

LATERALITY IN CATS: PAW PREFERENCE AND PERFORMANCE IN A VISUOMOTOR ACTIVITY

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INTRODUCTION

During the last decade, increasing attention has been paid to the question of functional asymmetries in forelimb usage by animals. The interest was essentially focused on manual laterality in nonhuman primates given their manipulative abilities and their phylogenetic closeness to humans (for reviews see: Fagot and Vauclair, 1991; MacNeilage, Studdert-Kennedy and Lindblom, 1987; Warren, 1980). The comparative approach to this question could however be considerably enriched by data obtained from other taxonomic groups. Cats are good candidates for such studies of forelimb specialization because, in a sense, they do manipulate and rely on fast and accurate paw movements to catch and seize their preys.

Very few studies directly addressing the question of laterality have been carried out in relation to paw usage in cats (Cole, 1955; Warren, 1958; Warren, Abplanalp and Warren, 1967; Tan, Yaprak and Kutlu, 1990). Additional data on paw lateralization are available from neurophysiological studies where the behavior of intact cats on various tasks was analyzed before lesion (e.g., Olmstead and Villablanca, 1979). For most studies, only the frequency of paw use was recorded. For example, Cole (1955) employed a baited transparent tube and recorded the paw used by the animal to extract the food. In another study, Burgess and Villablanca (1986) recorded the paw used in swiping movements when catching a dangling piece of food. The latter authors found that 14 of 17 intact cats were lateralized and showed a significant left preference. Other studies reported a tendency towards a group preference for the left side, but the left bias was not significant (Forward, Warren and Hara, 1962; Olmstead and Villablanca, 1979). In addition, no population level bias was found either by Tan et al. (1990) who tested 60 adult cats on simple reaching (34 right- versus 24 left-preferent and 8 ambilateral cats), or by Webster (1972) in a small group of 8 split-brain cats. However, Webster reported that the hemisphere ipsilateral to the preferred paw was more efficient than the contralateral hemisphere in a variety of visual discrimination problems. To summarize, the few available studies indicate that cats exhibit individual paw preferences on several tasks, but the data available are too scarce to allow clear-cut conclusions on their generality. The present study will address the question of paw asymmetries in a large

group of cats performing a visuo-motor task where they had to reach toward a moving spot of light. Data analyses will be conducted in two main directions. Firstly, in line with the previous investigations, we will focus on spontaneous paw preferences. Secondly, the visuo-motor performances (e.g., accuracy, reaction time, movement time) will be considered for each paw and for several subgroups of cats. To our knowledge, this is the first attempt to carry out in parallel a quantification of forelimb preferences and a detailed analysis of paw proficiency in cats. An abstract version of the results has been presented in Fabre-Thorpe, Fagot and Vauclair (1991).

MATERIALS AND METHOD

Subjects

Subjects were 44 intact adult male domestic cats weighting 3 kg to 4.5 kg and coming from different litters. All cats were usually kept in individual cages (50 cm × 50 cm). They were never food-deprived and were fed with dry food 5 days a week. They were water-deprived before the experiment but could drink *ad libitum* at the end of the daily testing session. They had unrestricted diet on the weekends.

Apparatus

The apparatus has been described in detail by Fabre-Thorpe, Viévard, Fuzellier, et al. (1984). Briefly, it consists of a bulb placed on the pen carrier of an XY-plotter moving below a translucent screen (47 cm × 42 cm) which is tilted at 40° from the horizontal plane (Figure 1). A capacitive proximity detector was fixed to the bulb and was set to deliver a signal that

