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3 **Visual priming influences olfactomotor response**
4 **and perceptual experience of smells**
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Abstract

Whereas contextual influences in the visual and auditory domains have been largely documented, little is known about how chemical senses might be affected by our multi-sensory environment. In the present study, we aimed to better understand how a visual context can affect the perception of a rather pleasant (floral) and a rather unpleasant (damp) odor. To this end, 19 healthy participants performed a series of tasks including odor detection followed by perceptual evaluations of odor intensity, pleasantness, flowery and damp characters of both odors presented at two different concentrations. A visual context (either congruent or incongruent with the odor; or a neutral control context) preceded odor stimulations. Olfactomotor responses as well as response times were recorded during the detection task. Results showed an influence of the visual context on semantic and motor responses to the target odors. First, congruency between context and odor increased the saliency of the olfactory feature of the memory trace, for the pleasant floral odor only (higher perceived flowery note). Clinical applications of this finding for olfactory remediation in dysosmic patients are proposed. Second, the unpleasant odor remained unaffected by visual primes, whatever the condition. In addition, incongruency between context and odor (regardless of odor type) had a disruptive effect on odor sampling behavior, which was interpreted as a protective behavior in response to expectancy violation. Altogether, this second series of effects may serve an adaptive function, especially the avoidance of, or simply vigilance towards, aversive and unpredictable stimuli.

Keywords

Olfaction, visual context, priming, intensity, pleasantness, sniffing

Introduction

Processing of environmental objects by our brain usually involves more than a single sensory input. A given object possesses attributes that can be processed by vision (such as shape, color), somatosensory system (e.g., softness, temperature, pain), audition (like sound volume, frequency), taste (e.g., bitter, sweet), trigeminal system (e.g., freshness, irritation), and olfaction (e.g., odor intensity, localization). Such multimodal integration contributes to the formation of percepts, where all pieces of solicited sensory information are associated together and compared with previous mental representations.

Beside this multimodal integration, there is also evidence for interactions between sensory modalities during the processing of environmental objects, including for instance auditory interferences on visual sensitivity (Chen & Spence 2011) or between olfaction, verbal materials and/or vision which have also been shown to interact with each other. These interactions can take two forms. The first form is an influence by *direct access* whereby a sensory modality facilitates / interferes with the processing of another modality during a multimodal perception (here, the two stimulations are presented concurrently) (Zellner and Kautz, 1990; Gottfried and Dolan, 2003; Herz, 2003; Sakai, 2005; Bensafi et al., 2007a, 2014). The second form is an influence by *reactivation* where a sensory modality facilitates / interferes with the processing of another modality via a priming paradigm (here, the first stimulus – the prime – is presented before the second stimulus – the target). Such priming paradigms are commonly used in psychological research to study how the prime can affect the processing of, and behavioral/motor response to, the target. The target may or may not share with the prime some sensory, affective or semantic properties. Priming tasks have been recurrently used in sensory studies in order to explore how olfactory stimuli influence the processing of visual information (Grigor et al., 1999; Castle et al., 2000; Bensafi et al., 2002a; Cook et al., 2015) and vice versa (van Beilen et al., 2011; Kowalewski and Murphy, 2012).

On a theoretical level, such a mutual influence between olfaction and vision can be explained using cognitive models of human memory, in particular the Activation-Integration ACT-IN model (Versace et al., 2014). In this model, percepts are defined as representations characterized by multiple components: shape, color, odor, sound, emotion, motor, etc. Such percepts are encoded in memory as multi-dimensional objects containing these inter-related components which altogether form a “memory trace”. This model predicts that any salient component of a given trace can reactivate the trace itself but also other components of the same trace. For instance, for environmental objects that contain smells (i.e., a rose) one may assume that its visual characteristics (materialized by, for instance, pictures of a rose or gardens) can influence the activation of the emotional (i.e.,

hedonicity of a rose, modulated by its intensity), semantic (i.e., smell of a rose) and motor (i.e., action of sniffing a rose) attributes. The main aim of the present study was to test this prediction. Here, we hypothesized that a visual image (prime) semantically associated with an odor would influence the subsequent processing of the odor in a priming paradigm. We further assumed that such influence of the visual prime on the smell target would be observed at different levels of processing, from emotional ratings, to semantic evaluations and olfactomotor responses. The experimental design included 2 concentrations of 2 odors differing in hedonic valence. In addition, the role of the semantic proximity between the prime and the target was examined: we predicted that congruent associations might have a facilitating effect while incongruent associations might have a disrupting effect on the processing of the target. During the experimental sessions, participants were required to perform a series of tasks related to the odorant: following prime presentation, they were asked to detect the smell as fast as possible after its presentation, to give estimates of intensity and pleasantness, and to qualify it using quality descriptors, while sniffing behavior was recorded. Four variables were thus collected: emotional and semantic ratings, olfactomotor response and response time.

