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A hedonically complex odor mixture produces an attentional capture effect in the brain

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ABSTRACT

A counter-intuitive property of many pleasant and attractive stimuli is that they are hedonically complex, containing both pleasant and unpleasant components. A striking example is the floral scent of natural jasmine, which may contain more than 6% of indole, a pure chemical which is usually rated as unpleasant. Using fMRI we investigate the hypothesis that the interaction between the pleasant and unpleasant components in the hedonically complex natural jasmine produces an attentional capture effect in the brain. First, to localize brain areas involved in selective attention to odor, we compared neural activity in response to jasmine without indole when participants explicitly and selectively attended to either its pleasantness or intensity, with neural activity when no selective attention was required. We then show that the superior frontal gyrus has increased activity both when selective attention is being paid to jasmine without indole, and also when no selective attention is required but an unpleasant component is added to it to produce a hedonically complex mixture. The attentional capture effect in the superior frontal gyrus by the mixture was related to the hedonic complexity of the mixture across subjects; could not be explained by salience, intensity, or pleasantness; and was specific to the superior frontal gyrus in that it was not found in other prefrontal areas activated by selective attention. The investigation supports the new hypothesis that the affective potency of stimuli with mixed pleasant and unpleasant components is related at least in part to the recruitment of mechanisms in the brain involved in attentional capture and enhancement.

Introduction

Many stimuli in our environment are hedonically complex, containing both pleasant and unpleasant components. An interesting property of hedonically complex stimuli is that the presence of an individually unpleasant component can enhance the pleasantness or attractiveness of the mixture. An example is that a vegetable odor that is unpleasant on its own may in combination with the taste of monosodium glutamate produce a consonant flavor that is experienced as highly pleasant (McCabe and Rolls, 2007). This is counter-intuitive, but appears to happen with many natural odors that are highly pleasant (Ohloff, 1994). A striking example is the pleasant floral scent of jasmine, which as it occurs naturally in *Jasminum grandiflorum* contains typically 2–3%, and sometimes more than 10%, of indole, a pure chemical which on its own at the same concentration is usually rated as unpleasant (Mookherjee et al., 1990). Why might this occur? One investigation has shown that parts of the brain such as the medial orbitofrontal cortex that represent the pleasantness of odors (Anderson et al., 2003; Grabenhorst and Rolls, 2009; Rolls et al., 2003) can respond even more strongly to jasmine when it contains the unpleasant component indole, compared to when it only contains individually pleasant components (Grabenhorst et al., 2007). Thus one brain mechanism that may underlie the attractiveness of hedonically complex stimuli is a principle that brain areas that represent the pleasantness of stimuli can do this in a way that is partly independent of unpleasant components, thereby emphasizing the pleasant component of a hedonically complex mixture.

Another hypothesis for a mechanism that may contribute to the pleasantness or enhanced impact of a hedonically complex mixture is that the interaction between the pleasant and unpleasant components produces an attentional capture effect in the brain, in that it might engage neural processing related to selective attention, which may enhance and prolong the activation of the brain by the mixture. Here we test this hypothesis by measuring whether brain areas where selective attention enhances neural activations to an odor, are also activated particularly effectively by a hedonically complex olfactory mixture even in the absence of explicit attentional instructions. If some brain regions are activated similarly by selective attention to odor and a hedonically complex odor mixture, then this is evidence that brain processing

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related to attentional capture may contribute to the efficacy of olfactory mixtures in enhancing subjective pleasantness. One candidate region where this effect might be expressed is the lateral prefrontal cortex, which is involved in attention and attentional capture across different sensory modalities (Corbetta and Shulman, 2002; Downar et al., 2000; Kanwisher and Wojciulik, 2000). Further, jasmine odor has been shown to elicit an enhanced early component of the contingent negative variation, a slow cortical potential which occurs between a warning stimulus and an imperative stimulus, specifically over left frontal areas (Taylor and Roberts, 1990). Thus attentional capture could be an interesting way in which some natural as well as other volatile chemical stimuli (including perfumes that contain extracts of natural materials, such as civet cat musk gland secretions) can produce strong and lasting subjective pleasantness, can contribute to making other stimuli pleasant and attractive, and thus may influence subjective preference, emotion, and choice. Interestingly, in a previous investigation (Grabenhorst et al., 2007) a non-linear enhancement effect of the pleasant and unpleasant components of the jasmine mixture in the medial orbitofrontal cortex was not reflected in the subjective hedonic ratings, and it could be that any attention-capturing effect of hedonically complex mixtures operates partly unconsciously.

We conceptualize *hedonic complexity* as the simultaneous presence of individually pleasant and unpleasant components in a sensory stimulus (Grabenhorst et al., 2007). This can be operationally defined as the absolute difference in ratings of subjective pleasantness given to the individual pleasant and unpleasant components. The concept of hedonic complexity is closely related to the topics of cost–benefit analysis and value-based decision-making, in that the pleasant and unpleasant components of an affective stimulus can be conceptualized as the intrinsic benefits and costs of a reward or a goal for action (Rolls and Grabenhorst, 2008). We propose that in value-based, economic decision-making, the subjective value of the benefits and costs of a reward must be independently computed before the net value of the reward can be evaluated, that is before a benefit–cost representation can be formed. The reason for this is that with our current understanding of how attractor-based decision-making networks in the brain operate (Deco and Rolls, 2006; Deco et al., 2009; Rolls and Deco, 2010; Rolls and Grabenhorst, 2008; Wang, 2002, 2008), there is one input for each possible choice into a neural decision mechanism, and the inputs must therefore represent the net intrinsic value of each choice.

We note that jasmine is just one example of many instances in which pleasant odor combinations may contain odor components that on their own may be unpleasant. Jasmine provides thus a useful model example for this functional neuroimaging study of what is a common effect. Other examples quoted by perfumers and flavorists include perfumes that sulfur components that on their own are unpleasant (like cat urine), but give a lift to and may even impart a fruity component to complex odor mixtures including tropical fruits and even Sauternes wine. Another example is that adding a musk odor (such as civet or castor glandular secretions (Ohloff, 1994)), unpleasant on their own, to a pleasant odor may, for at least some people, enhance the attractiveness of a perfume and may capture attention. Another example is that wintergreen contains methyl salicylate, which on its own is unpleasant. In the areas of flavor combinations, it is found that an odor which on its own is rather affectively unpleasant, such as vegetable odor, may as a component of a mixture with monosodium glutamate, become very pleasant (McCabe and Rolls, 2007). The addition of trace amounts of pepper to strawberries is also a good demonstration as to how a culinary ingredient that on its own produces an innately unpleasant "irritating" sensation (Rozin et al., 1981), in this case via the trigeminal nerve, may enhance the aroma of a sweet dish. Thus odors with mixed hedonic components are key for success in perfumery with certain creations, and the same principle is also important in the multimodality effects used in cuisine.

In the present study we used functional magnetic resonance imaging (fMRI) to investigate the hypothesis that the interaction between the pleasant and unpleasant components in a naturally hedonically complex odor mixture produces an attentional capture effect in the brain. First, we localized brain areas involved in focusing selective attention on the different properties of a pleasant odor. We then tested whether any of the brain areas involved in attention to odor also respond when an unpleasant component is added to the odor to produce a hedonically complex mixture, even in the absence of explicit selective attention. We also tested whether any attention-related effects were due to hedonic complexity or to other factors such as pleasantness, intensity, or salience.

Methods

Design

In the experiment described here, we compared brain responses to a chemically well defined model jasmine odor with 8 components that did not include indole and was pleasant (which we refer to as 'jas'), to the odor of indole, which was unpleasant (which we refer to as 'indole'), and to a mixture of these two olfactory stimuli, jas and indole, which is a model of the natural jasmine and which was pleasant (which we refer to as 'jasind'). The jasmine without indole, 'jas', was presented under two experimental conditions. In the attention condition, participants were instructed to pay attention to different properties of the odor (either its pleasantness or intensity) whereas in the no attention condition no such instruction was given.

The trial types were as follows: (1) jas: no attention, (2) indole: no attention, (3) jasind: no attention, (4) air: no attention, (5) jas: attention to intensity, (6) jas: attention to pleasantness. The timecourse of events for the attention and no attention trials is shown in Fig. 1.

