

OBSERVATION

High and Low Roads to Odor Valence? A Choice Response-Time Study

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Valence and edibility are two important features of olfactory perception, but it remains unclear how they are read out from an olfactory input. For a given odor object (e.g., the smell of rose or garlic), does perceptual identification of that object necessarily precede retrieval of information about its valence and edibility, or alternatively, are these processes independent? In the present study, we studied rapid, binary perceptual decisions regarding odor detection, object identity, valence, and edibility for a set of common odors. We found that decisions regarding odor-object identity were faster than decisions regarding odor valence or edibility, but slower than detection. Mediation analysis revealed that odor valence and edibility decision response times were predicted by a model in which odor-object identity served as a mediator along the perceptual pathway from detection to both valence and edibility. According to this model, odor valence is determined through both a “low road” that bypasses odor objects and a “high road” that utilizes odor-object information. Edibility evaluations are constrained to processing via the high road. The results outline a novel causal framework that explains how major perceptual features might be rapidly extracted from odors through engagement of odor objects early in the processing stream.

Keywords: olfactory perception, odor object coding, valence, emotion

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How are major perceptual features derived from an olfactory input? The present study proposes a novel theoretical framework for olfactory perception based on response-time (reaction time [RT]) measurements and mediation analysis.

Among the many possible perceptual attributes of an odor, the features of valence (unpleasant to pleasant) and edibility (low to high) explain a large proportion of the total perceptual variance among odors (Khan et al., 2007; Lawless, 1989; Schiffman, Musante, & Conger, 1978; Stevenson, 2010; Zarzo, 2008). The dominance of these two features reflects the evolutionary legacy of the olfactory system, which is closely affiliated with the limbic system. Even though valence and edibility ratings are often correlated, they can be dissociated; perfumes are typically rated as pleasant but not edible, whereas the smell of onion typically shows the opposite pattern (Royet et al., 1999).

Although little is yet known about how the brain determines the valence and edibility of an odor, recent findings support an “object-centered” approach to olfactory perception (see Gottfried, 2010; Olofsson, Bowman, Khatibi, & Gottfried, 2012; Wilson & Stevenson, 2006; however, see Yeshurun & Sobel, 2010; Figure 1A). As defined here, odor objects represent those unique qualities or characteristics of an odor (such as its mintiness or floweriness) that are encoded as memory-based olfactory templates and can guide further processing. Although object-centered perception is a relatively new development in olfactory research, it is a well-established concept in vision research (Hummel & Biederman, 1992; Logothetis, Pauls, Bulthoff, & Poggio, 1994; Reddy & Kanwisher, 2006; Tanaka, 1993). In our recent work, we showed that perceptual information about odor objects is accessed in advance of information about its valence, and that odor valence does not interfere with odor-object identification (Olofsson et al.,

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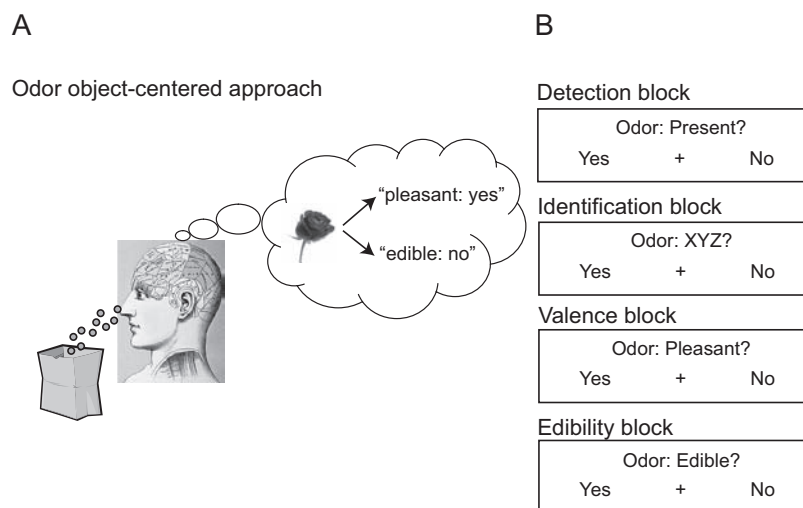


