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Effect of experimental setting on learning and performance of Auditory Delayed Matching-to-Sample task in dogs

Paweł Kuśmierek and **Danuta M. Kowalska**

Department of Neurophysiology, Nencki Institute of Experimental Biology,
3 Pasteur St., 02-093, Warsaw, Poland, Email: pq@nencki.gov.pl

Technical communication

Abstract. Twelve dogs were trained in a new task for auditory recognition memory: auditory Delayed Matching-to-Sample (DMS). The animals were tested in two experimental settings using approach (Setting 1) or bar-press (Setting 2) responses. At the early stages of training, the learning took more trials in Setting 2, which was caused by different instrumental response and/or different relationship among manipulanda, stimuli, and reward in these two settings. The performance of the final task did not differ between settings and showed a gradual decline with extended delays. No differences were found in responding patterns or in dynamics of learning. Therefore, we conclude that the auditory DMS, trained in either setting, offers a valuable and reliable tool for studies of neural substrate of auditory recognition memory. The detailed analyses of the dogs' behaviour will allow to evaluate the subtle effects of experimental manipulations in future experiments, and for many reasons the data obtained from these two settings may be combined in further analyses.

Key words: auditory DMS, approach, bar-press, dogs

INTRODUCTION

Global anterograde amnesia, i.e., a severe and permanent impairment of ability to form new memories, was described in humans after bilateral lesions to the medial temporal lobe (e.g., Scoville and Milner 1957, Milner et al. 1968). This evidence stimulated attempts to reproduce the syndrome in animals. Following the development of a test of one-trial recognition memory for monkeys (Gaffan 1974, Mishkin and Delacour 1975) it was found that bilateral medial temporal damage in animals did indeed produce a memory impairment; and further, like the clinical syndrome, it appeared to be global in nature, extending to all sensory modalities (for review, see Mishkin and Murray 1994). In fact however, recognition deficit in animals with medial temporal lesions has so far been observed only in the visual, tactile, and olfactory modalities, and the role of mammalian medial temporal lobe in auditory recognition is therefore still unknown.

Curiously, and for reasons that are still unknown, although vocal signals are important in nonhuman primate communication, monkeys have great difficulty learning auditory recognition memory tasks (e.g., Stępień et al. 1960, D'Amato and Colombo 1985, Kojima 1985, Wright et al. 1990, Fritz et al. 1997). Dogs, by contrast, appear to learn auditory task relatively easily (Brown and Sołtysik 1971, Pietrzykowska and Sołtysik 1975)

Recently, a behavioural test for studying auditory recognition memory in dogs has been proposed (Kowalska 1997): the trial-unique auditory Delayed Matching-to-Sample task (DMS), comparable to the visual and tactile recognition tasks used on monkeys. The test was carried out in a soundproof testing chamber, with bar-press instrumental response. The results have shown that dogs can also learn the auditory recognition DMS task much easier than can monkeys (e.g., Wright et al. 1990, Fritz et al. 1997). However, training still takes much longer than the learning of visual recognition memory tasks in monkeys (Mishkin and Delacour 1975). This may be caused by species and/or by modality related differences. On the other hand, learning and performance of the recognition task may also be influenced by independent variables of the experiment, and even small changes in the experimental environment (e.g., way of stimulus presentation or kind of reinforcement) affect learning of visual recognition memory tasks in monkeys (Elliott et al. 1977). The results obtained by Kowalska (1997) in dogs trained in a relatively small testing chamber with a quite precise bar-press instrumental response might reveal their ability to learn the task in this particular experimental setting only. It was possible therefore, that with another arrangement the learning of this difficult task would improve. Thus, in the current study, we trained a group of dogs in a different experimental environment, using the large room of the Nencki Testing Apparatus, in an auditory recognition task with simple locomotor instrumental response. Next, we compared the dogs learning and performance obtained in this condition with that described earlier.

In the previous experiment a considerable drop of performance was observed in the task with extended delays, when dogs were switched from the baseline delay of 1.5 s to 10-s delay (Kowalska 1997). Whether this drop was caused by the sudden increase of delay after several hundreds of trials with 1.5-s delay, or it actually reflected dynamics of the dogs auditory memory trace, was not assessed. To answer this question, in the present experiment for some dogs, during the performance task, we introduced an additional block with 5-s delay. If the drop of performance was an effect of sudden increase of the delay, the dogs pretrained with 5-s delay should improve performance level on 10-s delay, in comparison to animals lacking this pretraining.

Thus, in the current study we provided detailed analysis of learning and performance of the auditory recognition task in two different experimental conditions with emphasis on the dynamics of these processes. Such analyses will provide a basis for using the auditory DMS test in further experiments. If performance levels in the DMS task do not differ, and if analyses of learning do not show qualitative differences between the settings, then the future studies may be conducted in the two settings parallel with data pooled together. On the other hand, if significant differences are observed, then it will encourage us to change the experimental procedure in order to accelerate the learning, and improve the performance of the auditory recognition tasks. Detailed analyses of several performance indices in the DMS task could be used in further evaluation of the effects of lesions of brain structures, which may constitute the neural substrate of auditory recognition memory.

METHODS

Subjects

Twelve adult, experimentally naive male mongrel dogs weighing 8-24 kg were used in the study. The ani-

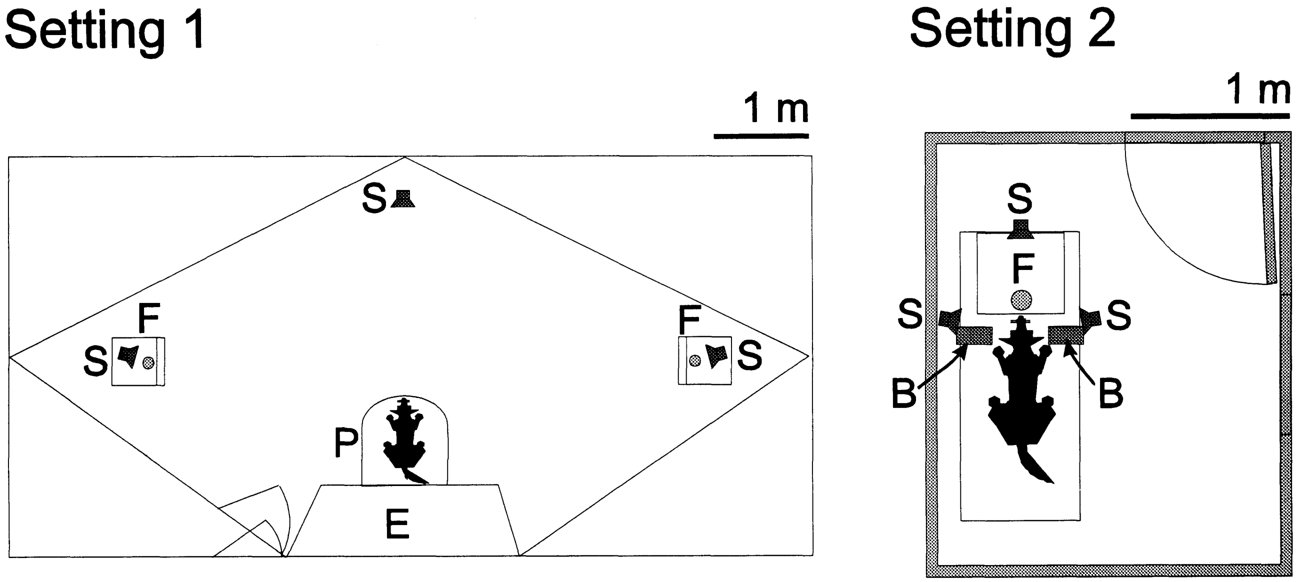


Fig. 1. Experimental Setting 1 (approach) and Setting 2 (bar-press). S, speakers; F, feeders; B, response bars; P, starting platform; E, experimenter.

mals were housed individually in cages (2.7 x 1.2 x 3.0 m) with free access to water. Animals were trained five days a week. Food was given once a day, 15-23 h before testing. The dogs were under continuous veterinary care.

