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Hemispheric Priming by Meaningful and Nonmeaningful Symbols in Language-Trained Chimpanzees (*Pan troglodytes*): Further Evidence of a Left Hemisphere Advantage

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Hemispheric priming was examined in 3 language-trained chimpanzees (*Pan troglodytes*) using a simple reaction time paradigm. Subjects were required to hold down a response button until the occurrence of a response cue. A warning stimulus was presented to either the left visual field (LVF) or the right visual field (RVF) before the response cue occurred. No warning stimulus was presented on control trials. The warning stimuli were geometric communicative symbols from two semantic categories: *foods* and *tools*. A third set of warning stimuli were *familiar* geometric symbols. Dependent measures included reaction time and the number of false-positive responses. Reaction-time data indicated an RVF advantage in priming when the warning stimuli were food or tool symbols. No significant visual half-field differences were found for familiar symbols, but a trend toward an RVF advantage was observed. These effects were enhanced when subjects responded with their left hand. False-positive data also indicated an RVF advantage for the food and tool warning stimuli. The data indicate that hemispheric asymmetries for processing communicative symbols are present in language-trained chimpanzees.

It has been hypothesized that hemispheric specialization and language functions have evolved in a parallel manner and that this relation is unique to humans (Corballis, 1989; Passingham, 1981). Others have argued that hemispheric specialization has had important evolutionary consequences independent of linguistic processing (Hamilton & Vermeire, 1988a; Levy, 1977; Witelson, 1987). Recent reports indicating that apes can acquire and use simple language systems (Gardner & Gardner, 1968; Rumbaugh, 1977; Savage-Rumbaugh, 1986; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986) have increased interest in these different hypotheses. Whether there are hemispheric asymmetries in the processing of symbols that have acquired "meaning" by apes has a number of important theoretical implications regarding the evolution of lateralization and language. Such information would shed light on the possible factors, including environmental, genetic, or morphological, that may drive the development of hemispheric asymmetries (see Geschwind & Galaburda, 1985).

A number of studies that used nonlinguistic stimuli have addressed the issue of differential hemispheric processing in nonhuman primates. Although most of the findings have been negative (for reviews see Hamilton, 1977; Warren, 1980), those studies with positive results have demonstrated differential hemispheric processing of species-specific vocalizations (Heffner & Heffner, 1984; Petersen et al., 1983; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978), pure tones (Dewson, 1977; Pohl, 1983), visual–spatial discriminations (Hamilton, 1983; Hamilton & Vermeire, 1988b; Hopkins & Morris, 1989; Hopkins, Washburn, & Rumbaugh, 1990; Jason, Cowey, & Weiskrantz, 1984), or species-specific facial expressions (Hamilton & Vermeire, 1988b). Morris, Hopkins, Bolser-Gilmore, and Washburn (in press) also found, using a hemispheric priming paradigm with chimpanzees, a greater reduction in reaction times (RTs) with nonspecific color warning stimuli when they were presented to the left visual half-field (LVF). These results were similar to those reported in adult human subjects (Heilman & Van Den Abell, 1979).

The hemispheric priming paradigm assumes that each hemisphere is "activated" (Pribram & McGuiness, 1975) or "primed" (Kinsbourne, 1973) when presented with a warning stimulus before the onset of a response cue. Activation is defined as the "readiness to respond" or as a prepatory state in response to a previously presented warning stimulus (Pribram & McGuiness, 1975). Previous research with humans has shown that verbal and nonverbal stimuli can differentially

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activate or prime the hemispheres (Bowers & Heilman, 1980; Kinsbourne, 1973).

Hopkins, Morris, and Savage-Rumbaugh (1991) recently addressed the issue of whether unilaterally presented warning stimuli would asymmetrically affect hemispheric activation in 2 language-trained chimpanzees. Subjects were required to depress a response button to initiate a trial. After trial onset, a foreperiod (FP) of random and varying duration was followed by presentation of a warning stimulus to either the LVF or the right visual half-field (RVF). For control purposes, no warning stimulus was presented on some trials. After a random delay, a response cue appeared at fixation. Subjects were to remove their fingers from the response button as quickly as possible once the response cue appeared (i.e., simple RT). Four different types of warning stimuli were used. The warning stimuli were either known, language-familiar, visually familiar, or unknown symbols. Known stimuli were geometric symbols that the subjects could label and comprehend under blind test conditions (see Savage-Rumbaugh, 1986). The results indicated an RVF priming advantage when language-known warning stimuli were presented. Symmetric priming was found for the remaining warning stimulus types.