Material and Methods

Subjects

Nineteen healthy participants (mean age $\pm$ standard deviation: 28.9 ± 9.5 ; 9 men and 10 women) were recruited at the University of Lyon, France. They declared having normal olfaction and *a posteriori* verification showed that *i*) the participants perceived the experimental odors at a satisfactory level of intensity (4.6 ± 0.9 on a scale from 1 to 9), and *ii*) none of the participants had lower intensity ratings than the others, as shown by a Grubbs test for outliers ($G = 2.11$, $U = 0.72$, $p = 0.2257$). Participants provided written informed consent prior to participation. They were tested individually and received monetary compensation for their participation. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local Lyon Sud-Est II review board.

Stimuli

Odors. Two odorants were used (odorant code, « quality » with verbatim extracted from www.thegoodscentcompany.com, CID): phenyl-2-ethanol (PEA, floral/rose/dried rose, 6054), terpinen-4-ol (TER, earthy/musty/damp, 11230) both provided by Sigma Aldrich. Each odorant was used at 2 concentrations (percentage in vol/vol): high (PEA: 1%; TER: 5%) and low (PEA: 0.5%; TER: 1%). Concentrations were chosen based on previous studies (Kermen et al., 2011; Licon et al., 2018) so that each odor has a low and high perceived intensity, that high concentrations of both odors are approximately iso-intense, and that low concentrations remain high enough to allow odor identity to be recognized (explaining why concentration intervals between high and low are not identical for both odors). Odorants were diluted in odorless mineral oil (Sigma Aldrich), absorbed on a scentless polypropylene fabric (3 × 7 cm; 3M, Valley) to maximize air exchange surface and dispensed in 15 mL brown glass jars (opening diameter: 1.8 cm; height: 5 cm; filled with 5 mL odorous solution). We also used “blank” jars containing only odorless mineral oil, to limit participants’ olfactory fatigue along the testing and to test for effective odor perception by comparing odorous vs. blank flasks. PEA and TER were chosen because they were perceived as different in terms of pleasantness and because they elicited distinct semantic descriptions in previous studies (Kermen et al., 2011). In that study, the analysis of verbatims revealed that: (i) the two odors elicited no words in common, (ii) the most frequent words for PEA were “Rose”, “Floral”, and “Alcohol” and for TER “Muddy”, “Woody”, “Damp”. These descriptions fit the organoleptic characteristics of these molecules (see <http://www.thegoodscentcompany.com>).

Pictures. Visual cues were high-resolution pictures displayed on a computer screen. Pictures were either copyright-free or from the authors’ personal shots. Two different contexts were used, and each context was represented by 3 different pictures (Fig. 1A): Context 1 was a woody, damp, musty environment, congruent with TER odor, and Context 2 was a floral, garden or perfume factory environment, congruent with PEA. The most suitable pictures of a series were chosen during a pilot study, during which 5 participants were asked to evaluate 30 candidate pictures chosen by the experimenters to visually illustrate the odor descriptors. Participants were asked to provide a rating of the congruence between the 6 descriptors given for PEA (3) and TER (3) and each picture, on a scale from 0 (descriptor not suited at all) to 10 (descriptor very well suited). For each odor, we identified and kept for the main study the 3 pictures with both the highest ratings of congruence with the target odor’s descriptors and the lowest ratings of congruence with the other odor’s descriptors. We thus obtained 6 pictures in total, 3 for each odorant.

