

Odor Recognition in Mandarin Vole (*Microtus mandarinus*) and Reed Vole (*M. fostis*)

TAI Fadao¹ LIAN Yi² WANG Tingzheng¹ SUN Ruyong³

(1 College of Life Sciences, Shaanxi Normal University, Xi'an, 710062, China)

(2 College of Life Sciences, East China Normal University, Shanghai, 200062, China)

(3 College of Life Sciences, South China Normal University, Guangzhou, 510631, China)

Abstract: The abilities to discriminate and recognize individuals' odors of mandarin voles (*Microtus mandarinus*) and reed voles (*M. fostis*) were investigated in present study using behavioral paradigm. Mandarin voles and reed voles were exposed to conspecific individual substrates for one hour, and after 15 min, 30 min and 60 min intervals, durations of investigating behavior such as visiting, sniffing and digging to this familiar substrate and another novel substrate were recorded in different groups of voles, each group were tested at just one interval. It was found that voles exposed to conspecific heterosexual substrates preferred to familiar substrates at different lengths of time after exposure. In the other hand, voles exposed to homosexual substrates preferred to the novel odor at different lengths of time. The mandarin voles exposed to homosexual substrates showed significant preferences for novel substrates at 60 min intervals after exposures. But reed voles did not show obvious preference to homosexual substrates exposed to them after 60 min interval. Female voles showed more significant preferences to different substrates than did male voles at 60 min intervals after exposure. The present results indicate that different species and different sexes of voles showed different patterns of olfactory recognition and memory. This difference may be because of their different social organizations, ecologies and life history strategies in different species.

Key words: Mandarin vole (*Microtus mandarinus*); Reed vole (*M. fostis*); Recognition; Individual odor

棕色田鼠和沼泽田鼠的气味识别

邰发道¹ 廉 漪² 王廷正¹ 孙儒泳³

(1 陕西师范大学生命科学院, 西安, 710062)

(2 华东师范大学生命科学院, 上海, 200062) (3 华南师范大学生命科学院, 广州, 510631)

摘要: 把棕色田鼠或沼泽田鼠暴露于同种个体底物(个体饲养箱内的锯末)1 h, 不同组别的田鼠在间隔 15 min、30 min、60 min 后, 记录对暴露过的熟悉底物和另一个陌生底物的访问、嗅闻、挖掘等社会探究行为(每组在每一个时间间隔只试验 1 次), 统计分析发现, 田鼠在暴露于同种异性底物, 然后间隔不同的时间后, 总是倾向于选择熟悉同种异性底物; 田鼠在暴露于同种同性底物, 然后间隔不同的时间后, 总是倾向于选择陌生同种同性底物; 棕色田鼠在暴露于同性底物 1 h, 然后间隔 60 min 后, 对陌生的同性底物有明显多的探究行为, 但沼泽田鼠在同种情况下却没有表现出这种选择倾向。在暴露底物 1 h, 然后间隔 60 min 后, 雌性田鼠比雄性田鼠表现出更明显的选择倾向。以上结果表明不同种类和性别的田鼠对气味表现出不同的识别模式。这种差异可能表明不同种具有不同的社会组织、生态和生活史对策。

关键词: 棕色田鼠; 沼泽田鼠; 识别; 气味

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A number of studies have found that odor cues play an important role in a variety of social activities in mammals, including kin recognition, mate selection, inbreed-

ing avoidance and juvenile dispersal from the natal area (Johnston, 1993; Maslak and Gouat, 2002). Several researchers have also found that lesions of the olfactory

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Biography: Tai Fadao (1967 -), male, main research fields are behavioral neurobiology and animal ecology. E-mail: taifadao@snnu.edu.cn

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bulbs impair basic recognition responses in male rats (Bluthe *et al.*, 1990; Popik *et al.*, 1991). The ability to discriminate, recognize and remember odor cues is very important in the social lives of rodents (Halpin, 1980; Ferkin, 2001). So the olfaction is the primary signal for social recognition in rodents. But the mechanisms of individual recognition, including the signals used, the sensory and perceptual mechanisms involved are not very clear (Halpin, 1986; Johnston, 1993).

