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Evidence of Odor Priming: Edibility Judgements are Primed Differently between the Hemispheres

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Abstract

In olfaction, there is only weak evidence of repetition priming. Repetition priming was therefore investigated in two experiments using birhinal presentation of odors at study and monorhinal at test. Experiment 1 demonstrated repetition priming for repeated judgements of edibility in terms of response latency, but not in terms of correctness. No differences were found between the hemispheres (nostrils). Experiment 2 utilized a slightly different design, in which identity of odors was studied and judgement of edibility was tested. This time, only the right hemisphere (RH) was associated with priming. This persistence of RH priming should be seen in the light of a general tendency for superiority of the left hemisphere for correctly judging edibility. It is concluded that the olfactory system benefits from previous exposure/processing just as do vision, audition and touch. In line with previous research in vision, it is suggested that RH priming may be more associated with perceptual priming and left-hemisphere (LH) priming with conceptual priming.

Introduction

Procedural memory (Cohen and Squire, 1980; Squire, 1987) or implicit memory (Graf and Schacter, 1985) has been under intense investigation during the last two decades. Repetition priming (henceforth referred to as 'priming'), especially, has been of considerable interest. Priming has been demonstrated and replicated for the spatial senses: vision, audition and touch, and is defined as the facilitation of task performance through prior experiences in the absence of conscious or intentional recollection (Schacter, 1987).

In olfaction, there is scarce evidence of odor priming, partly because there is very little published on implicit testing of olfactory memory. Schab and Crowder (Schab and Crowder, 1995) did, however, perform several experiments aimed at demonstrating priming for odors. The authors concluded that the results provided a surprisingly bleak picture of odor priming in cases where it would be expected for visual and lexical stimuli. For instance, detection thresholds were unaffected by previous exposure to an odor and/or its name. Odor identification thresholds were lowered by previous exposure to an odor's name, but not additionally so when the odor itself was included at study. Latency for pleasantness ratings were also unaffected by exposure to the odor name in combination with the odor itself or with the imagery of that odor. The most convincing result, according to the authors, concerned priming of suprathreshold identification. Exposure to name and odor at study gave significantly better identification scores in the test phase, 5 min later, than did the name-only condition (which by itself yielded significant priming). The authors interpreted this increase as 'odor priming', as opposed to just 'name priming'.

Because odors, in general, are quite difficult to identify (Cain *et al.*, 1998), it is possible that the condition where odors and names were both present in the study phase is contaminated with explicit learning of which name should go with which odor. This information was likely to enhance performance during the test phase. Indeed, only ~30% of the odors were correctly identified in Schab and Crowder's study when appearing as control odors. Schab and Crowder argued that using an odor-only condition would yield ambiguous results, since we do not know for sure whether or not participants subvocally verbalize the name of the odors at study. This is probably true. It should be noted that a paper in German on this topic did reveal better and faster naming for primed odors in an odor-only condition compared to control odors (Wippich, 1990).

In a study on olfactory priming (M.J. Olsson and W.S. Cain, submitted for publication), it was acknowledged that most theories on object naming would agree that at least three serial stages are present in this process: object identification, name activation, and response generation (McCauley *et al.*, 1980; Johnson *et al.*, 1996). Olsson and Cain attempted to avoid name priming by using odors without explicitly asking for, or presenting, the names during the study phase and then measuring the reaction times for

subvocal identification (i.e. no naming was required). In the test phase, faster latencies were found for primed compared to control odors. In another study (Olsson, 1999), participants were asked to judge whether or not primed and control odors matched a target odor. Results revealed both negative and positive priming (in terms of response latency), dependent on whether odors at study were correctly identified or not, respectively. To conclude, priming of odors may well occur. But, more research is needed to assess the existence, extent and nature of such olfactory priming.

With regard to cerebral lateralization of priming, there are some reports on differences between left-hemisphere (LH) and right-hemisphere (RH) priming for vision and audition. Schacter (Schacter, 1994) extended the proposal that priming reflects largely the operations of a perceptual representation system (Tulving and Schacter, 1990). He argued for further fractionation of visual and auditory word-form systems into lateralized subsystems: an LH subsystem that operates on abstract (but modality-specific) word-form information and an RH subsystem that operates on highly specific visual or auditory perceptual information. Moreover, Marsolek and colleagues (Marsolek *et al*., 1992, 1994; Marsolek, 1999) presented evidence for dissociable neural subsystems subserving different types of priming in LH and RH. Marsolek argued that LH works more effectively than the RH when priming is based on abstract-category information, whereas the contrary is true when priming is specific. In conclusion, there are reasons to believe that priming may reveal itself differently in different hemispheres for any modality tested.

