Acta Neurobiol. Exp. 2002, 62: 251-262

Effect of sound source position 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

Abstract. Spatial adjacency of stimulus source and response site has been proven important for learning of simple behavioural tasks, including auditory quality and location discrimination. We investigated effect of sound source position (adjacent or not adjacent to manipulanda) on learning and performance of a complex auditory recognition memory task. Spatial adjacency of stimuli and manipulanda improved learning of a simple auditory directional task, which was an intermediate stage of training. In contrast, no improvement of learning and performance of the recognition task was found.

Key words: auditory recognition, spatial adjacency, dog

INTRODUCTION

Neural substrates of recognition memory have been studied extensively for many years, chiefly in monkeys. Most of these studies have been limited to visual (e.g., Meunier et al. 1993), tactile (e.g., Suzuki et al. 1993), and olfactory (e.g., Otto and Eichenbaum 1992) modalities, while experiments on auditory recognition have been sparse. The reason is that despite numerous attempts, experimenters have been experiencing great difficulties developing an effective behavioural task for studying auditory recognition memory in monkeys (e.g., Stępień et al. 1960; Cowey and Weiskrantz 1976, Kojima 1985, Colombo and D'Amato 1986, Wright et al. 1990). Recently, an auditory version of delayed matching-to-sample (DMS) task has been devised and used successfully in dogs (Kowalska 1997) and monkeys (Kowalska et al. 1999). It has been shown that dogs can learn the task much faster than monkeys (Kowalska et al. 1999), and that performance on the task does not depend upon a particular experimental environment (Kuśmierek and Kowalska 1998) – a result that demonstrates the generalizability of DMS. The task has been used for studies on the neural substrate of auditory recognition memory (Kowalska et al. 1998, 2001).

Thus, so far dogs appear to be the most appropriate subjects for investigation of auditory memory. It has to be emphasised, however, that despite their superiority to monkeys, dogs still need a considerable number of trials to acquire the auditory DMS task. Moreover, the duration of training (contrary to subsequent performance levels) was shown to depend on the experimental environment, being longer in a bar-press situation than in an approach situation (Setting 2 vs. Setting 1 in Kuśmierek and Kowalska 1998). We suggested that this difference was caused either by the difference in the type of instrumental response (bar-press vs. approach) or by different spatial relationships among the manipulanda, stimuli sources, and reward (spatially contiguous in the approach situation vs. non-contiguous in the bar-press situation). Which of these factors contributed more to the result was not determined because they were not manipulated independently in the experiment.

Many studies have shown that placing manipulanda, stimulus sources, and reward in spatially adjacent positions improves learning and performance on various behavioural tasks. Particularly relevant are results of a series of experiments by Harrison and co-workers, which have shown a strong beneficial effect of spatial proximity (referred to as "adjacency" by these authors) of response and reward on learning and performance of simple auditory quality differentiation and simple auditory location differentiation (for review, see Harrison 1992). This proximity must be close: one experiment in rhesus monkeys has shown that locating response keys only 20 cm from the respective loudspeakers (while maintaining a much larger inter-key distance of 70 cm) retards learning of auditory location discrimination in comparison to training with keys located immediately in front of the loudspeakers. The magnitude of the retardation was similar to that obtained when the animal was required to avoid responding to a key located in front of the sounding speaker and to respond to a key located in front of the non-sounding speaker, that is, 90 cm from the sounding speaker (Harrison et al. 1977).

In our task, auditory location differentiation is trained directly in the course of auditory DMS acquisition, and both auditory quality differentiation and auditory location differentiation are embedded in the intermediate stage of recognition learning and in the final DMS task (Kowalska 1997). On the basis of Harrison's data, we hypothesised, therefore, that bringing the stimulus sources closer to the manipulanda in the bar-press situation would yield faster acquisition of the DMS task, and/or better performance. If the hypothesis were confirmed, Harrison's findings would be shown to extend to a complex auditory task. Moreover, such result would suggest that the adjacency of stimulus sources and response sites caused faster learning in Setting 1 in the previous experiment. On the other hand, if locating stimuli adjacent to the manipulanda did not improve learning indices, then we would reason that the faster learning in Setting 1 was related to the nature of the instrumental response. Furthermore, Harrison's postulate would then appear to be limited to simple auditory discrimination tasks only.

To test these alternatives, four dogs were trained in the bar-press situation (referred to as Setting 2 in Kuśmierek and Kowalska 1998), but with side speakers located directly under the response bars (group AD - adjacent). Their learning and performance scores were compared to four dogs trained with side speakers located 34 cm above the response bars (group NA – non-adjacent). Of these four, three had been reported in the previous paper, while the fourth was a replacement for one that had displayed anomalous behaviour (D-11, see Kuśmierek and Kowalska 1998).

METHODS

The methods were similar to those previously described (Kowalska 1997, Kuśmierek and Kowalska 1998).

Briefly, the behavioural procedure was based on instrumental training with food reinforcement, given in 15-trial (or 20-trial, stage C) sessions daily with 40-s inter-trial intervals. The training consisted of several stages, which gradually directed animals towards the DMS rule. After habituation and training of the instrumental bar-press response, simple directional responding to an auditory stimulus presented from either the left or right speaker was trained to a criterion of at least 80% correct responses in 30 consecutive trials (stage A). In the next stage, trial-unique stimuli were introduced and each trial was started with stimulus presentation from the central speaker, which was never associated with reward. This was followed after 1.5 s by the same stimulus playing from a side speaker. Proper directional responses (i.e., towards the sounding side speaker) were reinforced and training continued to a criterion of 90% correct responses in 90 trials (stage B). In stage C (modified Konorski's task (Konorski 1959, Kowalska 1997, Kowalska et al. 2001)), stimulus presentation from the central speaker was followed after 1.5 s either by presentation of the same sound from a side speaker (go trials), or by presentation of a different sound from a side speaker (no-go trials). Proper directional responses in go trials were rewarded as in stage B, whereas responses in no-go trials were never rewarded, and they did not turn off the sound. Withholding of response for 9 seconds in a no-go trial was not rewarded and was scored as correct (for analysis of dynamic of acquisition of the task, see below). The training continued until response latencies in go trials were significantly (Mann-Whitney test) shorter than in no-go trials in 6 of 10 consecutive 20-trial sessions. Next was the final task, auditory DMS with trial-unique stimuli (stage D). After presentation of a stimulus from the central speaker followed by 1.5-s delay, two stimuli were played in alternation, each from one of the side speakers. One of these stimuli was the same as the one played previously from the central speaker, the other one was different (novel). Either the same stimulus (S trials) or the novel stimulus (N trials) could be played first from a side speaker. Responses toward the same stimulus were rewarded and scored as correct, and training continued to a criterion of 90% correct in 90 trials. After a 14-day control pause, the same procedure as in stage D was repeated in order to test retention of the rule (stage E). This was followed by a DMS performance task given in four 90-trial blocks, with the delay extended to 10, 30, 60, and 90 s, respectively (stage F). In all stages, except for no-go trials of stage C, any response immediately turned off the sound stimulus.