This design allowed contrasting brain activation to the jas odor under the attention condition with activation to the jas odor under the no attention condition to localize brain areas involved in selective attention to odor. The different attention conditions, paying attention to pleasantness vs intensity, have been shown to differentially engage brain systems involved in processing the pleasantness and intensity of both taste and olfactory stimuli, and these findings, some in the same dataset show that top-down attentional instructions can modulate processing in taste, olfactory, and reward processing cortical areas (Grabenhorst and Rolls, 2008; Rolls et al., 2008). We emphasize that in previous analyses parts of the same dataset (Grabenhorst et al., 2007; Rolls et al., 2008) were used to address different questions about olfactory processing, and did not investigate attentional capture by a hedonically complex mixture. The design also allowed contrasting brain activation to the mixture of jasmine and indole (jasind) with activation to the jasmine without indole (jas). This effect of adding an unpleasant component to the jas odor to produce a hedonically complex olfactory mixture could then be compared with the effect of paying selective attention to the jas odor. In previous investigations of this dataset acquired in a common sample of subjects we have reported the results of performing regression analyses using the pleasantness and intensity ratings as regressors for brain activations, and comparing the attention to pleasantness and attention to intensity conditions (Grabenhorst et al., 2007; Rolls et al., 2008). By creating a precise and analytically defined jasmine model, to which we could add indole, we could thus investigate how in substances such as natural jasmine (which contains 2–3% indole) an unpleasant component can interact with other components to make a pleasant combination, and how different brain regions respond to this mixture.

Subjects

Fourteen healthy volunteers (7 male and 7 female, mean age 26) participated in the study. Ethical approval (Central Oxford Research

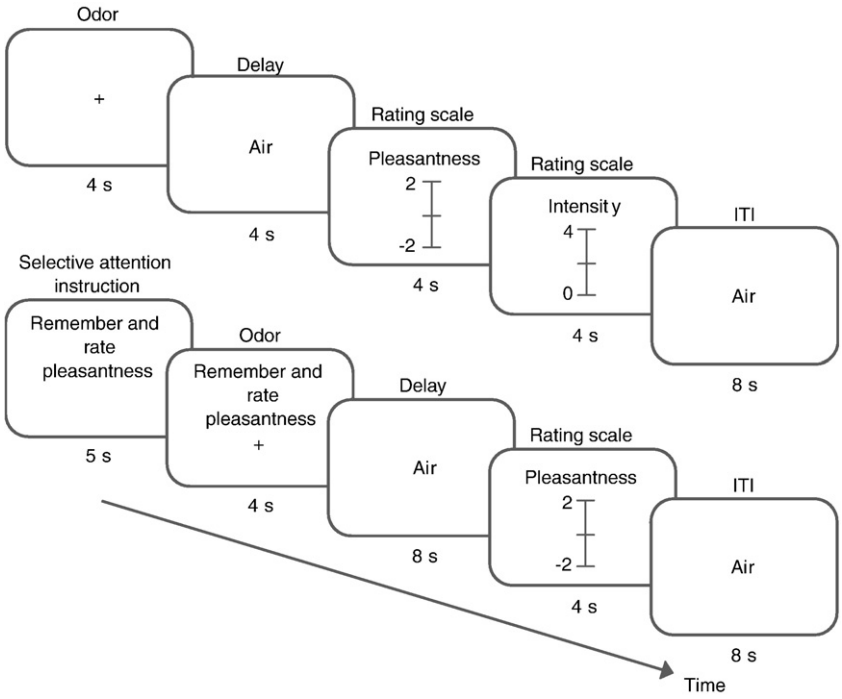

Fig. 1. Task design. The upper panel shows the timecourse of a trial where no instructions for selective attention were given. The lower panel shows the timecourse of a trial where instructions to direct attention to the pleasantness of the odor were given.

Ethics Committee) and written informed consent from all subjects were obtained before the experiment. The participants were selected from the normal population, subject to their finding the indole unpleasant (which some people do not, perhaps related to the expression of different olfactory receptor genes in different people (Dulac and Torello, 2003)) and the mixture pleasant, and were given practice in the task and in making the ratings in a psychophysical session that preceded the scanning session. We note that perfumers with great experience would probably be able to identify the indole in the jasind mixture, and would rate the mixture as pleasant. The participants in the present study typically could not identify the indole in the mixture, and found it similar to the jasmine without indole.

Stimuli

A chemically defined jasmine-like model odor ('jas') was made that contained the following: benzyl acetate 20.0%; hexylcinnamic aldehyde 24.0%; hedione® 15.4% (the natural parent unsaturated compound is methyl jasmonate); linalool 24.8%; jasmone 4.8%; eugenol 2.4%; Z3-Hexenyl benzoate 5.0%; and methyl anthranilate 3.6%. The indole stimulus was 6% indole ('indole'). The mixture consisted of the same concentration of all the substances in the jas odor, but in addition 6% indole ('jasind'). (Natural jasmine also contains para-cresol, also judged unpleasant. To simplify the experiment, we used only indole in jasind, but at a slightly higher level (6%) than in usual jasmine oil to compensate for the lack of para-cresol. We note that the components in the model jasmine we created are present in natural jasmine (Demole, 1982; Kaiser, 1988; Toda et al., 1983; Verzele et al., 1981) with the exception of hexylcinnamic aldehyde which has been found to be a useful building block of jasmine odor (Demole, 1982), and that the components in the model are sufficient to capture many aspects of natural jasmine.) All stimuli were diluted 1:5 in dipropylene glycol in such a way that the 8 components would be present at the same level in jas and jasind regardless of the presence of indole. The concentration of indole was chosen because it was unpleasant to the participants when presented alone, but did not make the jasind mixture unpleasant. (For four of the 14 participants, an indole concentration of 4% was used to satisfy these criteria.) Clean air was delivered whenever an odor was not being delivered. In the intertrial interval, limonene was delivered for 1 s, to help the olfactory system to be in a stable, non-adapted state, when one of the three test stimuli was presented at the start of each trial. (This was based on procedures developed by measuring neuronal responses in olfactory neurophysiology in which it has been found that provided that odors are changed in a pseudorandom way, olfactory adaptation effects with these short infrequent deliveries do not result in significant adaptation in brain regions such as the orbitofrontal cortex (Critchley and Rolls, 1996; Rolls et al., 1996.)

Stimulus delivery

A purpose-designed (C. Margot) continuous airflow six-channel computer-controlled olfactometer was used to allow odor stimuli to be delivered in the MRI scanner. The control and metal components of the system are kept outside the scanner room, and the system is free of any auditory, tactile or thermal shifts that could cue the subject to the onset of odor delivery. The flow of cleaned medical air is controlled using a pressure regulator and flow meter. The air is directed using solenoid-operated valves controlled by the stimulus computer using TTL pulses to one of the glass evaporation flasks containing one odor stimulus or air. The purpose of the flasks was to release an odor mixture by evaporation in a similar way to that in which an odor mixture would evaporate normally from a surface to which it had been applied. Each flask contained three filter papers held in glass flanges on each of which was spread 0.25 ml of the liquid odor stimulus less than three hours before an experiment began. Each flask is connected by its own teflon tube (to provide for low adhesion) to a single nozzle located within 1 cm of the nose to minimize dead space. The delivery nozzle provided two tubes, one placed just inside each nostril, to produce birhinal stimulation. All odor stimuli used in the present experimental design (jasind, jas, ind, limonene, and clean air) were delivered using a different channel of the olfactometer. The flow-rate of the air supply was kept constant for all odors and the clean air at 3 l/min to each nostril. The air line was on continuously by

default, and was switched off by its solenoid exactly at the time when another solenoid directed the clean air supply to another flask so that an odorant could be delivered. This resulted in a system with no perceptible pressure change when the air was replaced during stimulus delivery by an odor for 4 s.

Experimental protocol

During the fMRI experiment the subjects gave psychophysical ratings of pleasantness and intensity on every trial, so that correlation analyses between the ratings and the brain activations could be performed. The experimental protocol consisted of an event-related interleaved design presenting in random permuted sequence the different experimental conditions described above, and a clean air condition.