The focus of the current study expanded on the research conducted by Hopkins et al. (1991). First, the findings of hemispheric advantages by Hopkins et al. (1991) were limited to warning stimuli composed of food symbols. Whether the RVF advantage was specific to these types of meaningful warning stimuli was addressed in the current study by examining another meaningful set of warning stimuli, referred to as tool symbols, in addition to food symbols. A second focus of this study was to examine whether reduction in RT could be enhanced by cuing a semantic category with a fixation stimulus. Finally, we assessed whether semantic priming was greater within the LVF or RVF.

Method

Subjects

Three adult chimpanzees (*Pan troglodytes*), 2 males (Sherman and Austin, 16 and 17 years old, respectively) and 1 female (Lana, 20 years old) were tested using lexigrams as lateralized priming stimuli in a visual half-field paradigm. All subjects had received extensive language training using lexigram symbols over the past 12–18 years (Savage-Rumbaugh, 1986). Previous research with these subjects had indicated that Austin and Sherman were primarily right-handed, whereas Lana's hand preference was more ambiguous (Hopkins, Washburn, & Rumbaugh, 1989; Morris, Hopkins, & Bolser-Gilmore, in press; Morris, Hopkins, Bolser-Gilmore, & Washburn, in press).

Apparatus

Stimulus presentations and RT were controlled and recorded by a Zenith 159 microcomputer with an attached Metrobyte CTM05 millisecond timing board and a Samsung 351838-12 EGA color monitor.

Procedure

Subjects were trained to fixate on a stimulus presented in the center of a computer monitor via a computerized shaping procedure (Hopkins & Morris, in press). To initiate trials, the chimpanzees depressed a button placed directly in front of them. Trial initiation was followed by a 1- or 2-s FP, after which a 150-ms warning stimulus was presented to either the LVF or RVF. For control purposes, trials with no warning stimulus (NWS; i.e., no prime) were also presented. After the warning stimulus presentations or control trials, a 1- or 2-s delay (D) occurred. At the end of this delay, a response cue in the form of a 2 cm × 2 cm aqua-colored square appeared at central fixation. Upon the appearance of the response cue, subjects had to remove their finger from the response button as quickly as possible. During all testing, subjects were required to place their chins on a bar that was positioned 54 cm from the screen to ensure constant distance from the monitor. Warning stimuli were displaced at least 4° off center so that presentations were restricted to either the LVF or RVF.

The primary dependent measure was RT, which was measured in milliseconds from the response cue onset until the subjects removed their fingers from the button. In addition, false-positive and omission errors were recorded. False-positive responses were those on which the subjects removed their fingers from the button before the appearance of the response cue. Omission errors were counted on trials when subjects did not respond within 800 ms after the appearance of the response cue.

Nine different warning stimuli were used. These stimuli can be seen in Figure 1. Three were symbols that represented the semantic category *food* (beancake, bread, orange), three were symbols that represented the semantic category *tool* (straw, key, money), and three were symbols with unassigned meaning that were termed *familiar*. The symbols that represented foods and tools were defined as meaningful because subjects could both label and comprehend them reliably in controlled blind tests (Savage-Rumbaugh, 1986). Familiar warning stimuli were symbols that were visually familiar to these subjects but had no ascribed meaning. These symbols occupied a position on the subjects' keyboard, but they had never been paired with any exemplars.