Stimuli were 1.5-s long recordings of various sounds (animal voices, machines, melodies, etc.) stored in a computer and played with a SoundBlaster Pro sound card at an intensity level of about 60 dB(A). For the recognition task, the stimuli were arranged into pairs. For each pair, stimuli were chosen that differed across many features and that were easily and obviously discriminable to the human listener.

Eight naïve male mongrel dogs weighing 7-24 kg (7-18 kg for group NA, 15-24 kg for group AD, *P*=0.2, Mann-Whitney test) were used. The animals were food-deprived for 15-23 h prior to testing. All procedures and conditions complied with Polish animal welfare laws and were approved by the Nencki Institute Ethical Committee.

Testing was conducted in a sound-proof chamber equipped with two response bars (left and right), an automatic food reward dispenser, and two sets each of three speakers.

For group NA, the side speakers (two-way, Thompsonic operating in open-back configuration) were located 34 cm above the response bars, that is, at the approximate level of the dogs' ears (Fig. 1, see also Kowalska 1997, Kuśmierek and Kowalska 1998). For group AD, the side speakers (two-way, GDC 10/20/1,Tonsil, Poland, operating in sealed enclosures) were located just below the response bars (Fig. 1). The central speaker was located in front of the dog, 77 cm (group NA) or 95 cm (group AD) above the food dispenser and was identical to the respective side speakers. The speakers used in group AD were built into enclosures in order to protect them from possible damage by dogs. Moreover, the front of the AD speakers was protected by a custom-made perforated metal plate, whereas the front of the NA speakers was protected by the original plastic grille.

To assess the effect of using different speakers and different acoustic configurations, computer-generated white noise was emitted from the left speaker (either NA or AD or Setting 1 described in Kuśmierek and Kowalska 1998) and measured with a sound level meter (Brüel and Kjaer sound level meter 2209 with 4145 one-inch microphone). The speakers used in this study

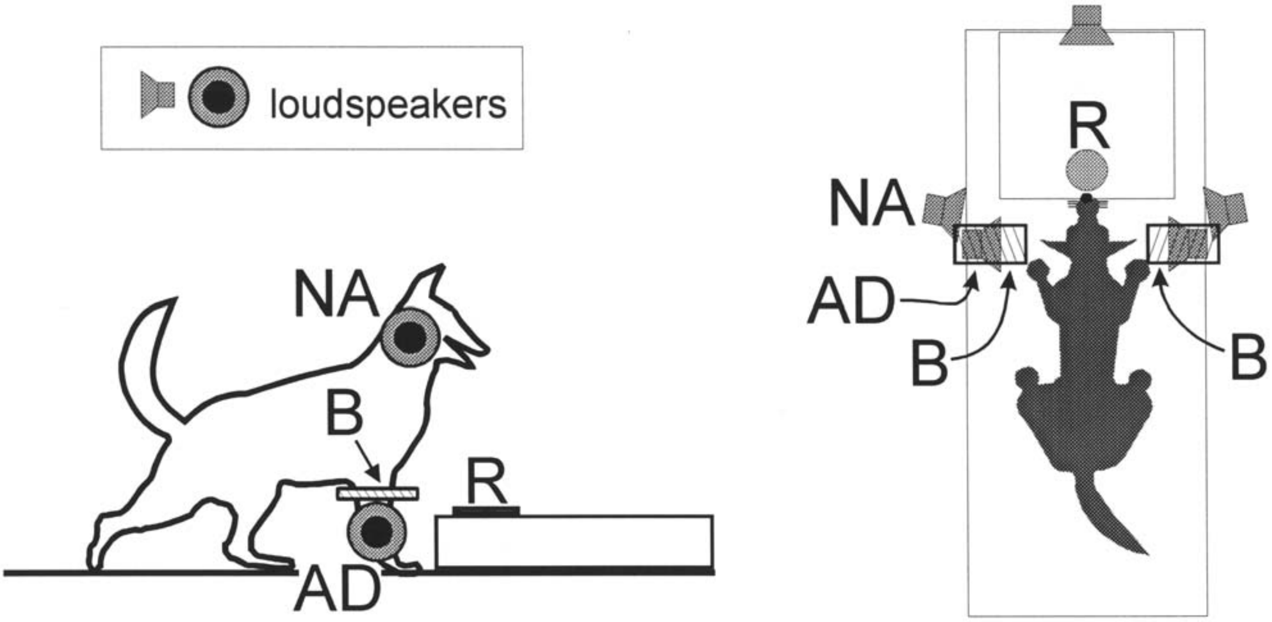

Fig. 1. Location of the non-adjacent (NA) and adjacent (AD) loudspeakers in respect to response bars (B), reward dispenser (R), and the animal. Left, view from the right side; right, view from the top of the platform. Central speaker are not shown on the left.

were compared to Setting 1 speakers because dogs trained in that setting showed fast learning and good performance on tasks identical to those described here (Kuśmierek and Kowalska 1998). The AC signal from the meter was fed into the SoundBlaster Live! sound card, digitised (sampling frequency 44.1 kHz, 16-bit resolution) and the amplitude adjusted in order to obtain equal intensity in all three recordings. 1/3-octave spectra were calculated from 4096 FFT spectra averaged over 1 second of recording with SpectraPlus 2.32.04 program (Sound Technology, Campbell, CA, USA). The three spectra were compared visually and Pearson correlation coefficients were computed. Moreover, spectral variation was calculated as the mean of the absolute differences between neighbouring 1/3-octave bands. This measure was then normalised by dividing by the sum of ascending and descending vertical (sound pressure level) ranges of the spectra. The ranges were computed by subtracting the value in the first band and the value in the last band, respectively, from the spectrum maximum.

