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Performance of Mice in Discrimination of Liquor Odors: Behavioral Evidence for Olfactory Attention

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Abstract

We examined performance of mice in discrimination of liquor odors by Y-maze behavioral assays. Thirsty mice were initially trained to choose the odor of a red wine in the Y-maze. After successful training (>70% concordance for each trained mouse), the individual mice were able to discriminate the learned red wine from other liquors, including white wine, rosé wine, sake, and plum liqueur. However, when the mice were tested to distinguish fine differences between 2 brands of red wine, their performance significantly varied among the individual trained mice. Among 10 mice tested, 2 mice were able to discriminate between the red wines (>75% concordance) whereas 6 mice failed to distinguish between them (50–67% concordance, where chance could be assumed to be 50%). More importantly, 2 other mice exhibited lower than 30% concordance, indicating that they were more attracted to the nonrewarded red wine compared with the learned one. This result suggested that the individual mice directed attention to different subsets of volatile components emanating from the rewarded red wine, when they were trained to choose the liquor odor in the Y-maze. Selective attention of mice was also observed in Y-maze behavioral assays using the mixtures of 3 or less pure odorants. Additionally, we also observed that the olfactory attention of mice could be modified through their learning experiences.

Key words: attention, liquor, mice, odor discrimination, Y-maze assay

Introduction

Attention can be defined as the selective aspect of perception and response (Treisman 1969). Selective attention is used to filter out irrelevant information, allowing cognitive processing resources and behavioral outputs to be concentrated on a small number of relevant sources of information (Luck 1998). Much has been learned in recent years about how attention influences the neuronal representation of visual and auditory stimuli. Boynton (2005) has recently proposed a simple computational model to provide a framework for predicting a variety of neurophysiological, neuroimaging, and behavioral studies of visual attention. Kayser et al. (2005) have also developed a saliency map model for the auditory system and demonstrated that it could serve as a conceptual basis for comparing the principles underlying auditory attention.

As rodents preferentially attend to olfactory cues, olfactory working memory provides a simple facet of cognition to assess (Roman et al. 2002). Turchi and Sarter (2000) have assessed the role of the basal forebrain cholinergic system in the olfactory working memory capacity in rats using an olfactory span task. Young et al. (2007) have also proposed an odor span task as a novel paradigm for assessing working memory in mice. They have reported that the mouse odor span task can detect subtle changes in olfactory working memory and that a olfactory working memory deficit can be reversed by acute nicotine administration at a dose previously shown to enhance attention in mice (Young et al. 2004).

Most naturally occurring odors are complex blends of volatile compounds. The way in which they are perceived depends upon the interactions between mixture components at the level of olfactory receptors (Derby 2000) as well as the way that component signals are processed in the olfactory bulb and olfactory cortex (Wilson and Stevenson 2003;

Tabor et al. 2004). Because most of these inputs are irrelevant at any given moment, it should be more efficient to focus neural resources on a subset of the available information and ignore the rest (Luck 1998). However, to our knowledge, few papers have reported experimental evidence for selective attention in odor discrimination. In the present paper, we report behavioral evidence for selective attention in odor discrimination of mice. We found this evidence in the course of behavioral studies on the discrimination of liquor odors in mice using a Y-maze. Our initial interest was to assess if mice could discriminate different brands of liquors just by taking a sniff of them like an expert flavorist. Additionally, we also demonstrate that selective attention in the olfactory system of mice could be modified through their learning experiences.

Materials and methods

Animals

A total of 30 male C57BL/6J mice were used in this study. The mice were approximately 8 weeks of age at the beginning of the experiment. They were maintained on a 12-h light: dark cycle in an animal facility where both temperature and humidity were controlled. Behavioral training and testing were conducted during the light phase of the 12-h cycle. Before the start of behavioral training, mice were provided with continuous food and water. Mice were treated in accordance with the guiding principles for the care and use of animals for scientific purposes in Hiroshima University.

Liquors and pure odorants

The liquors used in the present study were 3 red wines, Bon Rouge (referred to here as red wine A; Mercian Co., Tokyo, Japan), Bistro Red (red wine B; Mercian Co.), and Beaujolais Villages (red wine C; Manoir du Pave, Saint-Lager, France); 2 white wines, Bon Blanc (white wine A; Mercian Co.), and Bistro White (white wine B; Mercian Co.); 1 rosé wine, Bistro Rosé (Mercian Co.); 1 Japanese sake, Josensyu (Kamotsuru Shuzo Co., Hiroshima, Japan); and 1 plum liqueur, Umesyu (Choya Co., Osaka, Japan). The pure odorants used were isoamyl acetate (referred to as IA), citral (Ci), ethyl butyrate (EB), linalool (Li), L-carvone (Car), (R)-(+)-limonene (Lim), ethyl valerate (EV), geraniol (Ger), and methyl caproate (MC). Most of the chemical compounds are known to be involved in a variety of liquors. The pure odorants were purchased from either Sigma-Aldrich (Tokyo, Japan) or Nacalai Tesque Inc. (Kyoto, Japan). For Y-maze behavioral assays, pure odorants were appropriately diluted (typically 5% v/v) with odorless mineral oil.