Thirty blocks of 72 trials were presented to each subject. On 36 trials, the fixation stimulus was the lexigram that represented the food category (this symbol was constructed of a dot with a squiggly line that ran through the center). Previous findings indicated that these chimpanzees could classify symbols as either food or tool on the basis of symbolic information alone (Savage-Rumbaugh, 1986). On the remaining 36 trials, a meaningless lexigram served as the fixation stimulus. This symbol had never been seen by the chimpanzees before this study. Within these 36 trials, 12 warning stimuli were presented to

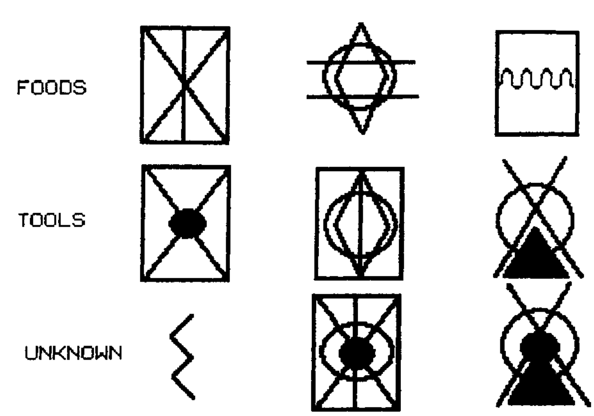

Figure 1. Three classes of warning stimuli presented unilaterally. (For the category FOOD, the lexigrams from left to right are "orange," "bread," and "chow." For the category TOOL, the lexigrams from left to right are "money," "straw," and "key.")

both the LVF and RVF. The remaining 12 trials had NWS presentations. The combinations of 1- or 2-s FPs and 1 or 2-s Ds resulted in four possible timing conditions (for Timing Condition 1, $FP = 1$ s and $D = 1$ s; for Timing Condition 2, $FP = 1$ s and $D = 2$ s; for Timing Condition 3, $FP = 2$ s and $D = 1$ s; and for Timing Condition 4, $FP = 2$ s and $D = 2$ s). Of the 12 trials presented in each visual half-field condition, one trial for each warning stimulus type (food, tool, familiar) and each timing condition (1, 2, 3, 4) were presented. Thirty test blocks were administered with subjects using either their left or right hand to respond within a test block. Hand use was counterbalanced across test blocks so that 15 test blocks were performed with each hand. This resulted in a total of 2,160 trials for each subject with 1,080 trials for each hand.

The fixation stimulus (food, nonmeaningful), timing condition (1, 2, 3, 4), visual half-field (LVF, RVF, NWS), and warning stimulus type (food, tool, familiar) were randomly selected for each trial. Randomized FPs and Ds were used so that subjects could not anticipate the occurrence of the warning stimulus or response cue within a trial. Trials on which the subjects committed an error were repeated later within the same block of trials so that a complete set of RT data was obtained within each session. All trials were reinforced with food.

Data Analysis

Consistent with other studies of hemispheric priming (Heilman & Van Den Abell, 1979; Shapiro & Hynd, 1985), a reduction value was calculated for each subject to determine the degree of priming or activation.[1] For each subject, the median primed RT for each warning stimulus, as a function of each visual half-field, hand, fixation, and timing condition, was subtracted from the median control trials (i.e., NWS trials) for each matching condition. This resulted in a reduction value indicative of the degree of priming. Negative values represent significant priming, whereas positive values reflect no priming. Thus, −150 ms would be considered greater priming than −100 ms.

These reduction values were analyzed using a five-way within-subjects-design ANOVA. Omission errors were rare (less than 2% of all trials), thus no analyses were performed on these data. Independent variables of interest included hand use, fixation stimulus, timing, warning stimulus type, and visual half-field. All main effects and interactions were evaluated with post hoc comparisons at alpha levels of $p < .05$.

Results

Reaction Time

The RTs, averaged across subjects for each hand, fixation, visual half-field, warning stimulus, and timing condition, are depicted in Table 1.

For the overall analysis, significant main effects for visual half-field, $F(1, 2) = 81.69$, $p < .01$, and timing condition, $F(3, 6) = 9.60$, $p < .01$, were found. A borderline interaction was also found between visual half-field and timing condition, $F(3, 6) = 3.44$, $p < .10$. The reduction in RT, averaged across subjects for each visual half-field and timing condition, are shown in Figure 2. Reduction in RT was significantly greater within the RVF ($M = -206$ ms) compared with the LVF ($M = -184$ ms). In addition, reduction in RT for Timing Conditions 1 ($M = -216$ ms) and 2 ($M = -209$ ms) were significantly greater than those observed in Timing Conditions 3 ($M = -172$ ms) and 4 ($M = -182$ ms). It is of note that reduction in RT for the RVF was significantly greater than reduction in RT for the LVF within Timing Conditions 3 and 4.