In order to evaluate the learning rate, the number of trials to criterion (excluding criterion trials, except for stage C) in stages A, B, C, D, and E was subjected to 2-way repeated measures ANOVA (group x stage (repeated measure factor, r. m.)). Performance levels in criterion trials of stages A, B, D, and E were also examined with a group x stage (r.m.) ANOVA. Performance level in the performance task with extended delays was assessed by means of a 3-way ANOVA (group x delay (r. m.) x trial type (S or N, r. m.)).

Dynamics of acquisition of the recognition tasks (stages C and D) was investigated with the vincentinising method (Hillgard 1938, see also Kuśmierek and Kowalska 1998). For each dog, acquisition was divided into five equal blocks, named "fifths" (criterion trials in stage D, as well as the first session with significant difference in response latencies and all following sessions of the stage C, have been excluded). For each fifth, the following measures were computed: percent correct responses in go and in no-go trials (stage C), or in S and in N trials (stage D), median of latencies in go and in no-go trials, or in S and in N trials. The data were analysed by 3 way (group x fifth (r. m.) x trial type (r. m.)) ANOVAs.

Distributions of response latencies were studied by percentile analysis. First, the 10th, 25th, 50th, 75th, and 90th percentiles of latency distributions were computed for 90-trial blocks at the beginning of stages B and E, for the final (criterion) blocks of stages A, B, and D, as well as for blocks with extended delays (stage F). Except for the criterion block of stage A, this calculation was also performed separately for trials scored as correct and those scored as incorrect. Next, the data were subjected to 3-way ANOVAs (group x block (r. m.) x percentile (r. m.)) and to 4-way ANOVAs (group x block (r. m.) x correctness (r. m.) x percentile (r. m.)) (for details, see Kuśmierek and Kowalska 1998). These analyses were conducted for the following sets of blocks: (i) final block of stage A (3-way ANOVA only), first block of stage B, and final block of stage B; (ii) final block of stage D and first block of stage E; (iii) final block of stage E and four consecutive blocks of stage F. For analyses (i) and (ii), only three dogs of group NA were used because the early version of our software did not allow recording of response latencies.

Prior to parametric statistical analyses, all percent correct data were subjected to arcsine transformation (see Ringo 1991) and all latency data were subjected to square root transformation, in order to improve distribution normality. ANOVAs were followed by Duncan *post-hoc* comparisons and/or contrast analyses for linear trend across consecutive levels of a repeated measures factor.

RESULTS

Number of trials to criterion in stages A, B, C, D, and E is shown in Fig. 2. This measure varied significantly across the stages of the experiment ($F_{4,24}$=18.2, $P<10^{-5}$). Given the obviously different difficulty of stages, this finding is rather trivial. More interestingly, the group x stage interaction was also significant ($F_{4,24}$=3.91, P=0.014). *Post-hoc* analysis revealed that in none of the stages was learning faster in group AD than in group NA. It is noteworthy, however, that all four dogs of group AD (but only one out of four dogs of group NA) reached the criterion of stage B immediately (i.e., in 0 trials). Quite unexpectedly, the number of trials to criterion in stage D was actually significantly higher in group AD (mean 649) than in group NA (mean 266, $P<0.01$), indicating slower acquisition of the DMS task in group AD.

Performance level in criterion trials of stages A, B, D, and E is shown in the inset of Fig. 2. A strong effect of stage ($F_{3,18}$=9.65, $P<0.001$) reflected the obvious difficulty of DMS (stages D and E) compared to the direc-

