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Gabriela Hossu, Luca Fantin, Céline Charroud, Jacques Felblinger, Muriel Jacquot, et al.. Neural mechanisms of odour imagery induced by non-figurative visual cues. *Neuropsychologia*, 2024, 196, pp.108836. 10.1016/j.neuropsychologia.2024.108836 . hal-04483316

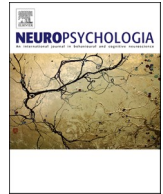
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Neural mechanisms of odour imagery induced by non-figurative visual cues

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ARTICLE INFO

Keywords:

Functional MRI
Olfaction
Mental imagery
Colour
Vision

ABSTRACT

Odour imagery, the ability to experience smell when an appropriate stimulus is absent, has widely been documented as being particularly difficult. However, previous studies have shown the beneficial effect of visual cues (e.g., pictures or words) to facilitate performance in numerous tasks of olfactory nature. Therefore, the use of visual cues to evoke odours seems relevant. In this study, our interest is directed towards non-figurative coloured arrangements, which result from a patented technology and aim at chromatically representing any smell from its chemical composition and sensory description. The aim of this study was to characterise the neural mechanisms of odour imagery facilitated by these non-figurative coloured arrangements. Using functional magnetic resonance imaging, we recorded and compared hemodynamic responses during odour imagery facilitated by non-figurative coloured arrangements and pictures. Our findings reveal that the use of non-figurative coloured arrangements during odour imagery solicits olfactory and non-olfactory brain regions (orbitofrontal cortex, insula, hippocampus, thalamus, dorsolateral prefrontal cortex and supplementary motor area), which are mainly involved in olfactory processing and multimodal integration. Moreover, very similar cortical activity was found between the use of non-figurative coloured arrangements and pictures during odour imagery, with increased activity in the supplementary motor area during the use of coloured arrangements only. Overall, non-figurative coloured arrangements could become a robust tool to visually evoke odours without requiring prior familiarity with the depicted odour. Future studies should use psychometric measures to determine the relationships between brain activation, odour imagery ability and vividness of the generated odour images.

1. Introduction

The existence of odour imagery, or “being able to experience the sensation of smell when an appropriate stimulus is absent” (Stevenson and Case, 2005), was long debated because of its difficulty to experience (Engen, 1987). Now commonly accepted in the scientific community, numerous studies have shown that successful odour imagery is still reported as less vivid than in any other sensory modality (Schiffstein, 2009; White et al., 1978). This phenomenon is usually discussed as the lesser importance of olfaction in our daily life compared to other sensory modalities, which negatively affects performance in all tasks of olfactory

nature. Yet, understanding odour imagery could contribute to some significant scientific advances, particularly in the field of healthcare. Indeed, it is well known that pleasant smells are effective at reducing transient states of discomfort, especially those induced by perceptual discrepancies (Keshavarz et al., 2015). However, odour diffusion also suffers from technological and psychophysical limitations, making its application in ecological environments difficult. Given the numerous psychometrical and behavioural resemblances between odour perception and odour imagery, some current studies are investigating the use of pleasant odour imagery for the alleviation of discomfort induced virtual environments. In order to have access to such applications which could

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benefit millions of users of virtual environments, it is nonetheless necessary to determine the best ways to facilitate the generation of mental images.

In this context, several studies have demonstrated that the use of visual cues such as colours and images can improve performance in olfactory tasks such as odour detection (Gottfried and Dolan, 2003), identification (Zellner et al., 1991), discrimination (Demattè et al., 2009), and influence orthonasal odour intensity (Koza et al., 2005), pleasantness (Zellner et al., 1991), or overall mental representation (Morrot et al., 2001). As suggested by Dalton (2002), these effects could be explained by the tendency of olfaction to be affected by top-down processes, notably when they are driven by visual stimulation. This highlights the importance of visual-olfactory crossmodal correspondences (*i.e.* the tendency for the human brain to associate information from one sensory modality with information in other modalities). Such associations are mainly explained by the integration of the statistical regularities of odour-colour pairings in our environment (Spence, 2011). Consequently, studies have shown that individuals internalize robust and reproducible associations between odours and colours (Dematte et al., 2006; Gilbert et al., 1996; Maric and Jacquot, 2013; Nehmé et al., 2016).

