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Evidence for Separate Perceptive and Semantic Memories for Odours: a Priming Experiment

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Abstract

Sixty-four subjects participated in an olfactory priming experiment comprising separate study and test phases. Priming was measured within the olfactory modality (intramodal condition) and from the visual modality to the olfactory modality (intermodal condition). In the study phase of the intramodal condition, subjects were exposed twice to a series of odours: once performing a semantic orientation task (deciding which of seven categories odour stimuli belonged to) and once performing a perceptual orientation task (judging the intensity, the hedonicity and the familiarity of odour stimuli). Half of the odour stimuli corresponded to edible products, the other half did not. The study phase of the intermodal condition was similar, with the exception that the names of the odours (instead of the odours themselves) were presented. In the test phase, subjects were presented with primed and non-primed odour targets and had to decide as fast as possible whether the target corresponded to an edible product or not. Response times and types were recorded by a computer. The analysis of response times revealed a priming effect in the intramodal condition only. Results are discussed in terms of separate perceptual and semantic subsystems that store odour representations.

Introduction

It has long been known that memory is not a single, undifferentiated cognitive ability. Instead, memory can be described in terms of different subsystems that store different kinds of information or carry on different types of processes. The fractionation of memory began when authors proposed dichotomies such as primary (or short-term) and secondary (or long-term) memories (Atkinson and Shiffrin, 1968). Most of the recent work about memory systems has been conducted within the long-term memory domain, and has concerned the explicit (or declarative) versus implicit (or non-declarative) memory dissociation (Squire, 1987; Schacter and Tulving, 1994). Studies with different types of amnesic patients have revealed a preservation of different forms of implicit memories, such as priming and skill learning, although explicit memory was severely impaired. If priming has received substantial experimental interest in the past 10 years to reveal intact memory performance in amnesic patients, it has also been used to assess the nature and the organization of information in memory in experiments with normal subjects.

Priming can be described as the influence of the processing of a previously encountered stimulus (the prime) on the processing of a second stimulus (the target), which can be either identical to the prime or related in some respect to the prime. It is usually assumed that priming rests on a 'spread of activation' process according to which the processing of the prime yields a pattern of activation in a neural network that propagates through the net (McNamara, 1992). When the same or a related stimulus is then perceived, the residual activation of memory traces facilitates (i.e. 'primes') the processing of the target.

It is common to distinguish perceptual from semantic priming, depending on the type of memory trace (i.e. representation) that is activated by the prime. Perceptual priming is observed when the prime and the target share perceptual attributes. This is the case, for example, when a visual prime and a visual target overlap with each other. In contrast, semantic priming is observed when a prime (e.g. doctor) and a target (e.g. nurse) are semantically related.

According to Kosslyn and Koenig (Kosslyn and Koenig, 1992), perceptual priming and semantic priming are mediated by distinct subsystems. Perceptual priming is mediated by a pattern activation subsystem that stores modality-specific patterns that correspond to the shapes of objects, whereas semantic priming is mediated by an associative memory subsystem that stores amodal representations. This distinction is consistent with the position of Tulving and Schacter (Tulving and Schacter, 1990; Schacter and Tulving, 1994). These authors suggest that perceptual priming takes place within a perceptual representation system made of a visual word-form system, an auditory word-form system and a structural description system. These systems operate at a presemantic level and do not require access to the meaning of the stimulus.

The Kosslyn and Koenig (Kosslyn and Koenig, 1992) and Tulving and Schacter (Tulving and Schacter, 1990) conceptions of memory functional architectures are in accordance with the fact that perceptual representations are stored in modality-specific subsystems, which implies that distinct networks are used to store visual form representations and auditory form representations, for example, whereas semantic representations are stored in an amodal subsystem. Therefore, semantic representations can be accessed by any perceptual channel. This architecture allows one to formulate critical predictions regarding results of priming experiments. For example, shifting modality from study to test stimuli should decrease or even suppress perceptual priming but not semantic priming. In addition, changing perceptual features between the prime and the target (i.e. reducing the perceptual overlap) should decrease perceptual priming but not semantic priming.