Although priming was largest in Timing Conditions 1 and 2, the priming effects in Timing Conditions 3 and 4 were substantially greater compared with our previous findings. For instance, in the study by Hopkins et al. (1991), for the 2 subjects Austin and Sherman, mean reduction in RT in Timing Conditions 3 and 4 combined was −52 ms. In contrast, for Austin and Sherman, mean reduction in RT for Timing Conditions 3 and 4 combined in this study was −175 ms. It is important to note that the timing conditions were identical for the two studies, with the only difference being the presence of a lexigram that served as the fixation stimulus. Thus, in this study, the use of a lexigram as a fixation stimulus appeared to facilitate response times significantly, particularly in the conditions with longer FPs (i.e., Timing Conditions 3 and 4). This finding is consistent with results in the human literature (Bellers, 1971; Rosch, 1975). In addition, between visual half-fields, RVF responses were significantly faster than LVF responses on trials with 2-s FPs (Timing Conditions 3 and 4). Therefore, to determine whether the longer FPs affected the expression of lateralized priming, the data from Timing Conditions 3 and 4 were combined and subjected to additional analyses. For comparison, the data from Timing Conditions 1 and 2 were also combined and analyzed.

The independent variables of interest included hand use, fixation stimulus, warning stimulus type, and visual half-field. As with the overall analysis, a five-way within-subjects-design ANOVA was performed. All main effects and interactions were evaluated with post hoc comparisons at alpha levels of $p < .05$.

For the combined data from Timing Conditions 1 and 2, the ANOVA revealed a significant main effect for hand use, $F(1, 2) = 24.83$, $p < .04$. Reduction in RT was significantly greater for the left hand compared with the right hand. For the combined data within Timing Conditions 3 and 4, the results revealed a significant two-way interaction between hand use and warning stimulus type, $F(2, 10) = 21.14$, $p < .002$, and a three-way interaction between hand use, warning stimulus

[1] A reviewer of this article suggested that we use RT values in all conditions instead of reduction values because we were ignoring important information from our experimental model, especially, for the NWS responses. Although an argument could be made for such a case, our inherent interest was not in simple RT responses but rather only in the primed responses. In addition, by including the NWS trials in the statistical model, we would have been artificially reducing the overall error term(s) for the following reason. Because we used a repeated measures analysis of variance (ANOVA), for each warning stimulus, a median NWS value would have needed to be inserted into the model to provide a complete set of data. However, NWS trials were never paired with any warning stimulus in the design. In other words, there was no such thing as a tool, food, or familiar NWS trial. Thus, by using the same median value at each level of warning stimulus, no error would have been found, and when averaged across visual half-field and warning stimuli, the overall error term would have been reduced. This, in turn, would have made detection of statistical differences much easier because the comparisons of interest (i.e., LVF vs. RVF) would have been evaluated as post hoc comparisons rather than main effects or interactions because the primed trials were statistically different from NWS trials.

Table 1
Mean Reaction Time (±SD; in Milliseconds) for Each Hand, Fixation (Food vs. Nonmeaningful), Visual Half-Field, and Warning Stimulus for the Four Timing Conditions Averaged Across Subjects