In the main protocol, each odor (PEA, TER) was presented after the 6 selected pictures (3 congruent, 3 incongruent), but also after a neutral context (grey rectangle). At the end of the experimental session (described hereafter in the Procedure section), participants were asked to rate the congruency between each odor (at high concentration) and the 6 pictures using a scale from 1 (not related at all) to 9 (very congruent). These evaluations confirmed that the pictures were chosen in an appropriate manner (Fig. 1C) since TER was rated more congruent with Context 1 than PEA (paired t-test: $t(17) = 2.41$, $p = 0.0274$), and PEA was rated more congruent with Context 2 than TER ($t(17) = 3.77$, $p = 0.0015$).

Procedure

Each trial was characterized by a combination of 3 factors: Odor (PEA, TER), Concentration (high, low), and Context (congruent, incongruent, neutral). A total of 36 olfactory trials were thus used (2 odorants $\times$ 2 concentrations $\times$ 3 contexts $\times$ 3 pictures per context). Note that to limit olfactory fatigue and/or adaptation, an empty flask was presented 9 times as a target (3 times per type of context, interspersed within the olfactory targets). Thus, in total, the experiment lasted about 35 minutes and included 45 trials (36 odors + 9 empty flasks). The presentation order of the 45 different combinations of odor/concentration/context/picture was fully randomized. Participants were seated in a comfortable chair, equipped with the sniffing measurement apparatus and facing an adjustable computer screen set at eye-level (1 m viewing distance). A nasal cannula (AirLife, CareFusion, USA) positioned in both nostrils and connected to an airflow sensor (AWM720, Honeywell, France) allowed to record sniffing behavior. The sniffing signal was amplified and digitally recorded at 256 Hz using LabVIEW software®. To record response time during the odor detection task, participants' dominant, i.e., right hand (all were right-handed) was placed on a button-box (see next paragraph). At the beginning of each trial (see trial description in Fig. 1B), after a 1-second resting time, a circle was presented in the middle of the screen during 4 s, followed by a picture presented for 5 s. The participant were then asked to breathe out (instruction appearing for 2s), before a cross appeared in the middle of the screen for 5 s during which an odor was presented by the experimenter. The flask was placed 1 cm under the participant's nostrils and the participant had to press a key of the button-box with his/her index finger as soon as an odor was detected (and before the end of the 5-s odor presentation). The flask was then removed, and a new screen was presented for 25 s, where the participants were instructed to answer the questions of the experimenter. At this stage, participants were asked to rate intensity, pleasantness, flowery note and damp note using scales from 1 (very little intense, very unpleasant, not floral at all, not damp at all) to 9 (very intense, very pleasant, very flowery, very damp). The terms "flowery"

and “damp” were chosen among the other most frequent descriptors (see *Odors* section) because they referred to perceptual characteristics of the odors rather than odor sources (like rose or mud). The responses of the participants were given orally and written down by the experimenter.

Figure 1

Data Analysis

The analyzed variables were *i*) perceptual ratings of the odors (intensity, pleasantness, flowery note and damp note), *ii*) characteristics of the first sniff during flask presentation, namely sniff volume (area under the curve) and sniff duration in seconds (between the inhalation starting point and the point where the flow returned to zero), and *iii*) reaction time (RT) during odor detection (i.e., time between the flask inhalation starting point and the button-press to indicate that he/she detected an odor; these two time-points were recorded in milliseconds by the sniff recording system described in the procedure). Only trials involving TER and PEA were considered in the analyses (not the blank, $N=684$ trials). There were missing data described as follows. In case the odor was not detected, participants made no perceptual ratings (6% of the ratings). Because of anticipated sniffing (i.e., inhalation starting point occurring before odor presentation) or because of technical issues, the olfactomotor data of two participants were discarded (11 % of the trials, $N=17$ subjects). RTs below 200 ms were discarded (not within the normal range of reactivity for this kind of task: Olofsson, 2014) as well as RTs above 5 s (which was the maximum allocated time). It must be added that several aberrant observations that were deleterious for the quality of the statistical models (see next paragraph) were identified by visual inspection of the graphs of residuals and of Cook’s distances: they were removed (for sniff volume: 3 trials; for sniff duration: 3 trials with 2 being the same as for sniff volume) before recomputing the final model. Additional RTs were missing due to technical problems or to non-usable sniffs (see above) since RT calculation was based on the start of the sniff (16% of the trials missing, $N=17$ subjects).