Gas chromatography

Chemical analysis of liquors was carried out on a Shimadzu GC-2010 series gas chromatograph with electronic pressure control. The gas chromatograph was fitted with an Innowax column (60 m × 0.53 mm × 1 μm; Agilent Technologies, Tokyo, Japan). Samples were analyzed by the direct injection method (Peinado et al. 2004). After injection, the column temperature was maintained at 35 °C for 10 min and then linearly increased at a rate of 3 °C/min up to 215 °C. The carrier gas used was helium at 90 kPa. Compounds emerging from the column were detected by a flame ionization detector at 300 °C. Representative peaks were identified using the database of volatile compounds in wines (Mercian Co.).

Y-maze behavioral assay

The Y-maze was constructed as described previously (Yamaguchi et al. 1981; Yamazaki et al. 1999). The Y-maze used in this study was made of acrylic plastics. Two arms of the maze were scented by air currents conducted through the left and right odor boxes. Each of the odor boxes had a lid to admit a 5.5-cm petri dish or a 1.5-ml microcentrifuge tube containing an odor source. Each mouse was individually allowed to run along the 350-mm-long maze from the starting compartment and choose one arm scented by the odor concordant with its training. The time taken for the trained mice to make a choice was 2 or 3 s. The time interval in the starting compartment was set at 15 s to allow for changing the petri dishes or microcentrifuge tubes in the odor boxes. Left–right placing was decided by a series of random numbers. The water bottle in each arm was also replaced randomly. Other blind tests were conducted to avoid unintentionally prompt the trained mice.

Behavioral training and testing procedures

A total of 30 mice were randomly divided into 3 groups (referred to as group A, B, and C). Each mouse was individually subjected to 24 consecutive trials in one session. The trainee mice had been deprived of water for 23 h prior to the training and testing. The reward for concordant choice was a drop (ca. 20 μl) of water that was supplied from a bottle placed at the end of each arm. The water bottles were placed at the end of each arm and randomly alternated to prevent the individual mice from using a cue from an odor of water. If the choice was discordant, the mouse was immediately returned to the starting compartment without giving access to the drop of water. If the choice was correct, the mouse was allowed to drink a drop of water as a reward. Ten mice of group A were trained to discriminate red wine A. Ten mice of group B were trained with IA, whereas 10 other mice of group C were trained with the ternary mixture of 5% (v/v) each of IA, Li, and Ci. Percent concordance was calculated from the number of concordant responses in 24 consecutive trials in one session. Even chance level could be assumed to be 50% concordance. When a concordance score of greater than 70% was obtained, we decided that the mouse could discriminate an odor from the other. The chi-square test showed that this level of percentage concordance was significantly different from even chance level ($P < 0.05$) (Daniel 1987). The overall concordance score was calculated as the mean of concordance scores of 10 individual mice. Student's *t*-test was used to determine the 95% confidence interval of the overall concordance score.

Results

Liquor odor discrimination by mice

To assess if mice can discriminate liquor odors, we first trained mice using operant conditioning in the Y-maze. Ten mice of group A were individually trained to discriminate red wine A from distilled water. The discrimination training in 5 sessions allowed the individual mice to exhibit greater than 70% concordance. After then, the overall concordance gradually increased up to 89.2 ± 4.7% (mean ± 95% confidence interval, *n* = 10). The trained mice were then tested for their ability to discriminate the learned red wine A from other liquors, including sake, plum liqueur, white wine A, white wine B, rosé wine, and red wine B (Figure 1). The trained individual mice showed greater than 70% overall concordance for all the liquors tested. Interestingly, however, they failed to discriminate the learned red wine A from red wine C (the overall concordance = 55.8 ± 12.8). Gas chromatography analysis revealed that the pattern of volatile compounds in the learned red wine A was essentially similar to that of red wine C (Figure 2). By visual inspection, only peaks 6, 7, 9, 11, and 12 which corresponded to ethyl hexanoate, ethyl lactate, an unknown compound, decanoic acid, and dimethyl phthalate, respectively, were significantly different between red wines of A and C. By contrast, the peak intensity pattern of red wine B was considerably different from red wines A