	Right hand						Left hand					
	Food			Nonmeaningful			Food			Nonmeaningful		
Warning stimulus	LVF	RVF	NWS	LVF	RVF	NWS	LVF	RVF	NWS	LVF	RVF	NWS
					Timing Condition 1							
Food												
M	232	238	455	277	246	447	247	245	482	247	243	482
SD	70	45	23	62	75	26	46	44	45	72	42	42
Tool												
M	251	258	455	247	242	447	249	219	482	230	225	482
SD	49	53	23	18	42	26	59	66	45	49	55	42
Familiar												
M	268	241	455	280	249	447	277	282	482	282	245	482
SD	10	53	23	61	59	26	63	30	45	70	67	42
					Timing Condition 2							
Food												
M	252	241	446	286	251	453	247	261	476	286	257	490
SD	29	81	23	46	43	23	73	42	45	83	62	38
Tool												
M	234	217	446	256	260	453	247	224	476	242	238	490
SD	37	70	23	26	59	23	86	31	45	51	42	38
Familiar												
M	295	269	446	274	257	453	266	288	476	270	265	490
SD	52	55	23	53	56	23	41	38	45	58	70	38
					Timing Condition 3							
Food												
M	191	229	391	230	225	385	222	181	409	271	195	418
SD	66	41	27	33	70	32	46	38	47	42	34	31
Tool												
M	243	185	391	257	192	385	258	200	409	249	187	418
SD	48	31	27	46	54	32	72	64	47	24	82	31
Familiar												
M	228	239	391	277	241	385	257	233	409	266	235	418
SD	20	29	27	34	39	32	57	29	47	37	50	31
					Timing Condition 4							
Food												
M	217	222	385	228	198	388	236	191	411	228	189	419
SD	29	9	31	53	53	40	46	45	24	55	46	32
Tool												
M	233	211	385	199	181	388	252	198	411	234	176	419
SD	37	42	31	37	42	40	83	36	24	21	53	32
Familiar												
M	247	231	385	250	212	388	209	205	411	272	220	419
SD	38	29	31	33	30	40	67	58	24	38	49	32

Note. LVF = left visual field; RVF = right visual field; NWS = no warning stimulus (i.e., control trial). For Timing Condition 1, foreperiod (FP) = 1 s and delay period (D) = 1 s; for Timing Condition 2, FP = 1 s and D = 2 s; for Timing Condition 3, FP = 2 s and D = 1 s; for Timing Condition 4, FP = 2 s and D = 2s. The mean reaction times and standard deviations for NWS trials within each time, fixation, hand, and warning stimulus condition are the same because it was not feasible to have an NWS trial paired with each warning stimulus condition.

type, and visual half-field, $F(4, 20) = 3.10, p < .04$. Averaged across subjects, reduction in RTs at each visual half-field and warning stimulus as a function of hand use are depicted in Figures 3 and 4. When using the left hand to respond, reduction in RT for RVF responses to food and tool warning stimuli were significantly greater than for LVF responses. In addition, within the RVF, reduction in RT for food and tool warning stimuli were significantly greater than for familiar stimuli. For the right hand, reduction in RT for tool warning stimuli differed between visual half-fields. No other visual half-field differences were found.

False-Positive Responses

For false-positive responses, the ANOVA revealed significant main effects for hand use, $F(1, 2) = 26.00$, $p < .04$, warning stimulus type, $F(2, 4) = 9.46, p < .02$, visual half-field, $F(2, 4) = 12.28, p < .03$, and a borderline three-way interac-

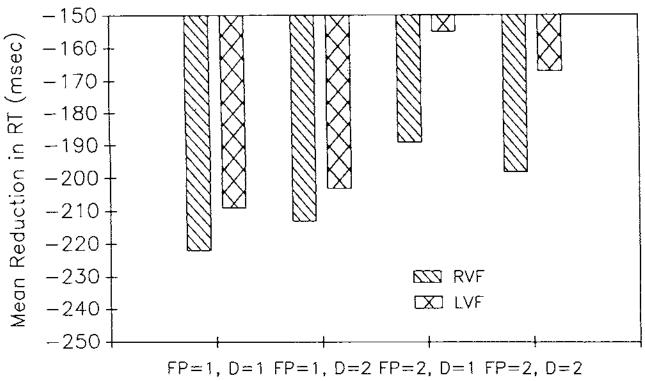

Figure 2. Mean reduction in reaction time (RT) at each timing condition and visual half-field. (LVF = left visual field; RVF = right visual field. FR = foreperiod [in seconds]; D = delay [in seconds].)