Each trial on which an odor was delivered without attention instruction started with a 4 s odor (or clean air) stimulus delivery, and an indication that a trial had started by a small white visual cue at the centre of a visual display backprojection screen being observed through prisms to allow the subjects to sample the odor synchronized with its onset. At t = 8 s after trial onset, the pleasantness rating scale appeared for 4 s, and the subject rated the stimulus for pleasantness on a continuous analogue rating scale (labeled with +2 for very pleasant and −2 for very unpleasant). At t = 12 s after trial onset, the intensity rating scale appeared for 4 s, and the subject rated the stimulus for intensity (0 to +4). The ratings were made with a visual analogue rating scale in which the subject moved the bar to the appropriate point on the scale using a button box.

An attention trial started at time t = 0 s with the visual instruction either “remember and rate pleasantness” or “remember and rate intensity”, shown for 5 s. The wording provided to the participants specifically referred to attention for this condition by stating that on some trials attention had to be paid to either the pleasantness or intensity and a corresponding rating had to be given. For the comparison trials, there was no message prior to the odor delivery to set up an attentional state. The odor was delivered from t = 5 s until t = 9 s. After the end of the odor delivery period the visual instruction was turned off and there was a delay period from t = 9 s until t = 17 s. The ratings of pleasantness or intensity were made at t = 17 until t = 21 s.

After the ratings on each trial the odor limonene was delivered for 1 s (to act as an inter-trial dishabituator), and there was then an intertrial interval of 8 s. We emphasize that the subjects did not know what each odor was nor of the number of odors in the experiment, and had to sniff at the start of each odor delivered in random sequence and then rate it for pleasantness and/or intensity. The clean air flow was on at all times that an odor stimulus was not being delivered. The subjects were not informed of the nature of the odors, nor of how many there were in the experiment. Subjects were pre-trained outside the scanner in the whole procedure and use of the rating scales, and had thus experienced all the odors on a number of different trials before the imaging experiment. Each of the six trial types ((1) jas: no attention, (2) indole: no attention, (3) jasind: no attention, (4) air: no attention, (5) jas: attention to intensity, (6) jas: attention to pleasantness) was presented in random permuted sequence 9 times. This general protocol and design has been used successfully in previous studies to investigate olfactory cortical areas (de Araujo et al., 2005; Grabenhorst et al., 2007; Rolls et al., 2003).

Functional imaging data: acquisition

Images were acquired with a 3.0-T Varian-Siemens whole-body scanner at the Centre for Functional Magnetic Resonance Imaging at Oxford (FMRIB), where 27 T2* weighted EPI coronal slices with in-plane resolution of 3 × 3 mm and between plane spacing of 4 mm were acquired every 2 s (TR = 2). We used the techniques that we have developed over a number of years (de Araujo et al., 2003; O'Doherty et al., 2001) and as described in detail by Wilson et al. (2002) we carefully selected the imaging parameters in order to minimize susceptibility and distortion artefact in the orbitofrontal cortex. The relevant factors include imaging in the coronal plane, minimizing voxel size in the plane of the imaging, as high a gradient switching frequency as possible (960 Hz), a short echo time of 28 ms, and local shimming for the inferior frontal area. The matrix size was 64 × 64 and the field of view was 192 × 192 mm. Continuous coverage was obtained from +62 (A/P) to −46 (A/P).

Functional imaging data: analysis

The imaging data were analysed using SPM5 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, London). Pre-processing of the data used SPM5 realignment, reslicing with sinc interpolation, normalisation to the MNI coordinate system (Montreal Neurological Institute) (Collins et al., 1994), and spatial smoothing with a 6 mm full width at half maximum isotropic Gaussian kernel. The time series at each voxel were low-pass filtered with a haemodynamic response kernel. Time series non-sphericity at each voxel was estimated and corrected for (Friston et al., 2002), and a high-pass filter with a cut-off period of 128 s was applied. In the single event design, a general linear model was then applied to the time course of activation where stimulus onsets were modelled as single impulse response functions and then convolved with the canonical hemodynamic response function (Friston et al., 1994). Linear contrasts were defined to test specific effects. Time derivatives were included in the basis functions set. Following smoothness estimation (Kiebel et al., 1999), linear contrasts of parameter estimates were defined to test the specific effects of each condition with each individual dataset. Voxel values for each contrast resulted in a statistical parametric map of the corresponding t statistic, which was then transformed into the unit normal distribution (SPM Z). In the second (group random-effects) stage, subject-specific linear contrasts of these parameter estimates were entered into a series of one-sample t tests, each constituting a group-level statistical parametric map. This random effects analysis with the number of participants in the study produced results that allow the inference to be generalized reliably to the population from which the subjects were selected (Friston, 2003). To ensure orthogonality of the contrasts involving the ‘jas: no attention’ condition, and thus to ensure the validity of the inclusive masking and conjunction analyses described in the results, we used half the trials of the ‘jas: no attention’ condition within each subject (determined by the odd–even method) for the contrast with the ‘jas: attention’ conditions, and the other half for the contrast with the ‘jasind: no attention’ condition. For contrasts involving the attention conditions, the analysis was performed by collapsing across both attention to pleasantness and attention to intensity trials. Additional control analyses confirmed that the significance levels and the location of the brain areas identified did not change when the contrasts where performed separately for the attention to pleasantness and attention to intensity conditions, and then inclusively masking the resulting statistical parametric maps, or when using a conjunction analysis between the two attention conditions as the inclusive mask for the jasind vs jas: no attention contrast. We also performed psychophysiological interaction (PPI) analyses (Friston et al., 1997) to identify brain areas where neural activity correlates with activity in a given seed region as a function of experimental condition. The PPI model performed at the single subject level included three regressors. The first regressor consisted of the timeseries of activity in a seed brain area identified in the contrast analyses. The timeseries was extracted in each subject by drawing a 6 mm sphere around the peak voxel from the group contrast analysis and then finding the individual's peak voxel within that sphere. The second regressor consisted of a stimulus-related contrast (jasind: no attention vs jas: no attention). The third regressor consisted of the interaction between the first and second regressors. The statistical parametric maps from each individual dataset were then

entered into second-level, random effects analyses. We report results for brain regions where there were prior hypotheses on the basis of previous studies, including subregions of the lateral prefrontal cortex where effects of attention have been demonstrated (Corbetta and Shulman, 2002; Downar et al., 2000; Hopfinger et al., 2000; Kanwisher and Wojciulik, 2000). Because our aim was to identify brain regions involved in processing related to attentional capture, which may operate non-specifically with respect to sensory modalities, we focused on the lateral prefrontal cortex as this brain region has been implicated in attention in different sensory modalities (Corbetta and Shulman, 2002; Downar et al., 2000; Hopfinger et al., 2000; Kanwisher and Wojciulik, 2000). We also included the medial dorsal thalamus, pyriform cortex, and orbitofrontal cortex in our hypotheses because of their role in olfaction and olfactory attention (Plailly et al., 2008; Rolls and Grabenhorst, 2008; Zelano et al., 2005). The regions of interest for these brain areas were constructed using the WFU Pickatlas SPM toolbox (Maldjian et al., 2003). We applied small volume (false discovery rate) corrections for multiple comparisons for which $p<0.05$ (though the exact corrected probability values are provided) (Genovese et al., 2002) with a radius corresponding to the full width at half maximum of the spatial smoothing filter used. In addition to the statistical criterion just described for a significant effect calculated for the peak voxel of a region of activation in an a priori defined region based on earlier findings, we used the additional statistical test (see Gottfried et al., 2002; O'Doherty et al., 2006; O'Doherty et al., 2003) that the results reported were in global contrast and/or correlation analyses significant using the criterion of $p<0.001$ uncorrected for multiple comparisons and with a cluster size of at least 15 contiguous voxels, and these additional statistics confirmed the same effects in the a priori regions in all cases except where indicated.

Our approach to testing the hypothesis described in the Introduction is as follows. First, we compare activations to the jas odor under the different attention conditions in order to identify brain areas that are activated when selective attention is being paid compared to when no explicit demand for selective attention is given. We then use the resulting statistical map as an inclusive mask for the contrast between the jasind and jas: no attention conditions in order to identify brain areas that are commonly activated by selective attention and by a hedonically complex odor mixture in the absence of explicit demands for selective attention. Having identified a commonly activated brain area we then relate the magnitude of the jasind vs jas: no attention effect across subjects to subject-specific measures of pleasantness, intensity, and hedonic complexity, as derived from the psychophysical ratings.