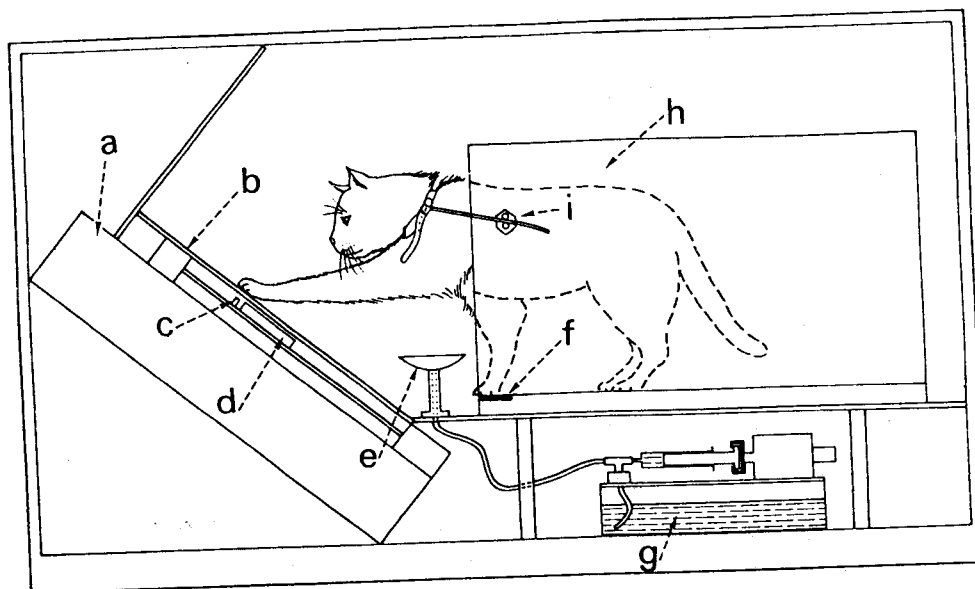


Fig. 1 - Schematic view of the apparatus. a: X-Y plotter; b: translucent screen; c: moving bulb; d: capacitive proximity detector; e: liquid reward supply; f: "starting plate"; g: milk reward distributor; h: lateral wooden wall; i: neck collar fixation.

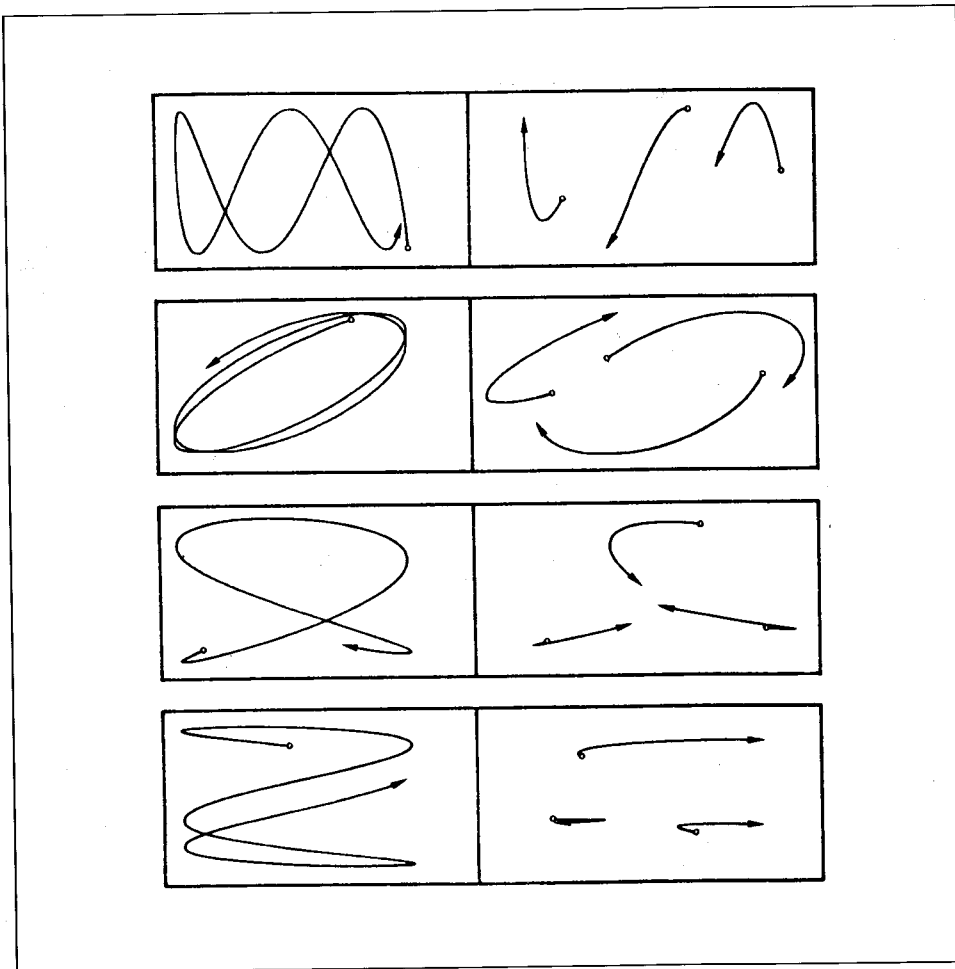


Fig. 2 – Left side: examples of Lissajous patterns used as target trajectories. Right side: target-spot trajectories during one second.