Therefore, use of visual stimuli to facilitate odour imagery seems an appropriate solution. In fact, odour labels have often been used in neuroimaging paradigms aiming at understanding the neural mechanisms of odour imagery. The majority of these studies revealed activations in the piriform cortex (primary olfactory cortex) as well as in associative olfactory brain regions such as the insula and orbitofrontal cortex (OFC – Bensafi et al., 2007; Djordjevic et al., 2005; Flohr et al., 2014; Plailly et al., 2012). The importance of the OFC in odour imagery may originate from its location at the intersection between the olfactory and visual pathways, resulting in its role in visuo-olfactory processing. Additional studies have revealed activations in the angular gyrus (Regenbogen et al., 2012) and inferior parietal lobule (Djordjevic et al., 2005; Lundström et al., 2019), which are also known for their role in multisensory integration. Therefore, odour imagery would require the recruitment of a multimodal network which has been suggested to be governed by the supplementary motor area (SMA – Leclerc et al., 2019). Yet, the use of odour labels to induce odour imagery has been subject to some debate. Criticisms have mainly argued that semantic information could influence the activated brain regions. More specifically, González et al. (2006) have shown that the simple action of reading odour-related words generated neural activity in the piriform cortex. This activity could reflect the anticipation of the arrival of a smell, or simply the action of sniffing rather than successful odour imagery itself (Royet et al., 2013). One way to address this bias would be to use non-figurative visual supports when facilitating odour imagery. Indeed, in addition to plain colours, Seo et al. (2010) have revealed the existence of robust associations between odours and abstract shapes. The absence of semantical meaning to these visual stimuli could cancel the anticipation phenomenon that constitutes the main limitation of often-used odour labels, or potentially other figurative visual supports. A good candidate corresponding to these expectations is non-figurative (non-semantic) coloured arrangements (Jacquot et al., 2013). Resulting from a patented scientific tool based on neural network algorithm (patent n° FR2992065), these arrangements represent any odour from its chemical composition and sensory description. Compared to plain colour patches, the complexity of non-figurative coloured arrangements allows for more efficient differentiation in the visually evoked smells. For example, smells of lavender, peppermint and cucumber are all usually associated to green hues (Maric and Jacquot, 2013; Spector and Maurer, 2012), whereas the respective non-figurative coloured representations evoke the appropriate odour percept and are significantly associated to their related odours (Jacquot et al., 2016).

The aim of this study was to characterise the neural mechanisms of odour imagery facilitated by non-figurative coloured arrangements in healthy volunteers. We expected activations in associative olfactory

cortices (insula and OFC) and SMA. The use of non-figurative coloured arrangements was compared to the use of pictures of odour objects, in order to explore the effect of semantics in complex, coloured visual facilitators of odour imagery. Because of the suggested effect of semantics on brain activity, we expected activity in the piriform cortex during the use of pictures only.

2. Material and methods

2.1. Population

Thirty right-handed female volunteers (mean age = 21.1 ± 1.9 years) took part in this study. All participants completed the Edinburgh Handedness Inventory test (Oldfield, 1971) and an 18-item version of the Ishihara colour test (Ishihara, 1918). To participate in this study, it was required to score at least 80% and 100% on these documents respectively, to ensure right-handedness and no colour blindness. All participants had normal or corrected-to-normal vision and reported a normal sense of smell with no olfactory dysfunction.

The study was conducted according to the Declaration of Helsinki and received ethical approval by the local ethics committee ("METHODODO" study; ClinicalTrials.gov Identifier: NCT02887053). This study was approved by ("Comité de Protection des Personnes EST-III", reference number 08.10.01) of the licensing ethics committee. Oral and written informed consents were obtained from each participant before inclusion.

2.2. Experimental procedure

The olfactory imagery fMRI paradigm consisted in two consecutive sessions (Fig. 1). In each session, a block design setup was used, comprising seven 60-s cycles, for a total duration of 420 s (7 min). Each cycle consisted in one control period during which a grey screen was presented for 25 s, followed by a 35-s stimulation period composed of seven different stimuli each presented for 5 s. Stimuli were either non-figurative coloured arrangements representing cucumber, orange blossom, cut grass, lavender, peppermint, rose and violet (session 1), or the corresponding pictures (session 2). The duration of presentation of visual stimuli was decided following pre-tests in healthy individuals. During these pre-tests, we observed that when odour imagery was successful, it occurred very fast. In order to limit boredom (which had been expressed when duration period was set to 7.5 s), we found 5 s as a good compromise, also being a multiple of our fMRI repetition time, allowing for synchronizing our paradigm with the MRI sequence. The presentation order of the visual stimuli was randomized for each cycle in each session. Throughout the study, participants were instructed to focus on odours evoked by the visual stimuli. They were informed that there was no correct or incorrect imagery, and that they were free to imagine any odour they thought corresponded to the visual stimuli. The sessions were deliberately ordered in a non-random fashion to avoid any influence caused by the presentation of non-figurative coloured arrangements right after the corresponding picture. Moreover, it was verified that the participants had never been exposed to or familiarised with the non-figurative coloured arrangements in the context of odour imagery. These measures ensured the spontaneous interpretation of the arrangements was preserved.