Results

The psychophysical ratings of pleasantness and intensity

The psychophysical ratings of pleasantness obtained during the neuroimaging were 0.96 ± 0.13 for jas: no attention, -0.83 ± 0.17 for indole, 0.80 ± 0.18 for jasind, 0.32 ± 0.07, for air, and 1.12 ± 0.10 for jas: attention to pleasantness. A within-subjects ANOVA ($F(4,52)=31.94$, $p<<0.001$) followed by post hoc LSD tests (accompanied by a Kolmogorov–Smirnov test for normality) showed that jas (under both the attention and no attention condition) and jasind were rated as more pleasant than the indole (both $p<<0.001$), and that there was no significant difference between jas (under both the attention and no attention condition) and jasind. The psychophysical ratings of intensity were for jas: no attention 1.95 ± 0.15, for indole 1.89 ± 0.17, for jasind 2.14 ± 0.11, for air 0.6 ± 0.10, and for jas: attention to intensity 1.99 ± 0.15. A within-subjects ANOVA ($F(4,52)=35.07$, $p<<0.001$), followed by post hoc LSD tests (accompanied by a Kolmogorov–Smirnov test for normality) showed that the only significant differences in intensity ratings were found between air and all experimental odors (all $p\ll0.001$) but not between any experimental odors. The finding of no significant differences in pleasantness and intensity ratings between jas: no attention and jasind indicates that the participants found these stimuli to be subjectively very similar.

We also calculated the intra-individual coefficient of variation for the pleasantness and intensity ratings of the jas odor on the attention and no attention trials to test whether the attention and no attention conditions differed in difficulty. The coefficient was defined as the standard deviation of an individual subject's ratings for a given condition divided by the subject's mean rating for this condition. This coefficient represents a relative measure of performance variability and has been shown to be sensitive to task difficulty effects in attention tasks (Brown, 1997; Brown and Merchant, 2007). No significant differences between the attention and no attention conditions were found for the pleasantness ($t(13)=0.85$, ns) and the intensity ratings ($t(13)=1.93$, ns). This makes it unlikely that any differences in brain activations between these conditions are the result of differences in difficulty.

Neuroimaging results

Brain areas involved in selective attention to odor

First, to localize brain areas involved in selective attention to odor, we compared neural activity in response to the jas odor under two conditions. In the jas: attention condition, participants were instructed to pay attention to either the pleasantness or the intensity of the jas odor, whereas in the jas: no attention condition, the identical jas odor was delivered but no instruction to pay attention was given. The analysis period started at the onset of the jas odor. A contrast of these conditions revealed higher activations to the jas odor under the attention condition compared to the no attention condition in the lateral prefrontal cortex, including parts of the superior frontal gyrus [−18 22 58] $z=3.76$ $p=0.002$, inferior frontal gyrus [−48 26 −4] $z=4.70$ $p<0.001$, and medial frontal gyrus [−32 6 46] $z=3.77$ $p=0.004$ (Fig. 2). No significant effects in other brain areas were found in a whole brain analysis. Fig. 2b shows the parameter estimates for these regions based on this contrast. To confirm that these effects were attributable to significant effects for both the attention to pleasantness and attention to intensity conditions and not due to a significant effect for only one type of attention condition, we also performed second-level, random-effects contrast analyses separately

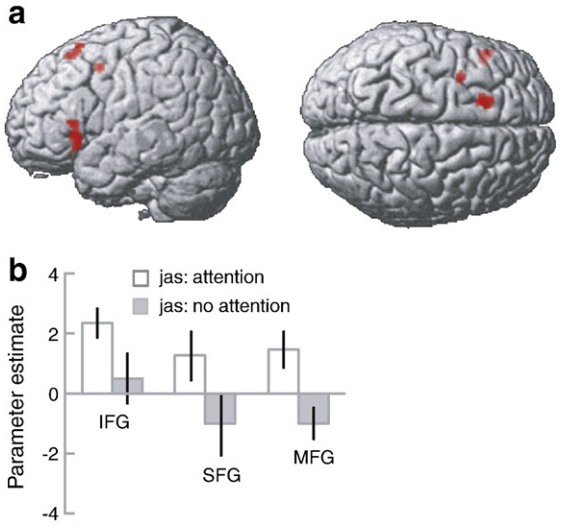

Fig. 2. (a) Brain regions involved in selective attention to odor shown by a contrast between activations produced by the jas odor when participants were instructed to pay attention to it compared to when no instruction to pay attention was given. Significant effects were found in different parts of the lateral prefrontal cortex including the superior frontal gyrus [−18 22 58] $z=3.76$ $p=0.002$, inferior frontal gyrus [−48 22 −4] $z=4.70$ $p<0.001$, and medial frontal gyrus [−32 6 46] $z=3.77$ $p=0.004$. (b) Parameter estimates for these effects (IFG: inferior frontal gyrus; SFG: superior frontal gyrus; MFG: medial frontal gyrus).

for these conditions. These separate analyses confirmed significant effects ($p<0.05$ corrected for false discovery rate, see Methods) for both types of attention trials in all regions. We also performed a conjunction analysis as implemented in SPM5 between the contrast of (jas: attention to pleasantness–jas: no attention) and (jas: attention to pleasantness - jas: no attention) to explicitly test for voxels that are commonly activated in both contrasts. To ensure orthogonality of the terms entering the conjunction analysis we split the trials of the jas: no attention condition for each subject in half and then used the different halves of trials for two contrasts. This analysis revealed significant effects in the superior frontal gyrus [−16 24 56] z = 3.88 $p<0.001$, inferior frontal gyrus [−48 22 −2] z = 4.36 $p=0.002$, and medial frontal gyrus [−32 4 46] z = 4.15 $p=0.002$ (Supplementary Fig. 1). Thus selective attention modulates responses to the jas odor in different regions of the lateral prefrontal cortex.

Common activations by selective attention and a hedonically complex odor mixture

Next, we searched for brain regions that are both involved in attention to odor and respond more strongly to the hedonically complex mixture jasind than to the pleasant component, jas, on its own. We performed a statistical comparison where neural activations produced by jasind were contrasted with activations produced by its pleasant component jas (under the no attention condition), and used the statistical parametric map generated in the jas: attention vs jas: no attention contrast as an inclusive mask (thresholded at $p<0.001$). The superior frontal gyrus was the only brain region to show a significant effect in both contrasts (Fig. 3). The effect of the jasind–jas: no attention contrast in the area with activations common to both contrasts was localized at [−16 18 64] z = 3.11 $p=0.011$. This peak identified using an inclusive masking procedure was part of a large cluster with peak at [−2 18 70] z = 3.36 $p=0.010$. No significant effects in other regions were found even when a more lenient threshold of $p<0.05$ for the inclusive mask was used. The medial orbitofrontal cortex also showed higher activations to jasind than jas: no attention (Grabenhorst et al., 2007) but showed no effect in the attentional contrast. In an exploratory whole-brain analysis of the jasind vs jas: no attention contrast no further brain areas showed a significant effect. To provide further evidence for a common effect in the superior frontal gyrus we performed a conjunction analysis as implemented in SPM5 between the contrasts of jas: attention vs jas: no attention and jasind vs jas: no attention. This revealed a significant effect only in the superior frontal gyrus at [−12 22 64] z = 2.91 $p=0.039$ (corrected for false discovery rate in a volume of interest and $p=0.002$ uncorrected for the whole brain; see Methods). The same superior frontal region also had higher activations to the jasind compared to its unpleasant component indole when masked inclusively with the jas: attention vs jas: no attention contrast at [−12 24 64] z = 3.05 $p<0.05$. This peak identified using an inclusive masking procedure was part of a large cluster with peak at [−12 14 68] z = 4.52 $p<0.001$. A conjunction analysis between the contrasts of jas: attention vs jas: no attention and jasind vs indole revealed a significant effect only in the superior frontal gyrus at [−12 22 64] z = 2.91 $p=0.046$ ($p=0.002$ uncorrected). To ensure that the effects were not specific to either the jas: attention to pleasantness or jas: attention to intensity condition, we repeated the inclusive masking procedure by using the statistical map resulting from the conjunction (jas: attention to pleasantness - jas: no attention) and (jas: attention to intensity - jas: no attention) as an inclusive mask for the jasind vs jas: no attention contrast. Using this masking approach did not change the location of the superior frontal gyrus effect or its significance level (Supplementary Fig. 2).