Experimental settings

SETTING 1 – APPROACH SITUATION

Eight dogs (D-1 to D-8) were trained in the Nencki Testing Apparatus (Fig. 1). The apparatus consisted of a room sized 8.5 x 4.25 m. A pentagonal testing area was limited by 2.15-m tall walls. Two automatic food dispensers, with 16 food cups each, were located on the floor, to the left and to the right of the starting platform. A 9-cm wide circular opening provided access to one cup at a time. Photoresistors, which were located just in front of the feeders, served as approach detectors. Two three-way side speakers (Thompsonic SP 309) were situated on food dispensers, 40 cm above the floor. An identical central speaker was placed 80 cm above the floor in front of the starting platform. Distance from each side speaker to the centre of the starting platform was 2.8 m, and from the central speaker to the centre of the starting platform – 2.3 m. The experimenter was sitting behind the starting platform and an 83-cm high wooden screen was interposed between the starting platform and the experimenter. Dogs were leashed on the starting platform. During a trial, they were released by the experimenter. Special precautions were taken in order to avoid accidental guidance of the dogs in making their choice. The moment of releasing was always at the very beginning of a testing trial. The experimenters were alternated every few weeks and performance levels were examined for experimenter related changes. No such changes were found.

The experiment was controlled by a PC-486 computer with SoundBlaster Pro sound card and a program Auditory Tasks designed by the first author. The computer was located inside the testing room. The testing room was not acoustically isolated. In the most quiet moments the background noise was about 35 dB(A) (measured with Brüel and Kjaer sound level meter 2209, time constant S). The computer monitor produced a constant ultrasonic noise between 25 and 40 kHz that was probably audible to dogs (Heffner 1983). A qualitative analysis of the ultrasonic noise with Mini-3 Bat Detector revealed that the ultrasonic noise appeared not to depend on any experimental condition, e.g., on required instrumental response.

SETTING 2 – BAR-PRESS SITUATION

Four dogs (D-9 to D-12) were trained in the Setting 2 (Fig. 1), which was set up in a soundproof chamber. Details were described previously (Kowalska 1997). The size of the chamber was 2.7 x 2.05 x 2.96 m. The two side speakers (two-way, Thompsonic) were located 34 cm above the response bars (on the left and on the right side of the dog) and 24 cm towards a single food dispenser. The central speaker was located above the food dispenser, 77 cm above the platform on which the dogs were standing. The chamber was acoustically isolated and the inner walls were covered with sound-absorbing tiles. The constant noise inside the chamber was 22 dB(A) and was caused mostly by the ventilating system. The experiment-controlling computer was located outside the chamber.

Stimuli

About 320 various sounds (1.5 s each) served as trial-unique stimuli. The sounds were of animals (e.g. wolves, birds, pigs, monkeys, elephants, crickets), tones, pulses, notes or short melodies played with various instruments (e.g., violin, piano, recorder, timpani) and other real-life sounds (e.g., rain, sea, table tennis game, helicopter, human laughter, bells, pencil sharpener, alarm clock, train). The preparation of stimuli was described previously (Kowalska 1997).

Procedure

The procedure was described in detail earlier by Kowalska (1997), thus, in this paper we give only a general outline with emphasis on differences between the two settings.

The experimental sessions consisted of 20 (Setting 1) or 15 trials (Setting 2). This difference was caused by limited capacity of the food dispensers (two dispensers with 16 food cups each in Setting 1 vs. one dispenser with 16 food cups in Setting 2). The side of stimulus presentation was changed from trial to trial in pseudorandom order (Gellerman 1933). Correct instrumental responses caused delivery of about 15 g of minced meat.

Two kinds of corrections were applied during the training: (1) intratrial correction – after an incorrect response, the presentation of sound was continued until the animal made a correct response, followed by reward. Such trial was always scored as incorrect. The intratrial corrections were used mostly in preliminary stages of the experiment, when a dog had great difficulty with acquisition of a task. (2) standard correction– in case of incorrect response, the sound was terminated and no reinforcement was delivered. After 20 s, the whole trial was repeated. In this situation, the trial outcome was always recorded as incorrect. The standard corrections were applied if performance level fell below 75% correct responses. Strong preference responses towards one side were extinguished with standard corrections. If necessary, a correction session with increased proportion of trials to the side opposite to the one that was preferred by the animal was applied.

Throughout the training, except for Konorski's Task (stage C, see below), if a dog refused to respond, the whole trial was repeated after 20 s. The intertrial intervals were 60 s (Setting 1) and 40 s (Setting 2), and they were constant through all stages of the experiment.

Before the regular training began, the dogs were familiarised with the testing situations for a few days. In Setting 1, the dogs were trained to walk towards a food dispenser on a noise made by the rotatory system delivering reinforcement, whereas in Setting 2, the dogs were encouraged to place a paw on the right response bar and such movements were reinforced with food. When the instrumental response was acquired, the dogs were switched to stage A.

STAGE A – PRELIMINARY TRAINING WITH ACOUSTICAL STIMULI

In this stage, 1–3 acoustical stimuli were introduced. In each trial, a stimulus was presented from one side speaker (left or right) in three 1.5-s bursts, each followed by 1.5-s silence (9 s overall). The dogs were allowed to respond from the beginning of the first presentation of the stimulus. Instrumental responses on the same side terminated the sound and were rewarded. The course of stage A differed somewhat between settings. In Setting 1, dogs were trained to approach the sounds emitted from the left or right speaker in pseudorandom order, while in Setting 2, dogs were first trained to perform response to the right bar on the sound presented from the right speaker. When the response to the right side stabilized then animals were trained to respond to the left side. Next, the pseudorandom presentation of sounds from both speakers was introduced. In the beginning of the stage, facilitating modifications could be applied: encouragement by the experimenter (either with voice or by forcing a correct response) or presentation of stimuli more than three times per trial. The training was continued to the criterion of at least 80% of correct responses in two consecutive sessions (40 trials in Setting 1 or 30 trials in Setting 2) without any facilitating modifications or corrections.

STAGE B – INSTRUMENTAL TRAINING WITH TRIAL-UNIQUE STIMULI

Starting from this stage, the trial-unique stimuli were used. The trial began with presentation of an acoustic stimulus from the central speaker in three 1.5-s bursts separated by 1.5-s silence periods (7.5 s overall). After 1.5-s delay, the same sound was presented through one of the side speakers in a similar way. Responses toward the sound terminated the stimulus and resulted in food reward. During the activation of the central speaker and during the delay period, the dogs trained in Setting 1 were leashed, so they could not perform the approach response. Animals trained in Setting 2 could press the bar on the activation of central speaker or during the delay, but this response was never reinforced by food and was not recorded. The dogs were allowed to respond from the beginning of the first presentation of the stimulus from a side speaker. These rules were kept up through all next stages of the experiment. The training was continued to a criterion of at least 90% correct responses in 100 (Setting 1) or 90 (Setting 2) consecutive trials (5 or 6 sessions without corrections, respectively).