Although little attention has been focused on sex differences in the learning abilities, some researchers have reported that male mice outperform females on spatial and nonspatial tests of learning and memory (Berger-Sweeney *et al.*, 1995; Mishima *et al.*, 1986). Bluthe and Dantzer (1990) have suggested that females have far lower levels of baseline investigatory behavior, but they retain recognition responses significantly longer than males. It is also found that olfactory recognition is different in different strains (Mihalick *et al.*, 2000). Previous study revealed that female prairie voles mated preferentially and spent more time with the familiar males; but montane voles showed no preference (Shapiro *et al.*, 1986). This same result was also found in mandarin vole and root vole (Zhao *et al.*, 2002). We do not know whether the difference is caused by their abilities of discrimination or by their memories of two species with different mating system.

Several paradigms have been used to measure social recognition and memory (Sawyer *et al.*, 1984). Because mice or rats have the natural tendency to intensely investigate novel individuals, when an unfamiliar conspecific is introduced for the first time into the home cage of an adult male rat or mouse, the resident male vigorously investigates the novel individual. If the novel animal is removed and then reintroduced to the same resident male a short time later, it will receive far less investigation during the second meeting. Based on this simple observation, it is possible to use changes in the duration of investigation during repeated pairings with the same stimulus animal as an index of memory for that individual. The repeated presentation of the same individual can prolong the duration of the memory (Sawyer *et al.*, 1984). In the other

hand, if a resident male is exposed to either urine or soiled bedding from a stimulus animal prior to testing, there is a significantly reduced level of initial investigation, indicating that the resident male has already formed a memory for that individual signature scent (Ferguson *et al.*, 2002). Using these paradigms, memory and recognition of scent signature have been investigated in various studies (Johnston, 1993; Poellinger *et al.*, 2001; Maslak and Gouat, 2002; Baum and Keverne, 2002). Some researchers found a sexual difference of the capacity to detect and investigate urinary odors in mice (Baum and Keverne, 2002). This method also has been used to explore odor discrimination ability in neonates (Fletcher and Wilson, 2001).

Several researchers have reported that two closely related microtine rodents, monogamous prairie voles (*Microtus ochrogaster*) and promiscuous montane voles (*M. montanus*) have different life strategies, neuroanatomies and social behaviors such as social preference, pair bonding and so on (Wang *et al.*, 1997; Liu *et al.*, 2001). It is found that mandarin vole is monogamous and reed vole is referred to be promiscuous according to reproduction characteristics and sexual dimorphism (Tai *et al.*, 2001a; 2001b). Recent study found that vomeronasal organ and accessory olfactory bulb were different in these two species also (Tai *et al.*, 2003). Mandarin voles and reed voles should have different social behaviors. We hypothesize that these two species must have different patterns of recognition and memory of social cues. Abilities of remembering and recognition of individual odors of two species were compared for the first time in the present study using behavior paradigms described above.

1 Materials and methods

The mandarin voles and reed voles used in the experiments came from an outbred colony reared in the College of Life Sciences, Shaanxi Normal University in Xi'an, The Peoples Republic of China. The colony of mandarin voles was established in 1997 with wild captured animals from Lingbao City, Henan Province. The reed voles were captured from Qingtongxia City, Ningxia Hui Autonomous Region. The animals were maintained in clear

plastic cages (40 cm × 28 cm × 50 cm). The breeding colonies were held at a photoperiod of 12L:12D and temperature of 18 – 20 °C. Hardwood shavings and cotton batting were provided as substrate and bedding. Rabbit chow (Lab. Anim. Center, Xi'an Medical University), carrot and malt were available ad libitum.