These results demonstrate that the superior frontal gyrus has activations that are increased both when attention is being paid to the jas odor, and when an unpleasant component is added to it to produce a hedonically complex mixture. Thus the mixture may produce an attentional capture effect in the brain and thereby modulate responsiveness to a jasmine odor in the same way as does an explicit instruction to pay attention to an odor, in that both conditions engage the superior frontal gyrus. The superior frontal gyrus does not though just represent the pleasantness of the odor stimuli, for activations in this region were not correlated with the subjective pleasantness ratings of the set of odor stimuli, whereas activations in other brain areas (such as the orbitofrontal cortex) were correlated with the pleasantness of the olfactory stimuli (Grabenhorst et al., 2007).

Relating neural activations to psychophysical ratings

Next, we investigated the nature of the effect produced by the mixture in the superior frontal gyrus. If the hedonic complexity of the mixture is the relevant factor that produces the attentional capture effect, then the effect should be related to the hedonic complexity across subjects. We tested whether the magnitude of the effect across individual participants is a function of the hedonic complexity of the mixture for each individual, defined as the difference in pleasantness between the jas: no attention and the indole for that participant. As a measure of the magnitude of the attentional capture effect by the jasind, we calculated the absolute difference in the % BOLD change in the superior frontal gyrus produced by the jasind and the jas: no attention (Figs. 3b, c). We then correlated this measure with the absolute difference in the pleasantness ratings given to the jas: no attention and the indole in each individual. The absolute difference of the % BOLD change in this superior frontal area was positively correlated ($r=0.54$ $p<0.05$) with the absolute difference in the subjective pleasantness of jas: no attention vs indole across participants (Fig. 3c). We further performed a partial correlation analysis to control for the effects of the pleasantness ratings of jasind on this relationship. When the effects of the jasind pleasantness ratings were removed the correlation was even more significant ($r=0.62$ $p=0.03$). In a control analysis, a similar correlation was not found for the absolute difference in intensity (Fig. 3d). (The correlation in this control analysis was not significant even in a partial correlation analysis which controlled for the effects of the jasind intensity ratings ($r=0.07$ $p=0.81$).) Thus, the more different in pleasantness the individual components were, the higher was the magnitude of the attentional capture effect produced by the jasind vs jas: no attention in the superior frontal gyrus. This supports the hypothesis that the superior frontal gyrus is a brain area involved in attentional capture by the hedonically complex mixture.

Comparison with other brain areas involved in attention

To test the specificity with which the superior frontal gyrus is related to attentional modulation of responses to odor and to the attentional capture produced by the hedonically complex mixture, we tested whether similar effects were found in the inferior frontal gyrus, an area as shown above where attention also modulates responses to jas odor. Of particular interest was whether the inferior frontal gyrus would also show greater activations to jasind than to jas. Figs. 4 (a, b) shows the parameter estimates for both brain areas for all conditions. The pattern of results suggests a difference in the functional specialization of the two brain areas, namely that the inferior frontal gyrus is not involved in attentional capture by the hedonically complex mixture. To statistically test for functional differences between the superior frontal gyrus and inferior frontal gyrus, we performed a two-factor within-subject ANOVA on the parameter estimates (obtained from the statistically significant SPM analyses described earlier), where one factor was the brain area, and the second factor was the experimental effect (jas: attention vs jas: no attention and jasind vs jas: no attention). A significant interaction was found with $F(1,13)=14.51$, $p=0.002$ (Fig. 4e). This result shows that there are differences between the two brain areas in how they respond to the mixture relative to its pleasant component. In particular, this analysis indicates that the inferior frontal gyrus is

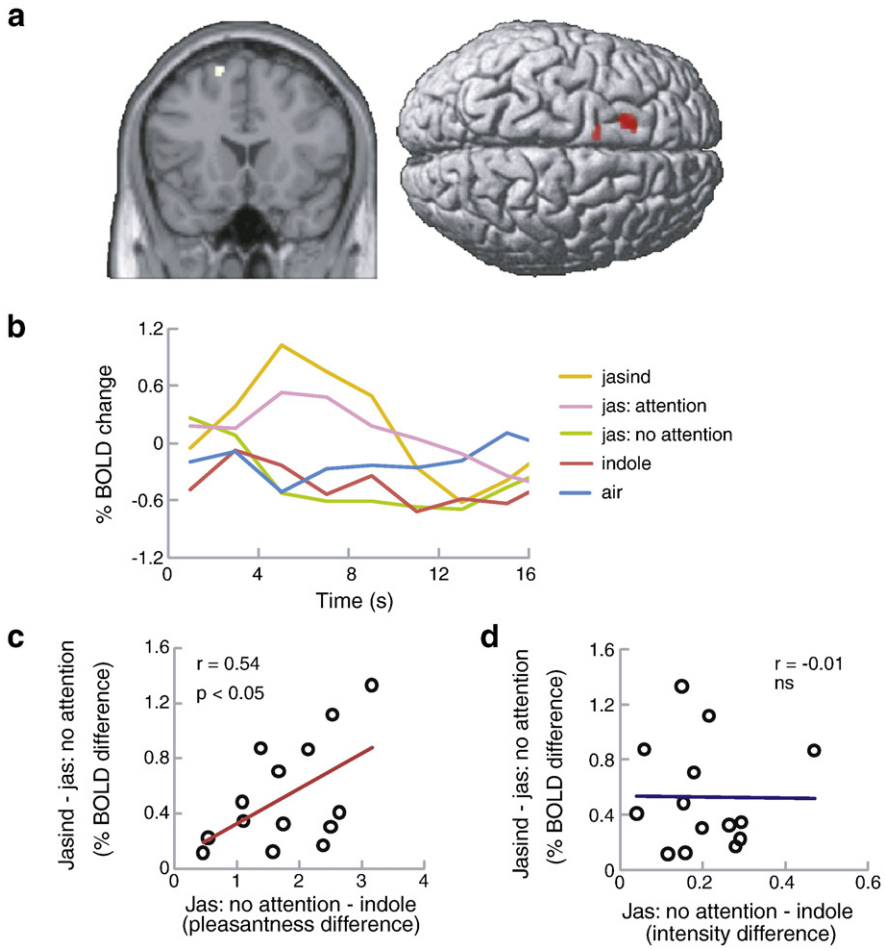

Fig. 3. (a) A contrast between activations produced by the hedonically complex odor mixture, jasind, and its pleasant component, jas, masked inclusively ($p<0.001$) by the contrast of paying attention to jas vs no attention. The superior frontal gyrus was the only brain area to show a significant effect ([−16 18 64] $Z=3.11$ $p=0.010$). (The right part of the figure shows the extent of the effect in the superior frontal gyrus at a reduced threshold of $p=0.005$ for the inclusive masking.) (b) Timecourses of the BOLD response in the superior frontal gyrus for the different olfactory stimuli. (c) Absolute difference in the % BOLD signal produced by jasind and jas in the superior frontal gyrus as a function of the absolute difference in subjective pleasantness ratings between jas and indole across subjects ($r=0.54$, $p<0.05$). (d) Absolute difference in the BOLD signal produced by jasind and jas in the superior frontal gyrus as a function of the absolute difference in subjective intensity ratings between jas and indole across subjects ($r=-0.01$, non-significant (ns)).

not involved in attentional capture by the mixture, and the comparison strengthens the evidence for a specific role of the superior frontal gyrus in attentional capture by the mixture. Further, there was a significant correlation across subjects between the parameter estimates for the contrasts jasind vs jas: no attention and jas: attention vs jas: no attention in the superior frontal gyrus (Fig. 4c) but not in the inferior frontal gyrus (Fig. 4d). This result indicates that the superior frontal gyrus responds very similarly under the attention condition and to the jasind mixture, suggesting that these stimuli recruit a similar type of processing in this region.