triggered the reward-system (milk delivery) whenever the paw of the cat reached the screen at the target location. The apparatus also comprised two lateral wooden walls with adjustable spacing from 12 cm to 18 cm depending on the size of the subject. A pair of capacitive “starting plates” (5 cm × 10 cm each) were located between the two walls on each side of the midsagittal plane of the apparatus.

Procedure

The cat, loosely restrained laterally between the two walls and antero-posteriorly by a collar, faced the tilted screen and adopted a quadrupedal stance with each forepaw resting on one “starting plate”. The experiment was controlled by a computer (Epson QX 10). A trial started when a 500 msec auditory warning stimulus was presented, after which, in order to trigger target onset, the cat had to keep its forepaws on the “starting plates” for a variable-delay (200–2000 msec). During this phase, a new delay period would be started if either paw was lifted from the “starting plates”. At the end of this delay, the bulb was turned on and a light spot (1 cm in diameter) appeared anywhere on the screen. The spot of light followed a Lissajous trajectory (Figure 2) generated by two variable frequency sinewave signals applied

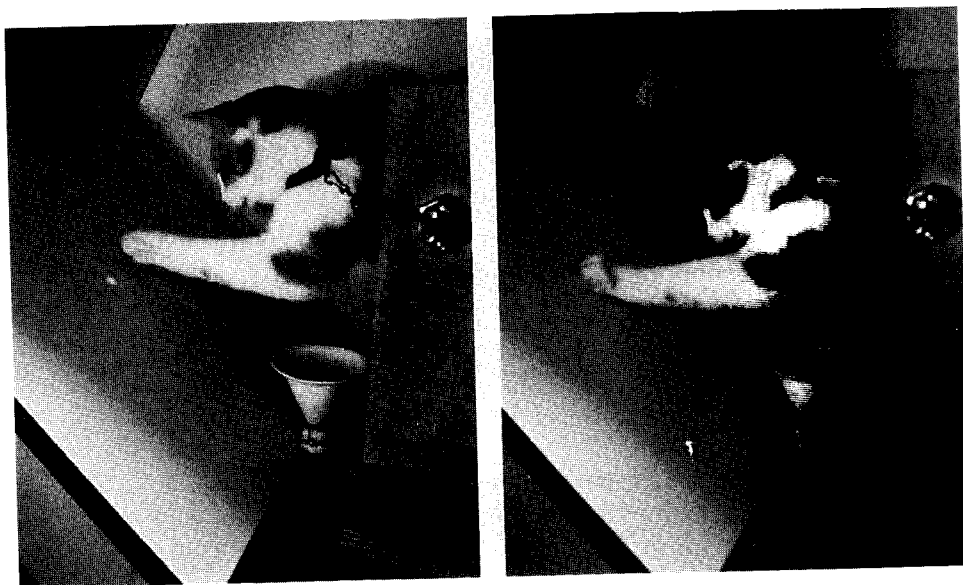


Fig. 3 – Two views of a reaching sequence. Left: forelimb extension towards the spot. Right: typical dorsiflexion of the paw when it is in contact with the screen.