The paradigms used to measure odor recognition were as follows: a vole was exposed to a novel vole's substrate for 60 minutes, 15 minutes later (or 30 minutes, 60 minutes later), the vole was simultaneously exposed to both the familiar substrate and another novel vole's substrate and durations of olfactory investigation to these two substrates were recorded and compared (Ferguson *et al.*, 2002). In each species, six groups of voles were divided according to different sex and different separate intervals (15 minutes, 30 minutes or 60 minutes). The different groups of voles were exposed to substrates of novel individuals for one hour (to become familiar with substrates). Then the voles were taken away and put in their nests for different lengths of time (15 minutes, 30 minutes or 60 minutes intervals). After these 15 minute, 30 minute or 60 minute intervals, the different groups of voles were put into a plywood rectangle box (60 cm × 20

cm × 33 cm) which was divided into three equal-size compartments. Voles were free to move between them. Substrate which was exposed to tested vole previously (familiar substrate) and another novel substrate were put into the two end compartments simultaneously. The durations of visiting the two compartments with different individual substrates were recorded. Durations of investigating behaviors were recorded including sniffing (Snout approached about 1 cm of substrate), digging and licking substrate within 10 min. Any test in which there was no visit nor investigating behaviors within 10 min was eliminated from samples.

Wilcoxon matched pair test was used to compare behaviors of subject voles in the two choice chambers.

2 Result

2.1 Investigating behaviors of mandarin voles to familiar and novel substrate at different intervals

When female mandarin voles were exposed to female substrates for one hour (as familiar substrate) and after 15 min, 30 min and 60 min intervals, the three groups of voles spent significantly more time investigating another novel substrate than the familiar substrate (Table 1).

Table 1 Comparison between durations of investigating homosexual familiar substrate and novel substrate at different intervals after exposure in mandarin voles

Intervals after exposure			15 min (n = 12)	30 min (n = 13)	60 min (n = 12)
Female investigating substrate of female	visiting	familiar substrate	116.83 ± 114.28	268.00 ± 149.62	42.50 ± 20.10
		strange substrate	502.17 ± 244.53*	474.00 ± 358.69*	792.00 ± 123.04**
	sniffing	familiar substrate	71.83 ± 38.86	32.67 ± 10.07	19.50 ± 7.58
		strange substrate	94.33 ± 57.34*	85.00 ± 77.31*	79.00 ± 39.60*
	digging	familiar substrate	40.83 ± 36.69	54.00 ± 40.15	14.50 ± 10.51
		strange substrate	50.00 ± 24.41*	152.33 ± 135.34*	111.00 ± 21.62**
Male investigating substrate of male	visiting	familiar substrate	167.00 ± 87.16	164.00 ± 70.27	154.00 ± 33.06
		strange substrate	452.75 ± 282.17*	439.40 ± 313.35*	463.50 ± 195.30*
	sniffing	familiar substrate	50.25 ± 18.30	66.60 ± 54.77	58.50 ± 48.45
		strange substrate	94.00 ± 65.43*	97.40 ± 85.13*	128.50 ± 86.45*
	digging	familiar substrate	17.00 ± 14.17	16.80 ± 10.35	45.75 ± 10.46
		strange substrate	41.00 ± 21.84*	23.80 ± 22.90	11.00 ± 8.08

* : $P < 0.05$; ** : $P < 0.01$

When male mandarin voles were exposed to a male substrates for one hour, after 15 min, 30 min and 60 min intervals, three groups of voles exhibited the same behavioral patterns as the females exposed to familiar and

strange female substrates (Table 1).

When female mandarin voles were exposed to male substrates for one hour and were taken away for 15 min, 30 min and 60 min intervals, the three groups spent sig-

nificantly longer time visiting, sniffing and digging familiar substrates than to novel substrates (Table 2).