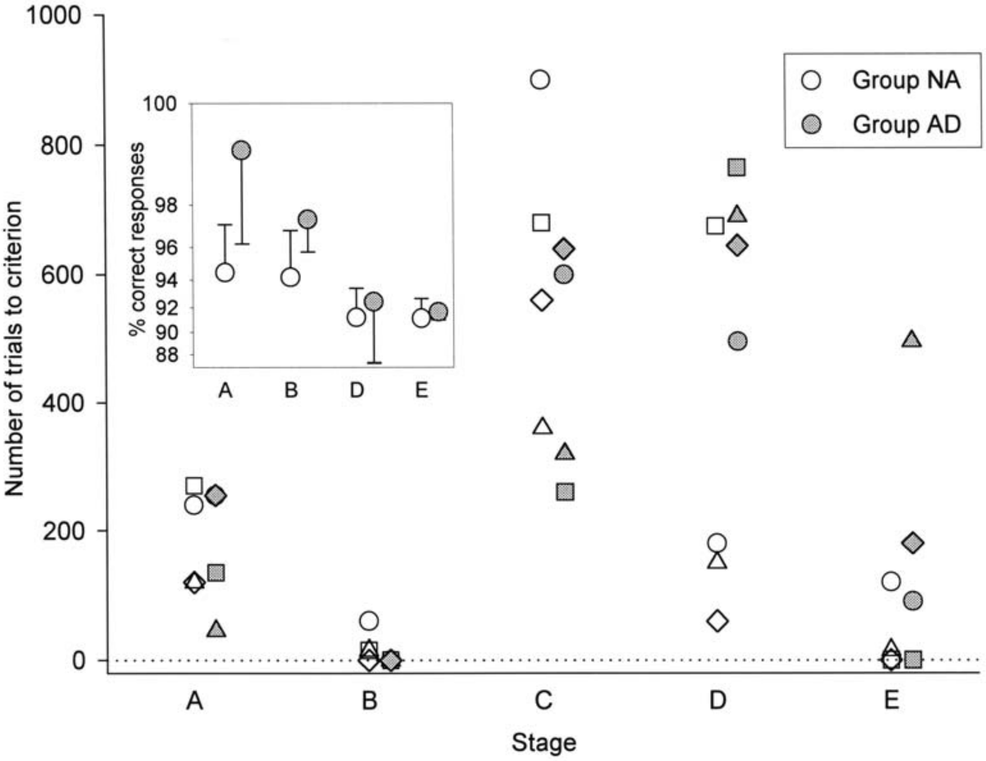

Fig. 2. Number of trials to criterion and performance level (inset) at various stages of the experiment for dogs trained with non-adjacent (NA, white symbols) and adjacent (AD, grey symbols) side speakers. Different symbols on the main plot indicate data from individual animals. Error bars show SDs. The non-linear vertical axis in the inset reflects arcsine transformation applied to data.

tional responses (stages A and B). Performance level in criterion trials was higher in group AD ($F_{1,6}$=6.01, P=0.05), supporting the hypothesis of an advantage of stimulus-response adjacency. Though the group x stage interaction fell short of significance ($F_{3,18}$=2.66, P=0.08), the detailed *post-hoc* analyses showed that in criterion trials of the directional response task group AD reached higher performance levels than in criterion trials of the DMS task, as well as higher performance than group NA in either task.

Performance with extended delays is shown in Fig. 3. A significant effect of delay was found ($F_{3,18}$=17.3, P<0.00002), indicating memory decay over increasing delays. The performance level was better in S trials than in N trials ($F_{1,6}$=13.5, P=0.01), reflecting the dogs' tendency to respond to the first stimulus presented from a side speaker. The effect of group on the performance level was close to significance ($F_{1,6}$=5.91, P=0.051): group AD appeared to perform slightly worse than group NA.

Results of the analyses of the dynamics of learning in stages C and D are shown in Fig. 4. In stage C, the performance level was higher in go trials than in no-go trials ($F_{1,5}$=114.9, P<0.0002). The performance level improved across fifths ($F_{4,\ 20}$=5.96, P<0.003, linear trend across fifths: $F_{1,5}$=14.79, P=0.012). Although the fifth x trial type interaction was not significant, it is noteworthy, that the linear trend across fifths was significant for no-go trials ($F_{1,5}$=13.39, P=0.015), but not for go trials ($F_{1,5}$=2.50, P=0.17), showing that the performance improved particularly in no-go trials. No significant effect related to experimental group was detected.

In contrast to our previous study, the difference in median latencies between go and no-go trials did not reach significance ($F_{1,5}$=4.74, P=0.081, in Kuśmierek and Kowalska 1998: $F_{1,8}$=6.53, P=0.034). As shown by a significant group x trial type interaction ($F_{1,5}$=8.26, P=0.035), the difference was caused by delaying of responses in group NA (P=0.018), but not in group AD (P=0.65). Consequently, median latencies in go trials did not differ between the groups (P=0.89), whereas median latencies in no-go trials were shorter in group AD than in group NA (P=0.014). It appears that response inhibition in no-go trials during course of the

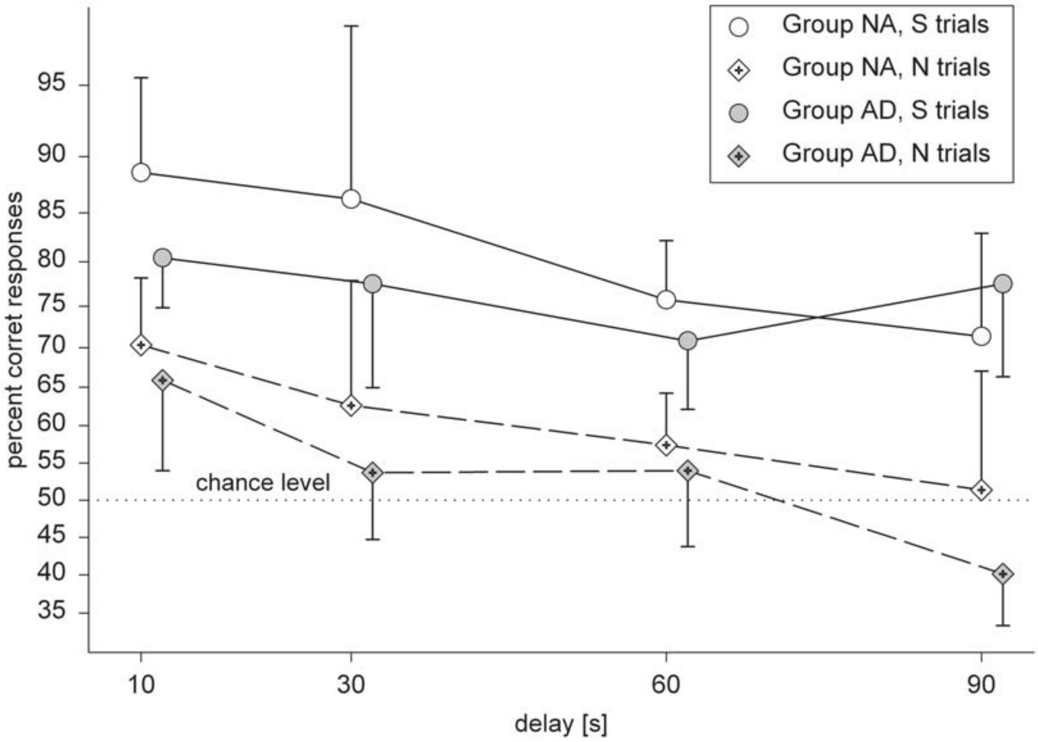

Fig. 3. Average performance level with extended delays (stage F) for dogs trained with non-adjacent (NA, white symbols) and adjacent (AD, grey symbols) side speakers. Circles show performance in S trials, squares, performance in N trials. Error bars show SDs. The non-linear vertical axis reflects arcsine transformation applied to data.