Following the odour imagery task, an oral interview was performed with each participant. In this interview, participants were invited to share any impressions on the experiment, and to qualitatively estimate their performance at the odour imagery task.

2.3. MRI data acquisition

The task stimuli were forward-projected onto a translucent screen located inside the MRI room using a projector placed directly outside the magnet bore. Participants viewed the screen via a mirror attached to the

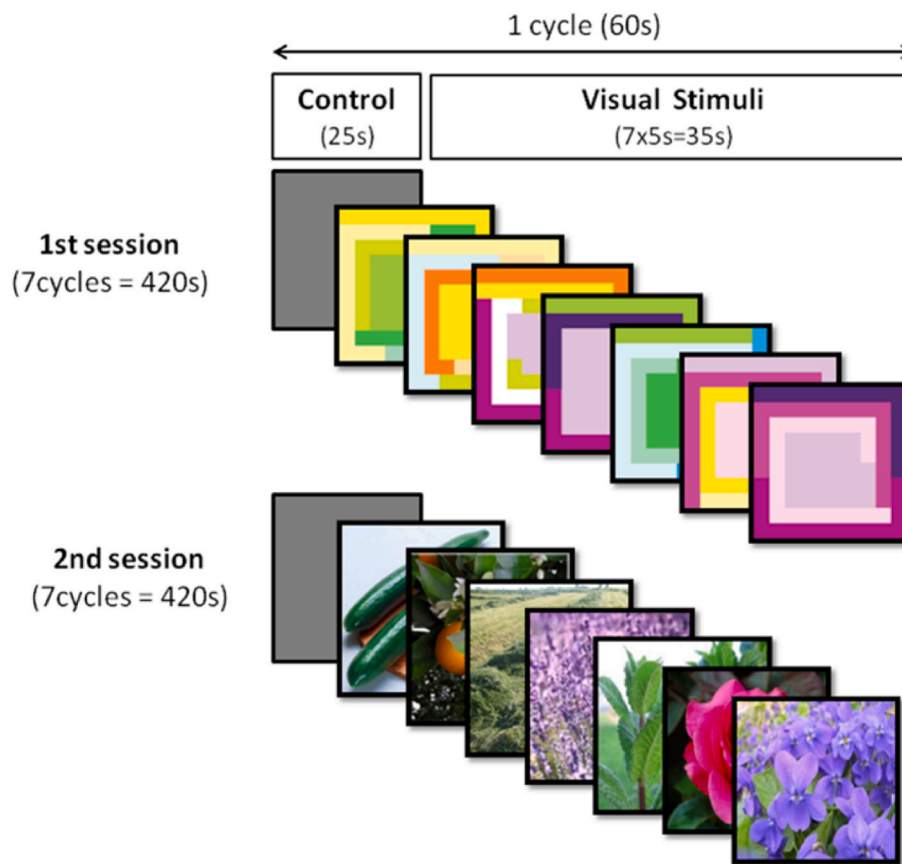


Fig. 1. Timeline of the fMRI paradigm.

head coil. All stimuli were projected onto the screen using ePrime software (Version 2.0, Psychology Software Tools Inc., Pittsburgh, PA, USA) and a calibrated projector (Panasonic PT-AE500E). The projection of stimuli was synchronized to the MRI scanner. Vision correction was performed using non-magnetic glasses, which can vary in the range of -5 to $+5$ with 0.5 dioptre steps.

Whole brain functional MR images were acquired using a 3-T magnet (Signa HDxt, GE Healthcare, Milwaukee, WI) equipped with an 8-channel receive-only head coil. One hundred sixty-eight volumes of BOLD Gradient Echo-echo planar images (GE-EPI) were obtained for each functional session with the following imaging parameters: repetition time (TR) = 2500ms, echo time (TE) = 30ms, 50 axial slices, slice thickness 3 mm, slices order: interleaved, in plane resolution $3 \times 3 \text{ mm}^2$, no interslice gap, flip angle 77 deg. One hundred and sixty-eight volumes parallel to the anterior–posterior commissural line covered the whole brain extending from vertex to the inferior parts of the cerebellum. For all participants, high-resolution anatomical images were acquired using a 3D fast spoiled gradient echo (FSPGR) sequence with the following parameters: TR = 11.2ms; TE = 5.1ms; flip angle 20 deg; in plane resolution $0.97 \times 0.97 \text{ mm}^2$; slice thickness 1.6 mm.