STAGE C – GO, NO-GO RECOGNITION TASK WITH TRIAL-UNIQUE STIMULi

In this stage, dogs were trained in go, no-go asymmetrically reinforced Konorski's Task (Konorski 1959) modified by (1) using trial-unique stimuli, (2) requiring responses to the left or right side. Eight sets of 20 pairs of stimuli were used in this stage (Kowalska 1997). Moreover, the position of the sound within each pair has been reversed; thus, each sound from the pair was used as a sample stimulus. In this way, the number of sets was duplicated to sixteen. Within each pair, the sounds were selected to be easily distinguishable by human ear (e.g., pencil sharpener noise and a short melody played by piano, loons voice and pizzicato strings, 1.4 kHz tone and tapping sound). Each trial consisted of two phases: (1) sample sound presentation through the central speaker, and, after a 1.5-s delay, (2) test sound presentation through one of the side speakers. The test stimulus was either same or different from the sample stimulus. In both phases, the sample or testing sounds were given in three bursts, each of 1.5 s, interrupted by 1.5-s periods of silence. In the testing phase, during the go (or same) trials, the identical sound to the sample was activated through one of the side speakers. Responses on the side of sample sound emission within 9.0 s automatically terminated the sound and caused food delivery. In case of no response, the trial automatically terminated after 9.0 s with no reinforcement. During the no-go (or different) trials, the sound differing from the sample sound was presented through one of the side speakers, in the same way as in the go trials. Instrumental responses in no-go trials did not interrupt the sound. No reinforcement was ever given in no-go trials. The next trial started with a completely new pair of sounds. The experimental session consisted of 20 trials (10 go, and 10 no-go trials) in both settings. Every session started with a new set of acoustic stimuli. The positions of pairs of sounds within the session were chosen randomly by computer, and relation between go (same) and no-go (different) trials changed according to Gellerman's series. Standard corrections were given only if performance level in go trials was very low. The dogs were trained until they responded differently on the same and different sounds (latency response comparison) with a significant difference (Mann-Whitney U-test, one--tailed) on 6 sessions within 10 consecutive sessions. In case of response inhibition, the response latency subjected to the Mann-Whitney test was 10 s.

STAGE D – DELAYED MATCHING-TO-SAMPLE TASK WITH TRIAL-UNIQUE STIMULI

In stage D, the dogs were trained in the final task, i.e., the auditory recognition Delayed Matching-to-Sample (DMS) task with trial-unique stimuli. Similarly to the previous stage C, the trial consisted of two parts: (1) the acquisition phase, when the sample stimulus was presented through the central speaker, in the way described for the stage C, and after a 1.5-s delay (2) the testing phase during which both the same (sample) stimulus and a new (different) stimulus were presented through the side speakers, in alternation. Each sound was presented three times. The testing phase might start pseudorandomly with the same stimulus (S trials) or with the new stimulus (N trials) (Fig. 2). Dogs were trained to approach (Setting 1) or to press the bar (Setting 2) on the side, where the sample sound was presented. Correct choice was reinforced by food. The training was continued to the criterion of at least 90% correct responses in 100 (Setting 1) or 90 (Setting 2) consecutive trials (5 or 6 sessions without corrections, respectively).

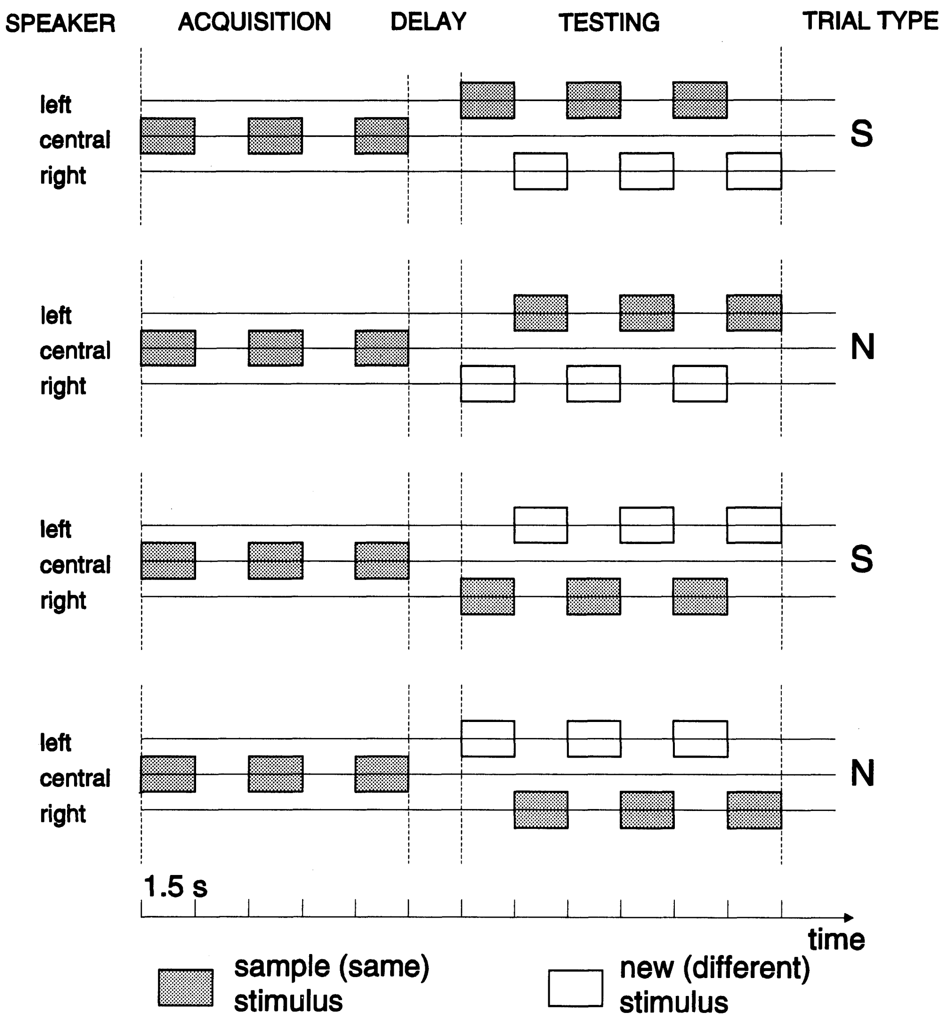


Fig. 2. The manner of presenting acoustic stimuli in DMS task (stages D, E and F). S, trials testing phase started with same stimulus; N, trials testing phase started with the new stimulus.

STAGE E – RETRAINING AFTER A REST PERIOD

After a two-week rest period, the dogs were retrained on the auditory DMS task in the same way, and to the same criterion as in the stage D.

STAGE F – PERFORMANCE TASK WITH EXTENDED DELAYS

The dogs were tested in the DMS task but the delay between acquisition and testing phase was extended to 10 s, 30 s, 60 s and finally to 90 s in separate blocks of 100 (Setting 1) or 90 (Setting 2) consecutive trials. Five out of eight dogs trained in Setting 1 (dogs D-2, D-4, D-5, D-6 and D-7) and two out of four dogs trained in Setting 2 (D-10 and D-11) received the additional block of trials with 5-s delay prior to testing with the 10-s delay. The remaining dogs (D-1, D-3, D-8, D-9 and D-12) were not pretrained with the 5-s delay. No corrections were applied in this stage.

Measurements and analyses

In each stage of the experiment, the number of trials and errors to criterion did not include the criterion trials. The exception was the stage C where criterion was calculated on Mann-Whitney statistics. In the stage A, the number of errors was not collected since at this early stage the dogs occasionally were encouraged or guided by the experimenters to make a correct response.

Latencies of response were collected in all stages except in the initial experiments when the software for such measurements had not yet been developed. Thus, for two dogs D-1 and D-9 latency data were not collected in the stages A, B, and C. For these dogs, the criterion for stage C was arbitrary and established by the experimenter. It is important to mention that the experiment-controlling program added some delays to the time of sound presentation. Thus, the longest possible response latency was not 9 s, as was predicted by the experimental procedure, but about 10 s. This delay was the same in the two experimental settings.

The latency data were square root transformed prior to ANOVA's in order to obtain as low as possible correlation of groups' means and variances. The percent correct data obtained in the stages C, D, and F were subjected to arcsine transform (see Ringo 1991) prior to parametrical statistical analyses. Other data were evaluated with distribution-free methods.