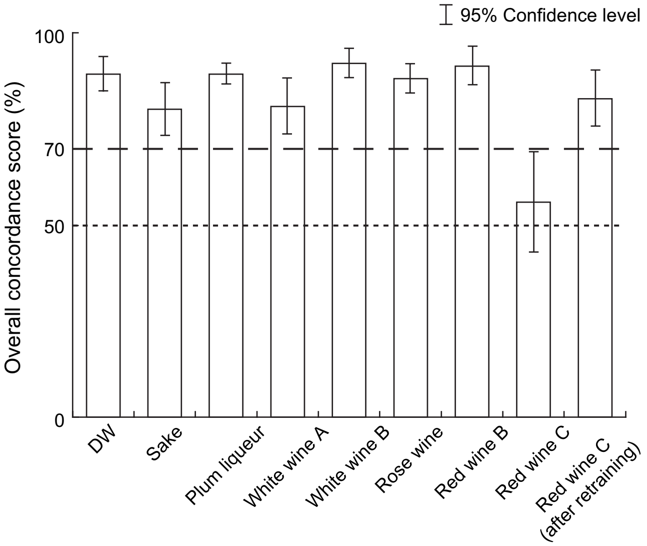

Figure 1 Behavioral discrimination of liquor odors in mice. Ten mice were individually trained to discriminate red wine A from distilled water (DW) in a Y-maze. After successful training (>70% concordance for each mouse), the individual mice were examined for their ability to discriminate the learned red wine A from other liquors, including Japanese sake, plum liqueur, white wine A, white wine B, rosé wine, red wine B, and red wine C. Percent concordance was calculated from the number of concordance responses in 24 consecutive trials in one session. The overall concordance score (mean ± 95% confident level) was calculated from the concordance scores obtained with the 10 individual mice. When the overall concordance score was greater than 70% (broken line), we decided that the trained mice were able to discriminate an odor from the other. Even chance level was assumed to be 50% (dotted line). The individual mice, which had been trained to discriminate between red wine A and DW, readily discriminated the learned red wine A from the liquors except red wine C (>70% overall concordance). The mice failed to discriminate between red wines A and C (overall concordance = 55.8 ± 12.8). However, after 5 retraining sessions, the mice could distinguish the red wine A from red wine C.

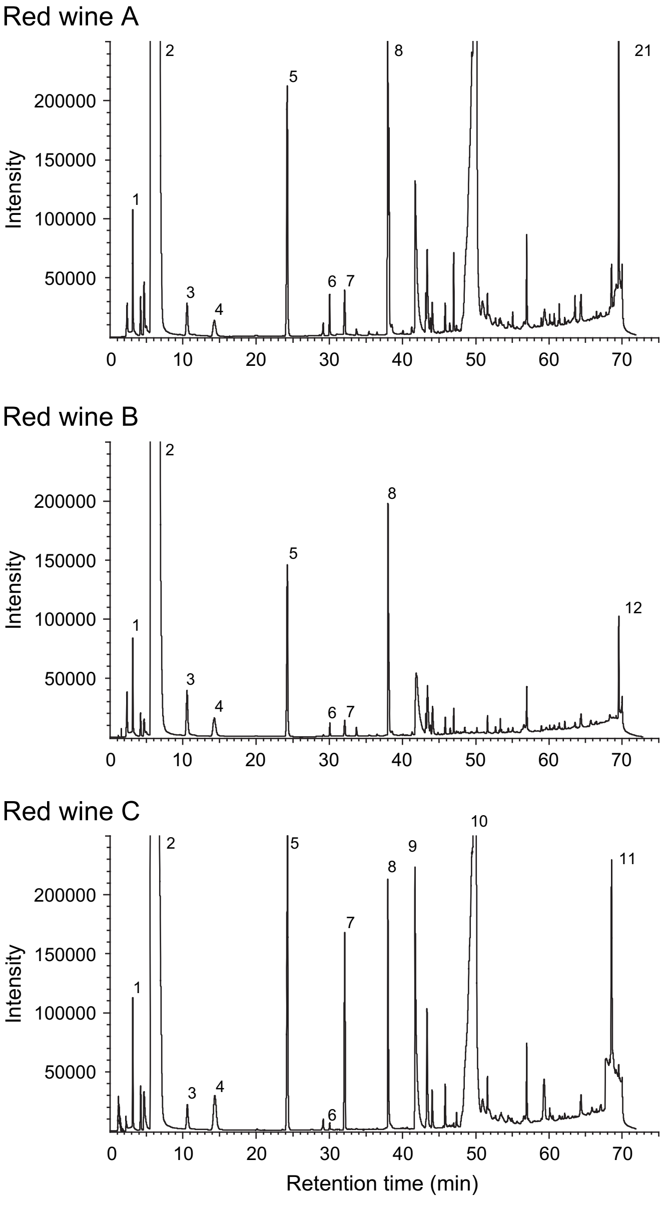

Figure 2 Chromatograms for red wines A, B, and C. Representative peaks were identified using the database of volatile compounds in wines (Mercian Co.). Peak 1, ethyl acetate; 2, ethanol; 3, 2-methyl propano1; 4, IA; 5, isoamyl alcohol; 6, ethyl hexanoate; 7, ethyl lactate; 8, ethyl octanoate, 9, unknown; 10, ethyl decanoate; 11, decanoic acid; 12, dimethyl phthalate.

and C. Particularly, the difference was distinct for the peaks that appeared at retention times of 40–55 min.