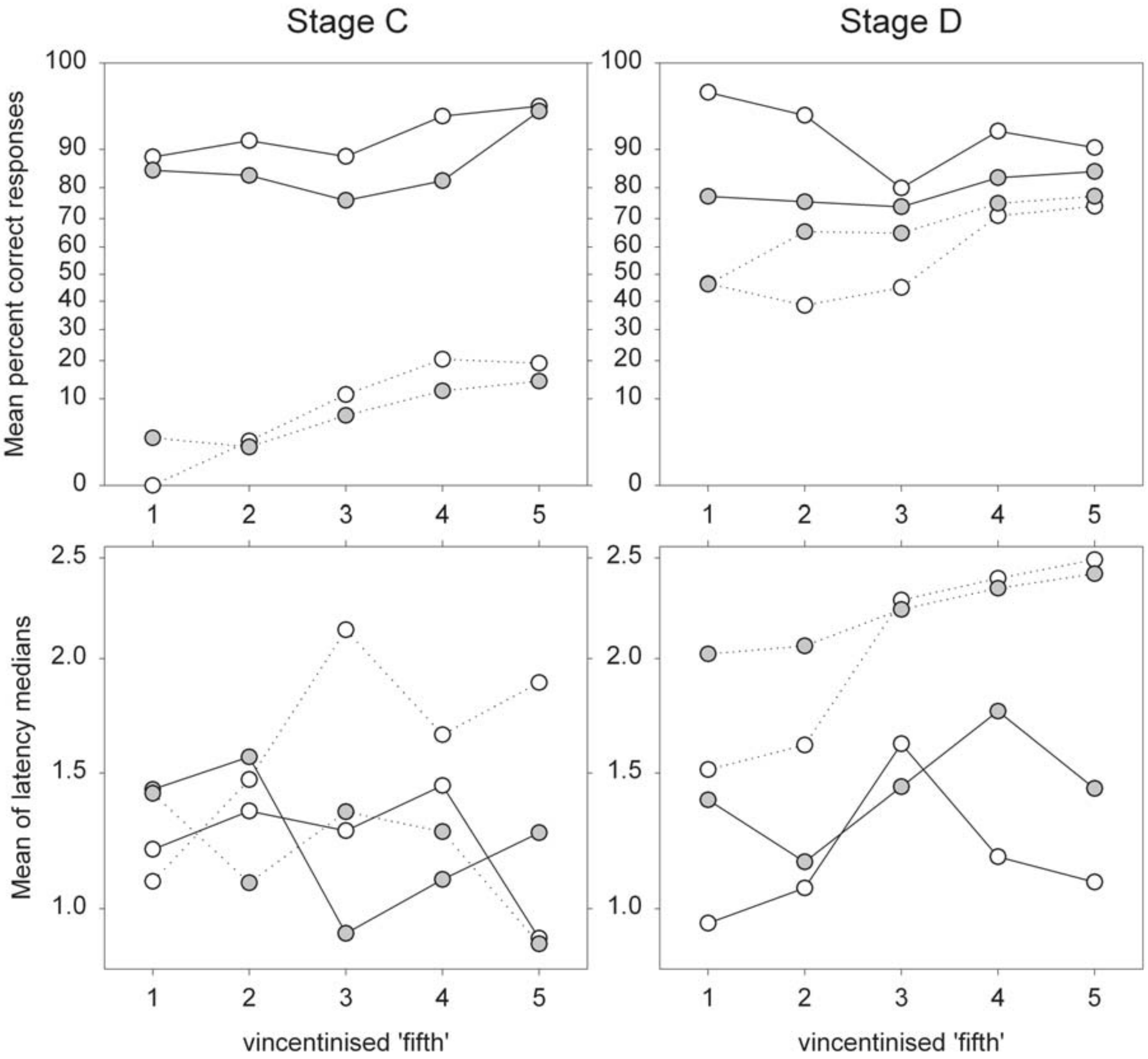

Fig. 4. Analysis of acquisition of stages C (modified Konorski's task, left panels) and D (delayed matching-to-sample, right panels) analysed with vincentinising method for dogs trained with non-adjacent (NA, white symbols) and adjacent (AD, grey symbols) side speakers. Upper panels, mean performance level, lower panels, average latency medians. Solid lines indicate go (Konorski's task) or S (DMS) trials, dotted lines indicate no-go (Konorski's task) or N (DMS) trials. The non-linear vertical axes reflect arcsine or square root transformations applied to data.

stage was limited to group NA. Although learning rate in stage C was not directly affected, the underlying behavioural mechanisms could differ for each group.

In stage D, the performance level was higher in S trials than in N trials ($F_{1,6}$=13.47, P=0.01) and showed overall improvement throughout the stage ($F_{4,24}$=5.55, P<0.003, linear trend: $F_{1,6}$=15.76, P=0.0074). This improvement arose from better performance in N trials (linear trend $F_{1,6}$=15,29, P=0.008), rather than in S trials ($F_{1,6}$=0.304, P=0.6). There was also a significant difference in median latencies between S and N trials ($F_{1,6}$=175.6, P=0.00011). However, no effect of experimental group was found in analysis of dynamics of learning in stage D.

Analysis of response latency distribution in stages A and B revealed that incorrect responses were performed with longer latencies than correct responses ($F_{1,5}$=7.79, P<0.04). More long-latency responses occurred in group NA (group x percentile interaction $F_{4,20}$=3.50, P=0.025). A significant group x stage x correctness x percentile interaction ($F_{4,20}$=3.43, P=0.027) indicated that in group AD (unlike in group NA), incorrect responses were performed with very short latencies, as well as that in group NA, latencies were less scattered at the end of stage B than in the beginning of the stage. We cannot state, however, that the latter effect was specific to group NA. All dogs in group AD reached the criterion of the stage immediately. Therefore, the first blocks of the stage and the last block of the stage overlapped so that changes of latencies in the stage could not be detected.