2.4. Data analysis

MRI data pre-processing and analysis were performed using SPM12 software (Statistical Parametric Mapping, Version 12, Revision 7219, Wellcome Department of Cognitive Neurology, London, UK). The standard pre-processing pipeline consisted of motion correction, spatial normalization and spatial smoothing using a $6 \times 6 \times 6 \text{ mm}$ full-width half-maximum Gaussian kernel. The difference between stimulation (non-figurative coloured arrangements or pictures) and control conditions (grey screen) was statistically evaluated using a general linear

model including realignment parameters, and by subtracting BOLD signal during the control condition to the stimulation condition ([Arrangements > Control]; [Pictures > Control]). The weight of the stimulation conditions was set to 1, and the weight of the control periods to -1 . Stimulation and control periods were modelled as boxcar regressors with durations corresponding to the full durations of the corresponding conditions for each cycle. A 128-s high-pass filter was used to remove non-physiological slow signal shifts. Contrasted parameter estimates images, describing brain activation for both stimuli (non-figurative coloured arrangements and pictures) were calculated at the participant level, then at the group level. Additionally, BOLD signal during both stimulation conditions was compared at the group level by subtracting one contrast to the other ([Arrangements > Control] – [Pictures > Control]) to compare the effect of arrangements versus pictures, and vice versa. For each visual condition and their comparison, brain activity was assessed using both whole-brain and region of interest (ROI) analyses. Prior to the analysis, the following were defined: the primary olfactory cortex (i.e., piriform cortex) and the “extended olfactory network” as described by Gottfried (2010) including the amygdala, orbitofrontal cortex (OFC), insula and the hippocampus (McNorgan, 2012). The thalamus, SMA (Leclerc et al., 2019), and dorsolateral prefrontal cortex (DLPFC) (Flohr et al., 2014) were also included. ROI masks were generated from the “neuromorphometrics” template (MNI space) introduced in SPM and were then registered to the functional space (Rolls et al., 2015). The piriform cortex was defined from a mask obtained from the authors of Seubert et al. (2013). The DLPFC was defined as the medial and superior frontal gyri. The OFC included the orbital and inferior frontal gyri. The ROI are represented in Fig. 2.

For whole brain analyses, a significance threshold of 0.05 was set at the voxel level, corrected for family-wise errors. For ROI analyses, the significance threshold was not corrected for the number of defined

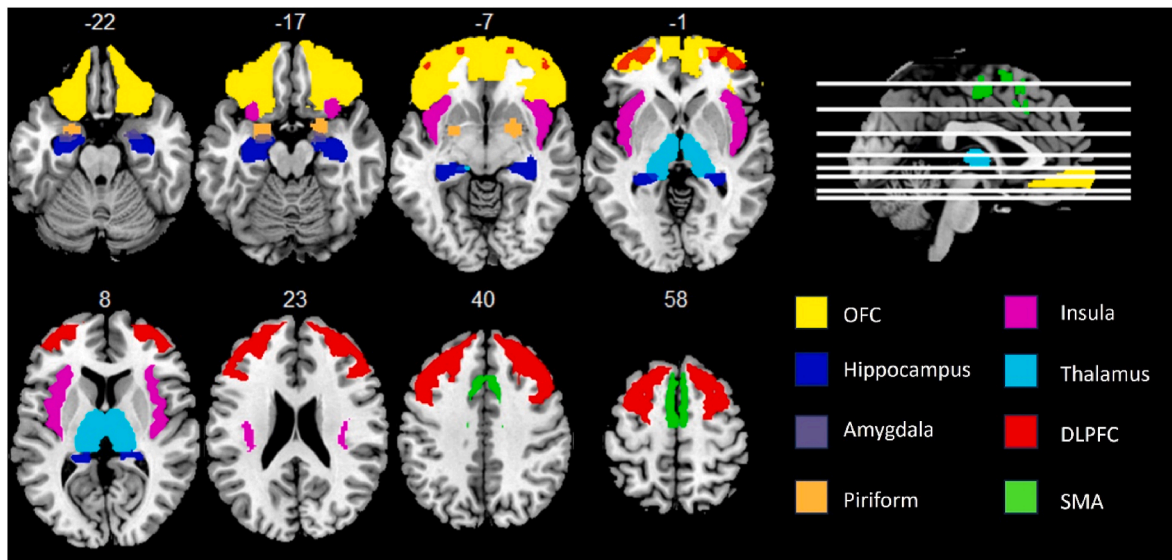


Fig. 2. Masks used for the ROI analyses.

regions accordingly with previous studies of odour imagery, for instance [Plailly et al. \(2012\)](#), which was compensated for by a more stringent threshold of 0.001 (uncorrected) at the voxel level. In both cases, a minimum of 10 voxels/cluster was defined. All graphical representations of brain activity were generated under MRICron using the ch2bet template.

3. Results

No data was lost or unusable due to excessive movement.