More interestingly, the discriminability of red wines A and C significantly varied among the individual trained mice (Table 1). Among 10 mice tested, 2 mice scored greater than 70% concordance. Six mice showed 50–67% concordance, indicating that they failed to distinguish between red wines A and C. More importantly, 2 other mice showed less than 30% concordance. Obviously, these mice were more attracted to the unrewarded red wine C compared with the learned red wine A. This difference in discriminability among the individual trained mice was surprising, considering that all the mice could readily discriminate the learned wine A from red wine B. To investigate if the ability of mice to distinguish the 2 red wines cosuld be improved by training, the mice were retrained to discriminate the rewarded red wine A from the unrewarded red wine C. Namely, red wines A and C were placed in either the left or right odor boxes. If individual mice chose the arm scented by the odor emanating from red wine A, they were allowed to drink a drop of water. After 5 learning sessions, nearly all the trained mice were able to distinguish the fine diff erence between red wines A and C (Table 1).

Concentration effects on odor discrimination

To assess if mice can discriminate concentration differences of the learned liquor odor, 10 mice of group A were individually subjected to odor discrimination tests using whole and diluted red wine A samples. As can be seen in Figure 3, the mice could easily discriminate the learned red wine A (referred to here as 100% red wine A) from lower than 75% red wine A (wine:water = 3:1). However, the overall concordance significantly declined for 80% red wine A (67.1 ± 8.3%). When the mice were tested for 90% red wine A, all the individual mice failed to distinguish between them (53.3 ± 9.6%). To further examine the effect of concentration difference on liquor odor discrimination, 2 petri dishes, which had been filled with red wine A, were placed in one of the odor boxes (referred to here as 200%). Interestingly, the overall concordance decreased down to 33.8 ± 8.4%, indicating that each mouse preferentially chose the arm scented by the unrewarded 200% red wine A. Even after several training sessions, the individual mice failed to choose the rewarded 100% red wine A as opposed to the unrewarded 200% red wine A in the Y-maze.

The influence of stimulus intensity on odor discriminability of mice was further studied using pure odorants. Ten mice of group B were individually trained to discriminate 5% (v/v) IA from mineral oil (Figure 4). After successful training (>70% concordance for each mouse), the mice were tested for their ability to discriminate concentration differences of IA. The mice could discriminate the learned 5% IA from the unrewarded IA of lower than 4% (>70% concordance for each mouse). However, the overall concordance declined to 60.4 ± 5.0 for 4.5% IA. Furthermore, the mice were more attracted to 10% IA compared with the learned 5% IA (the overall concordance = 20.8 ± 6.9). All the individual mice chose the arm scented by 10% IA as opposed to the learned 5% IA. By contrast, the mice could easily discriminate 5% IA from either 10% Ci (the overall concordance = 87.1 ± 6.2%) or 10% EB (83.8 ± 3.9%). In these discrimination tests, the concordance score did not differ significantly among the individual trained mice (data not shown).

Discrimination of pure odorant mixtures

Ten mice of group C were individually trained to discriminate a ternary mixture of 5% each of IA, Li, and Ci (referred to as IA + Li + Ci) from mineral oil (Figure 5). After successful training (>70% concordance for each mouse), the mice were able to discriminate the learned IA + Li + Ci from the ternary mixture of 5% each of Car, Lim, and EV (Car + Lim + EV) as well as the mixture of 5% each of Ger, EB, and MC (Ger + EB + MC). The mice were then subjected to odor discrimination tests between the learned IA + Li + Ci and binary mixtures of IA + Ci, Li + Ci or IA + Li (the concentration of each pure odorant was 5%).