The olfactory epithelia projects largely to the ipsilateral hemisphere with only one of six projections crossing the midline via the anterior commissure (Brodal, 1981). Several studies have shown that RH brain lesions have disrupted olfactory functioning more severely than LH lesions in tests of odor discrimination (Abraham and Mathai, 1983; Martinez *et al*., 1993; Rausch *et al*., 1977) as well as in a test of episodic recognition memory (Jones-Gotman and Zatorre, 1993), but see Eskenazi *et al*. (Eskenazi *et al*., 1983). In normal individuals tested monorhinally (which will be the case in this study), a right-nostril advantage has been seen for odor-quality discrimination (Zatorre and Jones-Gotman, 1990, 1991), absolute detection thresholds (Youngentob, 1982; Cain and Gent, 1991)—but see Betchen and Doty (Betchen and Doty, 1998) and Zatorre and Jones-Gotman (Zatorre and Jones-Gotman, 1990, 1991)—and episodic recognition (Martinez *et al.*, 1993) (M.J. Olsson and W.S. Cain, submitted for publication), but not in Bromley and Doty (Bromley and Doty, 1995). Monorhinal testing of odor identification has led to mixed evidence. Herz *et al*. (Herz *et al*., 1999) presented evidence of a substantial advantage for the left nostril, whereas Jones-Gotman *et al.* (Jones-Gotman *et al.*, 1997) did not find such a difference. Odor identification has been tied to LH functioning for split-brain patients (Gordon and Sperry, 1969) and patients with damage to the prefrontal cortex (Potter and Butters, 1980).

In brain-imaging studies of functional localization and lateralization of the human olfactory cortex, the orbitofrontal cortex exhibited right unilateral or higher activation during birhinal presentation of odors (Zatorre *et al*., 1992; Jones-Gotman *et al*., 1993; Dade *et al*., 1997; Yousem *et al.*, 1997; Sobel *et al.*, 1999). Although there is mixed evidence of functional differences between the hemispheres, our review would favor the RH as predominant in olfactory processing that does not involve explicit identification and naming of odors. However, more data as well as knowledge about how the hemispheres interact, are needed (Doty *et al*., 1997).

The first aim of the current study was to demonstrate repetition priming for olfactory stimuli using a test paradigm that involves processes specific to olfactory functioning. As noted before, identification scores for common odors rarely exceed 50% correct. With respect to this, it has been argued that veridical identification of odors with precise names does not appear as important from an ecological and evolutionary standpoint as does categorical identification (de Wijk *et al*., 1995). In our opinion, edibility may constitute such a category. Judgements of edibility also have the advantage of being an easier task for the participants than is naming. Edibility judgements do not require the knowledge of odor names or even precise odor identification. It should be noted, however, that edibility judgements are far from perfect, especially for the elderly (de Wijk and Cain, 1994).

The current study employed edibility judgements in response to repeated odor presentations in order to investigate odor repetition priming. A first experiment investigated whether the edibility judgements were enhanced if they were repeated for the same odors. A second experiment aimed at testing whether the priming effect observed in the first experiment was specific to the fact that the same task was repeated between study and test. Participants in the second experiment were therefore asked to identify odors (rather than to judge the edibility) at study and were later in the test phase asked to judge the edibility of these and control odors. In both studies, priming was measured as the facilitation of latency and correctness of edibility judgements.

The second aim of this study was to tap potential differences between the cerebral hemispheres with regards to priming as well as general speed and correctness of edibility judgements. Odors were therefore presented monorhinally at test.

Experiment 1

Materials and method

Participants

Thirty-two females and 32 males ranging in age from 20 to 46 years (arithmetic mean = 26.9; SD = 5.6) participated.

Participants were students from Uppsala and Stockholm Universities and were given movie tickets or course credits for their participation. To minimize individual differences with regards to side of hemispheric dominance, only right-handed people participated. The handedness was determined through the Edinburgh Inventory of Handedness—EIH (Oldfield, 1971). A maximally right-handed person scores 10, whereas a maximally left-handed person scores 0. The participants scored on average 9.80 (SD = 0.56).