Two male mandarin voles groups, being exposed to female substrates for one hour, after 15 min or 30 min intervals, spent significantly longer time visiting, sniffing

and digging these familiar substrates than novel substrates. But male mandarin vole did not show any significant preference for familiar or novel substrate after 60 minute intervals (Table 2).

Table 2 Comparison between durations of investigating heterosexuals familiar and novel substrate at different intervals after exposure in mandarin voles

Intervals after exposure			15 min (n=12)	30 min (n=13)	60 min (n=12)
Female investigating substrate of male	visiting	familiar substrate	519.00 ± 126.09	549.60 ± 239.93	397.00 ± 154.15
		strange substrate	172.00 ± 43.24*	120.40 ± 22.65*	122.50 ± 59.51*
	sniffing	familiar substrate	47.50 ± 23.54	66.20 ± 46.85	84.50 ± 24.75
		strange substrate	34.50 ± 18.79*	34.40 ± 31.42*	54.50 ± 4.95*
	digging	familiar substrate	100.00 ± 62.23	37.80 ± 12.87	0.00 ± 0.00
		strange substrate	44.00 ± 32.53*	24.40 ± 13.89*	2.50 ± 1.54
Male investigating substrate of female	visiting	familiar substrate	473.00 ± 243.24	387.50 ± 283.55	338.00 ± 221.32
		strange substrate	219.00 ± 126.09*	175.50 ± 170.41*	226.00 ± 152.43
	sniffing	familiar substrate	54.50 ± 28.79	67.50 ± 12.02	67.00 ± 32.52
		strange substrate	27.50 ± 13.54*	42.50 ± 30.41*	58.00 ± 28.57
	digging	familiar substrate	100.00 ± 62.23	51.00 ± 22.12	0.00 ± 0.00
		strange substrate	44.00 ± 32.53*	46.50 ± 23.03	0.00 ± 0.00

* : $P < 0.05$; * * : $P < 0.01$

2.2 Investigating behaviors of reed voles to familiar and novel substrate at different intervals

Female reed voles exposed to female substrates for one hour spent significantly longer time visiting, sniffing and digging novel substrate than familiar substrate after 15 min and 30 min intervals. The female reed vole groups did not show significant preference for familiar substrates after 60 min intervals (Table 3).

Male reed voles, exposed to male individual substrates for one hour, showed significant preference for the novel substrates after 15 min intervals. They spent longer time visiting the novel substrates, but they did not show obvious difference between visiting or digging familiar substrates and novel substrates after 60 min interval (Table 3).

Table 3 Comparison between durations of investigating familiar homosexual substrate and strange substrate at different intervals after exposure in reed voles

Intervals after exposure			15 min (n=12)	30 min (n=13)	60 min (n=12)
Female investigating female's substrate	visiting	familiar substrate	244.00 ± 45.07	72.33 ± 64.78	236.50 ± 161.33
		strange substrate	422.50 ± 36.06*	636.00 ± 286.20*	308.50 ± 236.28
	sniffing	familiar substrate	40.50 ± 17.28	36.67 ± 14.26	54.00 ± 28.49
		strange substrate	90.00 ± 21.62*	67.33 ± 43.89*	64.00 ± 40.71
	digging	familiar substrate	30.00 ± 22.43	13.67 ± 12.66	30.50 ± 13.13
		strange substrate	48.50 ± 28.59*	53.00 ± 41.22*	101.50 ± 29.40*
Male investigating male's substrate	visiting	familiar substrate	232.50 ± 59.71	235.40 ± 84.52	195.60 ± 67.28
		strange substrate	325.50 ± 182.86*	407.60 ± 166.97*	301.20 ± 213.92
	sniffing	familiar substrate	30.67 ± 23.80	20.80 ± 8.62	87.40 ± 41.80
		strange substrate	68.33 ± 40.18*	32.60 ± 11.66	69.60 ± 59.52
	digging	familiar substrate	28.17 ± 3.83	12.40 ± 3.51	21.80 ± 11.64
		strange substrate	26.67 ± 4.92	9.60 ± 7.63	20.80 ± 9.64

* : $P < 0.05$; * * : $P < 0.01$

Female reed voles exposed to male substrates for one hour, after 15 min, 30 min and 60 min intervals showed significant preference to familiar substrates (Table 4).