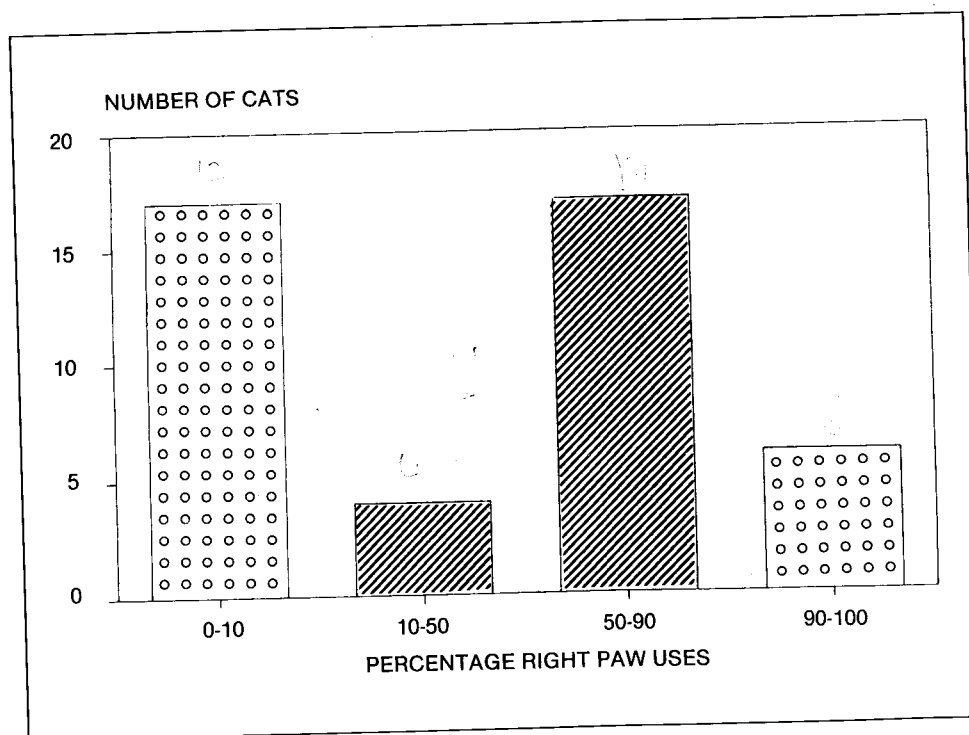


Fig. 4 – Distribution of the number of cats as a function of their percentage of right paw use. The shaded bars refer to nonlateralized subjects whereas dotted bars refer to lateralized cats.

respectively to the X- and Y-channels of the XY-plotter. The amplitude of the sinewaves were set to allow the target to move within the largest possible space that the cat could easily reach with its forepaw (action field 30 cm × 20 cm). A video camera, positioned from above the whole action field, recorded all movements.

On each trial, the light spot moved at a random speed (up to 30 cm/sec) and the cat had to reach for it with one forepaw. Reaching movements at the target location were detected by the proximity detector fixed on the bulb and led to the delivery of 2 ml of milk. The paw used to perform the reaching was recorded by the computer. That paw was indicated by the "starting plate" (left of right) that was released. For the present study, each trial was classified either as a "success" or as a "failure". The success being automatically recorded by the computer whereas failure was assessed by a human observer. Trials were considered as a "success" if the animal reached the target and turned the bulb off on the first reaching attempt. Trials were considered as a "failure" when the movement ended too far from the target to trigger the proximity detector. Paw contacts with the screen were easily seen on the video. When touching the screen, the paw extremity showed the typical dorsiflexion that is depicted in Figure 3. Any ambiguity with respect to the type of reaching could thus be raised by an off-line viewing of the video recording. Moreover, for each successful trial, the reaction time (RT), corresponding to the time elapsed (in msec) from target onset to paw lift, and the movement time (MT), corresponding to the time elapsed (in msec) from the paw lift to target offset by an accurate reaching movement, were automatically computed. Cats were tested 5 days a week for 60-80 trials a day over a period of 4-6 months. Six years of work were needed to train and to test the whole group.

Training

Animals were first trained to reach for an immobile spot of light. The location of the spot varied from one trial to another and the animal could use either paw. After this preliminary phase, training continued with the spot moving along one axis only (X or Y) at a frequency of .1 to .3 hertz. At that time, the last phase began with the light spot following Lissajous trajectories and visuo-motor performances were then recorded.

RESULTS

Overall Distribution of Paw Usage and Paw Preferences

A total of 23420 experimental trials were performed by the 44 subjects (mean = 532.3; S.D. = 209.6). On 69.6 percent of these trials (N = 16307; mean = 370.6; S.D. = 172.8), the cats successfully reached for the light spot. The remaining 30.4 percent of trials (N = 7113; mean = 161.6; S.D. = 117.1) were classified as "failures".