All participants reported good health, a functional sense of smell, and absence of severe asthma and allergies. None of them were taking any prescription drugs at the time of the test. Ten of the participants were smokers, but none of them had smoked in the hour prior to the test. None of the participants reported anything about their health status that could be considered relevant for their olfactory functioning at the time of the test.

Stimuli

A total of 48 odorants representing common items comprised the stimulus array. Only real-world items were used. Half of the odorants were edible and the other half were not. The total array was divided in two sets (A and B) balanced for edibility (see Appendix). Half of the time the A set served as the priming set and the B set as the control set, and for the other half their functions were reversed. Separate analyses of variance revealed no difference between stimulus sets A and B in Experiments 1 and 2. Odorants were placed in 250 ml jars of amber glass. Cotton pads obscured the sight of the odorant at the time of smelling.

Design

The experiment was divided in three different parts: a study phase and a test phase, for the measurement of priming, and a final phase for odor identification. In the study phase, 24 odors were judged for edibility following birhinal presentation. In the test phase, the 24 target odors and 24 new ones were judged for edibility. In this phase, odors were presented monorhinally. Half of the odors in the test phase were smelled via the left nostril and the other half via the right nostril. Half of the odors presented to each nostril represented something edible and the other half something inedible. Odor set (A or B) and gender were also balanced into this factorial design. All odors were presented in a randomized order unique for each participant in all phases. Priming was measured both in terms of response latency and correctness. In the identification phase, participants were exposed to all 48 odors birhinally and attempted to name or otherwise describe the odorous objects as precisely as possible.

Procedure

Before a session started, the participants answered some questions about their health, age and smoking habits. They also answered three questions about their hunger: (i) are you hungry? (yes/no); (ii) how long has it been since your last meal? (iii) what is your subjective estimation of your hunger at the present time on a scale from 1 to 10?

In the study phase, the set of 24 odors was presented to the participants one at the time. They were asked to take a single sniff and to vocalize 'yes' or 'no' to indicate whether the odor represented something edible or not. Between study and test phases, all participants filled out the EIH, which also served as a distraction task. The study–test interval also included some practice trials for the test phase.

In the test phase, odors were placed one at the time in front of the participant, who was asked to lean forward towards the jar under gentle exhalation and with the irrelevant nostril obstructed with the thumb. Participants inhaled the odor vapor in response to a sound. As soon as the participants knew the answer, they vocalized 'yes' or 'no'. The test phase was recorded on a tape recorder. The response latency, i.e. the time between the go signal and the participants' vocalization of their responses, was later measured from the tape recordings under circumstances that made the measurement of latency double blind.

The identification phase took place 5 min after the test phase. The participants smelled the 48 odors birhinally in the same order as in the test phase, but were here asked to identify the odors by name. Participants were given 10 s to name the odor before next odor was presented to them.

Results and discussion

Response latency

Analyses of individual response distributions of latencies were conducted to check for the positively skewed response distributions that can result from reaction time tasks. Mean skewness for linear latencies was 1.17 compared to 0.39 for logarithms of latencies (a symmetric distribution would yield a skewness of zero). This indicates that linear latencies, in particular, yield positively skewed response distributions. Therefore, geometric means of latencies were used to represent individual values of central tendency, whereas arithmetic means were used for the group. An alpha level of 0.05 was considered statistically reliable.

Response latencies were submitted to a 2 (male, female) × 2 (primed, control) × 2 (edible, inedible) × 2 (left, right) ANOVA with repeated measures on the last three factors. Only one significant main effect was observed: overall, primed odors yielded faster responses across participants (1746 ms) than did control odors (1850 ms) [$F(1,62) = 27.09$, $P < 0.0001$, $\eta^2 = 0.30$], evidencing odor repetition priming.