Table 1 Percent concordance of 10 individual mice for discrimination between red wines A and C

	Concordance score of individual mice (%)										Overall concordance (%)
	Mouse (arbitrary no.)										
	1	2	3	4	5	6	7	8	9	10	
Before retraining	75.0	79.2	54.2	58.3	50.0	66.7	66.7	62.5	16.7	29.2	55.8 ± 12.8
After retraining	95.8	87.5	79.2	83.3	87.5	87.5	91.7	87.5	70.8	58.3	82.9 ± 7.2

Ten mice were initially trained to discriminate red wine A from distilled water. They were then examined for their discriminability between red wines A and C (before retraining). After this discrimination test, the mice were individually retrained to discriminate between red wines A and C in 5 learning sessions. The retrained mice were then examined for their discriminability between red wines A and C (after retraining). The concordance score for each mouse was calculated from the number of concordance responses in 24 consecutive trials. The overall concordance was calculated as the mean of the concordance scores of the 10 individual mice (mean ± 95% confidence interval, n = 10). Student's t-test was used to determine the 95% confidence interval of the overall concordance score. The mice were numbered arbitrarily and were run in a random order in the discrimination test. Although the reason is unclear, the mouse number 10 was still only at chance level after retraining.

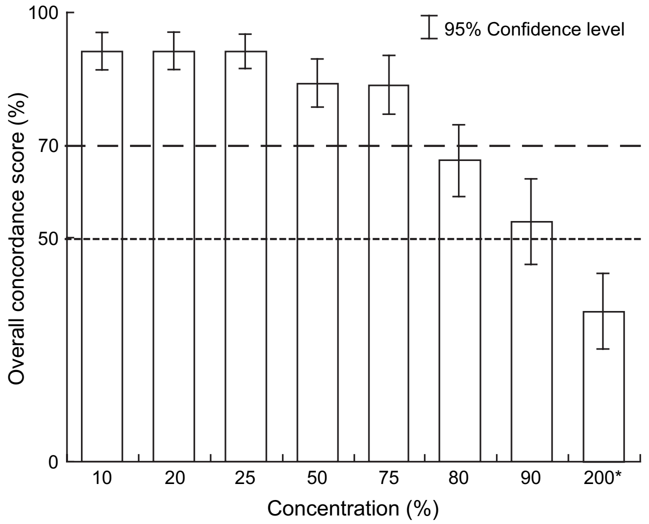

Figure 3 Testing of 10 trained mice for their ability to discriminate between whole and diluted red wine A samples. The individual mice were examined for their ability to discriminate the learned red wine A (referred to here as 100%) from diluted red wine A. Red wine A was diluted with distilled water to various concentrations (% red wine A) as indicated on the *x* axis. The overall concordance score was calculated as described in the legend of Figure 1. Asterisk indicates that the discrimination test for 200% red wine A was conducted by placing 2 petri dishes, which had been filled with red wine A, in a odor box in the Y-maze.

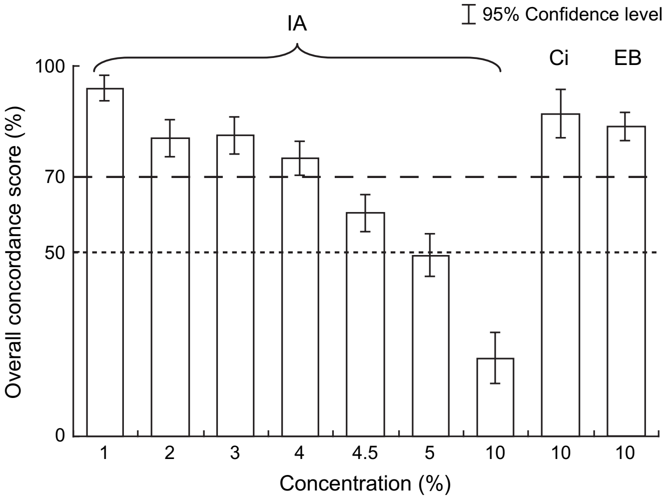

Figure 4 Testing of concentration influence on discriminability of IA in trained mice. Ten mice were individually trained to discriminate 5% IA from mineral oil. Then, the individual trained mice were tested for their ability to discriminate different concentrations of IA. IA was diluted with mineral oil to various concentrations (% IA) as indicated on the *x* axis. The individual mice were also examined for their ability to discriminate the learned 5% IA from either 10% Ci or 10% EB.