To provide further support for a role of the superior frontal gyrus in attention, we re-examined a previous dataset from an independent experiment in 12 subjects in which an attention design similar to the one in the present study was used with a taste stimulus, monosodium glutamate (Grabenhorst and Rolls, 2008). A contrast between trials in which subjects were paying attention to different properties of the taste stimulus (its pleasantness or intensity) compared to when no attention instructions were given revealed a significant effect in the same region of the superior frontal gyrus at [−20 20 64] $z=3.73$ $p=0.029$ (see Supplementary Fig. 3). This effect in the superior frontal gyrus of attention to taste overlapped with the effects of paying attention to odor, and with the attentional capture effect produced by the jasind (see Supplementary Fig. 4). This result indicates that the superior frontal gyrus is involved in attentional processing in different sensory modalities.

Comparison with olfactory brain areas

To ensure that the effects found in the superior frontal gyrus were not attributable to, and did not merely reflect interactions at an earlier cortical stage of olfactory processing (Wilson et al., 2006), we checked whether any of these specific effects were found in the pyriform (primary olfactory) cortex. No significant effects related to attentional capture were found in the pyriform cortex in the whole-brain SPM contrast analyses. To confirm that no effects in the pyriform cortex were present even at lower statistical thresholds, we extracted parameter estimates from a region of interest that was identified in this dataset as responding more strongly to jas when subjects where paying attention to the intensity of the odor, compared to when no attentional instruction was given ([30 −2 −16] $z=3.64$ $p=0.01$). The parameter estimates were for the contrast jas: attention vs jas: no attention 1.42 ± 0.31 and for the contrast jasind vs jas: no attention 0.18 ± 1.4, indicating that neural responses to jas in this region were not modulated by adding an unpleasant component to it. Further, a more anterior region of the pyriform cortex where neural activity correlated with subjective intensity ratings [−18 4 −16] did not show significant differences in the responses to jas, jasind, and indole (Grabenhorst et al., 2007). Moreover, no effects in the contrast analyses related to attentional capture were found in the medial dorsal thalamus or the orbitofrontal cortex. Thus the effects described here cannot be explained in terms of interactions between jas and indole at an early stage in cortical olfactory processing.

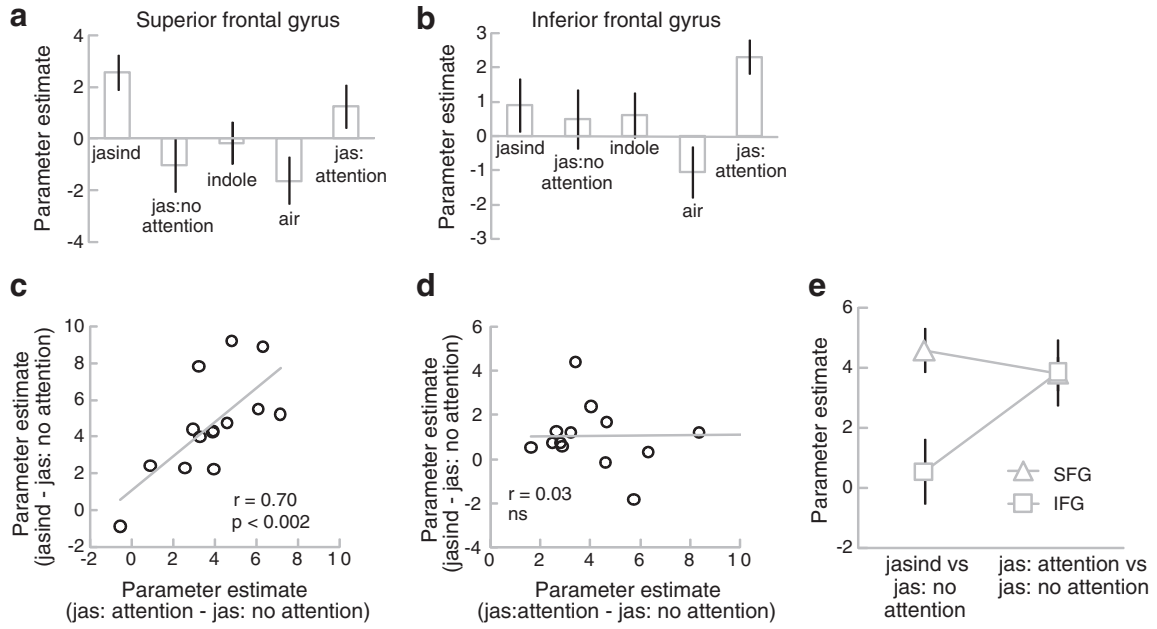

Fig. 4. Parameter estimates for the different conditions for the superior frontal gyrus (a) and the inferior frontal gyrus (b). (c) Superior frontal gyrus: Parameter estimates for the contrast jasind vs jas as a function of the parameter estimates for the contrast attention vs no attention ($r = 0.70$, $p < 0.001$). (d) Inferior frontal gyrus: Parameter estimates for the contrast jasind vs jas as a function of the parameter estimates for the contrast attention vs no attention ($r = 0.03$, non-significant (ns)). (e) A significant interaction ($p = 0.002$) was found between these two brain areas for the parameter estimates of the contrasts attention vs no attention and jasind vs indole.

Functional connectivity analysis

To investigate which brain areas are functionally connected with the superior frontal gyrus during the attentional capture effect we performed PPI analyses using the superior frontal gyrus [−16 18 64] as a seed region. We found that three brain areas showed increased functional connectivity with the superior frontal gyrus during the presentation of jasind compared with the presentation of jas: no attention (Fig. 5a): the lateral prefrontal cortex ([−42 48 18] $z = 2.91$ $p = 0.013$ and [50 36 −4] $z = 3.04$ $p = 0.033$), the medial orbitofrontal cortex ([14 44 −20] $z = 2.61$ with a reduced threshold of $p = 0.005$ uncorrected), and an area consistent with the location of the mediodorsal thalamus ([8 −16 6] $z = 2.92$ $p = 0.002$ uncorrected). Notably, the medial orbitofrontal cortex

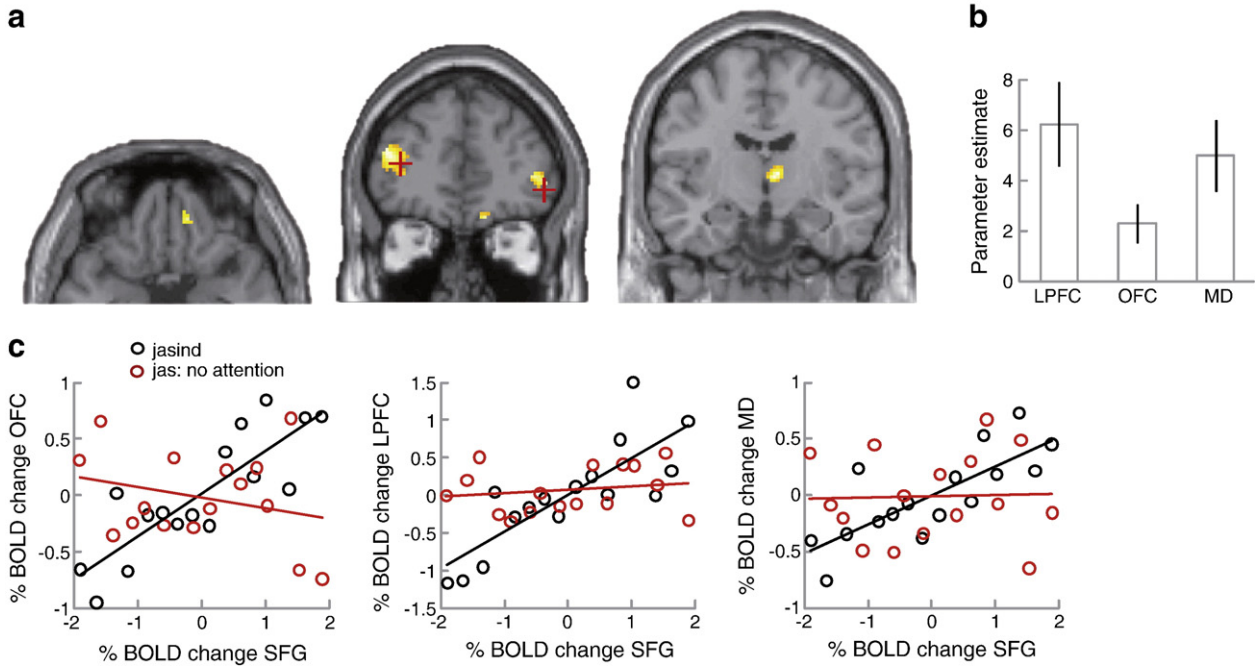

Fig. 5. (a) Brain regions where neural activity was more strongly correlated with activity in the superior frontal gyrus when the jasind odor was presented than when the jas odor was presented. Effects in a PPI analysis were found in the medial orbitofrontal cortex, left and right lateral prefrontal cortex, and the mediodorsal thalamus. The red crosshairs indicate peak coordinates from Grabenhorst and Rolls (2010) where lateral prefrontal cortex activity was differentially correlated with orbitofrontal and pregenual cingulate cortex when selective attention was directed to the pleasantness of a taste stimulus vs its intensity. (b) The parameter estimates ± sem from the PPI analysis. (c) The % BOLD signal in the superior frontal gyrus as a function of the % BOLD signal in the orbitofrontal cortex, lateral prefrontal cortex, and mediodorsal thalamus with the data plotted separately for the jasind condition (black) and the jas condition (red). LPFC: lateral prefrontal cortex, OFC: orbitofrontal cortex, MD: mediodorsal thalamus, SFG: superior frontal gyrus.