During the informal interviews following the fMRI exam, no participants verbalized being unable to perform the odour imagery task. All of them reported that they were more concentrated during the presentation of non-figurative coloured arrangements than pictures. Besides, about 30% of volunteers said that they used past experiences of taste and olfaction to associate odours to coloured arrangements.

3.1. Stimuli > control

The [Arrangements > Control] contrast revealed significantly higher

activation in multiple ROIs during the presentation of the non-figurative coloured arrangements as compared to the control condition (Fig. 3A). Bilateral clusters of activations were found in the OFC, insula, middle and superior frontal gyri, SMA and thalamus. A unilateral cluster of activation was revealed in the left hippocampus. The [Pictures > Control] contrast revealed bilateral activations in the hippocampus and SMA. Unilateral activations were revealed in the right insula, as well as in the left middle and superior frontal gyri and thalamus (Fig. 3B). Information on the activation clusters and local maxima for both contrasts are provided in [Tables 1 and 2](#). Outside of the ROI, our whole brain analyses revealed clusters of activity in the superior parietal lobule and middle frontal gyrus for the [Arrangements > Control] contrast only, and in the occipital gyrus and cerebellum for both [Arrangements > Control] and [Pictures > Control] contrasts. Details on the clusters of activity outside of the ROI are provided in [Table 3](#).

3.2. Comparisons between stimuli

Comparing the effect of arrangements versus pictures ([Arrangements > Control] – [Pictures > Control] contrast) revealed significantly

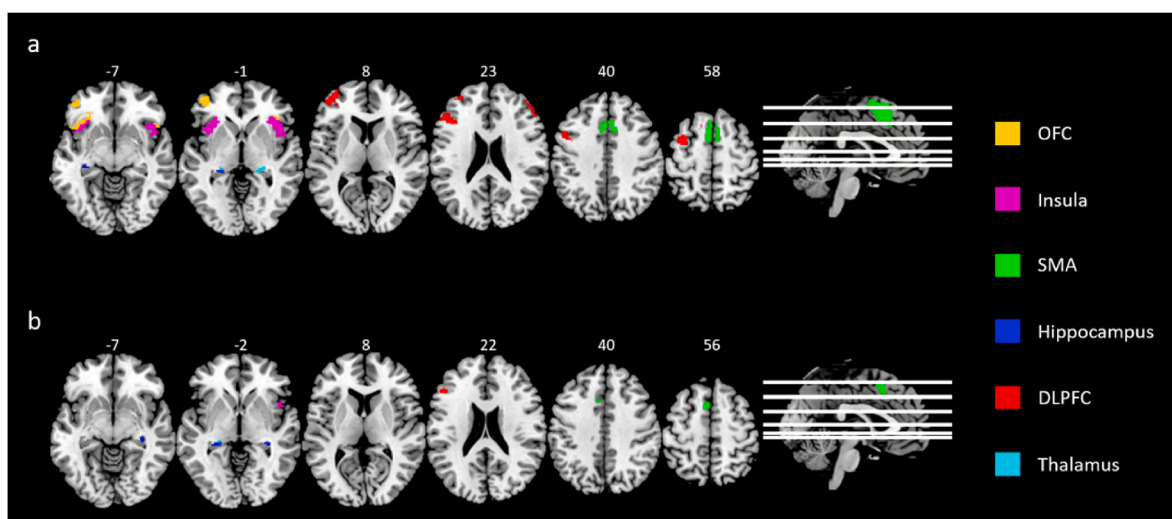


Fig. 3. Brain activity within the ROI for the [Arrangements > Control] contrast (panel a) and [Pictures > Control] contrast (panel b). Middle and superior frontal gyri were grouped into dorsolateral prefrontal cortex (DLPFC). Statistical threshold was set at $p < 0.001$ (uncorrected), $k = 10$.

Table 1

ROI results for the contrast comparing [Arrangements > Control]. Only regions of interest in which significantly activated clusters were observed are listed. 3-dimensional coordinates of the local maxima as well as t-scores are provided. L: left; R: right.

Contrast	Brain region	Hemisphere	Size	x	y	z	t
Arrangements > Control	OFC	L	135	-40	20	-4	6.51
		L	112	-40	46	-4	5.29
		R	45	44	26	-4	4.71
	Insula	L	345	-36	18	-4	8.62
		R	334	40	22	-4	6.79
	Hippocampus	L	33	-24	-30	-4	4.93
	Middle frontal gyrus	L	1008	-44	28	22	7.88
		R	59	52	36	22	4.42
	Superior frontal gyrus	L	170	-12	10	68	7.61
		R	88	10	14	64	6.82
	SMA	L	513	-4	16	44	10.00
		R	404	4	16	46	10.02
	Thalamus	L	16	-12	-30	2	5.74
		R	17	20	-32	-2	5.16

Table 2

ROI results for the contrast comparing [Pictures > Control]. Only regions of interest in which significantly activated clusters were observed are listed. 3-dimensional coordinates of the local maxima as well as t-scores are provided. L: left; R: right.