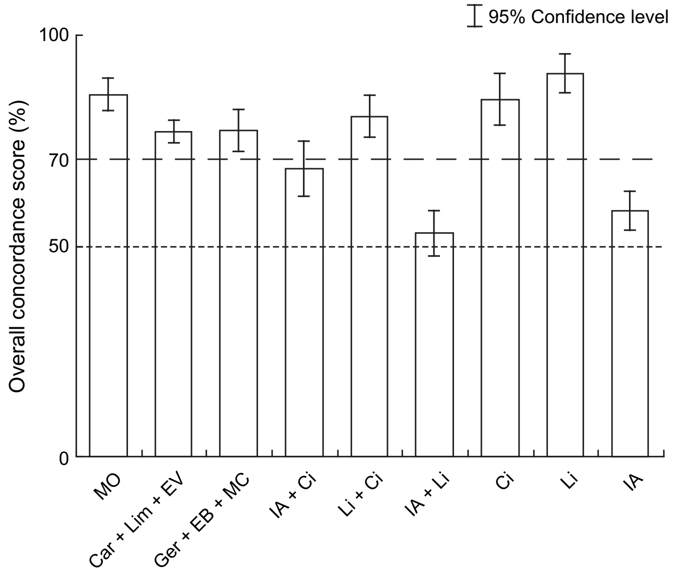

Figure 5 Discrimination of pure odorant mixtures in mice. Ten mice were individually trained to discriminate a ternary mixture of pure odorants containing 5% each of IA, Li, and Ci (referred to as IA + Li + Ci) from mineral oil (MO). After successful training (>70% concordance for each mouse), the individual mice were examined for their ability to discriminate the learned IA + Li + Ci from unrewarded mixtures of pure odorants. Discrimination tests were also conducted between IA + Li + Ci and single pure odorants (Ci, Li, and IA). The pure odorants used are IA, Ci, EB, Li, Car, (R)-(+)-lemonene (Lem), EV, Ger, and MC.

The trained mice showed greater than 80% overall concordance for Li + Ci (80.8 ± 5.0). In contrast, the overall concordance was significantly low for IA + Ci (68.3 ± 6.3) and for IA + Li (52.9 ± 5.3). Moreover, the mice could easily discriminate the learned IA + Li + Ci from 5% Ci (84.6 ± 6.3) and 5% Li (90.8 ± 4.6), whereas they failed to distinguish between IA + Li + Ci and 5% IA (58.3 ± 4.4). These results suggested that the trained mice could not discriminate the learned IA + Li + Ci from the unrewarded odors containing IA. In addition, there was no distinct difference in the discriminability of IA + Li + Ci among the individual trained mice (data not shown).

To assess if the discriminability of pure odorant mixtures could be modified by training, the mice of group C were retrained to distinguish between IA + Li + Ci and IA. Here, the mice were trained to choose the arm scented by IA + Li + Ci in the Y-maze where IA was used as the unrewarded odorant. After several training sessions, the overall concordance increased up to 90.3 ± 5.0% (Figure 6). Interestingly, although the retrained mice were able to discriminate the learned IA + Li + Ci from IA + Li (88.9 ± 5.0%), they showed significantly lower performance in discrimination of IA + Li + Ci from Li + Ci (72.2 ± 9.1%) compared with that observed before retraining (80.8 ± 5.0%; see Figure 5).

Discussion

Biological organisms are bombarded by sensory information. They need to select particular objects for action and successfully ignore other competing objects (Tripper

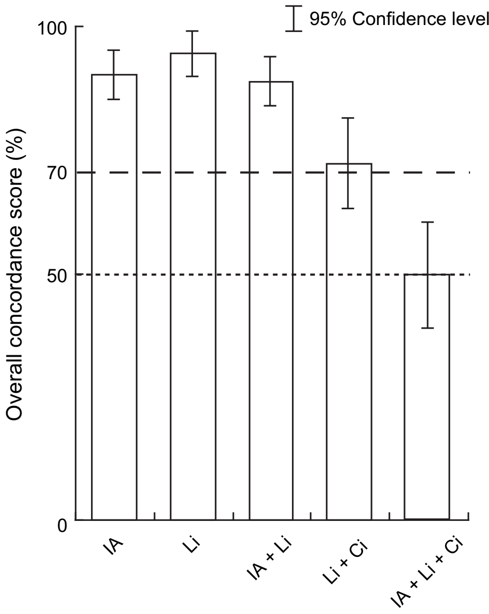

Figure 6 Discriminability of the learned ternary mixture of 5% each of IA, Li, and citral (Ci) by retrained mice. Ten mice, which had been individually trained to discriminate IA + Li + Ci from mineral oil were retrained to discriminate between IA + Li + Ci and IA. The odor sources were prepared using 5% pure odorants. Even chance level was confirmed by scenting both arms of the Y-maze by air currents containing the identical odor emanating from IA + Li + Ci.

1985). Although selective attention has intensively been discussed in the visual and auditory systems (Boynton 2005; Kayser et al. 2005), much less is known about this selective aspect of the olfactory system. In the present study, we demonstrated behavioral evidence for selective attention in the discrimination of liquor odors in mice. After successful training, all the individual mice were able to discriminate the learned red wine from other liquors, including white wine, rosé wine, sake, and plum liqueur (Figure 1). Unexpectedly, however, distinct differences were observed among the individual trained mice, when they were tested to distinguish fine differences between 2 brands of red wine (Table 1). As shown in Figure 2, liquor odors were complex blends of volatile compounds. The data presented here suggested that the individual mice selected different subsets of volatile components of the rewarded red wine when they were trained to discriminate the red wine from distilled water. It is highly likely that discriminability of the individual trained mice depended upon the similarity of the selected subset of volatile components between 2 brands of red wine. If the similarity is low, it is possible that the trained mice readily discriminate between them. Conversely, if the similarity is high, the discrimination of 2 brands of red wine is probably difficult. We also observed that the trained mice were more attracted to higher concentrations of the learned odor in the Y-maze (Figures 3 and 4). Consequently, if the selected subset of volatile components is similar between 2 brands of red wine, it is possible that the trained mice are more attracted by higher concentrations of the selected subset of volatile compounds.