Overall paw preferences for all trials (success and failure) were determined by considering the paw more frequently used at (1) a 50 percent criterion, and at (2) a 90 percent criterion. For the 50 percent criterion, 21 subjects more frequently used their left paw while the remaining 23 cats showed a preference for their right paw (two-tailed chi-square, $\chi^2 = .09$, d.f. = 2, ns). These data are depicted in Figure 4. Using a 90 percent criterion, the data indicate that 17 cats had a left paw preference, 6 had a right paw preference and 21 had no preference. Cats were not evenly represented among these 3 classes of preference (two-tailed chi-square, $\chi^2 = 8.2$, d.f. = 2, $p < .02$) and left-pawed cats significantly outnumbered right-pawed cats (two-tailed chi-square, $\chi^2 = 5.26$, d.f. = 1, $p < .02$). Additionally, there were significantly fewer left-pawed cats in the 50-90 percent category (N = 4) than right-pawed cats (N = 17; two-tailed chi-

square, $\chi^2 = 8.04$, d.f. = 1, $p < .01$). This result demonstrates that left-pawed cats were more strongly lateralized than right-pawed.

Accuracy of the Reaching Movements

Trial accuracy was evaluated for each subject using an accuracy ratio (AR) corresponding to the total number of successful trials divided by the total number of trials (success and failure). For the group of cats, the mean AR was equal to .70 (S.D. = .16) indicating that, on a majority of trials, subjects were successful in reaching for the spot of light.

No overall significant AR difference were found between lateralized and nonlateralized cats at the 90 percent criterion (mean lateralized = .73, mean nonlateralized = .7, two-tailed Mann-Whitney U test, $U = 184$, ns).

We also comparatively examined the performance of the left and right paw. This analysis was restricted to the 31 cats that had performed at least 10 trials with each paw. No overall AR difference emerged between the left and the right paws when considering either the 31 cats (mean left = .70; mean right = .68; two-tailed Wilcoxon T test, $T = 241$, ns) or the subgroup of 20 subjects using their right paw in more than 50 percent of the trials (mean left = .73, mean right = .77, two-tailed Wilcoxon T test, $T = 60$, ns). By contrast, the subgroup of 11 left-pawed cats at the 50 percent criterion showed a significant performance advantage with their left paw (mean left = .72, mean right = .64; two-tailed Wilcoxon

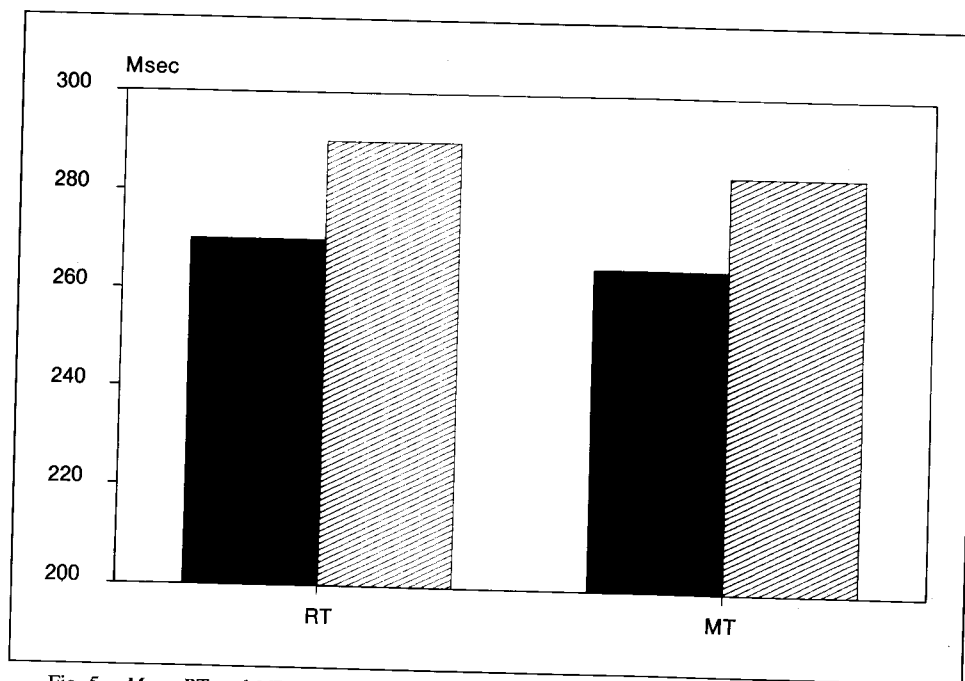


Fig. 5 - Mean RT and MT for the preferred (black bars) and for the nonpreferred (shaded bars) paws.