We used RStudio 1.1.453 on R 3.5.0 (R Core Team, 2018) and lme4 package (Bates et al., 2015) to perform a linear mixed effects analysis of the effects of Odor, Context and Concentration on participants’ responses, i.e. ratings of intensity, pleasantness, flowery and damp notes, sniff volume and duration, and odor detection time. As fixed effects, we entered Odor (PEA, TER), Context (congruent, incongruent, neutral) and Concentration (high, low) into the model, integrating only 2-way interactions because 3-way interactions were not significant for any of the variables (likelihood ratio test – with the *anova* function – comparing models with

and without the triple interaction). As random effects, we had intercepts for subjects, which was found to be highly relevant due to the important inter-individual variability (between 31 and 68% of the residual variance depending on the variable considered). We also included the random intercept for pictures, but likelihood ratio test model comparison showed that the complete model with both subjects and pictures was not significantly better than the model with only subjects, which was thus used. Sniff parameters (duration and volume) as well as RTs were log-transformed. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Following (Luke, 2017), p-values were obtained using Kenward-Roger approximation in the *anova* function of lmerTest package in R (Kuznetsova et al., 2017) and non-significant interaction were removed to keep only the best model including the main effects and the significant interactions. Post-hoc contrasts were performed using the *multcomp* function of the emmeans package in R (Lenth et al., 2019) and are reported in the results section with a significance level of 0.05.

Results

Detailed statistics regarding the main effects and interactions are reported in Table 1, and post-hoc contrasts allowing us to describe these significant effects are reported in Table 2 and illustrated in the Figures. Non-significant main effects or interactions are not mentioned in the text and only appear in the tables.

Emotional ratings

Intensity. Linear mixed model showed a significant Odor $\times$ Concentration interaction ($p < 0.0001$), as well as main effects of Concentration ($p < 0.0001$) and Odor ($p < 0.0001$) (see Table 1). Both odors were perceived as significantly more intense when they were at high concentrations compared to low concentrations (significant post-hoc contrasts: PEA-high vs. PEA-low, and TER-high vs. TER-low), but TER at high concentration received even higher intensity ratings (significant contrast: TER-high vs. PEA-high, while the contrast TER-low vs. PEA-low was not significant).

Pleasantness. A main effect of Odor was found ($p < 0.0001$, see Table 1), due to PEA's higher pleasantness ratings (Table 2).

Semantic ratings

Flowery note. The Odor $\times$ Context interaction was found to be significant ($p < 0.05$, see Table 1). As illustrated in Fig. 2A showing all significant post-hoc contrasts, while flowery ratings of TER were stable across contexts, flowery ratings of PEA were significantly higher in the congruent (flowery) than in the incongruent (damp) or neutral contexts (Table 2). In line with this, on average PEA was rated more flowery than TER (main effect of Odor, $p < 0.0001$, see Tables 1 and 2). Also, the congruent context was associated to higher flowery ratings (main effect of Context, $p < 0.01$, see Table 1; significant contrasts: congruent vs. neutral, and congruent vs. incongruent, while the contrast neutral vs. incongruent was not significant, see Table 2).

Damp note. First, there was a significant Odor $\times$ Context interaction ($p < 0.05$, see Table 1). As illustrated in Fig. 2B showing all significant post-hoc contrasts, while damp ratings of TER were stable across contexts, damp ratings of PEA were significantly higher in the incongruent (damp) than in the congruent (flowery) context (Table 2). Second, the Odor $\times$ Concentration interaction was significant as well ($p < 0.01$, see Table 1). Indeed, TER was rated damper at high compared to low concentration (significant TER-high vs. TER-low contrast), while this was not the case for PEA (PEA-high vs. PEA-low contrast was not significant), and TER received higher damp ratings than PEA at both concentrations (significant contrasts: TER-high vs. PEA-high, and TER-low vs. PEA-low, see Table 2). In line with this, on average TER was rated more damp than PEA (main effect of Odor, $p < 0.0001$, see Tables 1 and 2), and high concentrations were associated to higher damp rating than low concentrations (main effect of Concentration, $p < 0.05$, see Tables 1 and 2).