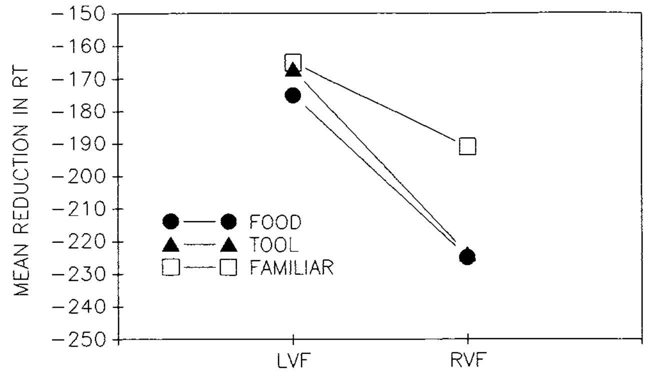

Figure 4. Mean reduction in reaction time (RT) for right-hand responses within each visual half-field and warning stimulus type. (LVF = left visual field; RVF = right visual field.)

tion between hand, warning stimulus type, and visual half-field, $F(4, 8) = 3.60$, $p < .06$. The total number of false-positive responses for each hand, fixation, visual half-field, and warning stimulus are shown in Table 2.

Post hoc comparisons indicated that the mean number of LVF ($M = 4.08$) and RVF ($M = 6.83$) false-positive responses were significantly greater than NWS ($M = 1.16$) responses, averaged across warning stimulus and hand use. Within the RVF, significantly more false-positive responses were made to food ($M = 7.5$) and tool ($M = 9.0$) warning stimuli compared with familiar ($M = 4$) warning stimuli. Finally, within the RVF, significantly more false-positive responses were made to food warning stimuli by the right hand ($M = 11$) compared with the left hand ($M = 4$).

Discussion

Reduction-in-RT data from this study suggest that these chimpanzees show significant hemispheric priming advantages when meaningful lexigrams are presented to the RVF (i.e., left hemisphere) compared with familiar lexigrams. Within the RVF, reduction in RT was significantly greater for food and tool warning stimuli compared with familiar warning stimuli. However, these results were limited to timing conditions with 2-s FPs. Results for false-positive data were similar to the RT data. When food and tool warning stimuli were presented to the RVF, significantly more false-positive responses were made compared with familiar warning stimuli. In contrast, false-positive responses occurred equally often between visual fields and with either hand when familiar warning stimuli were presented.

The RVF advantage findings for the food and tool warning stimuli were specific to left-hand responses. The reason this occurred requires some explanation because this result differs from that of our previous study (Hopkins et al., 1991) and could be interpreted as an inconsistent finding between studies. Moreover, because 2 of the 3 subjects are "right" handed and 1 is ambiguous by way of hand preference (Morris, Hopkins, & Bolser-Gilmore, in press), one might assume that the effect would be more robust for the dominant hand. We believe that this finding is due to a relation between the frequency of false-positive responses and RT that emerged in this study. Recall that no significant differences were found between visual half-fields in RT for the food warning stimuli (see Figure 3) when subjects were using their right hand to

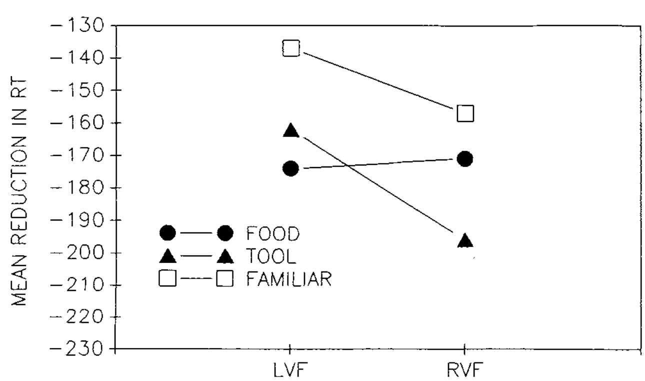

Figure 3. Mean reduction in reaction time (RT) for left-hand responses within each visual half-field and warning stimulus type. (LVF = left visual field; RVF = right visual field.)