There is some uncertainty concerning that the unexpected difference in the performance of mice on discrimination between red wines A and C may be caused by the lack of training. In the present study, we assessed if mice could distinguish between 2 odors (2 different liquors) after they had been successfully trained to discriminate between odor (red wine A) and nonodor (distilled water). To do this, 10 individual mice were first trained to discriminate between red wine A and distilled water in a total of 120 trials (24 consecutive trials in 5 sessions). The individual mice were then examined for their ability to discriminate red wine A from other liquors in a total of 144 trials (24 consecutive trials for 6 different liquors). In the liquor discrimination trials, the mice were also rewarded with a drop of water if their choice was correct. This indicates that the individual mice had been trained in a total of 264 trials (120 trials for training against nonodor and 144 trials in discrimination between 2 odors) before they were examined for their ability to discriminate between red wines A and C. As we demonstrated in Figure 1, the individual mice, which had been trained to discriminate between odor (red wine A) and nonodor (distilled water), were able to discriminate the learned red wine A from other liquors including red wine B. Importantly, they never randomly chose 2 different liquors, even in the discrimination trials between 2 red wines (learned red wine A and unlearned red wine B). We, therefore, think that 264 trials for each mouse were practically sufficient for training and that increasing the initial training period could probably produce the same results.

Our observation also suggested that mice can select the odor mixture with the greater concentration (Figures 3 and 4). Rinberg et al. (2006) reported that the accuracy of odor discrimination increased with the duration of imposed odorant sampling in the modified Knosys olfactometer and that the rate of this increase is slower for harder tasks. In our Y-maze assays, it was not possible to change the duration of odor presentation. However, we found that the mice prefer higher concentrations of liquor and pure odorants to the concentrations used for the training. The time taken for the trained mice to make a choice in the Y-maze was only 2 or 3 s, and thus, the time that the individual mice spent for odor discrimination was less than 1 s. We think that higher concentrations allowed the mice to obtain sufficient information to make a correct choice in the short period of time in Y-maze assays. It is highly possible that accuracy of odor discrimination in the Y-maze increased with increasing the concentration of the learned odor.

Selective attention of mice was also observed in Y-maze behavioral assays using pure odorant mixtures. As shown in Figure 5, when the mice was trained with IA + Li + Ci, they failed to discriminate the learned ternary mixture from untrained odors containing IA. In contrast to liquor odor discrimination, however, no significant difference was detected among the individual trained mice (data not shown). This result suggested that all the individual mice attended only IA when they were trained to discriminate IA + Li + Ci from mineral oil. Namely, the mice exhibited bias attention toward IA, thereby providing a weighted representation of the trained odor IA + Li + Ci. It seems likely that mice directed attention to different subsets of volatile components, only when complex odor sources such as liquors are used for the training. In this respect, one concern may be related to the possibility that IA is simply more pleasant or less aversive for the trained mice. If IA is more pleasant, the trained mice might choose IA, even when a preference test is conducted with all odors being rewarded equally. However, as shown in Figure 6, the mice were readily retrained to distinguish between IA + Li + Ci and IA, and after several retraining sessions, the mice were able to discriminate between IA + Li + Ci and IA + Li. It might be expected that the retrained mice could choose randomly 2 odors, given that if IA is more pleasant.

After 5 retraining sessions, almost the individual mice were able to discriminate between 2 brands of red wine (Table 1). Although one mouse failed to discriminate even after 5 retraining sessions, this result is likely to suggest that the olfactory attention of mice could be modified through their learning experiences. It may be that the retraining mice allowed the individual to focus attention on a subset of volatile compounds that were present differently between 2 red wines. Similarly, modification of selective attention was also observed in discrimination tests using pure odorant mixtures (Figure 6). The mice were able to discriminate IA + Li + Ci from IA after retraining. Concomitantly, they also showed lower performance in the discrimination of IA + Li + Ci from Li + Ci compared with that observed before retraining. It has been reported that odor discrimination is established based on a combinatorial receptor code model in which the identities of different odorants are encoded by a combination of odorant receptors (Buck and Axel 1991; Mori et al. 1999; Rubin and Katz 1999; Buck 2000; Uchida et al. 2000). More recently, Salcedo et al. (2005) have investigated the training-induced changes in ethyl acetate odor maps using a computational tool to map the glomerular layer of the olfactory bulb in mice. They demonstrated that training upregulated the number of glomeruli that became *c-fos* positive after stimulation with ethyl acetate. It seems likely that the training-induced changes in odor maps in periglomerular cells may be involved in the modification of selective attention in mice.