Figure 2

Olfactomotor responses

Sniff Volume. Results on log-transformed sniff volume revealed a significant main effect of Context ($p < 0.01$, Table 1), due to the fact that sniff volume was smaller in the incongruent than the neutral context (Table 2, Fig. 3A: incongruent vs. neutral was the only significant post-hoc contrast). The Odor $\times$ Concentration interaction was significant ($p < 0.05$, Table 1). Indeed, sniffs had smaller volume when smelling TER at high concentration compared to TER at low concentration (significant TER-high vs. TER-low contrast), and compared to PEA at high concentration (significant TER-high vs. PEA-high contrast) (the other contrasts, PEA-high vs. PEA-low, and TER-low vs. PEA-low, were not significant, see also Table 2). There were also significant main effects of Odor ($p < 0.01$) and of Concentration ($p < 0.01$, Table 1), because sniff volume was smaller for TER than for PEA, and smaller for high compared to low concentrations.

Sniff Duration. As for sniff volume, results on log-transformed sniff duration revealed a significant main effect of Context ($p < 0.001$, Table 1), due to the fact that sniff duration was shorter in the incongruent than the neutral context (Table 2, Fig. 3B: incongruent vs. neutral was the only significant post-hoc contrast). In addition, there was also a significant main effect of Concentration ($p < 0.0001$, Table 1), because sniff duration was shorter for high compared to low concentrations.

Figure 3

Odor Detection Time

There was a significant Odor $\times$ Concentration interaction ($p < 0.01$, Table 1), due to the fact that TER at high concentration was detected faster than TER at low concentration (significant TER-high vs. TER-low contrast), and faster than PEA at high concentration (significant TER-high vs. PEA-high contrast) (the other contrasts, PEA-high vs. PEA-low, and TER-low vs. PEA-low, were not significant, see also Table 2). Odor and Concentration had significant main effects ($p < 0.0001$ and $p < 0.0001$ respectively, Table 1), due to faster detection of TER than of PEA, and to faster detection of high compared to low concentrations (Table 2).

Discussion

In the present study, we aimed to test the hypothesis that a visual prime semantically associated with an odor would modulate the subsequent processing of this odor. We tested this assumption by manipulating the congruency between the visual prime and the olfactory target, and by measuring emotional, semantic and motor responses to olfactory targets according to whether they were congruent or not with the visual prime. The visual prime did influence odor processing, and this modulation depended on the nature of the odor. Indeed, when considering the odor of PEA, which is rather pleasant and has a flowery quality, we found that a congruent visual prime increased the flowery semantic quality attributed to this odor. Not only flowery but also damp ratings of PEA were affected by visual context: PEA was evaluated as damper when presented after the damp context. On the contrary, TER, which is a rather unpleasant odor that has damp/humid qualities, was unaffected by visual priming since none of the perceptual ratings (intensity, pleasantness, flowery and damp ratings) for this odor varied as a function of visual context congruency. The results on PEA are consistent with previous studies reporting that visual environmental cues can prime odor processing and render odors more salient (Schifferstein

and Verlegh, 1996; Gottfried and Dolan, 2003). This also suggests a more vivid activation of the memory trace, on several aspects including smell, by the related visual information (Versace et al., 2014). Note that, although the damp visual context was clearly more congruent with TER than with PEA, it can still be part of memory traces involving rose odor: indeed, plants and flowers, due to their vegetable nature, have a certain degree of humidity that can express through olfactory notes. This would explain why the damp visual context increased damp notes perceived when smelling PEA. The discrepancy observed between TER (unaffected) and PEA (more flexible) with regards to visual priming may reflect that for unpleasant odors such as TER, their adaptive value (i.e., indicating a potentially noxious odor source to be avoided) makes them less susceptible to cognitive modulation. This asymmetry between positively and negatively valenced odors with regard to top-down influences, with unpleasant odors being less prone to such influences, has been reported in previous studies (Ferdenzi et al. 2013; Herz 2003).