In order to examine changes of response latency distribution in the course of training and/or differences between experimental settings or between correct and incorrect responses, the10th, 25th, 50th, 75th, and 90th percentiles of response latency distributions were calculated in blocks of trials in the beginning of stages, starting from stage B (100 trials for Setting 1 and 90 for Setting 2), and during criterion trials, starting from stage A, as well as in blocks with extended delays of stage F. Then they were subjected to 3-way ANOVAs (experimental setting x block x percentile (10th, 25th, 50th, 75th or 90th)). The percentile factor was known to be significant *a priori*. However, its interactions with the other factors indicate their influences on latency distribution, which may have a behavioural importance. For example, a decrease of the 10th and 25th percentile values in some conditions may indicate that more short-latency responses occur in these conditions, which means that animals accelerate instrumental responses. Such changes may not affect the median (the 50th percentile) if they are limited to tails of distribution.

We examined also whether correct response latency distributions differed from incorrect response latency distributions by means of separate 4-way ANOVAs, performed with factor "correctness" added (i.e., experimental setting x block x correctness x percentile). Such analysis may allow finding sources of errors. The reason for doing two separate ANOVAs (rather than a single analysis with the factor correctness) was that usually the number of correct responses greatly exceeded the number of incorrect responses. However, as the percentile values rather than raw data were subjected to the analysis, the number of data obtained from the correct responses was equal to those obtained from incorrect responses. Therefore, the data from correct responses and from incorrect responses contributed equally to evaluation of factors other than "correctness" whereas they should be rather weighted according to the proportion of correct to incorrect responses. In order to avoid possible errors, only the "correctness" factor and its interactions with the other factors were assessed with the 4-way ANOVAs, while these other factors and their interactions were evaluated with the previously described 3-way analysis.

The dynamics of learning and responding in stages C and D was analysed using the vincentising method (Hilgard 1938). The total number of training trials was divided into five equal blocks (named fifths), for each dog separately. The criterion trials (in stage C: the first session with significant difference in response latencies and all following sessions of the stage) had been excluded. For each fifth of trials and each dog, the following measures were computed: mean performance levels (percent correct responses) in go and in no-go trials (stage C), or in S and in N trials (stage D) trials, median of latencies in go and in no-go trials, or in S and in N trials. There was a nonlinearity in response latencies above 9 s (theoretically, but in fact close to 10 s – see above). In the stage C, inhibition of the instrumental response was recorded as a response with latency of 10 s. In the stage D, there was a cut of responses above 9 s because after an inhibition of response the whole trial was repeated. Therefore, we used median rather than mean of latencies in the analysis. The data were subjected to 3-way (experimental setting x fifth x trial type) ANOVAs.

All ANOVAs were followed by Tukey post-hoc comparisons or, when suitable, contrast analyses for linear trend across levels of a repeated measures factor. For repeated measures factors with more than two levels Huynh-Feldt adjusted (H-F) P values are reported in addition to nonadjusted values of P.

In order to analyse response patterns in the DMS task, histograms of correct response latencies in the first block and in the criterion block of both stages D and E, and in blocks with extended delays (10-90 s) in stage F, were calculated for each dog, for S and N trials separately. The bins of 0.25-s width were centred on 0, 0.25, 0.5 s, etc. Cross-correlation was used to find lags between response latency distributions in S and N trials for each block and each dog. Autocorrelation was applied in order to detect periodicities in distributions of latencies of S or N trials, and to find their period values. The histograms of latencies obtained in each of the experimental settings were pooled and (1) lags between response latency distributions in S trials and N trials were found for each block and each experimental setting; (2) lags between latency distributions in Setting 1 and Setting 2 were found for each block and each type of trials.

RESULTS

Acquisition of the instrumental response

ANALYSIS OF PERFORMANCE

The mean trials to criterion in stage A, and trials and errors to criterion in stage B are shown in Fig. 3. The dogs trained in Setting 2 required significantly more trials than the dogs trained in Setting 1 to reach the criterion in stage A ($P<0.01$, Mann-Whitney test). No differences were found in either number of trials or errors to criterion in the stage B. Average performance levels (percent correct responses) in criterion trials did not differ between the experimental settings in both stage A and B ($P>0.15$, Mann-Whitney test).

ANALYSIS OF RESPONSE LATENCIES

The response latencies shortened during acquisition of instrumental response across stages A and B (main effect of block: $F_{2,16} = 9.78$, $P=0.002$, linear trend: $F_{1,8} = 13.5$, $P<0.01$). Medians of latencies did not differ between the two settings. However, analysis of percentiles revealed that in Setting 2 more long-latency responses occurred than in Setting 1 (experimental setting x percentile interaction: $F_{4,32} = 6.1$, $P<0.001$, H-F $P<0.005$).

In the criterion trials of stage A, some dogs performed on an almost perfect level and made one or no incorrect responses, thus the analysis with the correctness factor was calculated for stage B only. This analysis, followed by the Tukey test, revealed that erroneous responses

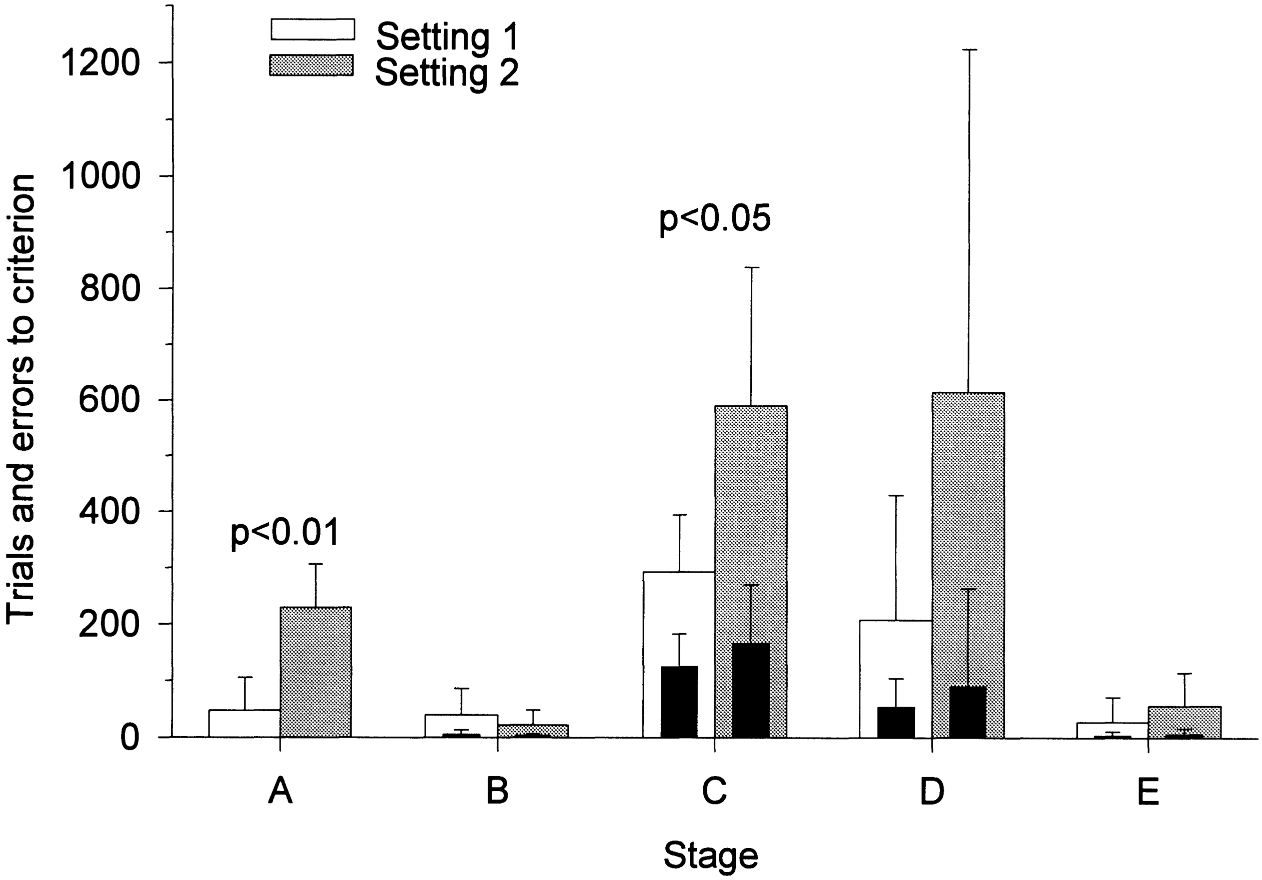


Fig. 3. Trials (wide bars) and errors (narrow bars) to criterion in consecutive stages of the experiment. Vertical lines show SDs.

made with very short latencies were eliminated in the course of stage B. The errors due to choice difficulties (indicated by higher 75th and 90th percentile values for incorrect responses) did not extinguish during stage B (block x correctness x percentile interaction: $F_{4,32}$ = 3.25, $P<0.025$, H-F $P=0.034$).