In conclusion, we demonstrated that mice can be trained to readily distinguish between liquor odors in Y-maze. More importantly, the data presented here suggested that the mice directed attention to different subsets of volatile components emanating from a liquor when they were trained to discriminate the liquor from distilled water. Additionally, it was also observed that the olfactory attention of mice could be modified through their learning experiences.

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References

Boynton GM. 2005. Attention and visual perception. Curr Opin Neurobiol. 15:465–469.

Buck L, Axel R. 1991. A novel multigene family may encode odorant receptors: a molecular basis for odor recognition. Cell. 65:175–187.

Buck LB. 2000. The molecular architecture of odor and pheromone sensing in mammals. Cell. 100:611–618.

Daniel WW. 1987. Biostatistics: a foundation for analysis in the health sciences. New York: John Wiely & Sons.

Derby CD. 2000. Learning from spiny lobsters about chemosensory coding of mixtures. Physiol Behav. 69:203–209.

Kayser C, Petkov CI, Lippert M, Logothetis NK. 2005. Mechanisms for allocating auditory attention: an auditory saliency map. Curr Biol. 15: 1943–1947.

Luck SJ. 1998. Neurophysiology of selective attention. In: Pashler H, editor. Attention. East Susex (UK): Psychology Press Ltd. p. 257–295.

Mori K, Nagao H, Yoshihara Y. 1999. The olfactory bulb: coding and processing of odor molecule information. Science. 286:711–715.

Peinado RA, Moreno JA, Munoz D, Medina M, Moreno J. 2004. Gas chromatographic quantification of major volatile compounds and polyols in wine by direct injection. J Agric Food Chem. 52:6389–6393.

Rinberg D, Koulakov A, Gelperin A. 2006. Speed-accuracy tradeoff in olfaction. Neuron. 51:351–358.

Roman FS, Marchetti E, Bouquerel A, Soumireu-Mourat, B. 2002. The olfactory tubing maze: a new apparatus for studying learning and memory processes in mice. J Neurosci Meth. 117:173–181.

Rubin BD, Katz LC. 1999. Optical imaging of odorant representations in the mammalian olfactory bulb. Neuron. 23:499–511.

Salcedo E, Zhang C, Kronberg E, Restrepo D. 2005. Analysis of training-induced changes in ethyl acetate odor maps using a new computational tool to map the glomerular layer of the olfactory bulb. Chem Senses. 30:615–626.

Tabor R, Yaksi E, Weislogel JM, Friedrich RW. 2004. Processing of odor mixtures in the zebrafish olfactory bulb. J Neurosci. 24:6611–6620.

Treisman A. 1969. Strategies and models of selective attention. Psychol Rev. 76:282–299.

Tripper SP. 1985. The negative priming effect: inhibitory effects of ignored primes. Q J Exp Psychol A. 37:571–590.

Turchi J, Sarter M. 2000. Cortical cholinergic inputs mediate processing capacity: effects of 192 IgG-saporin-induced lesions on olfactory span performance. Eur J Neurosci. 12:4505–4515.

Uchida N, Takahashi YK, Tanifuji M, Mori K. 2000. Odor maps in the mammalian olfactory bulb: domain organization and odorant structural features. Nat Neurosci. 3:1035–1043.

Wilson DA, Stevenson RJ. 2003. The fundamental role of memory in olfactory perception. Trends Neurosci. 26:243–247.

Yamaguchi M, Yamazaki K, Beauchamp GK, Bard J, Thomas L, Boyse EA. 1981. Distinctive urinary odors governed by the major histocompatibility locus of the mouse. Proc Natl Acad Sci USA. 78:5817–5820.

Yamazaki K, Beauchamp GK, Singer A, Bard J, Boyse EA. 1999. Odortypes: their origin and composition. Proc Natl Acad Sci USA. 96: 1522–1525.

Young JW, Finlayson K, Spratt C, Marston HM, Crawford N, Kelly JS, Sharkey J. 2004. Nicotine improves sustained attention in mice: evidence for involvement of the α7 nicotinic acetylcholine receptor. Neuropsychopharmacol. 29:891–900.

Young JW, Kerr LE, Kelly JS, Marston HM, Spratt C, Finlayson K, Sharkey J. 2007. The odor span task: a novel paradigm for assessing working memory in mice. Neuropharmacology. 52:634–645.

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