Concerning the lateralization of priming, the current study did not evidence any explicit tendencies towards a left or right side advantage [$F(1,63) = 0.34$, n.s.] (Table 1). The priming effect, measured as savings of latency, in the left and right sides were 112 and 95 ms, respectively, which are reliable differences according to pairwise, two-tailed t-tests [$t(63) = 4.09$, $P = 0.0001$ and $t(63) = 4.17$, $P < 0.0001$,

Table 1 Response latencies and correctness for edibility judgements following exposure of primed and control odors to left and right nostrils, and for overall data

	Response latency (ms)		Correctness (%)	
	Control	Primed	Control	Primed
Left	1873	1759*	78.7	81.7**
Right	1828	1733*	77.5	79.1
Overall	1850	1746*	78.1	80.4

Significantly different from control odors at $*P \leq 0.0001$ or $**P < 0.10$.

respectively]. Hence, the observed repetition priming was not lateralized between the nostrils. There was also no evidence of a general difference in processing speed between the nostrils [$F(1,63) = 1.07$, n.s.] or between edibles and inedibles [$F(1,63) = 1.46$, n.s.].

The only (marginally) significant two-way interaction observed was between nostril and edibility factors [$F(1,62) = 3.92$, $P = 0.05$, $\eta^2 = 0.06$]. Response latencies for edibles presented to the right side (1776 ms) were ~4% faster compared to the left side (1845 ms), whereas left and right latencies for inedibles were close to identical between the sides (1787 and 1785 ms, respectively).

The three different measures of state of hunger showed weak and non-significant correlations (product-moment) with the size of priming that were assessed for each individual (ratio of mean response latency for primed and control odors), also when calculated for each nostril. Participants' state of hunger did therefore not seem to influence the size of priming. Interestingly, it could be noted that time of day did influence the size of priming. According to 95% confidence intervals, participants that were tested before noon showed significantly more priming than those tested in the afternoon. There were no significant main or two-way interaction effects associated with smoker status.

Edibility judgements

An ANOVA (as above) was performed on percentage of correct edibility judgements. Inedibles were more often correctly classified (84%) than were edibles [75%; $F(1,62) = 16.90$, $P = 0.0001$, $\eta^2 = 0.21$]. With regards to the rather low performance levels, it could be speculated that what is nominally edible may not always be found edible to the particular participant at all times. There were no other significant main effects. Proportion of correct edibility judgements for primed odors was just non-significantly higher for primed odors compared to control odors [$F(1,62) = 2.75$, n.s.] (Table 1). Thus, the priming observed in this experiment is reflected in facilitation of processing speed rather than correctness.

The comparison between the nostrils did not reveal any significant differences, although the left nostril tended to be more accurate [$F(1,62) = 2.46$, n.s.] (Table 1). There were no significant two-way interactions.

Interestingly, there was no correlation between primability and the correctness scores for edibility judgements across the 48 odors ($r = 0.01$). There were no significant main or two-way interaction effects associated with smoker status.

Odor naming

In the third phase of the study, participants were birhinally presented all 48 odors again and asked to name them. Responses were coded as hits (to say 'orange' for orange), close misses ('citrus fruit' for orange) and far misses ('apple' for orange). To form individual correctness scores for identification (ID), hits were scored as one point, close misses as half a point, and far misses as zero.

An ANOVA of three two-level factors was conducted on the ID scores: primed/control × edibility × gender. Edible odors were correctly named more frequently (36%) than inedibles (22%) [$F(1,62) = 82.46$, $P < 0.0001$, $\eta^2 = 0.57$]. There were also significant differences between odors that had been presented in the study phase (32%) and those that had not (26%) [$F(1,62) = 9.13$, $P = 0.004$, $\eta^2 = 0.13$]. No other reliable main or interaction effects were observed. Moreover, smokers were not significantly different from non-smokers in terms of correctness of odor names.

To see whether the identifiability of an odor would have any implication for its primability, correlations (r) between ID scores and latency ratios (primed/control) were calculated using the odor as the statistical unit ($n = 48$). The correlation was $r(47) = -0.08$, n.s., indicating that the identifiability of odors could only account for <1% of the variance in primability. The same comparison made between identifiability and primability of odors tested via left [$r(47) = 0.00$] and right nostrils [$r(47) = -0.11$] also yielded non-significant correlations.

Correlations were also calculated across the 48 odors between the ID and edibility scores. If successful identification would be necessary for accurate judgements of edibility, this correlation should be very high. However, the correlation was quite low, $r(47) = 0.286$, and marginally significant at the 5%-level.

