation was counterbalanced across test sessions. All subjects received one test session per day and were tested twice on each behavioral task. After completing testing on the MTS and INSPECT task, visual analysis of the data indicated asymmetries in temperature change between ears for each task. Whether the observed effects were due to the cognitive tasks could not be determined from the existing data because of at least two rival hypotheses. First, 5 of the 6 chimpanzees preferred to use their right hand to manipulate the joystick, and it was reasoned that observed asymmetries in the MTS and INSPECT tasks could be due to the motor demands of the joystick testing system. Therefore, all subjects received one test session on the

MOTOR task (see above for description) following the same test procedure as the MTS and INSPECT tasks. Second, all subjects received one test session with no behavioral task (herein referred to as the CONTROL task). During the CONTROL test session, the computer cart was positioned in front of the cage, and the joystick was attached to the subject's home cage but no behavioral task was administered to the subjects. However, the subjects received reinforcements at random intervals during the 20-min test session. This test was done to rule out the potential effects of food reinforcement on changes in TM temperature.

Data Analysis

For each behavioral test (MTS, INSPECT, SIDE, and CONTROL), a difference score was determined for the TM temperatures of each ear. Specifically, the observed TM temperatures at 5, 10, 15, and 20 s were subtracted from the temperature at 0 s for each ear. These data reflected the relative change in temperature from the baseline reading for each ear and cognitive task. These data served as the primary dependent variable of interest. In addition, the average percentage correct for the MTS and INSPECT tasks and average response time for the SIDE task were calculated for each subject and test session. These data allowed for assessment of overall performance and the opportunity to link the behavioral performance with changes in TM temperature. The data were analyzed using inferential statistics (*t* test and analysis of variance) with alpha set to $p < .05$. Post hoc analyses were conducted using Tukey's honestly significant difference test with alpha at $p < .05$.

Results

Task and Laterality Effects

The difference scores were averaged across the four time conditions for this analysis. A within-subjects design analysis of variance (ANOVA) was performed with task (MTS, INSPECT, SIDE, and CONTROL) and ear (LEFT, RIGHT) serving as repeated measures. The mean TM temperature was the dependent measure. A significant interaction was found between task and ear, $F(3, 15) = 45.76, p < .001$. The average change in TM temperature as a function of task and ear can be seen in Figure 1. Post hoc analysis indicated between-ear differences in the MTS and INSPECT tasks, with the left-ear temperatures significantly higher than the right-ear temperatures. For the SIDE task, post hoc analyses indicated that temperatures were higher for the right ear as compared with the left ear. No between-ear differences were found for the CONTROL task. In addition, right-ear temperatures were higher for the SIDE task as compared with the MTS, INSPECT, and CONTROL tasks.

Time and Task Effects

For these analyses, the MTS, INSPECT, SIDE, and CONTROL task data were analyzed separately. For each task, a within-subject design ANOVA was performed with time (5, 10, 15, and 20 min) and ear (left and right) serving as repeated measures. The average change in temperature was the dependent measure. For the MTS task, $F(3, 15) = 24.25, p < .001$, and the INSPECT task, $F(3, 15) = 10.69, p < .001$, significant two-way interactions were found between time and ear. Post hoc tests indicated significant differences in the change in TM temperature between the left and right ears at all four time intervals for each task. For the SIDE task, significant main effects for time, $F(3, 15) = 14.89, p < .001$, and ear, $F(1, 5) = 69.42, p < .001$ were found, but no significant interaction was evident. Finally, no main effects or interactions were found for the CONTROL task. The average change in TM temperature as a function of time and ear for the MTS and INSPECT tasks can be seen in Table 1.

Correlates With Behavioral Performance

Listed in Table 2 are the individual performance data for each subject and task. In addition, the mean differences in TM temperature between the left and right ears for each task are listed in Table 2. The mean percentage correct for the MTS and INSPECT tasks were 88% and 77%, respectively. A paired t test revealed a borderline significant difference in performance between the two tasks, $t(5) = 2.37$, $p < .07$. The average response time for the SIDE task was 2.74 s. The individual performance data for the MTS, INSPECT, and SIDE tasks were correlated with the magnitude of difference in TM temperature between the left and right ears (mean left ear – mean right ear) for each subject. None of these correlations were significant.