Table 2
Total Number of False-Positive Responses as a Function of Hand Use (Left vs. Right), Fixation (Food vs. Nonmeaningful), Visual Half-Field, and Warning Stimulus Type

	Food			Nonmeaningful		
Warning stimulus	LVF	RVF	NWS	LVF	RVF	NWS
		Left hand				
Food	4	6	0	5	2	1
Tool	2	3	1	3	15	1
Familiar	4	5	1	2	7	2
		Right hand				
Food	5	7	3	5	15	0
Tool	7	10	2	5	8	1
Familiar	2	0	1	5	4	1

Note. Values are cumulative frequencies. LVF = left visual field; RVF = right visual field; NWS = no warning stimulus (i.e., control trial).

respond. However, the number of false-positive responses for food warning stimuli when using the right hand to respond was significantly greater than when using the left hand. Thus, as the RT demands increased, the number of false-positive responses also increased. This, in turn, may have limited the RT responses with the right hand and thereby influenced the distribution of RT values.

One final note regarding the relation between hand use and asymmetrical priming. An examination of Table 1 indicates that mean RTs to NWS trials were consistently faster for right-hand responses ($M = 419$ ms) compared with left-hand responses ($M = 448$ ms). However, for the primed trials, no differences between right- ($M = 239$ ms) and left-hand ($M = 239$ ms) responses were observed. Thus, a right-hand asymmetry exists in simple RT, an artifact that biases the data in favor of greater priming for the left hand. The right hand bias for NWS trials may reflect a component of hemispheric specialization related to "handedness." Alternatively, this effect may reflect residual priming for NWS trials as determined by the type of warning stimulus presented on the preceding trial ($n - 1$). Data from another study suggest that right-hand responses to NWS trials are significantly faster than left-hand responses when the preceding trial was a meaningful symbol compared with familiar or nonmeaningful symbols (Hopkins & Morris, in press). In short, the relation between priming and hand use across the course of a test session is a complex process and requires further investigation.

Interpreting the findings for the familiar warning stimuli is somewhat difficult but relevant from the standpoint of concluding that lateralized processing was evident in this study. Post hoc analysis indicated that the RVF responses failed to statistically differ from the LVF responses in Timing Conditions 3 and 4. However, given the limited number of subjects in this study, it could be argued that the lack of significant findings reflect Type II error and that a more liberal probability level could be used. In this case, an RVF advantage could be claimed for the familiar warning stimuli. In contrast, given the large number of independent variables and the number of levels within each independent variable (144 cells), it could also be argued that the probability of Type I error is high with so few subjects. That is, some visual half-field advantages could be found simply on the basis of chance. We would point out that guarding against Type I or II error by using a liberal or conservative probability level does not necessarily affect our interpretation of the findings from this study. Even if we conclude that an RVF advantage was found for the familiar warning stimuli, this would not account for the significant differences found within the RVF among food, tool, and familiar warning stimuli. Thus, using the most liberal criterion, the interpretation of the findings would be that all three warning stimuli prime the left hemisphere better than they do the right; but within the left hemisphere, priming is significantly greater for food and tool warning stimuli compared with familiar warning stimuli.

The results indicate that meaningful warning stimuli, whether semantically or nonsemantically related to a fixation stimulus, result in greater left hemisphere priming than do familiar warning stimuli. Although it was hypothesized that overall RT to meaningful warning stimulus lexigrams (i.e., food) that were semantically related to the meaningful fixation stimulus (concept "food") would significantly differ from warning stimuli that were nonsemantically related (i.e., tool) and nonmeaningful (i.e., familiar), these effects failed to reach significance. Why the effects were not found in the overall analysis may have been due to the total number of mismatch conditions that existed in the design of the experiment. For example, within a 72-trial test session, only 8 trials matched the correct cuing condition (i.e., food fixation + food warning stimulus). Thus, in initial testing, the subjects may have responded reliably to this cue; but across test sessions, they may have come to interpret this cue as indiscriminant to their performance.