Before and after the control pause, incorrect responses were made with longer latencies than correct responses ($F_{1,5}$=6.99, P=0.046). In group NA more long-response latencies occurred, particularly before the pause (group x stage x percentile interaction: $F_{4,20}$=4.02, P=0.015).

Examination of response latency distributions in stages E and F has also shown that incorrect responses were made with longer latencies than correct responses ($F_{1,6}$=28.54, P=0.0018). This difference depended on delay (block x correctness interaction: $F_{4,24}$=4.52, P=0.0073), being very significant in stage E (delay 1.5 s, P=0.00003), significant at delays 10 and 60 s (*Ps*=0.041 and 0.017, respectively), and not significant at 30 and 90 s (*Ps*=0.12 and 0.38, respectively). It appeared that latencies of correct responses increased monotonically across delays (linear trend $F_{1,6}$=14.72, P=0.0086), whereas latencies of incorrect responses, which were quite long at 1.5-s delay, decreased across 10 and 30-s delay blocks and then increased across 60 and 90-s delay blocks. However, in general, latencies increased across delays ($F_{4,24}$=5.84, P=0.0068, linear trend: $F_{1,6}$=12.07, P<0.014).

Results of spectral analyses of white noise emitted through each kind of speaker are shown on Fig. 5. Apparently, different acoustic configurations did influence sound spectra. The speakers used for NA group reproduced frequencies below about 1 kHz with low efficiency, probably due to cancelling out of sound waves produced by back and front of the membrane, which were in opposite phases. Obviously, such an effect was not present in group AD speakers, because the rear side of the membrane was isolated from the environment by the enclosure. On the other hand, these speakers reproduced frequencies between about 1.8 kHz and 4 kHz with relatively low efficiency. It is possible that this was caused by the perforated plate, which served as a

Fig. 5. 1/3-octave spectra of white noise stimulus played and recorded in Setting 1 (Kuśmierek and Kowalska 1998), and with nonadjacent (NA) and adjacent ((AD) speakers). The recordings have been normalised to equal overall intensity.

speaker grille. The correlation coefficient between spectra produced by NA and AD speakers was 0.61, whereas between AD and Setting 1 speakers it was 0.78, and between NA and Setting 1 speakers it was 0.81. The spectral variation measure was 0.075 for AD speakers, 0.055 for NA speakers, and 0.051 for Setting 1 speakers.

DISCUSSION

In accord with Harrison's findings (Harrison 1992), placing the loudspeakers closer to the manipulanda was beneficial at the very beginning of the experiment, when simple auditory directional responses were trained. Though no significant reduction in number of trials to criterion was achieved, the dogs from group AD reached higher performance levels than those from group NA in stages A and B. Moreover, the immediate acquisition of criterion at stage B by all dogs of group AD further supports the hypothesis. It is also backed indirectly by the occurrence of more long-latency responses in group NA than in group AD, suggesting that choice of the proper response was more difficult in group NA.

On the other hand, placing the loudspeakers adjacent to the manipulanda did not improve learning or performance on recognition (modified Konorski's or DMS) tasks. Rather, attaining the DMS criterion took more trials, and the performance level with extended delays was worse in group AD than in group NA. These results indicate that the modification of the experimental setting, which was expected to improve learning, actually impaired learning and performance of the DMS task. In particular, poorer results achieved in the performance task with extended delays argue against placing side speakers close to manipulanda in studies on auditory memory. This unexpected finding deserves some attention. Three possible causes will be discussed.

First, aiming side speakers almost directly towards the dog's ears in group NA could have made the stimuli more salient than in group AD, which received stimuli from loudspeakers located near the paws, resulting in better learning and performance on the DMS task in group NA. Events that occur in close vicinity to the head are obviously of special importance as they may signal an immediate threat. In monkeys, the ventral premotor cortex contains neurones that respond to acoustic stimuli that originate in that space, but not further from the head. These neurones are often trimodal, i.e., they respond also to visual stimuli that originate from the approximately same place and to tactile stimuli applied to respective parts of the head (Graziano et al. 1999). Apparently, the stimuli that originate in the peri-head space are processed in a specialised manner by the brain. Though no evidence exists for such a specific region in the canine brain, it is reasonable to believe that sounds whose sources are located close to the head, are also processed in a specialised manner by the dog's nervous system, and that their salience is high. Such specialised processing could be responsible for different results obtained with loudspeakers located in different positions. However, greater salience of sound stimuli in group NA should cause better learning and/or performance on directional responses tasks (stages A and B). Such a prediction is contradicted by our findings. It may be concluded that even if the stimulus salience was somewhat higher in group NA, it cannot fully account for our results.

The loudspeakers used for the experimental groups were of different brands (though approximately similar in size and general quality). More importantly, the speakers were operating in different acoustic conditions (open-back in group NA and sealed enclosures in group AD). Therefore, the acoustic signal could be modified by the loudspeakers, and some stimulus features, which are important either for sound localisation or for discrimination, could be lost or diminished in group AD. Spectral analyses of white noise emitted through each speaker revealed considerable differences in sound spectra due to speaker differences. It is unlikely, however, that enhancement of the low frequency band and the trough around 3 kHz in group AD's speakers impaired recognition performance due to reduced localizability of the stimuli. First, it is doubtful that such an easy task as left/right discrimination could be impaired due to this variation in the sound spectrum. Left/right discrimination can be performed accurately even if pure tones are used as stimuli. Though systematic studies on localizability of pure tones of various frequencies by dogs are lacking, such ability has been shown in other carnivores, such as the cat and the least weasel (Heffner and Heffner 1987, Martin and Webster 1987, Rauschecker and Kniepert 1993). Also, pure tones have been successfully used as stimuli for various location discriminations tasks in dogs (e.g., Ławicka 1969, Szwejkowska and Sychowa 1971, Stępień et al. 1990). Therefore, wide-frequency-range cues are by no means necessary for sound localisation in dogs, and the irregularities of speaker spectral characteristics in our experiments should not impair stimulus localisation.

More importantly, reduced localizability of stimuli in group AD would impair learning and performance of directional response tasks (stages A and B), contrary to the actual results.