Contrast	Brain region	Hemisphere	Size	x	y	z	t
Pictures > Control	Insula	R	17	50	12	-4	4.34
	Hippocampus	L	34	-28	-34	0	4.69
		L	23	-36	-34	-18	4.56
		R	35	34	-28	-6	4.95
	Middle frontal gyrus	L	100	-52	26	28	4.44
		L	34	-12	12	68	5.78
	Superior frontal gyrus	L	21	-20	20	62	4.94
	SMA	L	171	-8	10	52	5.29
		R	15	8	6	58	3.59
Thalamus	L	13	-22	-32	-4	4.25	

Table 3

Whole brain results for each [Stimulation > Control] contrast. Only activated clusters outside of the ROI are displayed. 3-dimensional coordinates of the local maxima as well as t-scores are provided. L: left; R: right.

Contrast	Brain region(s)	Hemisphere	Size	x	y	z	t
[Arrangements > Control]	Occipital gyrus, Cerebellum	R	3018	32	-84	4	13.40
		R		20	-84	-10	13.04
		R		34	-84	14	12.36
		L	2148	-22	-88	0	12.69
		L		-36	-86	-8	12.49
		L		-32	-86	2	12.02
		R		2	16	46	10.31
	Medial frontal gyrus	R	460	10	14	62	6.97
		R		2	6	62	6.72
		L		-24	-64	44	8.60
	Superior parietal lobule	L	288	-26	-66	54	8.38
		L		-24	-68	34	7.11
		L		-42	6	28	7.93
	Precentral gyrus	L	68	-42	6	28	7.93
	Medial frontal gyrus	R	11	24	-74	-50	7.71
		L		-12	10	68	7.61
		L		30	-44	-40	40
L		26		-52	6	44	6.89
L		-54		10	36	6.78	
R		22		-90	0	13.23	
R		16		-92	-8	12.99	
[Pictures > Control]	Occipital gyrus, Cerebellum	R	2164	32	-86	-6	11.58
		L		-16	-90	-10	12.03
		L		-26	-92	6	10.49
		L	-20	-94	-2	10.24	

higher activation in the left SMA during the presentation of the non-figurative coloured arrangements as compared to the presentation of pictures (Fig. 4). Detail regarding this cluster is provided in Table 4. Conversely, comparison between the effect of pictures versus arrangements ([Pictures > Control] - [Arrangements > Control] contrast) revealed no significant clusters within the selected ROI, but the whole

brain analysis did highlight a cluster in the medial and inferior occipital gyri. Details on this cluster are provided in Table 5.

4. Discussion

The aim of this study was to characterise the neural mechanisms of

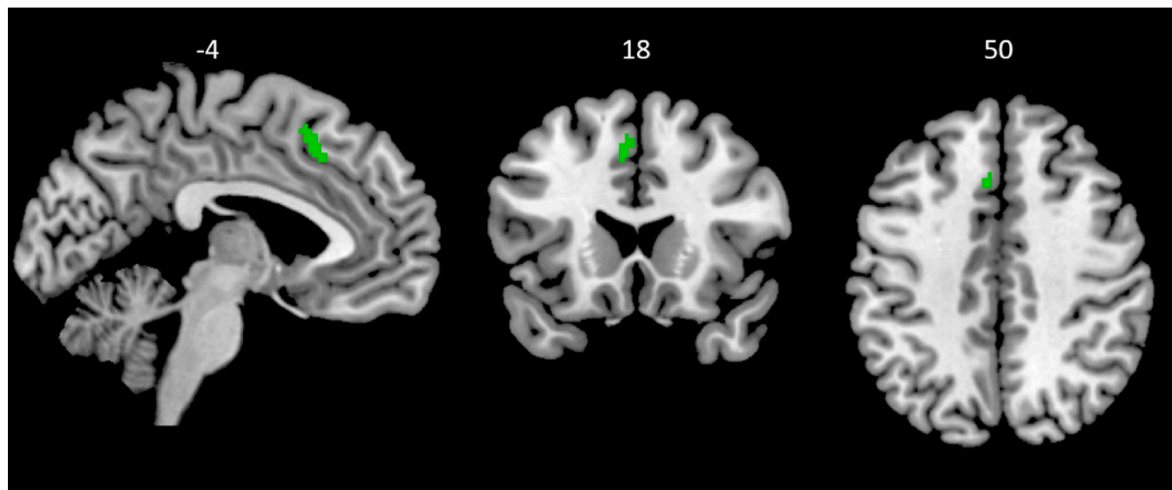


Fig. 4. Activity in the left SMA when comparing the effect of arrangements versus pictures]. Statistical threshold was set at $p < 0.001$ (uncorrected), $k = 10$.