Discussion

The overall results suggest that measurement of TM temperature is sensitive to lateralized changes in brain temperature and that the effects are selective, depending on the type of cognitive task used. The results of these experiments do not clearly determine which hemisphere is dominant in the execution of a specific task. This ambiguity reflects the uncertainty in interpreting increases or decreases in TM temperature in relation to each task. Meiners and Dabbs (1977) argued that reductions in temperature would reflect the active half of the brain because blood cools the brain. On the basis of this interpretation, the data from the chimpanzees reflect a right-hemisphere asymmetry for the MTS and INSPECT tasks, a finding consistent with the previously reported behavioral data (Hopkins & Morris, 1989; Hopkins et al., 1990). In contrast, Swift (1991) argued that increases in TM temperature reflect increased activity by a given hemisphere. Previous studies have reported increased cognitive performance in relation to increases in temperature for either cerebral cortices or the hypothalamus (e.g., Ahlers, Thomas, & Berkey, 1991). Thus, Swift argued that increased brain temperatures are related to greater use within a hemisphere. On the basis of this interpretation, a left-hemisphere asymmetry would be inferred for the MTS and INSPECT tasks, a finding inconsistent with the previously published behavioral data. Additional research is needed to determine the exact nature of the relation between increased or decreased TM temperature and hemispheric metabolic activity. Moreover, direct measures of performance and changes in TM temperature are needed to further clarify these issues.

The findings in the chimpanzees differ from those of previous studies in humans in one important aspect. The magnitude of difference in TM temperature between ears was substantially higher in the chimpanzees than in the humans tested by Meiners and Dabbs (1977) as well as by Swift (1991). The mean differences in TM temperature in the studies in humans has been .02–.04 °F. In contrast, the range of difference in TM temperature for the chimpanzees was from .50 to .92 °F (see Table 2). It is not clear what factors account for these differences, but they may include the type of device used to measure TM temperature, differences in the procedures or tasks used, or differences in the arterial or venous systems of human and nonhuman primates (see Falk, 1993). Boyce et al. (1996) noted a larger range of difference in TM temperature in rhesus monkeys than in the human children. Thus, the evidence of larger asymmetries in TM temperature in the chimpanzees is consistent with previous findings in rhesus monkeys.

In conclusion, the results of this study suggest that a relatively inexpensive device designed to measure core body temperature can detect differences in the left and right TM temperature in relation to specific cognitive tasks. This is the first report of laterality in physiological processes in chimpanzees, particularly in relation to specific cognitive demands. Whether the asymmetries are due to endogenous or exogenous factors remains unclear. Specifically, our results do not address whether the asymmetries are due to increases in the temperature of tissue surrounding the ear canal (see Kagan, 1994) or are generated by blood flow in and around the TM. Additional research should focus on the use of this temperature gauge in areas outside of

the domain of cognition, such as in studies of motor functions or emotions (see Zajonc & McIntosh, 1992). Finally, the potential application of this device in clinical settings warrants further investigation.

Acknowledgements

This investigation was supported in part by National Institutes of Health Grant RR-00165 from the National Center for Research Resources to the Yerkes Regional Primate Research Center. Additional support was provided by National Institutes of Neurological Disorders and Stroke Grant NS-29574.

We appreciate the helpful comments and contributions of Robin Morris and James Dabbs. The supportive services provided by the Veterinary Department and care staff of the Yerkes Center are greatly appreciated. We thank Charles Hyatt for his assistance in testing and training the chimpanzees for ear temperature presentation. The Yerkes Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

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Figure 1. Mean changes in tympanic membrane (TM) temperature (°F) for each task averaged across time intervals. Bars represent standard errors in each condition.

Table 1
Mean Tympanic Membrane Temperature Changes (°F) for Each Task and Time Interval

Task ^a	5 min		10 min		15 min		20 min	
	M	SE	M	SE	M	SE	M	SE
MTS								
Left ear	.23	.03	.33	.05	.42	.05	.49	.05
Right ear	-.12	.03	-.33	.03	-.36	.03	-.43	.04
INSPECT								
Left ear	.08	.05	.15	.05	.23	.05	.32	.06
Right ear	-.06	.04	-.14	.05	-.13	.06	-.18	.06

Note. Means and standard errors reflect change from baseline tympanic membrane temperature at the specified time (see text for description) and are presented in 100th of a degree Fahrenheit.

^aMTS and INSPECT are names of tasks (see Method section for description).

Table 2

Individual Behavioral Performance Data on Each Task

Subject	Behavioral task			Difference in temperature (°F)		
	MTS (%)	INSPECT (%)	SIDE	MTS	INSPECT	SIDE
Jarred	88	82	3.16	.613	.188	.100
Lamar	77	84	3.12	.638	.125	-.025
Scott	94	82	2.42	.563	.400	-.350
Katrina	95	68	2.60	.725	.313	-.050
Winston	94	82	2.55	.700	.488	.000
Carl	76	61	2.60	.813	.400	-.025

Note. MTS, INSPECT, and SIDE are names of tasks (see Method section for description). MTS and INSPECT values are percentages correct. SIDE values represent response times in 100th of a second. With respect to difference scores, the mean tympanic membrane (TM) temperature for the right ear was subtracted from the mean TM temperature for the left ear for each behavioral task and subject.