The different sound spectrum produced by group AD speakers could selectively impair performance of the recognition tasks due to reduced discriminability of stimuli. Proper stimulus quality discrimination is essential for correct recognition performance, but not for performance on directional response tasks. Consequently, reduced discriminability could contribute to recognition impairment in group AD. Results of the acoustic measurements show that speakers used for group AD produced the most variable spectrum, and they differed from Setting 1 speakers and particularly from NA speakers with respect to spectral shape (as indicated by correlation coefficients). Therefore, we cannot exclude reduced discriminability of the stimuli due to loudspeaker properties as a cause of the poorer learning and performance of the DMS task in group AD. On the other hand, several facts argue against this. If the spectral shape difference was responsible for differences in learning and performance of recognition tasks, then, given results obtained by the three groups, the spectral shape produced by NA speakers should lie in-between the shapes produced by Setting 1 speakers (best behavioural results) and AD speakers (worst behavioural results). Or at least the spectrum produced in Setting 1 should be similar to that produced by NA speakers (similar performance level with extended delays) and should differ from that produced by AD speakers (worse performance level with extended delays). However, according to the correlation coefficients and to visual inspection, the spectral shape produced by Setting 1 speakers fell in-between the two other spectral shapes. Secondly, despite the considerable trough around 3 kHz in the AD speakers' spectrum, within the dog's best sensitivity range (4-16 kHz, Heffner 1983) all three spectra are very similar. Next, the stimuli used in the study were complex natural sounds and therefore many differentiating features were provided, some of them being completely independent of spectral variation due to speaker properties. Even if we consider spectral shape as a feature that differentiates two given stimuli, then their spectra would be modified in the same manner by the loudspeaker, thus leaving the relative inter-stimulus difference unchanged. Finally, and most importantly, the stimuli were easily discriminable by the human listener when they were played through any of the speakers.

The factors described above, that is, stimulus salience related to speaker-ear distance and acoustical factors, were not related to Harrison's findings, which emphasise adjacency of speaker and response as a naturalistic feature. A new sound in a friendly environment evokes orienting and exploratory responses, which, when rewarded, can be easily transformed into instrumental responses. If the acoustic signal is distant from the response site, then such orienting and exploratory responses direct the animal's activity away from the response site, thus hindering learning of simple auditory behavioural tasks (Grastyán and Vereczkei 1974, Harrison 1992).

In our experiment, placing the loudspeakers close to the response site facilitated learning of simple directional responses in group AD, probably because the orienting response and the required instrumental response were spatially congruent. The proper instrumental response could have been chosen solely on the basis of the orienting response. As a result, a stronger association of orienting response and instrumental response could develop in this group. Such a strong association is obviously helpful for a task which requires little inhibition of responses and which requires instrumental responses that can be determined exclusively on the basis of the orienting response, such as the directional response task. However, the recognition tasks differ from the directional response task in both aspects. Correct instrumental responses cannot be chosen solely on the basis of the orienting response because stimulus quality is as important as stimulus location. Consequently, instrumental responses to some stimuli must be inhibited.

In stage C, inhibition of the instrumental response was the correct behaviour in no-go trials. Though it was not rewarded directly, there was some indirect reinforcement. Each response has energy costs, and so withholding non-rewarded responses in no-go trials spares this energy. That energy cost is a factor in learning stage C was shown in our previous experiment: criterion in this stage was attained more quickly in an approach task (i.e., more energy consuming) than in a bar-press task (less energy consuming) (Kuśmierek and Kowalska 1998). In stages D, E, and F, inhibition of responses towards the novel stimulus is required, particularly in N trials, i.e., when the novel stimulus is presented as the first one from a side speaker. The tendency to respond towards the first stimulus was present during the entire experiment, as shown by better performance throughout in S trials than in N trials (Fig. 3).

Therefore, the strong association of orienting response and instrumental responses that was probably developed in group AD during training of stages A and B could then impair inhibition of responses to no-go and novel stimuli, and consequently learning and performance on the recognition tasks. In stage C, the vincentinising method revealed that response inhibition in no-go trials developed in a different manner in the two groups. In group NA, it was detected in the course of stage C, whereas in group AD it was not visible even in the final fifth. It was also detected in the previously reported experiment, which included dogs trained in the approach situation (Setting 1) (Kuśmierek and Kowalska 1998). Taken together, group NA dogs and Setting 1 dogs, which learned the DMS task relatively quickly and performed well with the extended delays, displayed a weak but detectable tendency to inhibit responses in no-go trials in the course of stage C. The opposite findings in group AD suggest that their poorer learning and performance on the recognition tasks may be related to impairment of inhibition. The stronger orienting response-instrumental response association in group AD is further suggested by the analysis of response latency distributions. In stages A and B, as well as at the end of stage D and at the beginning of stage E, more long-latency responses occurred in group NA than in group AD. This indicates that responses in group AD were fast and unhesitant, possibly because they were directed by the orienting responses, while group NA experienced greater difficulty in the choice of the correct directional response.

On the other hand, two effects should have been detected if the stronger orienting response-instrumental response association existed in group AD. First, response latency distributions should differ between the groups in stage F, as in the previous stages. Second, the tendency to respond to the first stimulus from a side speaker in the DMS task should be stronger in group AD than in group NA, yielding a significant group x trial type interaction in analysis of performance in stage F. However, neither effect was found.

This experiment has demonstrated that modification of the experimental setting, which was expected to improve learning and performance of delayed matching-to-sample in dogs, yielded equivocal findings. Though training of early directional response stages was facilitated, learning and performance of the complex auditory memory task was actually disturbed. Although we cannot be certain of the explanation, it seems that the factor that led to more rapid learning in Setting 1 than in Setting 2 (Kuśmierek and Kowalska 1998) was the difference in type of response (approach vs. bar-press) rather than in the degree of stimulus-response proximity.