Acquisition of the recognition memory tasks

ANALYSIS OF PERFORMANCE

The mean trials and errors to criterion in stages C and D are shown in Fig. 3. In stage C, both numbers of trials and errors to criterion were significantly higher in Setting 2 than in Setting 1 ($P<0.05$, Mann-Whitney test), whereas in stage D, differences in both trials and errors to criterion were not significant, though considerably high ($P>0.1$, Mann-Whitney test).

Average performance levels (percent correct responses) in criterion trials did not differ between the experimental settings in either stages C or D.

ANALYSIS OF DYNAMICS OF LEARNING AND OF RESPONSE LATENCIES (FIG. 4)

In stage C, performance levels (percent correct responses) were better for go than no-go trials (main effect of trial type: $F_{1,8}$ = 216.4, $P<0.0001$). The performance level was systematically improving in the course of the stage (main effect of fifth: $F_{4,32}$ = 5.37, $P=0.002$, H-F $P=0.002$; trend: $F_{1,8}$ = 25.2, $P=0.001$). This was caused by improvement of performance in no-go trials (fifth x trial type interaction: $F_{4,32}$ = 3.31, $P<0.022$, H-F $P=0.04$; trend for no-go trials: $F_{1,8}$ = 59.75, $P=0.0001$, for go trials: $F_{1,8}$ = 3.52, $P=0.1$). There was a significant interaction of experimental setting x fifth x trial type ($F_{4,32}$ = 3.13, $P=0.028$, H-F $P=0.047$) indicating that in the 3rd and 4th fifths, the mean performance level of dogs trained in Setting 2 was lowered in go trials and increased in no-go trials, in comparison to other fifths. However, inspection of individual data revealed that this interaction was caused by behaviour of one dog (D-11), which, in the 3rd and 4th fifths, often did not respond either in go or no-go trials.

Median latencies in go trials were shorter than in no-go trials (main effect of trial type: $F_{1,8}$ = 6.53, $P=0.034$). However, no significant differences related to experimental setting or to dynamics of learning (effect of "fifth") were found for this measure in stage C. The lack of fifth x trial type interaction and of linear trend of latencies across fifths in no-go trials suggests that the inhibition of responses in no-go trials developed late and rapidly, and was not apparent before the criterion trials. However, as noted previously, there was a significant increase of performance level in no-go trials. Such an increase could be achieved only by inhibition (i.e., increase of latencies) of responses in no-go trials. The explanation may be that only a small fraction of responses to different (no-go) stimuli was inhibited whereas a majority was accomplished with short latencies, resulting in a small but significant increase of performance level without changes to the medians of latencies. In order to evaluate the dynamics of response latencies during stage C, we repeated the analysis using means of latencies, which are sensitive to changes in tails of distribution. This analysis confirmed, though indirectly, that a fraction of latencies in no-go trials did increase: latency means became higher across fifths (main effect of fifth: $F_{4,32}$ = 5.09, $P=0.003$, H-F $P=0.003$; trend: $F_{1,8}$ = 14.35, $P=0.0053$), and this increase was caused by an increase of latencies in no-go but not in go trials (fifth x trial type interaction: $F_{4,32}$ = 14.94, $P<0.0001$, H-F $P<0.0005$; trend for no-go trials: $F_{1,8}$ = 51.57, $P=0.0001$; for go trials: $F_{1,8}$ = 3.20, $P=0.11$). Experimental setting affected neither medians nor means of latencies in stage C.

During learning of the auditory DMS task (stage D), performance level (percent correct responses) was better in S trials than in N trials (main effect of trial type: $F_{1,9}$ = 8.24, $P<0.02$). This difference changed across the fifths: there was a significant increase of performance across the fifths in N trials but not in S trials (fifth x trial type interaction: $F_{4,36}$ = 4.93, $P<0.003$; trend in N trials: $F_{1,9}$ = 13.1, $P=0.006$; in S trials: $F_{1,9}$ = 1.6, $P=0.24$). The overall change in performance across fifths was not significant (main effect of fifth: $F_{4,36}$ = 1.96, $P=0.12$, H-F $P=0.13$; trend: $F_{1,9}$ = 2.7, $P=0.13$). No differences in performance level between two experimental settings were observed.

The median response latencies in learning the DMS task were shorter in S trials than in N trials (main effect of trial type: $F_{1,9}$ = 14.04, $P=0.005$). The response latencies were short at the beginning of stage D and became longer towards the end of the stage (main effect of fifth: $F_{4,36}$ = 3.85, $P=0.01$, H-F $P=0.01$; trend: $F_{1,9}$ = 7.47, $P=0.02$). This effect was caused by lengthening of response latencies in both S and N trials: the separate contrast analyses for trials S and N did not show significant linear trends ($F_{1,9}$ = 4.73, $P=0.058$, $F_{1,9}$ = 2.04, $P=0.19$, S