Beyond the effects of visual context on participants' conscious responses (perceptual ratings), an original finding of this study is that the olfactomotor behavior associated to the perception of the smell targets was modulated as well. The volume and duration of the olfactomotor activity (sniffing) were significantly lower after the participant was primed with an incongruent visual context (compared to a neutral context). Sniffing, i.e. the active sampling of olfactory information, is an implicit behavior that accompanies odor perception in the very first seconds after stimulus presentation (Ferdenzi et al., 2015). Its volume and duration determine the amount of inhaled odor, which confers to sniffing behavior a function of protection against toxic substances (decreased volume and duration in response to strong and unpleasant odors: Johnson et al., 2003; Bensafi et al., 2007b). Here, the reduced sniffing behavior in the incongruent context may be explained by expectation effects. When the target odor is inconsistent with the previous visual prime, participants may experience expectancy violation and may therefore quickly stop sniffing as an expression of vigilance regarding an unpredictable stimulus. It must be noted that this effect was disconnected from the nature of the odor (PEA or TER), probably because this behavior occurs precociously in the chain of responses to the odor, before the more complex cognitive processing measured through verbal evaluations.

In conclusion, this study showed the influence of the visual context on the processing of a smell (semantic and motor attributes in particular). On the one hand, incongruency between a visual prime and an olfactory target seems to have a disruptive effect on odor sampling behavior since it was associated with reduced overall olfactomotor behavior. Congruency on the other hand increased the saliency of the trace only for the pleasant odor PEA. Although our findings cannot be generalized to all pleasant and unpleasant odors, they make

sense in an adaptive perspective and should be tested in future studies by including more contrasted odorants and a larger set of stimuli. Other observations were made in this experiment, namely that i) sniffing volume and duration were lower for higher odor concentrations, which replicates previous findings (Mainland and Sobel, 2006), and ii) the most aversive odor TER was detected faster and sniffed less intensely (lower sniff volume), all the more so that it was presented at high concentration, which is in line with Bensafi et al. (2002b) and Boesveldt et al. (2010). These elements reinforce the validity of the protocol used in our study. We expected visual congruent prime to shorten odor detection time, based on Olofsson et al. (2012)'s study, but this assumption could not be verified. One explanation could be found in the nature of the primes (Loersch and Payne 2011): indeed, congruency between the primes and the targets that we chose may have not been strong enough to facilitate odor detection, and this parameter could be improved in the future (by reinforcing the semantic content of the visual prime, e.g., with the addition of verbal information to the picture).

As a perspective, applications of this research could be developed for example in rehabilitation strategies for patients with hyposmia (partial olfactory loss) where odors are perceived as relatively weak. Several studies showed that the prevalence of hyposmia is relatively high (10-15 %) (Brämerson et al. 2004; Landis et al. 2004; Hummel et al. 2007), and increases with aging (Gaines, 2010). Moreover, significant alteration of the quality of life is typically associated with this sensory impairment (Croy et al., 2014; Manesse et al., 2017). Concrete solutions to enhance olfactory perception would thus be extremely useful. Remediation of olfactory perception through daily training has positive outcomes, both on the level of perception (Hummel et al. 2009) and on activation of brain areas involved in semantic and memory functioning (e.g. hippocampus) (Gellrich et al., 2017). Therefore, setting up a training protocol that would enhance the saliency of the odor memory trace (or at least some of its components), for example by combining odor with relevant visual contexts, may be beneficial in improving olfaction in people with olfactory deficits.

Acknowledgments

This study was funded by a grant from the Auvergne-Rhone-Alpes French Region (ARC2 Program, Qualité de vie et Vieillessement) to MB. The authors wish to thank Romain Bouet for helping with statistical analyzes and two anonymous reviewers for their comments.

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Figure Legends

Figure 1. Protocol. (A) The experimental design comprised 45 trials that were combinations of the factors Context (6 pictures + 1 neutral), Odor (2 odors + 1 blank) and Concentration (2 levels). (B) Sequence of a trial. (C) Congruency ratings (Mean $\pm$ SEM; * $p < 0.05$ in a paired t -test).

Figure 2. Semantic ratings (Mean $\pm$ SEM). Odor by Context interaction for (A) Flowery ratings ($p = 0.0175$), and (B) Damp ratings ($p = 0.0115$). * $p < 0.05$ post-hoc contrasts by pairs.

Figure 3. Olfactomotor responses (Mean $\pm$ SEM). Effect of Context on (A) Sniff volume (Area Under the Curve) ($p = 0.0082$), and (B) Sniff duration (in seconds) ($p = 0.0009$). * $p < 0.05$ post-hoc contrasts by pairs.