T test, $T=7$, $p<.05$). Finally, we compared the performance of the preferred paw (whether left or right) with the performance of the non-preferred paw, considering only, as previously, the 31 cats that performed at least 10 trials with each forelimb. It was found that the preferred paw was significantly more accurate than the non-preferred paw (mean preferred = .78; mean non-preferred = .71; Wilcoxon two-tailed T test, $T=107$, $p<.02$).

Paw Reaction Time

The mean RT was equal to 259 msec (S.D. = 75.6). Comparison between lateralized and nonlateralized cats at the 90 percent threshold showed that cats with a preference exhibited a shorter mean RT (234 msec) than cats without preference (283 msec, two-tailed t-test, $t=2.25$, d.f. = 42, $p<.05$). However, no difference emerged between left- and right-pawed cats at the 90 percent criterion (left-pawed: mean = 236 msec; right-pawed: mean = 231 msec, two-tailed t-test, $t=.21$, d.f. = 20, ns). The mean RT for the more-used paw (270 msec) was significantly shorter than the mean RT of the less-used paw (290 msec; two-tailed paired t-test, $t=2.52$, d.f. = 27, $p<.02$) for the group of 28 cats that made at least 10 successful reachings with each paw. That result is depicted in Figure 5.

Movement Time

For the first five cats, the software was not set to record movement time. Thus, data on paw MT were only available for 39 animals. For those subjects, the overall mean MT was 264 msec (S.D. = 48.9). Analysis shows that lateralized cats at the 90 percent level ($N=21$ in this case) did not differ significantly, in terms of overall MT, from nonlateralized cats ($N=18$ in this case, mean = 257 and 270 msec respectively, two-tailed t-test, $t=.84$, d.f. = 37, ns).

Interpaw statistical comparisons for the movement time were carried out considering only subjects ($N=23$) that made at least 10 successful trials with each paw.

It appears that the preferred paw had a shorter MT on average (mean = 265 msec, S.D. = 52.1) than the nonpreferred one (mean = 284 msec, S.D. = 77.7, two-tailed paired t-test, $t=2.18$, d.f. = 22, $p<.05$, see Figure 5). Results also indicate a shorter MT for the right paw (mean left = 285.6, mean right = 264.9, paired t-test, $t=2.41$, d.f. = 22, $p<.05$). This latter result is due to the large number of right preferent cats in the considered group (18 of 23). In effect, the 18 right preferent cats at the 50 percent criterion exhibited a shorter MT with their right (preferred) paw (mean left = 297, mean right = 271, paired two-tailed t-test, $t=2.47$, d.f. = 17, $p<.05$). No significant interpaw difference emerged for the subgroup of 6 left preferent cats (mean left = 244.6, mean right = 240.8, two-tailed paired t-test, $t=.3$, d.f. = 5, ns).

DISCUSSION

This study considers paw preference and performance in a group of 44 adult cats reaching with one paw for a mobile target. The main results can be summarized as follows.

Measure of Paw Preference. The overall distribution of paw preferences for all reaching attempts indicates that, at the 90 percent criterion, there were more left-pawed ($N=17$) than right-pawed cats ($N=6$). However, the asymmetry in the distribution of paw preferences disappeared when a 50 percent criterion was employed (23 right and 21 left).

Measure of Paw Performance. Two main effects were found regarding paw performance. First, it was found that the preferred paw had a shorter RT, a shorter MT and was also more accurate than the non-preferred paw. Secondly, lateralized cats exhibited a shorter RT than nonlateralized cats.

Although the frequencies of left and right paw uses for the group as a whole were almost equal, the distribution of paw preferences shows a significant asymmetry in favor of the left side. That finding is consistent with the left-paw preferences found in a previous study where cats had to reach for a mobile object (Burgess and Villablanca, 1986). Slightly left skewed distributions have been reported in cats for different types of visuo-motor activities towards fixed objects (e.g., Cole, 1955; Forward et al., 1962; Olmstead and Villablanca, 1979), but none of these previous studies found a significant population bias. Thus, the only studies that showed left preferences for the group measured reaching towards mobile objects (Burgess and Villablanca, 1986, and the present study). This results suggests that the mobility of the target, possibly by increasing the spatial demand, was an important characteristic of the task which led to the demonstration of a left bias in the group of cats investigated.