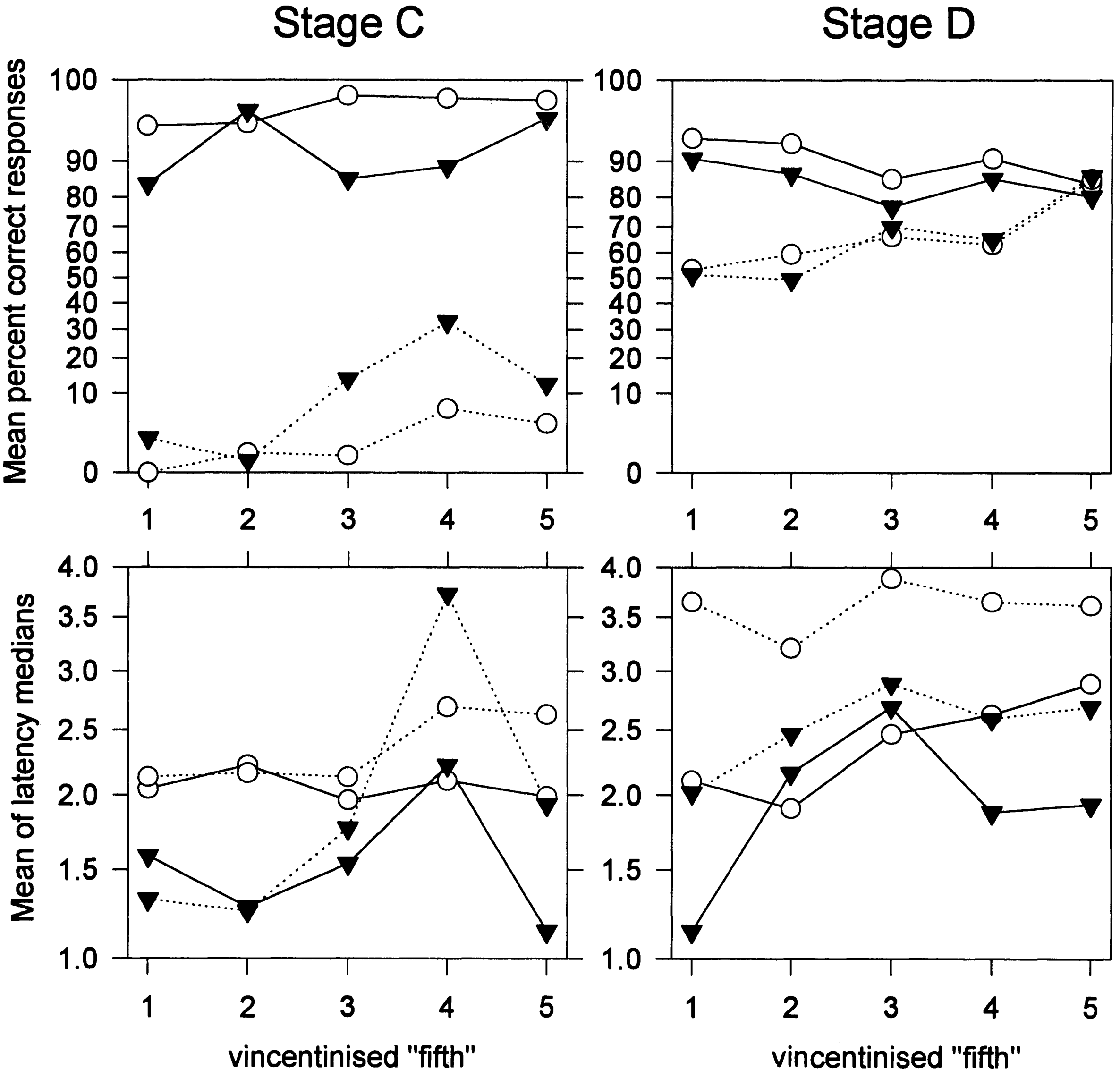


Fig. 4. Dynamics of performance level (upper panels) and of latencies (lower panels) in stages C (left) and D (right) in the two settings (circles: Setting 1, triangles: Setting 2). Solid lines indicate go (stage C, left) or S (stage D, right) trials. Dotted lines indicate no-go (stage C, left) or N (stage D, right) trials. The non-linear vertical axes reflect transformations applied to the data: arcsine (upper panels) and square root (lower panels) (see Measurements and analyses in Methods section). The S and N abbreviations are explained in Fig. 2.

and N, respectively). It is noteworthy, however, that the effect for S trials was stronger than for N trials. Again, the analysis did not show influence of experimental setting on response latencies during auditory DMS training.

Retention of the task rule after the rest period

The mean trials and errors to criterion in stage E did not differ in the two settings (*P*>0.2, Mann-Whitney test; Fig. 3). In Setting 1, five dogs reached the criterion immediately, whereas three needed an average of 73 trial and 11 errors (ranges: 40-120 and 7-18, respectively) of additional training. In Setting 2, one dog reached the criterion immediately and three needed an average of 75 trials and 13 errors (ranges: 15-120 and 2-21, respectively) of additional training. There was also no difference in mean performance level (percent correct responses) in the criterion trials between dogs trained in the two settings or between the criterion trials of stages D and E.

No differences between response latencies between two experimental settings were found either in criterion trials of stage D or in the beginning of stage E. However, detailed analysis showed that values for the 10th, 25th, and 75th (but not for the 50th and 90th) percentile were significantly higher in Setting 1 than in Setting 2 (experimental setting x percentile interaction: ($F_{4,40} = 3.54$, P=0.015, H-F P=0.032; Tukey tests: $P<0.01$).

Performance of the DMS task with extended delays

ANALYSIS OF PERFORMANCE

The mean performance scores in stage F are shown in Table I. The 4-way (experimental setting x pretraining with 5-s delay x delay (10-90 s) x trial type (S or N)) repeated measures ANOVA revealed that the performance level (percent correct responses) depended neither on experimental setting nor on pretraining with 5-s delay. Moreover, percent correct responses for 5-s delay and for 10-s delay in respective dogs did not differ.

The delay factor influenced the performance level heavily ($F_{3,24}$ = 24.5, $P<0.0001$, H-F $P<0.0001$): this was reflected by a gradual decay of performance on the task with increasing delay (trend for all data: $F_{1,8}$ = 27.94, $P<0.001$; for the experimental settings, trial types, or pretraining conditions separately: $Fs(1,8)>10$, $Ps<0.011$).

The performance level in N trials was lower than the performance in S trials by about 20% (main effect of trial type: $F_{1,8}$ = 18.5, P=0.0026; Table I). More detailed analyses showed that in Setting 1 (but not in Setting 2), dogs had significantly higher performance level in S trials in comparison to N trials (experimental setting x trial type interaction $F_{1,8}$ = 7.44, P=0.026; Tukey test for Setting 1: P=0.0013, for Setting 2: P=0.77). Moreover, opposite to the dogs that were pretrained with 5-s delay, the dogs that had no pretraining with 5-s delay performed significantly better in S trials than in N trials (pretraining with 5-s delay x trial type interaction: ($F_{1,8}$ = 6.72, P=0.032; Tukey test for dogs without the 5-s pretraining: P=0.0063, with the 5-s pretraining: P=0.53). It has to be stressed however, that the performance levels for S trials as well as for N trials, separately, did not differ between the two experimental settings or between the pretraining conditions.