These predictions have been confirmed in several studies using, for example, word stem completion priming, which is known to mostly engage perceptual representations. Other authors (Graf *et al.*, 1985; Bassili *et al.*, 1989; Craik *et al.*, 1994) have reported less priming when the primes and the targets do not appear within the same modality. Moreover, Gibson *et al.* reported less priming when the primes and the targets did not appear in the same typography (Gibson *et al.*, 1993).

Although most of the critical priming work has been carried out in the visual and auditory modalities—where stimuli are relatively easy to control—we believe that shifting the modality and manipulating the surface feature of stimuli have similar effects in other modalities, such as olfaction. Indeed, we suggest that the principle of separating perceptual and semantic representations extends beyond the visual and auditory modalities and consists on a general principle of the architecture of our cognitive system.

In the present study, we conducted a priming experiment in which subjects had to decide whether odour targets corresponded to an edible product or not, to explore how shifting from the olfactory to the visual modality influences the processing of an olfactory target. We hypothesized that more priming would be observed in an intramodal, olfactory–olfactory condition than in an intermodal, visual–olfactory condition. However, the first aim of our study was to determine if intramodal olfactory priming could be elicited in the first place, given the difficulty to manipulate odours. Indeed, previous attempts to demonstrate a priming effect with odours have not yielded clear-cut results (Olsson and Cain, 1995; Schab and Crowder, 1995; Olsson, 1999).

Materials and methods

Subjects

Sixty-four (32 female and 32 male) students from the University Lyon 1 volunteered for participation in this experiment. The subjects ranged in age between 18 and 30 years. Each subject had normal or corrected to normal vision and no one had trouble breathing through the nose at time of testing. Thirty-two subjects (16 females and 16 males) participated in the intermodal condition, the other 32 subjects (16 females and 16 males) participating in the intramodal condition.

Stimuli, materials and apparatus

Twenty-four olfactory stimuli, half of which corresponded to edible products, were divided into two series of 12 odours (list a and list b) comprising six ‘edible’ and six ‘non-edible’ odours (Table 1). These odours have been selected in accordance with the results of a previous experiment in which 185 odours (pure chemical or mixtures) were rated in terms of intensity, familiarity, hedonicity, edibility and ease of naming by 71 subjects (Royet *et al.*, 1999). Only odours that were rated extremely high in terms of ease of naming and extremely high or low in terms of edibility were used in the present experiment. In addition, stimuli were distributed into list a or list b so that means and standard deviations of intensity, familiarity and hedonicity were as close as possible in each set of six odours (six ‘edible’ and six ‘non-edible’ stimuli per list).

Odours were maintained in white, 100 ml polyethylene squeeze bottles provided with a dropper (Osi, Strasbourg, France). They were diluted in mineral oil to form 5 ml of a solution (10% v/v) that was adsorbed by compressed filaments of polypropylene. In the case of ether, the concentration was only 1% v/v given its high volatility.

Twenty-four visual stimuli that corresponded to the name of each olfactory stimulus were drawn in New Century Schoolbook 24 typeface to appear in the center of the computer screen.

An air flow was generated with a compressor (Atlas Copco, France) and the air was then treated with a charcoal filter before reaching an air-dilution olfactometer. An odour was injected into the olfactometer by squeezing the polyethylene bottle. The odour was carried by the air flow and reached an anesthesia mask (Respiron, Europe Médical) placed on the subject’s face after a 100 ms interval. A thermic probe was attached to the mask and was located near the right nostril. The probe allowed the experimenter to monitor breathing by transmitting a signal into headphones supplemented by light emitting diodes. As the air flow was

Table 1 Stimuli used in list a and list b

List a	List b
Sea	banana
Lipstick	lily
Caramel	tangerine
Gardenia	smoked salmon
Anise	pine
Chocolate	ether
Jasmine	strawberry
Lemon	hyacinth
Chewing-gum	grapefruit
Paint	coconut
Peach	citronella
Tar	lavender

running continuously, odours were cleared from the mask before the next odour was presented.