Figure 1. (A) Illustration of the object-centered framework and the decision tasks. The object-centered account predicts that initial formation of a perceptual odor-object representation (in this example, a rose odor-object) then activates systems that determine other perceptual characteristics (valence and edibility). (B) Perceptual decisions were performed with button-press responses. Boxes represent examples of visual cues displayed during the different trials and tasks (XYZ indicates individual odor names that varied across trials). At the start of each trial, a 3-s countdown was followed by the appearance of a red crosshair on the computer monitor, cuing the participants to sniff synchronously with the odor pulses. Labels were provided during the prestimulus countdown.

2012). These findings are in strong agreement with the object-centered approach to olfactory perception.

A key assumption in the object-centered approach is that odor objects provide causal links to downstream olfactory processes (Wilson & Stevenson, 2006). As odor-object RTs appear to vary systematically across individuals and odors, they might therefore constitute a temporal relay to valence and edibility (Olofsson et al., 2012). Such observations predict that odor-object identification RTs would be a statistical mediator of processing speed in the pathway from rapid odor detection to slower valence and edibility decisions. To test this hypothesis, we devised a speeded two-alternative (yes/no) RT experiment in which participants made rapid decisions regarding odor detection, edibility, valence, and object identification (Figure 1B; some results from one of the experimental conditions in this study were presented as part of a previous study; Olofsson et al., 2012, Experiment 2).

Method

Twenty subjects (12 women; mean age = 23.7 years; $SD = 2.3$ years) with no history of cigarette smoking, breathing problems, allergies, asthma, smell or taste problems, or neurological or psychiatric illness participated in the study. Their odor detection thresholds were in the normal range (min = 7.25, max = 16.00; $M = 13.51$, $SD = 2.42$; 16 is highest possible score; Sniffin' Sticks, Burghard Instruments; Hummel, Kobal, Gudziol, & Mackay-Sim, 2007). Participants provided informed consent to take part in the study, which was approved by the Northwestern University Institutional Review Board. The stimulus set consisted of eight familiar, moderately intense odorants that were selected to systematically vary in valence and edibility: lemon, almond, garlic, fish, rose, wood, gasoline, and marker pen (see online supplement

for details). The odors were presented using an olfactometer (Plailly, Howard, Gitelman, & Gottfried, 2008). A PC laptop computer was used for stimulus presentation and response collection, and for triggering the olfactometer to deliver odors. Participants were instructed to exhale during a 3-s countdown, and to take a sniff at the onset of a following sniff cue (red crosshair). Odor delivery was synchronized with the sniff cue and lasted for 1,000 ms. Breathing belts were used to measure respiratory patterns throughout the experiment (Plailly et al., 2008). During baseline perceptual ratings (i.e., prior to the main RT tasks), participants evaluated the following odor characteristics: intensity, pleasantness, familiarity, edibility, and perceptual quality (i.e., how well the odor corresponded to its word label; scales ranged from -10 to $+10$). Individual odor assessment of each perceptual attribute was based on the mean of three trials. Each participant performed a total of 120 ratings. The procedure was self-paced, with each new trial starting 5 s after the previous rating.