region identified in the PPI analysis is the same region that, as reported previously (Grabenhorst et al., 2007), had an increased activation to the jasind compared to jas: no attention and showed a correlation with the subjective pleasantness ratings of the odors. Both lateral prefrontal cortex areas are at the same locations where neural activity in a recent investigation (Grabenhorst and Rolls, 2010) was differentially correlated with the orbitofrontal and pregenual cingulate cortices when selective attention was directed to the pleasantness of a taste stimulus vs its intensity. The peak coordinates of the effects found by Grabenhorst and Rolls (2010) are indicated by the red cross hairs in Fig. 5a. The parameter estimates from the PPI analysis for the different brain areas are shown in Fig. 5b. The correlations between neural activity in the superior frontal gyrus and the three brain areas during the presentation of the jasind vs jas: no attention stimuli are shown in Fig. 5c.

Main effect of olfactory stimulation

To validate our general olfactory task design we also performed a global contrast analysis in which we compared the activations produced by all experimental odors (jasind, jas: no attention, indole) with activations produced by air. The analysis revealed extensive activations in primary and secondary olfactory cortical regions (Carmichael et al., 1994; Haberly, 2001; Price, 2006) (including the medial orbitofrontal cortex [−6 52 −16] $z = 3.64$ $p = 0.005$, parts of the mid orbitofrontal cortex [30 46 −12] $z = 4.32$ $p < 0.001$, [−24 26 −18] $z = 3.98$ $p < 0.001$, [14 30 −22] $z = 3.82$ $p < 0.001$, the amygdala [24 −4 −16] $z = 3.20$ $p = 0.01$ and the olfactory tubercle [14 −6 −12] $z = 3.57$ $p = 0.01$.) Two effects in brain regions outside the main olfactory regions of interest were found in the brainstem [−4 −30 −40] $z = 5.19$ and lateral frontal cortex [12 48 50] $z = 5.09$ (using a statistical criterion of $p < 0.05$, family-wise error corrected with a volume of 15 voxels or greater).

Discussion

Our findings show that neural activity in the superior frontal gyrus is modulated both by selective attention to odor, in that it has enhanced activations when subjects are instructed to pay selective attention to either the pleasantness or the intensity of jasmine without indole, and when indole is added to jasmine to produce a hedonically complex mixture. Thus it is a brain area in which a hedonically complex stimulus with both pleasant and unpleasant components may, even in the absence of explicit attentional demands, produce effects related to attentional processing because of the unusual combination of pleasant and unpleasant components. These findings were made with an odor that is known to most people and found pleasant, jasmine, and thus the results are likely to apply to many people. We emphasize that in its natural form jasmine contains indole in addition to its pleasant components, and that this study was made possible by formulating a chemically-defined model jasmine odor with only pleasant components, to which indole could be added as part of the experimental design. We also emphasize that by including a condition where subjects were instructed to pay selective attention to the jasmine without indole we were able to perform a direct, within-study comparison between brain areas involved in attention to odor and where responses to jasmine with indole compared to jasmine without indole are enhanced. Further, we were able to show in a within-subjects comparison that the magnitude of the attentional capture effect produced by the mixture in the superior frontal gyrus is related to the magnitude of the attentional modulation (Fig. 4c), providing further support for a similar type of processing under both conditions.

In an earlier study (Royet et al., 2000) a more anterior part of the superior frontal gyrus was activated more strongly by affective compared to neutral olfactory and visual stimuli. However, the neural attentional capture effect we report here is not explained simply by affective salience because the region did not respond differently to the affective (pleasant and unpleasant) individual components compared to the neutral air control stimulus (Fig. 4a). It is also important to note that the neural attentional capture effect cannot be explained in terms of pleasantness per se, as no significant effects in this region were found in analyses where the pleasantness ratings were used as subject-specific regressors for neural activity. Moreover, the region did not differentiate between the pleasant and unpleasant components of the mixture when presented individually (Fig. 4a). It is also unlikely that the effects reported were related to differences in task difficulty between the conditions for the following reasons. First, analyses of the variability in the pleasantness and intensity within each participant, measured by the intra-individual coefficient of variation, showed no differences between the attention and no attention conditions indicating that these conditions did not differ in difficulty (Brown, 1997; Brown and Merchant, 2007). Second, all participants were pre-trained in rating olfactory stimuli in the attention condition and the no attention condition using a larger set of odors to ensure that they could perform the task easily.

An interesting finding was that the magnitude of the attentional capture effect in the superior frontal gyrus was a function of the hedonic complexity of the mixture across subjects, defined as the absolute difference in pleasantness between its pleasant and unpleasant components (Fig. 3c). A similar effect was not found for the difference in intensity. This finding indicates that the capacity of the mixture to produce attentional capture in the superior frontal gyrus may be explained by the interactions between its pleasant and unpleasant components. Previous research on odor mixtures has shown that the interactions between components include suppression, the formation of new representations that are different from the components (Giraudet et al., 2002; Shepherd, 2006; Wilson et al., 2006), and difficulty in identifying the chemical components of mixtures with more than a few components (Jinks and Laing, 1999; Laing and Francis, 1989; Livermore and Laing, 1998). The interactions may take place at various stages of the olfactory pathways including the olfactory bulb, and areas that receive inputs from the olfactory tract including the pyriform cortex (Wilson et al., 2006). However, the effects described here cannot be explained in terms of interactions at early stages in cortical olfactory processing, for example in the pyriform cortex, in that no significant effects in this region were found in the whole-brain SPM contrast analyses or in control analyses using regions of interest in the pyriform cortex, medial dorsal thalamus or orbitofrontal cortex. Moreover, the capacity to recruit attentional processing is not simply a general property of all odor mixtures. For example, in the present study the pleasant component, jas, is a chemically complex mixture itself but it did not produce an attentional capture effect in the brain as shown in Fig. 4a which shows no difference in the activations in the superior frontal gyrus between jas (chemically a complex mixture with 8 components) and indole (a pure chemical). This provides further support for the conclusion that it is the *hedonic* complexity of the odor mixture that produces a neural effect of attentional capture, and not chemical complexity per se.

A strength of the present study is that we used a chemically well-defined model of a sensory stimulus that is naturally hedonically complex, consisting of pleasant and unpleasant components. It is known for other naturally complex sensory stimuli that the specific combinations of different components can produce non-linear or synergistic effects in brain areas involving the orbitofrontal cortex and anterior cingulate cortex. These include combinations of monosodium glutamate taste with a consonant vegetable odor (McCabe and Rolls, 2007); sweet taste and vanilla odor (Small et al., 2004); the combination of sweet taste, vanilla odor, and oral fat texture (Grabenhorst et al., 2010); and monosodium glutamate taste with the ribonucleotide inosine 5′-monophosphate (de Araujo et al., 2003). In contrast, non-linear interactions especially with respect to affective stimuli are typically less evident for combinations that may not normally be part of a familiar natural stimulus, for example monosodium glutamate and rum odor or salty taste and vanilla odor (McCabe and Rolls, 2007; Small et al., 2004).