The DMS task is a complex one, and many behavioural, cognitive, and perceptual factors are involved, such as response inhibition, trial-unique stimuli, memory, or the abstract concept of "same/different" (Wright at al. 1990). Our present data suggest that stimulus-response adjacency, though it facilitates training on simpler tasks, may not be critical for learning and performance of the DMS task. In designing such tasks, the principles found to be crucial for simple tasks may be of less importance. Many factors must be carefully controlled in order to obtain successful learning and reliable performance (e.g., Kowalska et al. 1999).

CONCLUSIONS

Stimulus-response adjacency contributed to efficient training of a simple auditory directional task. However, it had an adverse effect on learning and performance of a complex auditory memory task, namely delayed matching-to-sample with trial-unique stimuli.

ACKNOWLEDGEMENTS

Preliminary results were presented at the Forum of European Neuroscience, Berlin, 1998. The authors are grateful to Dr. Mortimer Mishkin for valuable comments on the manuscript and to Joanna Sadowska for training the animals. Supported by JSMF grant No. 95-13.

REFERENCES

Colombo M. and D'Amato M. R. (1986) A comparison of visual and auditory short-term memory in monkeys (*Cebus apella*). Q. J. Exp. Psychol. B. 38: 425-448.

Cowey A. and Weiskrantz L. (1976) Auditory sequence discrimination in *Macaca mulatta*: the role of the superior temporal cortex. Neuropsychologia 14: 1-10.

Grastyán E., Vereczkei L. (1974) Effects of spatial separation of the conditioned signal from the reinforcement: a demonstration of the conditioned character of the orienting response or the orientational character of conditioning. Behav. Biol. 10: 121-146.

Graziano M.S., Reiss L.A., Gross C.G. (1999) A neuronal representation of the location of nearby sounds. Nature 397: 428-430.

Harrison J.M. (1992) Avoiding conflicts between the natural behavior of the animal and the demands of discrimination experiments. J. Acoust. Soc. Am. 92: 1331-1345.

Harrison J.M., Iversen, S.D. Pratt S.R. (1977) Control of responding by location of auditory stimuli: adjacency of sound and response. J. Exp. Anal. Behav. 28: 243-251.

Heffner H.E. (1983) Hearing in large and small dogs: absolute thresholds and size of the tympanic membrane. Behav. Neurosci. 97: 310-318.

Heffner R.S., Heffner H.E. (1987) Localization of noise, use of binaural cues, and a description of the superior olivary complex in the smallest carnivore, the least weasel (*Mustela nivalis*). Behav. Neurosci. 101: 701-708.

Hilgard E.R. (1938) A summary and evaluation of alternative procedures for the construction of Vincent curves. Psychol. Bull. 35: 282-297.

Kojima S. (1985) Auditory short-term memory in the Japanese monkey. Int. J. Neurosci. 25: 255-262.

Konorski J. (1959) A new method of physiological investigation of recent memory in animals. Bull. Acad. Pol. Sci. Biol. 7: 115-119.

Kowalska D.M. (1997) The method of training dogs in auditory recognition memory tasks with trial-unique stimuli. Acta Neurobiol. Exp. 57: 345-352.

Kowalska D. M., Kuśmierek P., Kosmal A. (1998) The effects of auditory association areas lesions on the sound recognition memory in dogs. Soc. Neurosci. Abstr. 24: 1305.

Kowalska D. M., Kuśmierek P., Mishkin M. (1999) Comparison of learning and performance of an auditory Delayed Matching-to-Sample in monkeys and dogs. Neural Plast., (Suppl.) 99: 113.

Kowalska D. M., Kuśmierek P., Kosmal P., Mishkin M. (2001) Neither perirhinal/entorhinal nor hippocampal lesions impair short-term auditory recognition memory in dogs. Neuroscience 104: 965-978

Kuśmierek P., Kowalska D.M. (1998). Effect of experimental setting on learning and performance of Auditory Delayed Matching-to-Sample in dogs. Acta Nerobiol. Exp. 58: 291-307.

Ławicka W. (1969) Differing effectiveness of auditory quality and location cues in two forms of differentiation learning. Acta Biol. Exp. 29: 83-92.

Martin R.L., Webster, W.R. (1987) The auditory spatial acuity of the domestic cat in the interaural horizontal and median verical planes. Hear. Res. 30: 239-252.

Meunier M., Bachevalier J., Mishkin M., Murray E. A. (1993) Effects on visual recognition of combined and separate ablations of the entorhinal and perirhinal cortex in rhesus monkeys. J. Neurosci. 13: 5418-5432.

Otto T., Eichenbaum H. (1992) Complementary roles of the orbital prefrontal cortex and the perirhinal-entorhinal cortices in odor-guided delayed-nonmatching-to-sample task. Behav. Neurosci. 106: 762-775.

Rauschecker J.P., Kniepert U. (1993) Auditory localization behaviour in visually deprived cats. Eur. J. Neurosci. 6: 149-160.

Ringo J.L. (1991) Memory decays at the same rate in macaques with and without brain lesions when expressed in d' or arcsine terms. Behav. Brain Res. 42: 123-134.

Stępień I., Stępień L., Łubińska E. (1990) Function of dog's auditory cortex in tests involving auditory location cues and directional instrumental response. Acta Neurobiol. Exp. 50: 1-12.

Stępień L. S., Cordeau J. P., Rasmussen T. (1960) The effect of temporal lobe and hippocampal lesions on auditory and visual recent memory in monkeys. Brain 83: 470-489.

Suzuki W. A., Zola-Morgan S., Squire L. R., Amaral D. G. (1993) Lesions of the perirhinal and parahippocampal cortices in the monkey produce long-lasting memory impairment in the visual and tactual modalities. J. Neurosci. 13: 2430-2451.

Szwejkowska G., Sychowa B. (1971) The effects of lesions of auditory cortex on discrimination of sound localization in dogs. Acta Neurobiol. Exp. 31: 237-250.

Wright A. A., Shyan M. R., Jitsumori M. (1990) Auditory same/different concept learning by monkeys. Anim. Learn. Behav. 18: 287-294.

Received 29 August 2002, accepted 14 November 2002