In four different (randomly ordered) RT tasks, subjects decided as quickly as possible whether odors corresponded to word labels that had been presented just prior to odor onset. The tasks were: detection (word label: "Odor: Present?"), edibility (label: "Odor: Edible?"), valence (label: "Odor: Pleasant?"), and identification (label: "Odor: XYZ?" where XYZ = Lemon, Almond, Garlic, Fish, Rose, Wood, Gasoline, or Marker Pen, on separate trials; Figure 1B). Before each block, participants received instructions in the following format:

In the valence task, if you perceive that the odor is *pleasant*, you press the yes-button, but if it is *unpleasant*, you press the no-button. For all odor trials, you have to make a quick button-press response based on whether you perceive it to be pleasant or unpleasant. (see SI)

Odor edibility was defined as “whether or not the odor comes from something people normally eat or drink. It does not matter whether you personally like to eat or drink it or not,” in an attempt not to conflate edibility with valence (see SI). Each odor was presented 4 times in each task, except for the detection task, in which each odor was presented 2 times, as half the trials were odorless. Only odor trials were considered for statistical analyses. Trials were constructed so that “yes” and “no” responses would be balanced. Responses were evaluated from 200 to 5,000 ms post-onset of the sniff cue. Odor presentation order was randomized in all tasks. Trials were separated by an 11-s stimulus onset asynchrony to limit sensory habituation. Each block lasted about 6 min, with a short break in between blocks.

All RT measures were log-transformed to yield normal distributions before further analyses were performed. Kolmogorov–Smirnov tests indicated that our log-transformed RT distributions did not deviate from normality, $p(\text{det}) = 0.915$; $p(\text{ple}) = 0.283$; $p(\text{edi}) = 0.199$; $p(\text{id}) = 0.148$. Hypotheses were tested by means of ANOVAs and regressions. To assess the mediation hypothesis, we used the recommended product-of-covariance approach with bootstrapping to empirically estimate variance from 5,000 samples of the indirect effect ab (please note that the bootstrapping method and its expression of product variances as confidence intervals are motivated by the fact that product variances are rarely normal; see Preacher & Hayes, 2004).

Results and Discussion

Ratings, Sniffing, and Behavioral Accuracy

Odors were perceived as being of high intensity ($M = 5.08$, $SE = 0.56$) and familiarity ($M = 5.01$, $SE = 0.88$), and well matched to their word label (high quality; $M = 5.21$, $SE = 0.79$). Analyses of breathing data showed that sniff magnitudes and onsets were similar across tasks ($ps > 0.40$; see SI), ensuring that respiratory differences could not have accounted for behavioral differences. In the decision tasks, behavioral accuracy was high for both detection ($M = 95.9\%$, $SD = 3.7\%$) and identity ($M = 94.4\%$, $SD = 3.6\%$). Binary decisions on the valence RT task corresponded well with preexperimental individual baseline ratings of valence (i.e., whether the valence of an odor was rated as being higher or lower than 0; $M = 87.0\%$, $SD = 7.8\%$), and the same was true on the edibility RT task when referenced to baseline edibility ratings ($M = 85.3\%$, $SD = 11.1\%$). No response was recorded in $<1\%$ of trials, and such trials were excluded from further analysis. To the extent that odor valence and edibility decisions are subjective assessments that may fluctuate over time, a lack of agreement between preexperimental ratings and later decisions should not be interpreted strictly as error rates. Unless otherwise stated, all responses were included in the analyses of RTs (see SI).

Response Times: Identification Precedes Valence

We compared the mean RT data from the four experimental tasks. There was a significant effect of task, $F(2.46, 44.74) = 19.31$, $p < .001$, $\eta^2 = 0.504$ (Figure 2A), with follow-up tests revealing that detection responses were significantly faster than valence responses, $p < .001$, $\eta^2 = 0.576$, edibility responses, $p < .001$, $\eta^2 = 0.628$, and identity responses, $p = .002$, $\eta^2 = 0.403$.

Identity responses were faster than valence responses, $p = .039$, $\eta^2 = 0.205$, and edibility responses, $p < .001$, $\eta^2 = 0.572$, and valence and edibility responses approached significance, $p = .064$, $\eta^2 = 0.169$. The temporal precedence of identity responses before valence and edibility responses is congruent with previous findings that odor-object evaluations are faster than odor-valence evaluations for familiar odors (Olofsson et al., 2012).