Table 4

ROI result for the contrast comparing the effect of arrangements versus pictures. Only regions of interest in which significantly activated clusters were observed are listed. 3-dimensional coordinates of the local maxima as well as t-scores are provided. L: left; R: right.

Contrast	Brain region	Hemisphere	Size	x	y	z	t
[Arrangements > Control] - [Pictures > Control]	SMA	L	46	-4	18	50	3.85

odour imagery facilitated by non-figurative coloured arrangements. Our ROI analyses when using these non-semantic visual cues revealed significant clusters of activity in the OFC, insula, hippocampus and thalamus, which are known to be part of the olfactory system (Royet and Plailly, 2004). Despite an absence of significant activity in the amygdala, these findings are mostly consistent with those of multiple studies demonstrating the role of olfactory regions during odour imagery (Djordjevic et al., 2005; Flohr et al., 2014; Leclerc et al., 2019) and particularly the OFC and hippocampus. In the case of visually facilitated odour imagery, the well-documented pivotal role of the OFC can be explained by its involvement in visuo-olfactory associative conditioning (Gottfried et al., 2002). As discussed by Gottfried and Dolan (2003), its structural organization may be the cause of its role in the synthesis of multimodal information during unimodal stimulation. On the other hand, the hippocampus is known to be involved in mnemonic processes, allowing for complex retrieval of multimodal associations (Gottfried and Dolan, 2003; Stark and Squire, 2000; Sperling et al., 2003) based on learnt visuo-olfactory pairing. Additionally, significant clusters of cortical activity were revealed in the SMA and dorsolateral prefrontal cortex (DLPFC: middle and superior frontal gyri), which are non-olfactory regions known to be involved in sensory imagery across modalities with distinct functions (Djordjevic et al., 2005; Pratt et al., 2003). While the SMA has been discussed as governing a multimodal processing network (Leclerc et al., 2019), the DLPFC is known to be an indicator of working memory effort during sensory imagery tasks. This

Table 5

Whole brain results for the contrast comparing the effect of pictures versus arrangements. Only significantly activated clusters outside the ROI are listed. 3-dimensional coordinates of the local maxima as well as t-scores are provided. L: left; R: right.

Contrast	Brain region(s)	Hemisphere	Size	x	y	z	t
[Pictures > Control] - [Arrangements > Control]	Inferior and Medial occipital gyri	R	56	28	-94	-4	8.08

was notably demonstrated by increased activity in the DLPFC during odour imagery in patients with olfactory loss (Flohr et al., 2014) and during visual imagery in visually impaired (Dulin et al., 2011).

The present study compared for the first time, the effects of two complex multi-coloured visual cues: non-figurative coloured arrangements, and pictures which have been demonstrated as robust facilitators of odour imagery (Krishna et al., 2014). Our ROI analyses revealed significantly superior activity in the SMA during the use of non-figurative coloured arrangements. A recent study demonstrated increased activity in the SMA during odour imagery in poor odour imagers (Han et al., 2022). It is therefore possible that the difference in SMA activity revealed in our study be the result of increased attentional resources during the use of non-figurative coloured arrangements, as compared to pictures, in line with what has already been shown for the DLPFC in patients with smell loss (Flohr et al., 2014). Moreover, decreased activity in several brain regions implicated in odour imagery (e.g. OFC and hippocampus) had previously been shown in professional perfumers compared to students (Plailly et al., 2012). More localized neural activity could therefore be understood as increased efficiency in generating odour images, in a similar way to practice-related working memory tasks (Garavan et al., 2000) and motor imagery (Chang et al., 2010). This interpretation in regards to cognitive load is also consistent with the fact that all participants reported being more concentrated during the odour imagery task driven by non-figurative coloured arrangements, compared to pictures. On the other hand, the observed difference in SMA activity could also be accounted for by a difference in visual processing. Indeed, studies have shown the implication of the SMA in high-level visual tasks (Gazzaley et al., 2007; Tang et al., 2006). In fact, the performed whole brain analyses showed increased activity in the middle and inferior occipital gyri in the pictures condition, which could be attributed to the quantity of visual information contained in these visual cues. A comparison of odour imagery versus passive viewing of the visual cues could provide answers regarding the precise role of the SMA during the viewing of both types of visual stimuli. The addition of eye-tracking would be particularly relevant in order to potentially distinguish different visual strategies.