A Macintosh SE computer was used to present instructions, attention signals and visual stimuli. The computer also recorded response times and the keys used to respond on the computer keyboard. The Macintosh was connected to the olfactometer so that the internal clock of the com- puter was triggered when a stimulus was injected into the olfactometer.

The experiment was conducted in a room of ~40 m^3. In order to eliminate any undesirable odour from the experimental room, two air extractors (ELGE, Villeurbanne, France and Nather, Portes-les-Valence, France), with a flow of 225 m^3/h each, were operating continuously during the experiment.

Design and procedure

Each subject participated in a study phase in which they were exposed twice with a series of odours and in a test phase where they had to judge whether odour targets corresponded to edible products or not. The experiment was presented as if it consisted of three different experiments. The task to perform at test remained unknown for the subjects until the second study phase was over.

Subjects were seated in a quite room, in front of the computer screen. The anesthesia mask remained on the subjects' face during the whole experiment, and instructions were presented on the computer screen and complemented verbally—if necessary—by the experimenter. Subjects were asked to breath regularly without sniffing.

In one of the study phases (categorization) of the intramodal condition, subjects had to decide which (among seven) category best characterized the stimuli. The categories were 'chemical', 'fruit', 'nature', 'flower', 'cookies', 'fish' and 'others'. An attention signal appeared on the computer screen at the beginning of each trial. The odour prime was injected into the olfactometer just before the beginning of the next breathing phase and the signal 'odour' appeared on the screen simultaneously. Subjects had 10 s to select the most appropriate category by marking the response with a X on a sheet of paper. After the 10 s period, the attention signal of the next trial appeared again on the screen. The order of presentations of the stimuli was pseudo-random, with the constraint that no more than three edible or non-edible trials appeared in a row.

In the other study phase (description) of the intramodal condition, subjects had to rate each odour according to a 10-point scale in terms of subjective intensity, hedonicity and familiarity. The procedure was identical to the one of the categorization study phase, with the exception that subjects had different instructions and response sheets.

Different pseudo-random trial orders were used for the categorization and the description study phases, and half of the subjects were presented with the categorization study phase first the other half with the description study phase first. In addition, half of the subjects (group A) were presented with the stimuli of list a, whereas the other half (group B) were presented with the stimuli of list b.

The study phases of the intermodal condition were identical to the study phases of the intramodal condition, with the exception that the name of the odour was presented instead of the odour itself. The name appeared on the computer screen, replacing the signal 'odour' of the intramodal condition. The presentation was also synchronized with subjects' breathing.

The test phase was identical for all subjects. They were told that they would participate in a new experiment unrelated to what they had done before. They were asked to read carefully the instructions that appeared on the computer screen and were then presented with 24 odour targets (odours from lists a and b), half of which had been encountered in the study phases, the other half being new. The stimuli were presented in a pseudo-random order with the constraints that no more than two stimuli of the same list and no more than two edible stimuli appeared consecutively. The stimulation procedure was identical to the one used in the study phases of the intramodal condition. Subjects were required to decide as fast as possible whether each stimulus target corresponded to an edible product or not by activating the appropriate key of the computer keyboard. Subjects had to respond with their left or right index finger, half of the subjects being instructed to respond 'edible' with the left index finger, the other half with the right index finger. Response times and response types were recorded directly by the computer.

Results

Separate analyses of variance (ANOVAs) were performed on mean response times and numbers of errors on the data of the test phase. All effects or interactions not reported here did not reach the 0.05 probability criterion. We may, however, report non-statistically significant results when they are of theoretical interest.

Response time analysis

We performed an ANOVA on the means of correct response times with Condition (intramodal, intermodal) and Group (A, B) as between-subjects factors, and Response (edible, non-edible) and Type (prime, non-prime) as within-subjects factors. Before performing the means, response times higher than twice the mean of their corresponding cell (defined by the crossing of the factors Response and Type) and response times of <150 ms were replaced by the mean of the cell. This procedure only concerned <3.1% of the trials.