Results from a follow-up analysis showed that excluding “error” trials did not change the outcomes (see SI). Moreover, when comparing odors that were highly pleasant or unpleasant to odors that were rated as more neutral, or when comparing odors of high or low edibility to odors rated as more ambiguous, the main outcomes were unchanged (Figure 2B; see SI for details). The order of task completion were thus unlikely to be accounted for by speed-accuracy trade-offs, or by odors that were ambiguous or inconsistently categorized with regards to valence or edibility.

A Causal Path From Identification to Valence

Given the temporal precedence of identity responses before valence and edibility responses (cf. Figure 2) and our previous results of a processing advantage for object-based decisions (Olofsson et al., 2012), it is reasonable to hypothesize that the valence and edibility of an odor is causally determined after extracting information about its object identity (Wilson & Stevenson, 2006). Whether odor-object identity represents a causal step linking stimulus input to valence (or edibility) determination was modeled using mediation analysis (Figure 3), which is helpful for characterizing the temporal, sequential unfolding of psychological processes (Collins, Graham, & Flaherty, 1998). In this model, we used all eight odors for all 20 subjects as data points, because even if a given odor object might be activated at different times for different individuals, the temporal associations outlined above should remain (see Figure 3B). However, because we were only interested in within-subject variations, we controlled for effects related to subject (Bland & Altman, 1995; Collins et al., 1998).

We constructed a mediation model of the RT data that included a “direct” processing route from detection (the predictor) to valence (the outcome), and an “indirect” route linking detection and valence by way of identification (the mediator). By determining the significance of the direct and indirect routes, the model tested whether the relationships between our key variables would conform to either parallel routes (no mediation), a serial (mediated) route, or dual processing routes (both mediated and unmediated; Figure 3B, 3C). Either of the two latter possibilities would constitute evidence of identification as a mediator (Zhao, Lynch, & Chen, 2010) of valence, and help validate an object-based account of human olfactory perception. The results showed a significant effect of the indirect route (path ab), $\beta = 0.197$, 99% CI [0.0890, 0.3275], consistent with mediation (note that this product variance is better expressed in CI rather than as a p value because it is typically not normally distributed; see Preacher & Hayes, 2004). There was also an effect of the direct route (path c) from detection to valence RTs, $\beta = 0.284$, $p < .001$. This pattern of findings thus conforms to a dual route (Figure 3D, left) by which odor valence can be accessed by both direct and indirect routes. The proportion explained variance (R^2) of the model was 41.0%. In a follow-up analysis, the rated absolute deviation from the valence midpoint