Another result was the absence of activity in the OFC during the use of pictures. Nevertheless, since the comparison between the use of

arrangements and pictures did not reveal any significant differences in this region, it is likely the use of pictures induced weaker, subthreshold yet existent clusters of activity in the OFC. In any case, our data as it stands does not provide sufficient information to determine whether one type of visual cue induced more vivid odour imagery. In order to answer this question and assess the relationship between neural activity and vividness of generated odour images, CANOE an ongoing clinical trial (NCT05308433) will couple subjective ratings of odour imagery vividness to brain imaging on a wider sample. Nevertheless, brain activity could be influenced by the ability to imagine odours, as it is the case in other modalities of imagery such as motor imagery (Chang et al., 2010). Therefore, these measures should be interpreted with regards to odour imagery ability, for which tools have been developed in several languages (Fantin et al., 2020; Gilbert et al., 1996; Kollndorfer et al., 2015). Additionally, future studies could use specific tools such as the NASA TLX (Hart and Staveland, 1988) to assess the relationship between workload induced by odour imagery, and activity in non-olfactory brain regions such as the DLPFC. Such measures could provide insight on the attentional solicitation for odour imagery relative to the type of visual cue used as a facilitator.

One surprising result is the absence of activity in the piriform cortex during the use of both non-figurative coloured arrangements and pictures. Provided the satisfactory number of participants for an fMRI experiment with no loss of data, there is little chance that his result be caused by a lack of statistical power (Desmond and Glover, 2002). It is also conceivable that the absence of activity in the piriform cortex could be caused by an insufficient success in the odour imagery task, since this factor was not quantitatively controlled during the fMRI exam. However, participants reported having been able to generate mental odour images during the interviews following the fMRI session. We are therefore fairly confident that our participants did in fact globally succeed in the odour imagery task, suggesting that activity in the piriform cortex may not be a robust neurophysiological marker of success in odour imagery. This interpretation is in line with previous studies shown in perfumery students and professionals (Plailly et al., 2012). Activity in the piriform cortex may not respond to any semantical representation of odours, but may actually be driven by specific aspects of reading odour labels. Alternatively, it has been suggested that decreased activity in the piriform cortex during odour imagery could be the manifestation of functional reorganisation in individuals capable of generating mental odour images with ease. In any case, while our findings do not confirm our hypothesis, they still tend to corroborate the influence of top-down cognitive processes on the activity of the primary olfactory cortex during odour imagery (Royet et al., 2013). However, the present study did not directly compare the use of non-figurative coloured arrangements and pictures to the use of odour labels. Therefore, in order to confirm this hypothesis, the ongoing trial CANOE (NCT05308433) aims at comparing neural activity during odour imagery facilitated by the presentation of several types of visual cues, including odour labels. This could also provide more information related to the effects of characteristics of visual cues (e.g. complexity) during odour imagery.

Overall, our results demonstrate that the use of non-figurative coloured arrangements during odour imagery does not differ from the use of figurative pictures in terms of neural activity in the olfactory network. These findings could signify that semantics *per se* do not affect brain activity during odour imagery. The enhanced activity in the SMA during the use of the non-figurative coloured arrangements, however, could reflect increased attentional demands, perhaps in relation to a need to mentally reconstruct visual context to succeed in the odour imagery task. Nevertheless, there is a possibility that in some cases, non-figurative coloured arrangements may evoke odours more robustly than pictures. Indeed, figurativeness or semantics in a visual cue could be limiting if one is not familiar with the depicted odour. By contrast, it is possible the use of abstract (non-figurative or non-semantic) visual cues such as coloured arrangements may provide one the possibility to freely interpret the visual stimulation and thereby unconstrainedly

imagine a familiar odour. These assumptions remain to be answered by coupling neurophysiological and psychological measures.

Funding

This work is co-funded by the French State-Region contract CPER 2015–2020 (Contrat de Plan Etat Région– IT2MP Innovations Technologiques, Modélisation et Médecine Personnalisée), by the European Union through the European Regional Development Fund “FEDER-FSE Lorraine et Massif des Vosges 2014–2020” program and by CHRU of Nancy, France.

CRediT authorship contribution statement

Gabriela Hossu: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luca Fantin:** Writing – review & editing, Writing – original draft, Validation, Software, Formal analysis, Data curation. **Céline Charroud:** Writing – review & editing, Writing – original draft, Software, Investigation, Formal analysis, Data curation. **Jacques Felblinger:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition. **Muriel Jacquot:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Hadrien Ceyte:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Muriel JACQUOT has been a senior researcher at GIVAUDAN company since 2021. The non-figurative coloured arrangements used in this study are the property of GIVAUDAN, but were not at the time of the design and implementation of the study.

Data availability

Data will be made available on request.

Acknowledgements

The authors thank the staff of the Nancy CIC-IT and the staff of the MRI service of the CHRU de Nancy-Brabois for their daily work.

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