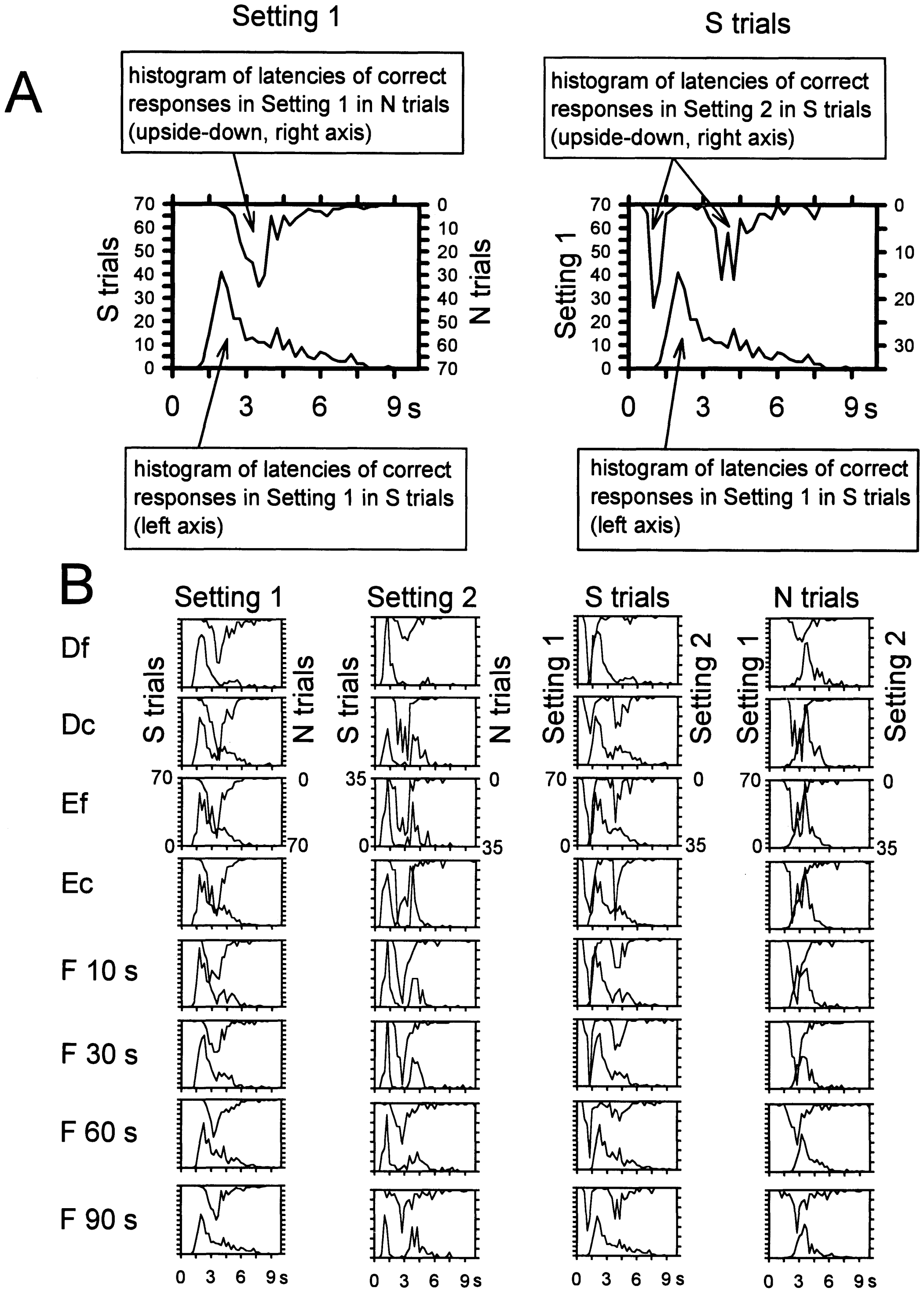
ANALYSIS OF LATENCIES

The response latencies increased gradually from the criterion block of stage E (with delay 1.5 s) across different delay of stage F (main effect of block: $F_{4,40}$ = 4.17, P=0.006, H-F P=0.006; trend: $F_{1,10}$ = 10.23, P=0.01). The response latencies for incorrect responses were longer than for correct responses (main effect of correctness: $F_{1,10}$ = 10.35, $P<0.01$).

TABLE I

Percent correct responses in blocks with extended delays (stage F)

Group	Delay: 5 s	10 s	30 s	60 s	90 s	average 10-90 s
Setting 1 (n = 8)	86.6 (n = 5)	84.4	73.3	69.5	65.5	73.1
Setting 2 (n = 4)	81.1 (n = 2)	81.9	75.5	65.9	61.7	71.3
with 5-s delay pretraining (n = 7)	85.0	84.4	75.2	67.8	64.0	72.9
without 5-s delay pretraining (n = 5)	-	82.4	72.3	68.9	64.5	72.0
S trials (n = 12)	83.5 (n = 7)	91.0	86.8	76.6	74.7	82.3
N trials (n = 12)	86.4 (n = 7)	76.1	61.2	59.8	53.7	62.7
Total mean (n = 12)	85.0 (n = 7)	83.6	74.0	68.3	64.2	72.5



Setting 1

S trials

histogram of latencies of correct responses in Setting 1 in N trials (upside-down, right axis)

histogram of latencies of correct responses in Setting 2 in S trials (upside-down, right axis)

histogram of latencies of correct responses in Setting 1 in S trials (left axis)

histogram of latencies of correct responses in Setting 1 in S trials (left axis)

Setting 1

Setting 2

S trials

N trials

Fig. 5. Comparisons of histograms of response latencies (response patterns) in blocks of the DMS tasks. A: explanation of the way of presenting data. Left: comparison of S trials to N trials within an experimental setting. Right: comparison of Setting 1 to Setting 2 within same type of trials. B: first column: histograms of latencies in Setting 1, S trials compared to N trials. Second column: histograms of latencies in Setting 2, S trials compared to N trials. Third and fourth column: same data, but latencies in Setting 1 are compared to latencies in Setting 2, for S (third column) and N (fourth column) trials separately. Df, Dc, Ef, Ec, F 10 s, F 30 s, F 60 s, F 90 s: first block of stage D, criterion block of stage D, first block of stage E, criterion block of stage E, and blocks with extended delays of 10, 30, 60 and 90 s, respectively. The unit on each vertical axis is 5. The S and N abbreviations are explained in Fig. 2.

Response patterns in the recognition memory task

In most dogs, the latency distributions of N trials were usually lagged 1.0-2.0 s in comparison to latency distributions of S trials. The responses appeared to be locked to presentations of the sample stimulus in both S and N trials. In S trials, periodicities occurred in some dogs: sometimes the dogs responded not to first, but to second or even third presentation of the S stimulus. Such periodicities usually appeared in the course of stage D and sometimes they became more pronounced with extended delays in stage F. Periods ranged 1.25-3.75 s, but most common values were 2.0-3.0. Periodicities were very rarely seen in N trials, indicating that in these trials, dogs usually responded to first presentation of the sample stimulus.

Three dogs showed different patterns of responding. Dogs D-1 and D-7 showed no apparent locking to stimuli and a smear of latency distributions. However, as the distributions of latencies in N trials were still delayed to distributions of latencies in S trials in most blocks, the smear was probably due to changes in motor act duration, while locking to the presentation of the sample stimulus was still present. Dog D-11 showed a reversed pattern of responding: distributions of latencies in S trials were lagged to distributions of latencies in N trials. This dog responded to first presentation of the sample stimulus in N trials and to second presentation of this stimulus in S trials.

Analysis of histograms of latencies pooled within experimental settings confirmed the 1.0-1.75-s lag of N trial responses versus S trial responses in both settings (Fig. 5, first and second column). In the pooled data, the periodicities are clearly visible for Setting 2 only. Individual data showed that they occurred in Setting 1, too; however, the picture is obscured by individual differences. Moreover, response latency distributions were lagged in Setting 1 *versus* Setting 2 by 0.75-1.0 (S trials) or 0.5-0.75 s (N trials) in all blocks (Fig. 5, third and fourth column) indicating, that in Setting 1 response latencies were longer than in Setting 2.

The obtained values of the N trials to S trials lag (around 1.5 s) as well as the values of periods in cases when periodicities were detected (close to 3 s) support the notion of locking the responses to presentations of the same stimulus.

DISCUSSION

Influence of experimental setting on rate of learning

The results obtained in this experiment strongly support the supposition that dogs can learn an auditory recognition memory task with trial unique stimuli easier and faster than monkeys (D'Amato and Colombo 1985, Kojima 1985, Fritz et al. 1997). Moreover, in both experimental paradigms recognition training with trial-unique stimuli was shorter than the training on an auditory Konorski's Task with two stimuli, reported by Brown and Sołtysik (1971).

The course of learning was shorter for animals trained in Setting 1 in comparison to animals trained in Setting 2. However, the significant differences between the two experimental settings were observed only at the early stage of the instrumental response acquisition (stage A), and at the early stage of recognition training, where the Konorski's Task with trial-unique stimuli was introduced (stage C). Such differences did not appear on the later stage of instrumental training (stage B) and during acquisition of the final DMS task (stage D). The difference which appeared in the course of learning was probably caused by the two different instrumental responses required in the two paradigms; the bar-press response is more difficult to acquire, because it is a more precise motor act than the locomotor approach response. The greater difficulty in responding in Setting 2 in the beginning of training was confirmed by the distribution of response latencies. Dogs trained in Setting 2 had more long-latency responses than those trained in Setting 1, possibly due to more difficulty with making the response.

The factor just described is directly associated with the motor component of the instrumental response. The dogs had to perform the appropriate motor act in order to reach the criterion of stages A and B. Moreover, the shortening of response latencies observed during acquisition of the instrumental response indicates that, in both settings, the dogs improved their instrumental responding in the course of training. Therefore, the factor might influence learning of the instrumental response in stage A but it is unlikely that it could be responsible for differences that occurred in learning the recognition memory tasks.