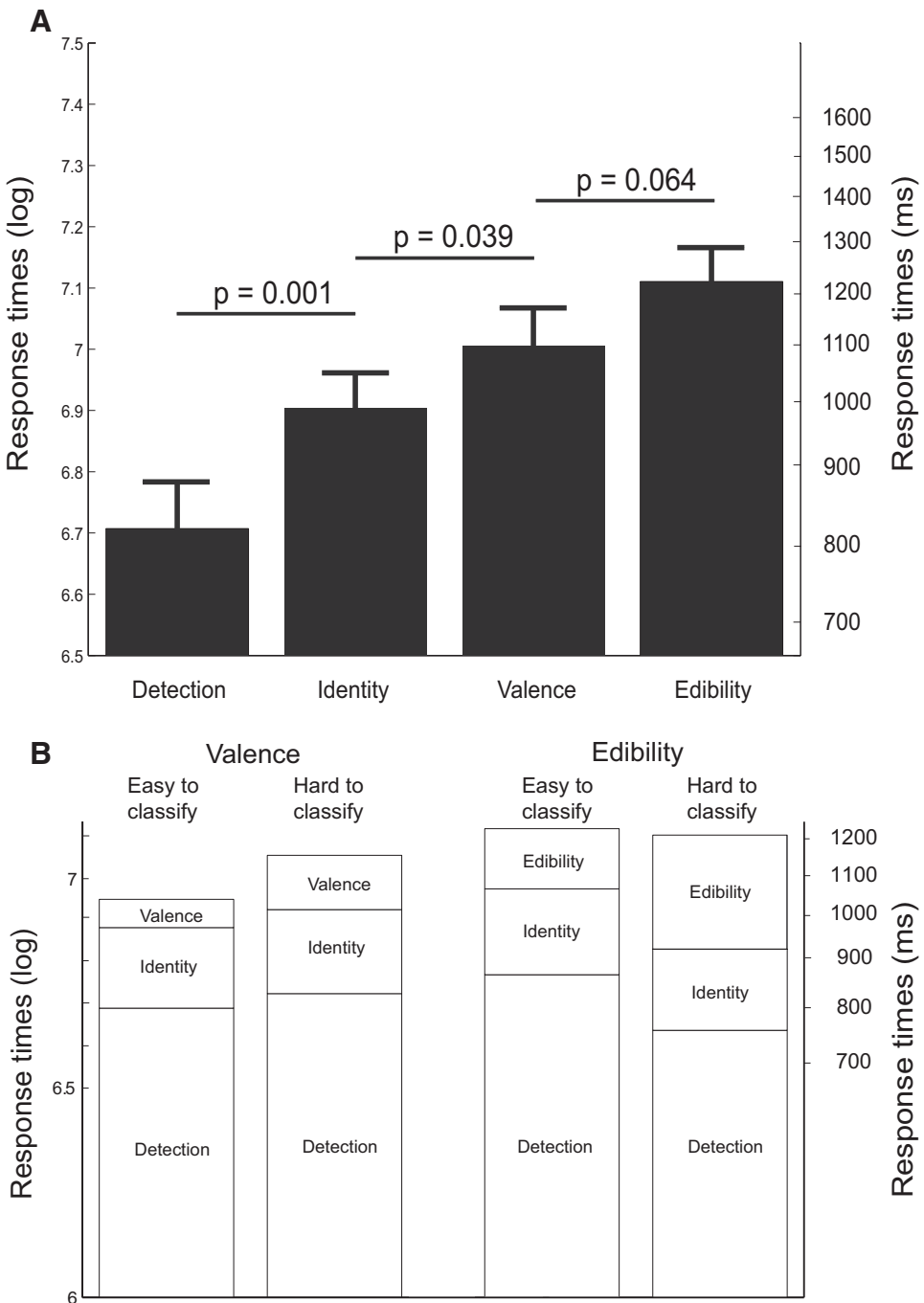


Figure 2. (A) Identification RTs precede valence and edibility RTs. (B) Mean RTs (+SE) associated with the four different task RTs were calculated separately for odors that were divided into “easy” and “hard” to classify based on how much they deviated from the midpoint of the valence and edibility rating scales. Four odors were placed in each category, based on the preexperimental ratings of each participant. The stacked graphs illustrate that the temporal order by which the RT tasks were completed did not differ for “easy” versus “hard” odors.

(determined for each individual and odor) was used as a covariate. Although this variable explained a significant portion of the variance in valence RT, $p = .002$, indicating that an effect was present at the valence response stage, it is important to note that it did not

diminish the mediation effect of the indirect route, $\beta = 0.179$, 99% CI [0.0848, 0.2959], indicating that the original model was robust. Applying the same approach to edibility responses (the “outcome” in the mediation model), we also found evidence for me-