In the classic Rosch (1975) study of semantic priming and in other priming studies (Posner, 1978), subjects are required to make same–different judgments after the presentation of the warning stimulus. The same–different judgment is based on whether the warning stimulus falls within the same category or within a different semantic category. In this study, the subjects were not required to make such conditional–categorical discriminations between the fixation and warning stimulus. Another finding from the Rosch study was that pictures yielded greater priming effects than did words. Pictures were not used in the current study, but it would be of interest to determine whether pictures could be used in the current paradigm to produce semantic priming. Nonetheless, given the procedural differences that exist between this study and more typical semantic priming studies, further research will be necessary before any definitive conclusions can be made regarding the semantic organization of these chimpanzees' lexigrams.

The relation between the different fixation stimuli and the time course of hemispheric activation should be further examined in subsequent research. From our earlier research (Hopkins et al., 1991), it was apparent that hemispheric activation was greatest during time conditions with a 1-s D, particularly when they were preceded by a 1-s FP. This finding was consistent with other reports on the relation between simple RT and FP (Niemi & Naatanen, 1981). In this study, hemispheric activation was largest in Timing Condition 1, but in comparison, priming was much greater in Timing Conditions 3 and 4. For example, in our previous research (Hopkins et al., 1991), with a 2-s FP and a 2-s D, the mean reduction in RT was -35 ms. In this study, the mean reduction in RT for the same timing condition was -175 ms. Furthermore, this difference was not due to practice because response times for the NWS trials were similar between the two studies (401 ms vs. 387 ms). Thus, it appears that having a lexigram serve as a fixation stimulus altered the pattern, timing, or strategy that the subjects used in responding in this paradigm.

The basic findings from this study, as well as those from our previous research (Hopkins et al., 1991), differ significantly from other reports of laterality in nonhuman primates in which asymmetries have been described. For example, in the studies by Petersen et al. (1978, 1983), species-specific vocalizations were used as stimuli. In contrast, the stimuli used in this study were lexigrams, that is, stimuli that were learned by the chimpanzees. Thus, it cannot be argued that the hemispheric asymmetries found are species-specific for these subjects. Also, because the familiar stimuli were visually familiar to the subjects, these results cannot be attributed to greater familiarity with meaningful lexigrams compared with the nonmeaningful lexigrams (Sergent, 1981). Finally, the results of this study indicate that RVF advantages in priming are not specific to a single semantic category of stimuli in these chimpanzees (i.e., food). Because the results were similar for both the food and tool warning stimuli, both semantic categories of stimuli appear to be differentially processed when compared with nonmeaningful stimuli within the left hemisphere.

Because of the procedural and methodological limitations of this study, several cautions should be emphasized with regard to these findings. First, with only 3 subjects, global statements about lateralization in chimpanzees would be premature. Much larger groups of subjects need to be evaluated before any definitive conclusions can be made. An additional limitation of this study involves the duration of the fixation stimulus. The FP between the onset of the trial and presentation of the warning stimulus was either 1 or 2 s. However, it was possible for the fixation stimulus to appear on the monitor before the onset of each trial. In other words, the FP began when the subjects initiated the trial by depressing the button. However, it was possible for the fixation stimulus to be displayed on the monitor before the onset of the trial because on some trials the intertrial interval may have expired. This may or may not have effected the results, but future research should more systematically control this variable.

Whether the subjects were exactly fixating on each trial was not directly monitored in this study. Although their eye movements were monitored during each trial, and the chimpanzees were very good at continually directing their visual gaze to the fixation point, continued research should further explore the influence of this factor on such results. It is unlikely that uncontrolled fixation could account for the present findings primarily because the effects are replicable (Hopkins et al., 1991), and uncontrolled fixation would predict a random pattern of results, which was not observed.

In summary, the results from this study support our earlier findings of a left hemisphere advantage in priming by warning stimuli that are meaningful (Hopkins et al., 1991). Nonmeaningful warning stimuli were processed in a manner that was in the direction of a left hemisphere advantage, but this advantage was not significant. Collectively, the data suggest that the manner in which these chimpanzees perceive symbols that have acquired functional meaning may be similar to that observed in human subjects in the processing of words. Further research using traditional lateralized recognition and memory paradigms should help to determine the relation between these simple priming effects and other higher cortical processes. Through such studies, the debate regarding the relation between hemispheric specialization and language functions should broaden to include primates other than humans.

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