The most important result was that subjects responded generally faster for primed stimuli than for non-primed ones [$F(1,60) = 6.318$, $P < 0.015$]. Contrast analyses comparing primed and non-primed stimuli for each condition revealed that priming was found in the intramodal condition [$F(1,60) = 8.12$, $P < 0.007$], whereas no priming was found in the intermodal condition [$F(1,60) < 1$, NS]. This result is illustrated in Figure 1.

The ANOVA also revealed that subjects of group A exhibited more priming than subjects of group B for the interaction of the factors Type and Group [$F(1,60) = 4.056$, $P < 0.05$]. However, this effect in turn depended on the response for the interaction of the factors Type, Group, and Response [$F(1,60) = 6.80$, $P < 0.015$]. In order to better understand the nature of this interaction, we performed contrast analyses comparing response times for primed and non-primed targets for each subjects group and response level. These analyses revealed that subjects of group A exhibited significant priming for both edible [$F(1,60) = 4.37$, $P < 0.05$] and non-edible stimuli [$F(1,60) = 9.62$, $P < 0.003$], whereas subjects of group B exhibited priming for edible stimuli [$F(1,60) = 5.71$, $P < 0.025$] only. Indeed, a trend towards an inverse-priming (i.e. interference) effect occurred in group B for non-edible targets [$F(1,60) = 3.30$, $P < 0.08$].

We then investigated whether this trend was due to the selection of the non-edible stimuli of list b or, more generally, to subjects' sampling. As the same stimuli—but different subjects—were used in the intramodal and intermodal conditions, we performed additional contrast analyses on the Type, Group, Response and Condition interaction that compared response times for primed and non-primed non-edible stimuli of group B in each condition. These analyses revealed that an inverse priming occurred in the intermodal condition only [$F(1,60) = 8.43$, $P < 0.006$], which makes it unlikely that differences in the stimuli could explain the trend towards an inverse-priming effect in group B for non-edible stimuli; rather, it seems more plausible that the trend occurred as a consequence of subjects' sampling.

Error analysis

We performed an ANOVA on the number of errors similar to the one performed on response times. First of all, the analysis revealed that relatively few errors occurred (16.02% errors in the intramodal condition and 16.28% errors in the intermodal condition). The ANOVA showed that more errors occurred for edible responses than for non-edible ones [$F(1,60) = 152.16$, $P < 0.00001$]. Thus, subjects could more easily reject non-edible stimuli than accept edible ones. This ANOVA also revealed an interaction of the factors Response, Condition and Group [$F(1,60) = 4.57$, $P < 0.04$]. However, this interaction has no theoretical interest. The most important result here is that no effect or interaction that involved the factor Type was significant in the error analysis. Hence, results observed in the response time analysis cannot be the consequence of a speed–accuracy tradeoff.

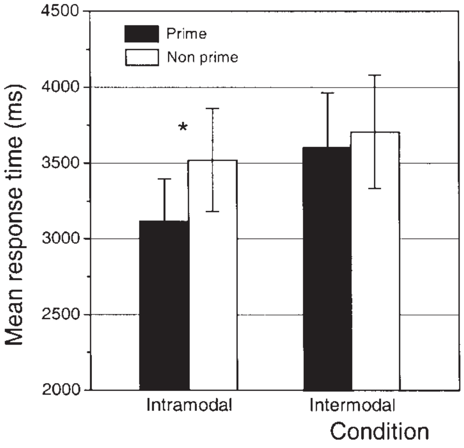

Figure 1 Mean response times for judging the edibility of prime and non-prime stimul in the intramodal (olfactory–olfactory) condition and in the intermodal (visual–olfactory) condition. Asterisk, significant difference between prime and non-prime ($P < 0.05$); vertical bars, SEM.