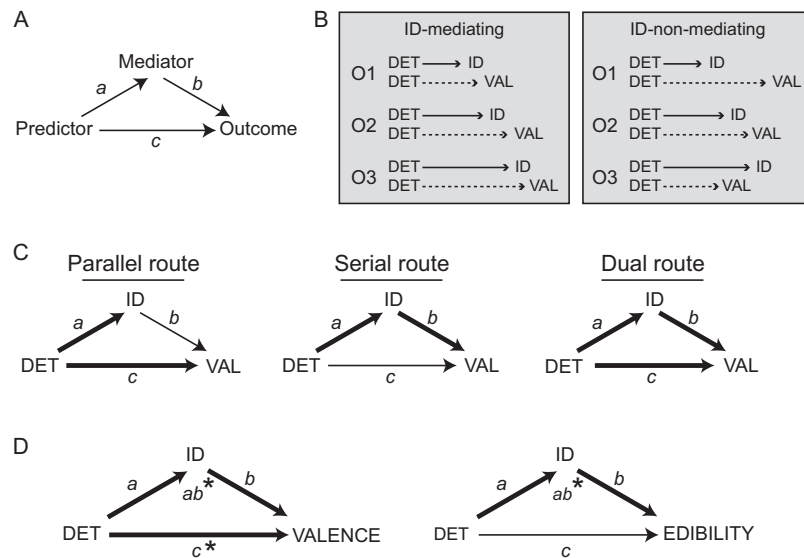


Figure 3. (A) Results from the mediation analyses. This schematic depicts a canonical mediation model that includes both direct (c) and indirect effects ($a \times b$); specifically, c is the association between predictor and outcome that remains after the indirect effect ab is included in the regression (B). Hypothetical comparative RT profiles for three odors (O1–O3) in a case where identification mediates valence (left box) and in a case where it does not (right box). These profiles illustrate a systematic relationship between identification (ID) RTs and valence (VAL) RTs only if ID mediates access to valence information. Here, the RTs are referenced to odor detection (DET), which is considered the “predictor” in the model (C). Possible outcomes of the mediation analysis, with thick arrows indicating significant relationships, including models in which the link from DET to VAL is direct and independent of ID (parallel routes to ID and VAL, no mediation), indirect and reliant on ID (serial route), or a combination of direct and indirect effects (dual route). Separate analyses were conducted with valence replaced by edibility (D). Results indicate that valence is processed through dual routes (both ab and c are significant), whereas edibility is processed through a serial route (only ab is significant). * $p < .001$ for direct effects and 99% CI for indirect effects.

diation, such that the indirect path ab was significant, $\beta = 0.233$, 99% CI [0.1171, 0.3650]. However, there was no evidence of a direct path c from detection to edibility responses, $\beta = 0.045$, $p = .461$. The proportion explained variance (R^2) of the model was 34.6%. The rated absolute deviation from the edibility midpoint (determined for each individual and odor) was used as a covariate in a follow-up analysis. Although this variable explained a significant portion of the variance in edibility responses, $p = .01$, indicating an effect present at the response stage, it did not influence the mediation effect of the indirect route, $\beta = 0.233$, 99% CI [0.1189, 0.3672]. This pattern conforms to the serial route (Figure 3D, right), whereby the extraction of odor-object information mediates odor edibility with no direct pathway. Other analyses included odor intensity and odor familiarity as covariates in the mediation model, but these covariates had no significant influence ($ps > 0.50$) and did not affect the results. In sum, the results from the mediation analyses of RTs show that object identification mediates valence and edibility upon detecting an odor.

Although much research on the human olfactory system focuses on outlining its spatial characteristics by means of functional neuroimaging, in this study we focus instead on the time domain, using RTs to outline the olfactory perceptual cascade. Previously, the notion of “high” and “low” roads has been invoked to describe information flow toward the amygdala via cortical and subcortical circuits to generate affective responses (LeDoux, 2000; Morris, Öhman, &