Male reed voles exposed to female individual substrates spend significantly longer time visiting, sniffing fa-

miliar substrates at 15 min and 30 min intervals after exposure. But at 60 min intervals, male did not exhibit any significant preference to familiar and novel substrates (Table 4).

Table 4 Comparison between duration of investigating heterosexual familiar substrate and novel substrate at different intervals after exposure in reed vole

Intervals after exposure			15 min (n = 12)	30 min (n = 13)	60 min (n = 12)
Female investigating male's substrate	visiting	familiar substrate	297.00 ± 88.91	536.00 ± 151.32	495.00 ± 42.43
		strange substrate	144.00 ± 82.43 *	284.50 ± 117.08 *	223.00 ± 63.64 *
	sniffing	familiar substrate	74.50 ± 51.82	105.00 ± 22.63	134.00 ± 32.53
		strange substrate	36.50 ± 27.58 *	65.50 ± 14.85 *	30.50 ± 10.61 *
	digging	familiar substrate	18.50 ± 10.16	74.50 ± 25.56	112.50 ± 43.13
		strange substrate	26.50 ± 7.48 *	40.00 ± 36.77 *	36.00 ± 29.70 *
Male investigating female's substrate	visiting	familiar substrate	317.72 ± 223.56	339.17 ± 65.74	278.00 ± 42.43
		strange substrate	144.00 ± 82.43 *	238.00 ± 35.86 *	234.00 ± 63.64
	sniffing	familiar substrate	56.50 ± 37.58	89.00 ± 68.45	114.00 ± 54.67
		strange substrate	34.50 ± 11.82 *	56.00 ± 23.29 *	92.45 ± 61.71
	digging	familiar substrate	18.50 ± 6.16	24.00 ± 12.75	53.45 ± 37.34
		strange substrate	26.50 ± 7.48	15.23 ± 13.67	42.76 ± 34.53

* : $P < 0.05$; * * : $P < 0.01$

3 Discussion

The data reported here suggests that mandarin voles were able to discriminate novel substrates from familiar ones successfully over intervals that ranged from 15 to 60 min. Reed voles discriminated novel substrates successfully only over intervals from 15 to 30 min. Discrimination of individually distinctive odors at different intervals between trials and different species was observed first time in present study. Previous studies of other species have shown that discrimination of individually distinctive odors occurred at interval of few seconds apart in rats (Brown *et al.*, 1987), a few minutes apart in gerbils (Halpin, 1974), 1 day apart in dogs, wolves and sugar gliders (Schultze-Westrum, 1969; Brown and Johnston, 1983); 1 second to 10 days in hamster (Johnston, 1993) or even 4 weeks apart in guinea pigs (Beauchamp and Wellington, 1984). These inconsistent results can be explained by assuming that different experiments of various species may exhibit different social recognition. This short term test of recognition (roughly 60 min) in present experiment may be only one form of social memory. Recognition

of mates and kin involve memories that last days, weeks, or even months and may involve cognitive and neural systems distinct from those required for short-term social recognition (Ferguson *et al.*, 2002).