Experiment 2

Our main goal in Experiment 1 was to demonstrate repetition priming for olfactory stimuli. The results indicated that primed odors were categorized as being edible/inedible significantly faster, but not more accurately, than were control odors. In the literature, repetition priming tasks are typically characterized as either predominantly perceptual or conceptual in nature (Roediger and McDermott, 1993). It has been argued, however, that a growing number of tasks in the literature are difficult to classify in terms of this dichotomy (Roediger, 1990; Gabrieli, 1998). For the priming in Experiment 1, it is possible that the critical processing

concerned some aspect of stimulus meaning, which would point to conceptual repetition priming. For instance, participants may have been engaged in some categorization of odors in a number of edible and inedible subcategories. On the other hand, since not only the task but also the stimulus form was identical between study and test, perceptual priming may well have predominated.

To further investigate the nature of the olfactory priming observed in Experiment 1, the experiment was replicated with one major change. In the study phase, participants were asked to identify odors instead of judging their edibility. Odors were, however, still judged for edibility at test, as in Experiment 1. If priming persisted here, it could be argued to be perceptual rather than conceptual, since the perceptual representation is the same between the study and test in the two experiments. If priming were to disappear in Experiment 2, it could be argued that the priming effect in Experiment 1 was dependent on repeated judgements, rather than repeated exposure (perception). Of course, this reasoning holds only if edibility judgements are independent of odor identification. We have earlier argued that edibility judgements do not require knowledge of odor names or even precise odor identification. This notion is also supported, as we will see below, by the fact that edibility judgements on the average are considerably faster than judgements of identification.

Materials and method

The experimental method was identical to that of Experiment 1 with some exceptions reported below.

Participants

Sixteen females and 16 males who ranged in age from 19 to 43 years (AM = 23.21; SD = 4.41) participated. Participants were students at Uppsala University and were given movie tickets or course credits for their participation. All participants were right-handed (EIH scores averaged 9.69, SD = 0.69).

All participants reported good health in general, a functional sense of smell and absence of severe asthma and allergies. None took any prescription drugs at the time of the test. Fifteen of the participants were smokers, but none of them had smoked in the hour prior to the test. None of the participants reported anything about their health status that could be considered as relevant for their olfactory functioning at the time of the test.

Design and procedure

Two changes from Experiment 1 should be noted. First, the timing of the edibility judgement was done differently. In the Experiment 2, participants started to smell the test odorant upon an audible signal that coincided with the start of a timer. When the participant knew the answer, they stopped the timer by pressing a button on a handheld device with their right thumb. Response latencies from Experiment 1 and 2 are therefore not comparable in size. Second, there was no identification phase in the Experiment 2.

Table 2 Response latencies and correctness for edibility judgements following exposure of primed and control odors to left and right nostrils, and for overall data

	Response latency (ms)		Correctness (%)	
	Control	Primed	Control	Primed
Left	1324	1313	80.8	82.0
Right	1384	1291*	77.0	78.3
Overall	1348	1308	78.9	80.1

*Significantly different from control odors at $P < 0.05$ according to a paired *t*-test (two-tailed).

Results and discussion

Response latencies

Latencies for judgements of edibility were averaged geometrically across trials for each individual and condition (Table 2). The individual means were then submitted to an ANOVA (primed/control × edibility × nostril × gender). Overall, response latencies for primed odors were non-significantly lower than latencies for control odors [$F(1,30) = 2.64$, n.s.]. However, when priming was analysed for each side separately, priming was evident when tested via the right nostril but not via the left. The analysis of interaction between the primed/control and nostril factors yielded $F(1,30) = 5.26$, $P = 0.03$, $\eta^2 = 0.15$ (Table 2). No other significant interactions were found for response latency.

Overall response latencies for odors presented to the left nostril (1318 ms) were non-significantly lower than those for the right nostril (1338 ms) [$F(1,30) = 0.15$, n.s.]. In other words, there was no general difference in processing speed between left and right sides of the nose. Latencies for edibles (1312 ms) were somewhat, but non-significantly, faster compared to those for inedibles (1344 ms) [$F(1,30) = 2.20$, n.s.]. There were no significant main or two-way interaction effects associated with smoker status.