What might be the nature of the attentional capture effect? The superior frontal gyrus does not represent the pleasantness of the odors involved, so it does not contribute as a hedonic analyser. Nor is it an olfactory region in the sense that it does not respond to the other odors in any way different from air (Figs. 3b, 4a). However, by reflecting attentional capture to the complex hedonic mixture, it may prolong and enhance brain processing of the hedonically complex mixture. Where could such an effect be expressed in the brain, as a result of top-down effects from the prefrontal cortex (Rolls, 2008; Rolls and Deco, 2002)? A likely candidate is the medial orbitofrontal cortex, where responses to jasind are larger than to either of its components (Grabenhorst et al., 2007), and where the activations reflect the pleasantness of the stimuli (Anderson et al., 2003; Grabenhorst and Rolls, 2009; Grabenhorst et al., 2007; Rolls et al., 2003). Consistent with this hypothesis, we found in the present study that activity in the superior frontal gyrus was correlated with activity in the medial orbitofrontal cortex and that this correlation was stronger when the mixture was presented compared to when its pleasant component was presented. Thus part of the efficacy of hedonically complex odor mixtures is that they may operate by recruiting neural mechanisms related to attention, which then via top-down influences modulates processing by enhancing processing and perhaps reducing habituation in areas such as the orbitofrontal cortex where the pleasantness of the stimuli is represented (Grabenhorst et al., 2007; Rolls and Grabenhorst, 2008). We note that two of the participants in the present study did show enhanced pleasantness in that they rated the jasind mixture as being significantly more pleasant than the jas odor alone. Even if in all subjects the mixture with different hedonic components does not lead to increased pleasantness ratings, the larger activations in the medial orbitofrontal cortex by jasind (Grabenhorst et al., 2007) might represent preferences that are not conscious, but can influence decision-making and behavior, and may draw attention back later to the odor, which could prolong its pleasantness.

This newly investigated attentional capture mechanism in the superior frontal gyrus may act together with a separate mechanism by which activations in brain regions such as the medial orbitofrontal cortex to pleasant odors reflect primarily the pleasantness of odor mixtures, and much less any unpleasant components they may have (Grabenhorst et al., 2007). It is of interest that this mechanism dominates sensory experience, in that although the unpleasant components of the jasmine mixture are represented in other brain areas that represent the unpleasantness of olfactory stimuli, such as the dorsal anterior cingulate cortex (Grabenhorst et al., 2007), the pleasantness of the complex mixture dominates the affective experience. An interesting question for future research is whether processing related to attentional capture in the superior frontal gyrus can be produced by a hedonically complex stimulus that is overall unpleasant. A recent positron emission tomography study found that parts of the orbitofrontal cortex responded more strongly to a binary odor mixture of pleasant citral and unpleasant pyridine than to its individual components (Boyle et al., 2009). The mixture was overall less pleasant than its pleasant component. However, correlations with subjective pleasantness, intensity or hedonic complexity were not investigated in that study, nor were effects related to salience, selective attention or attentional capture. Thus, the nature of these 'odor impurity' responses remains unclear.

Because of the close relationship between emotion and olfaction, odors play an important role in making many sensory stimuli pleasant and attractive, including in food selection and social affiliative behavior. This may be an important way in which hedonically complex odor mixtures that are especially effective in activating brain regions involved in attention and hedonic evaluation (Grabenhorst et al., 2007) can influence value-based choices and behavior. The present investigation is also relevant to the much broader issue of how pleasant and unpleasant stimuli combine to produce what is overall a pleasant experience, and indeed what can sometimes be a more pleasant experience than the pleasant component alone. Our findings suggest that at least part of the affective potency of stimuli with mixed pleasant and unpleasant components is that they become more pleasant by recruiting superior frontal mechanisms involved in attentional capture and enhancement. The finding that the magnitude of the attentional capture effect in the superior frontal gyrus was related to the hedonic complexity of the mixture also indicates that there may be individual differences in the extent to which a hedonically complex stimulus such as an odor mixture captures attention, and this may be related to differences in subjective preferences and value-based choices. Interestingly, the same superior frontal gyrus region has previously been shown to respond more strongly to cues related to smoking in abstinent compared to satiated smokers (McClernon et al., 2005, 2008), providing further support for a function of this brain region in attentional capture and responses to hedonic cues. An interesting question for future studies is whether the attentional capture effect produced by hedonic complexity in a sensory stimulus can interact with the effect produced by explicit selective attention in the superior frontal gyrus.

We also found in a PPI analysis that neural activity in the superior frontal gyrus was correlated with activity in the mediodorsal thalamus and that this correlation was stronger on trials when the mixture was presented compared to when its pleasant component was presented (Fig. 5). The mediodorsal thalamus has previously been shown to be part of a functional system that underlies attention to olfactory stimuli (Plailly et al., 2008). Our present finding further implicates the mediodorsal thalamus in olfactory attention and suggests that it plays a role even under conditions when attentional processing is recruited by a hedonically complex odor mixture.

The lateral prefrontal cortex including the superior frontal gyrus has been shown to be involved in attention to sensory stimuli across modalities (Corbetta and Shulman, 2002; Hopfinger et al., 2000; Kanwisher and Wojciulik, 2000). The superior frontal gyrus occupies a large area of the frontal cortex. Thus when comparing superior frontal activations across studies it is important to consider the exact location of the effect. While a single functional contribution of the superior frontal gyrus to cognitive function has not yet been identified there is much evidence that implicates this brain area in attentional processing. In one study the superior frontal gyrus was activated in response to attention-directing cues (Hopfinger et al., 2000), and their region overlaps with that described here. A further study found that the same area was commonly activated by joint and non-joint attention in a social attention paradigm (Williams et al., 2005). A study which compared brain activations in healthy individuals and patients with schizophrenia during a continuous performance test, a widely-used measure of attentional functions, found reduced functional connectivity between the superior frontal gyrus, in a region overlapping with the one found in the present study, and other cortical areas involved in attention (Honey et al., 2005). In one study, transcranial magnetic stimulation of the superior frontal cortex selectively impaired performance in a visuo-spatial working memory task but not a visual-object working memory task (Oliveri et al., 2001). The authors of that study relate this finding to a possible function of the superior frontal gyrus in covertly directing attention from one spatial location to another. This interpretation is consistent with our proposal that the superior frontal gyrus is involved in neural processing related to selective attention, and that a hedonically complex odor mixture can implicitly engage this processing. We note that a strength of the present investigation is the within-study comparison of a functional localizer contrast for selective attention with a contrast for hedonic complexity in an odor mixture. This strategy of comparing activations produced in different conditions in the same study is a stricter test than comparing effects across different studies where the exact location of an effect may vary for example due to differences in subject samples, experimental procedures, and fMRI data acquisition protocol.

The inferior frontal gyrus region in which we found effects has also been implicated in top-down attention (Chong et al., 2008; Downar et al., 2000). In the present investigation no effects of attentional capture were observed in olfactory brain areas such as the pyriform cortex or the orbitofrontal cortex. We have previously reported in a different analysis of the present dataset that the pyriform cortex is specifically involved in attention to intensity whereas the orbitofrontal cortex is specifically involved in attention to pleasantness (Rolls et al., 2008). The present findings indicate that the superior frontal gyrus may be involved in processing related to attention independently of what specific aspect of the stimulus attention is being paid to. We also report that in an earlier study in which an attention design similar to the one in the present study was used with a taste stimulus, monosodium glutamate (Grabenhorst and Rolls, 2008), the superior frontal gyrus also showed enhanced activation by a contrast between trials in which subjects were paying attention to different properties of the taste stimulus (its pleasantness or intensity) compared to when no attention instructions were given (see Supplementary Fig. 2). Moreover, using PPI analyses we found in the present investigation that neural activity in the superior frontal gyrus was differentially correlated during the jasind and jas: no attention conditions with areas in the lateral prefrontal cortex (Fig. 5a). The specific areas in lateral prefrontal cortex where PPI effects were found have recently been shown to be involved in the effects of top-down selective attention to the pleasantness vs intensity of taste (Grabenhorst and Rolls, 2010). Thus the superior frontal gyrus is involved in attentional functions in different sensory modalities including olfaction and taste. The novel finding of this investigation is that this brain region is also involved in attentional capture to hedonically complex stimuli, even in the absence of explicit attentional demands.

Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.12.023.

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