Dolan, 1999). Based on our findings, we propose, analogously, that odor valence is determined in part by input from a “high road,” which involves object recognition of familiar odors. The odor objects are thus not defined by their valence, but rather define valence, that is, odor objects activate emotional responses downstream. The perceptual aspect of the odor object is likely represented in the piriform cortex; this region has extensive projections to and from other associative cortices (Carmichael, Clugnet, & Price, 1994; Johnson, Illig, Behan, & Haberly, 2000), enabling perceptual learning and odor quality coding, which comprise essential features of object perception in the olfactory domain (Gottfried, Winston, & Dolan, 2006; Haberly, 2001; Howard, Plailly, Grueschow, Haynes, & Gottfried, 2009; Li, Luxenberg, Parrish, & Gottfried, 2006). Semantic attributes of the odor object might be represented in the anterior temporal lobes (Olofsson, Rogalski, Harrison, Mesulam, & Gottfried, 2013; Patterson, Nestor, & Rogers, 2007), and the orbitofrontal cortex and amygdala might represent emotional intensity and olfactory reward value (Gottfried & Dolan, 2004; Gottfried, O’Doherty, & Dolan, 2003; Zald & Pardo, 1997). In the context of this framework, it seems plausible that for familiar odors, the high road involves causal engagement of odor objects in piriform cortex and heteromodal regions, but the low road does not. In contrast to valence, edibility might only be accessed indirectly through the high road, and we speculate that there may thus be no such thing as a general perceptual class of intrinsic “food odors” that would include smells as diverse as fish and

lemon. Such judgments might always require perceptual analysis provided by the high road.

Our mediation analysis was informed by modern approaches that have largely replaced the traditional “causal steps approach” (Baron & Kenny, 1986) because of its conceptual and empirical shortcomings (Hayes, 2009; MacKinnon, Lockwood, Hoffman, West, & Sheets, 2002). We note that statistical mediation analysis does not require establishing a temporal sequence of response variables, and indeed, mediation analysis is often used in survey-based psychological research without consideration of RTs, but mediation models should only be used when they are theoretically justified. In the present study, because only object identification was a priori hypothesized as a mediator, we were conservative in elaborating on more complex mediation models. However, an exploratory analysis indicated that, second to object identification, odor valence might constitute a secondary mediator to determine edibility RT responses within the high road (see SI for details). Future studies may investigate the role of such complex mediation pathways, as well as differences related to prior olfactory exposure and learning (Stevenson & Wilson, 2007), and the role of retro-nasal and orthonasal stimulation of food odors, within the general framework of high and low roads in olfactory object perception. Our study shows that probing the temporal characteristics of the perceptual cascade might yield unique information about the processing pathways of the human olfactory system.

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Call for Nominations

The Publications and Communications (P&C) Board of the American Psychological Association has opened nominations for the editorships of **History of Psychology**; **Journal of Family Psychology**; **Journal of Personality and Social Psychology: Personality Processes and Individual Differences**; **Psychological Assessment**; **Psychological Review**; **International Journal of Stress Management**; and **Personality Disorders: Theory, Research, and Treatment** for the years 2016–2021. Wade Pickren, PhD, Nadine Kaslow, PhD, Laura King, PhD, Cecil Reynolds, PhD, John Anderson, PhD, Sharon Glazer, PhD, and Carl Lejuez, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2015 to prepare for issues published in 2016. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- **History of Psychology**, David Dunning, PhD
- **Journal of Family Psychology**, Patricia Bauer, PhD, and Suzanne Corkin, PhD
- **JPSP: Personality Processes and Individual Differences**, Jennifer Crocker, PhD
- **Psychological Assessment**, Norman Abeles, PhD
- **Psychological Review**, Neal Schmitt, PhD
- **International Journal of Stress Management**, Neal Schmitt, PhD
- **Personality Disorders: Theory, Research, and Treatment**, Kate Hays, PhD, and Jennifer Crocker, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to <http://editorquest.apa.org>. On the Home menu on the left, find "Guests." Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Sarah Wiederkehr, P&C Board Search Liaison, at swiederkehr@apa.org.

Deadline for accepting nominations is January 11, 2014, when reviews will begin.