We found data indicating that laterality in paw proficiency is congruent with asymmetry in paw preferences, at least within the limits of our testing conditions. In other words, the spontaneously preferred paw was also the more accurate in performing the reaching. Although this question has not been raised concerning the cat, it has been suggested on several occasions, both in human and in nonhuman primates, that lateralization in forelimb proficiency is not always related to lateralization in forelimb preference (e.g., in nonhuman primates: Preilowski, 1983; Ettlinger, 1988; in humans: Kimura and Vanderwolf, 1970; Nakamura and Saito, 1974; Todor and Doane, 1977). However, most of the comparisons between preference and proficiency measures were usually not established within the same task. Typically, in human studies, preferences are inferred from a questionnaire of laterality, whereas performances are evaluated on a specific motor task such as tapping or pointing. To our knowledge, the present study is one among few (see, for example, Hopkins, Wahsburn and Rumbaugh, 1989) where preferences and performances have been evaluated on the same motor task and therefore on identical movements.

The main result concerning RT was that lateralized subjects exhibited a RT that was, on average, about 50 msec shorter than RT for nonlateralized subjects. A shorter RT was also observed (about 20 msec on average) when comparing the more- and the less-used paw. RT differences could be explained

within two, non exclusive, frameworks. The first explanation refers to processes of motor programming. During RT, the cats need to take into account the target's position when it appeared, together with its direction and speed in order to correctly anticipate its future location at the time of contact. Moreover, animals had to select the paw to be used for the reaching and to initiate its movement (muscular mobilization). It has been shown for a long time, mostly with the method of precuing, that RT increases with the number of alternatives in a set of responses (e.g., Hyman, 1953; Rosenbaum, 1980; Bonnet, Requin and Stelmach, 1982). The differences in RTs between lateralized and nonlateralized subgroups could then reflect the need, in the latter group, to program the paw that will be used in each reaching. In other words, RT could in fact be interpreted as a choice RT (in terms of paw) for cats with no established preference, but not for animals with a strong or exclusive preference. This uncertainty difference gives a RT advantage to lateralized subjects. The second interpretation of RT differences refers to a possible postural adjustment prior to movement execution. According to this hypothesis, the lateralized cat, but not the ambilateral cat, would prepare its posture with the aim of using the preferred, more-used paw. Such postural anticipations are well known to occur in quadrupeds (Mori and Brookhart, 1968; Gahéry and Nicoullon, 1978). A study specifically directed at this issue is needed to decide between the programming and posture hypotheses.

Analyses of MT revealed that the preferred paw was more rapid than the non-preferred one. Such an effect, which has also been found in nonhuman primates (Hopkins et al., 1989) and in humans (e.g., Todor and Smiley, 1985), may simply be explained by practice effects, leading to better hand control of the preferred compared to the nonpreferred limb.

Our laboratory study takes advantage of a behavior that belongs to the spontaneous repertoire of the cat, that is catching fast moving targets. A detailed analysis of the reaching movements demonstrated that such a task elicits lateral differences, opening a new future to the consideration of lateralized processes in cats and in other mammals.

ABSTRACT

Laterality in paw use was investigated over a period of 6 years in 44 domestic cats trained to perform a reaching movement toward a moving spot of light. Both paw preference and paw performance were recorded. At a 50 percent criterion, no significant paw preference was found at the level of the group. When a 90 percent criterion was considered, 23 subjects had a significant preference for one paw. Among these strongly lateralized animals, there were more left- (N=17) than right-pawed (N=6) cats. The analysis of visuo-motor performances included reaction time, movement time, and reaching accuracy. Lateralized cats had a faster reaction time than nonlateralized cats. The more-used paw had a shorter reaction time, a shorter movement time, and was also more accurate than the less-used paw. Thus, the findings demonstrate a functional advantage of being lateralized. Moreover, the results confirm the existence of an asymmetry of paw preference in cats and show a consistent relation between paw preference and performance.

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