Other factors, related to non-motor components, might influence the acquisition of the recognition memory tasks. The approach distance might be beneficial for learning in Setting 1. Zabłocka and Żernicki (1990) showed that cats learned visual discrimination substantially worse when a partition between stimuli was inserted. The partition prevented the cats to correct an initially wrong response. Such a self-correction was possible only when the partition was removed. Similarly, in Setting 1, the distance between platform and feeder might cause a delay between choice and accomplishment of the approach response. Such a delay may allow the dog to self-correct an initially wrong choice, and from this point of view might be beneficial for the learning. Additionally, while performing the approach response, the dogs were allowed to hear the stimuli for a longer time before they made their response, which might facilitate localisation and discrimination of auditory stimuli in Setting 1.

Moreover, the approach response requires spending more energy than the bar-press response. Therefore, the lack of food reinforcement, after an incorrect response, could better facilitate extinction of these responses in dogs trained in Setting 1, than in Setting 2. Particularly in no-go trials of stage C, the non-reinforced approaches might be more discouraging than non-reinforced bar-presses.

Another factor, which could influence learning of the instrumental responses and the recognition tasks, is spatial relationship between source of the stimulus, manipulandum, and reward. It was shown that spatial non-adjacency of stimulus and manipulandum impairs learning of auditory location discrimination in monkeys (Harrison et al. 1971, Downey and Harrison 1972, Harrison et al. 1977). A similar effect was observed in rats (Harrison et al. 1971). In addition, auditory quality discrimination was impaired in rats when the positive stimulus was presented through a remote speaker and the negative stimulus was presented through a speaker which was adjacent to the response bar (Harrison 1988). In our study, auditory location discrimination was trained at the early stages of the experiment, and later the animals were trained in tasks that required both auditory location and quality discriminations (stages C-F). In comparison to conditions of the approach situation, in the bar-press situation, there was certain spatial non-adjacency of stimuli (speakers), manipulanda (response bars) and reward (food dispenser): the food dispenser was located in front of the dog, the bars on the left and on the right (about 35 cm from the food dispenser opening), and the side speakers 34 cm above the bars. The distance between the food dispenser's opening and the side speakers was about 55 cm. In terms of angular distances, these distances were about 80° (food dispenser to side speaker), 100° (food dispenser to response bar), and 40° (response bar to side speaker), measured from approximate position of the dog's head. In the Setting 1, the angular distance between the speaker and the food dispenser opening was about 8°. In Setting 1, however, there was no separate manipulandum, the approach responses were directed towards the food dispenser. Taken together, although in Setting 2 the side speakers were located on the same side of the dog as the respective response bars and at the approximate height of the dogs ears, the components were less adjacent to each other than in Setting 1. This difference might also contribute to the rate of learning.

It should be stressed, however, that all of these factors differentiating the two experimental settings could influence the learning and performance at the early stages of training, but they did not significantly change the rate of learning during the final recognition DMS task.

Thus, we may conclude that the type of instrumental responses was the main factor, affecting the speed of learning in the two experimental settings. The spatial relationship of the elements of the experimental settings could also contribute to this difference. Contribution of other factors (e.g., acoustical conditions in settings or presence of experimenter and computer in Setting 1) cannot be excluded. All these factors should be considered in order to improve learning rate in future experiments.

Influence of experimental setting on the performance task

The performance level with the extended delay was not affected by the experimental setting. The number of factors that influenced learning the task had no effect on memory measures. Thus, the memory decay shown in Table I represents a valid measure of dogs auditory recognition memory abilities.

Additional behavioural observations

Several phenomena were observed that might allow justifying the experimental procedure proposed by Kowalska (1997). During stage B, an extinction of short-latency errors was observed. At this stage, the emission of the sound from the central speaker was introduced, and animal learned to extinguish response to this sound, and during the following delay period. In Setting 1, the response was not possible due to the leash, and in Setting 2 that response was possible. However, in both settings, the short latency erroneous responses appeared at the beginning of stage B, which may indicate that the dogs tried to decide about response side on the sound emitted through the central speaker. This behaviour was extinguished in the course of instrumental learning, preparing animals to smooth transition to the more complicated recognition task.

In the Konorski's recognition task, the results concerning level of performance and response latencies (both medians and means) show, that, in both settings, only a small fraction of the responses was inhibited before the criterion sessions, whereas latencies of other responses in the no-go trials did not increase. This result may suggest that the same/different concept had been acquired by the dogs before they dissociated the response latencies in go and no-go trials, as shown by significant Mann-Whitney test outcome. This may indicate the dynamics of the dissociation of the discrimination and differentiation processes in the course of recognition training. During this stage, the dogs learned that the response to the side of the sample sound activation is rewarded by food, while the response to the side where the different (new) sound is emitted, is not rewarded. This rule was transferred to the next, final recognition DMS task. Analysis of learning dynamics shows that at the beginning of stage D, the mean correct performance in trials when testing phase started with the new (different) sound exposition (N trials), was about 53% (Fig. 4). If dogs had responded always to the first stimulus in the testing phase, which was possible strategy used on the stage B, the correct performance level in N trials would be 0%. We may conclude therefore, that the training in Konorski's Task resulted in acquisition of same/different concept followed by differentiation of responses to the same and different stimuli. The training on the modified version of Konorski's recognition task was beneficial for subsequent auditory DMS learning.

Several other phenomena were observed during training. Analysis of the latencies revealed that during the final recognition task the dogs had some tendency to respond during emmision of the same stimulus and to wait during the different stimulus, rather than to respond during emission of the different sound to the opposite side. Such tendency was shown with the analysis of response patterns (Fig. 5, first and second column). The locking of responses to the presentations of the same stimulus may be a consequence of the whole previous training. In stages A-C, reinforcement could be obtained after a response towards a familiar sound, but never after a response to the side where no familiar sound was presented. Moreover, responding towards a sound rather than to the opposite side is easier (e.g., Stepień et al. 1990) because it is contiguous with the orienting reflex.

During learning of the DMS task, the increase of response latencies across the fifths was observed. This resulted mainly from the increase of response latencies in S trials (when the testing phase started with the sample stimulus) rather than in N trials. It is probable that with advance of learning the dogs were less excited and could develop a kind of inhibition of delay.

In the task with extended delays, the performance level was better in S trials than in N trials, and this difference remained unchanged across the delays. Apparently, in some trials, dogs tended to respond to the first stimulus of the testing phase. However, the detailed analysis of individual data does not affirm a clear relation between strategies used by the dogs in responding to the S and N trials and independent variables used in the experiment.

With extended delays of the performance task the latencies of responses increased. This may be an effect of an increasing difficulty of the task. Dogs might need to listen to stimuli more than one time before making a choice. This notion is supported by response pattern analysis showing, in some dogs, more pronounced periodicity in final blocks of stage F.

Individual differences

The number of behavioural indices that are collected in our experiment allows detecting dogs' whose behaviour differs much from the other dogs behaviour. Dog D-11 may serve as an example: he showed unusual dynamics of learning and of response latencies in stage C and an atypical responding pattern in the DMS task. Moreover, his learning in stage D was almost twice as long as the second-worst dog.

Effect of pretraining with the 5-s delay

The important finding was that introducing additional delay between the original 1.5-s delay and 10-s delay that was used in the previous study, did not change the level of performance to the 10-s delay, and to subsequent delays. This result supports the view that the drop of performance on the task with 10-s delay was not caused by the sudden elongation of the delay, but reflected rather the auditory memory capacity in the dog. From this point of view, in further experiments, there is no need to include the 5-s delay in the performance task.

Summary

The purpose for using the auditory DMS task is to investigate auditory recognition memory. We have been tracing the learning of the recognition DMS task rules, the retention of the recognition task, and recognition memory ability in the performance task. In all of these stages, no significant differences between the results collected on dogs trained in the two experimental settings were observed. The data from these two paradigms can thus be pooled in future experiments. Moreover, the similarities observed in the two settings suggest that there was no unintentional cueing by the experimenters in the approach situation.

The data provide a basis for further experiments on auditory recognition memory. With the proposed analyses, subtle effects, such as changes of response patterns or of response strategies can be evaluated after lesions of temporal lobe structures or after other experimental manipulations.

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