The mandarin voles exposed to homosexual substrates showed significant preference for familiar substrates at 60 min intervals after exposure, but reed voles did not show obvious preference to homosexual substrates exposed to them 60 min ago. These results hypothesized that mandarin vole may have the better recognition ability than reed vole. This may be because mandarin voles and reed voles have different mating systems. The social behaviors of the former are more meticulous than those of the latter. This adds evidence to previous hypotheses that social interactions of monogamous species are more meticulous than those of polygamous species. Shapiro *et al.* (1986) found that each vole species has a unique number and pattern of sources of sexually distinct scents. They also established that the greater the numbers of sources of scents for signaling opposite-sex conspecifics, the greater the numbers of encounters those individuals within that species have with opposite-sex conspecifics. The montane vole, a semisocial

species, has six sources of scents, which is intermediate between the numbers found in the meadow vole (*Microtus pennsylvanicus*), an asocial species, and the prairie vole (*Microtus ochrogaster*), a social species. These results suggest that the numbers, patterns, and locations of sexually distinct scents are positively associated with the frequencies with which individuals encounter the scent marks of neighboring conspecifics. These two species have different neuroanatomical distribution of vasopressin V sub (1a) receptors which are related with social organization and social recognition (Young *et al.*, 1999). Another interpretation may be that different species have different temperaments. This phenomenon had been found in a comparison of learning and memory performance between squirrel monkeys and common marmosets (Matthias and Karin, 1998). The third possibility may be because the dependence on olfactory cues is different in mandarin voles and reed voles. Mandarin voles have the habit of living underground and might be more prepared to rely on olfactory cues than the reed voles.

It is possible that female voles showed more significant preference to different substrates than male voles at 60 min intervals after exposure. This result may imply that female voles have better abilities to discriminate, recognize, and remember individual odors. Our result may be consistent with study on root voles (Zhao *et al.*, 1999). Female root voles showed significant preference for familiar rather than novel male, the partner rather than unfamiliar males, the partner rather than familiar males in the social behaviors. But the males made no preference for the familiar versus the novel females, or the partner versus the novel females. Our results may also add evidence to the hypothesis that the ability to detect and investigate volatile urinary odors is sexually different in mice (Baum and Kevern, 2002). Baum and Kevern (2002) have found that females were able to show habituation/dishabituation responses to 1:40 and 1:80 urine/water dilution while males only showed response to the dilutions of 1:1 to 1:20. The dramatic sex differences in recognition described above may be consistent with the sexually dimorphic and exquisitely sensitive olfactory pathway to the effects of gonadal steroids (Dantzer, 1998). However, the results of the

present studies are contrary to hypothesis in recent studies that male mice outperform females on olfactory discrimination learning (Mihalick *et al.*, 2000). This may be because of different species and different scent sources. The scents in mice discrimination are nonsocial odors such as cinnamon and nutmeg which are unrelated with individual recognition and social behaviors (Mihalick *et al.*, 2000). But scent in present experiment comes from substrates of voles which contain a great deal of specific information concerning gender, social status and reproductive state.

Preferences for familiar and novel odors by mandarin voles and reed voles exposed to heterosexual substrates are different from those by voles exposed to homosexual substrates. Voles exposed for heterosexual substrates preferred for familiar substrates at different intervals after exposure. In the other hand, voles exposed to homosexual substrates preferred to the novel odor at different intervals. We have not found sound interpretation on this inconsistency by far.

Some researchers suggest that one must be careful in interpreting any experiment concerning memory, because the behavior exhibited is not a direct measure of memory; the performance observed is influenced by memory but may also be influenced by other factors (Johnston, 1993). The choice of stimulus animal is most critical among the factors (Ferguson *et al.*, 2002). Intact males and females do bring about increased levels of aggression and sexual behavior in the test subjects. Because juvenile males provided relatively neutral stimulus value and ovariectomized females make excellent stimulus animals and can be used repeatedly over weeks or even months, they have been used in several experiments. Our results also indicate that the behavioral paradigms in the present paper may be useful for investigating recognition for individual scent signatures and the ability to recognize familiar versus novel individual scents using substrates as stimulus.

Using this behavioral paradigm, our findings support the hypothesis that the different vole species and different genders may have different social recognition abilities. It is likely that social organization, sexual behavior, ecology and life history strategy may affect the social recognition. Future research can explore what specific signal used in

social recognition, sensory, perceptual mechanism and neuroendocrine bases involved.

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