Discussion

Odours are more difficult to manipulate than visual or auditory stimuli, and the first aim of the present experiment was to investigate whether a priming effect could be elicited with odours. The observation that subjects responded generally faster to the stimuli they had encountered in the study phase revealed that we succeeded in eliciting such a priming effect. This observation was not contradicted by the analysis performed on the number of errors. Therefore, under the specific conditions we used in our study, everything happens as if odour processing were facilitated by the residual activation of memory traces (i.e. representations) due to a previous presentation of the same stimulus. Thus, our results parallel those observed with visual and auditory stimuli. We believe that the decision of edibility (as opposed to naming, for example) we used in the present experiment helped us to obtain the observed effects, since subjects could process odours with a reasonably low error rate.

The second aim of this experiment was to study the effects of shifting modality on olfactory priming. We expected more priming in an intramodal, olfactory–olfactory condition than in an intermodal, visual–olfactory condition.

Our results revealed that a robust priming effect occurred in the intramodal condition only. This result is consistent with a model of memory organization that predicts separate perceptual, modality-specific representations and semantic, amodal representations (Tulving and Schacter, 1990; Kosslyn and Koenig, 1992). According to such a model, shifting from the visual to the auditory modality would result in decreasing or even suppressing priming by losing the contribution of perceptual priming.

Thus, we suggest that perceptual olfactory priming is mediated by an olfactory pattern activation subsystem that stores modality-specific patterns that correspond to the ‘shapes’ of odours, just as the visual and the auditory pattern activation subsystems store visual and auditory shapes, respectively.

The fact that no significant priming occurred when we shifted from the visual to the olfactory conditions suggests that the priming task we used was perceptual rather than semantic. That is, the different types of processes performed in the study phases apparently did not yield the activation of those semantic representations that were necessary to judge the edibility of odours in the test phase.

Subjects were presented twice with each odour in the study phases in order to enhance perceptual encoding of the stimuli. It could be claimed that this procedure could have encouraged subjects to use explicit memory strategies in the test phase. We believe, however, that priming was not contaminated by explicit memory strategies for two reasons. First, explicit memory strategies would have occurred both in the intramodal and in the intermodal condition, and priming would have appeared in both cases. Second, subjects did not acknowledge having noticed that some of the stimuli presented in the test phase were identical to those they had encountered in the study phases. Thus, it appears that priming performance was probably not contaminated by or even did not result from explicit memory strategies.

It is important to note that odours are not like visual and auditory stimuli, because they cannot be easily decomposed into perceptual, explicit features. Nevertheless, we described in the present paper an example of priming within a modality, with such stimuli that could not be decomposable into explicit features. It seems difficult in such a case to explain perceptual priming in terms of an overlap of perceptual features. In addition, no mediation by words was encouraged in the intramodal condition where priming was found. Thus, the kind of priming we found here does not seem trivial, since it does not depend on the presentation of explicit perceptual features and is not mediated by words. It has to be understood in terms of the recurrence of a pattern of neuronal activation elicited by an odour stimulus, with no need for an explicit recognition of features.

There is considerable behavioural and neurological evidence that verbal mediation is only occasionally present, and is not essential in olfactory cognition (Herz and Engen, 1996). This particularity demonstrates a profound difference between olfactory cognition and cognition mediated by other sensory modalities. It explains why our results did not reveal a priming effect in the intermodal condition, as no semantic priming could be demonstrated. By contrast, it is well known that human experience of odours is primarily hedonic or aesthetic, and that odour-evoked memories are better than other cue-elicited memories because the former are more emotionally potent (Hinton and Henley, 1993; Herz and Cupchik, 1995; Herz and Engen, 1996; Herz, 1998). The stronger ability of odorants to induce emotional states explains why odours can successfully play a role as prime stimuli in a model of cross-modal affective priming (Hermans *et al.*, 1998). This specificity of odours is finally underlined by recent neuroimaging studies demonstrating evidence of functional dissociation between the left and right hemispheres (Zald and Pardo, 1997; Zald *et al.*, 1998; Royet *et al.*, 1999, 2000). Thus, our data and others clearly support a model of parallel processing in the left and right orbitofrontal cortices. The relative level of activation of left and right orbitofrontal cortices would depend on whether the olfactory judgement involves emotion or recognition, respectively.

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