Edibility judgements

Correctness scores for edibility judgements were calculated as proportion of correct responses given to edibles and inedibles and were then submitted to an ANOVA (primed/control × edibility × nostril × gender). As in Experiment 1, priming did not enhance correctness of edibility judgements. The tendency from the previous experiment for higher general correctness scores to be associated with left nostril rather than right persists in the results of the current experiment [$F(1,30) = 2.39$, n.s.] (Table 2). When data from both experiments were analysed in a repeated-measures ANOVA with experiments (1 and 2) as a between-subjects factor, the results were $F(1,94) = 5.40$, $P = 0.02$, $\eta^2 = 0.05$, indicating that overall edibility judgements were, indeed,

reliably more correct when odors were presented to the left nostril or hemisphere. Concordant with the previous experiment, edibility judgements were more accurate for inedibles than for edibles [$F(1,30) = 12.99$, $P = 0.001$, $\eta^2 = 0.30$]. This result possibly reflects an adaptive decision bias pointing to the importance of not ingesting inedible substances. There were no significant main or two-way interaction effects associated with smoker status.

General discussion

There is only weak evidence of olfactory priming. Olfactory priming was therefore investigated. In Experiment 1, repeated judgements of edibility of odors yielded priming in terms of response latency, but not in terms of correctness. Response latencies for primed odors were ~6% faster than for control odors. No differences were found between the hemispheres (nostrils). The conclusion is that task performance is facilitated by previous exposure/processing in olfaction just as in vision, audition and touch.

The second experiment utilized a slightly different design, in which identity was studied and judgement of edibility was tested. This time, only RH tests demonstrated priming, which was of the same size as in Experiment 1; latency savings averaged ~7%. Why priming was not evident when probing LH functioning is not clear. As mentioned earlier, experiments in vision indicate that RH priming is more dependent on perceptual agreement between study and test than is LH priming (Marsolek *et al*., 1992; Marsolek, 1999). Similarly, it could be speculated for the current data that left and right hemispheres were primed for different reasons in Experiment 1. Since RH priming persisted when judgements differed between study and test and LH priming did not (Experiment 2), it is possible that RH priming primarily is driven by perceptual processes, whereas LH priming is dominated by conceptual processing. More specifically, RH priming could be dependent on the overlap in perceptual processing between study and test, and less dependent on the similarity between study and test tasks. LH priming, on the other hand, may be dependent on some conceptual processing necessary to make the edibility judgement—for instance, the categorization of odors into some number of edible and inedible subcategories, such as spices, cleaning products, etc.

In terms of methodology, it is interesting to note three things with respect to using edibility judgements in a repetition priming design. First, the task is easier to perform than is identification. This means that we will get fewer missing values for judgements of edibility than of identity. Second, the reaction times are relatively fast for edibility judgements. Mean response latency for participants to indicate that they knew whether a control odor was edible or not was ~1350 ms in the current study (Experiment 2), which should be compared to ~2100 ms to indicate identification in Olsson and Cain's study (M.J. Olsson and W.S. Cain, submitted for publication). This is probably a conservative measure of the latency difference, since Olsson and Cain used 12 highly identifiable (i.e. fast) odors and the current study used 48 odors that varied in identifiability. This indicates that edibility judgements are not conditional on previous decisions of identity. Third, it should also be noted that there was no correlation, across odors, between the primability of odors and their identifiability or between the former and their edibility judgement scores. The outcome of the current priming procedure is therefore unlikely to vary with the selection of odorants. This may be an advantage, since there are reasons to believe that odor memory performance as measured by many tests (Olsson, 1999) may depend on different memory processes for odors that can be identified and those that cannot.

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Appendix

Set A		Set B	
Edible	Inedible	Edible	Inedible
Orange (peel)	detergent	lemon (peel)	dish detergent
Chocolate	snuff (Swedish)	coffee	cigarette butt
Curry	bar of soap	thyme	baby powder
Meat bouillon	nail polish remover	peanut butter	marking pen
Cloves	soft soap	nutmeg	kitchen cleaner
Cinnamon	glue	vanillin sugar	plastic padding
Tea	gasoline	ginger	engine oil (used)
Liquorice	bleach	fruit gum	furniture polish
Pickled cucumber	paint (water based)	soy sauce	shoe cream
Black pepper	window cleaner	dill	tobacco
Vicks (pastilles)	shampoo	strawberry jam	hair gel
Anise	tar	potato chips	toilet refreshener