nature neuroscience

Preferring one taste over another without recognizing either

Ralph Adolphs[1,2], Daniel Tranel[1], Michael Koenigs[1] & Antonio R Damasio[1]

Stimuli can be discriminated without being consciously perceived and can be preferred without being remembered. Here we report a subject with a previously unknown dissociation of abilities: a strong behavioral preference for the taste of sugar over saline, despite a complete failure of recognition. The pattern of brain damage responsible for the dissociation suggests that reliable behavioral choice among tastes can occur in the absence of the gustatory cortex necessary for taste recognition.

The study was carried out in subject B., a 72-year-old, premorbidly normal man who had a severe *Herpes simplex* encephalitis in 1975. He had complete bilateral destruction of the amygdala, hippocampus, adjacent temporal cortices and basal forebrain, as well as extensive bilateral damage to the anterior insula, posterior and medial orbitofrontal cortices and anterior cingulate cortices (**Fig. 1**), resulting in one of the most severe cases of amnesia and agnosia ever reported[1]. His memory span is about 40 s without rehearsal; he fails to recognize familiar people and many objects, yet he shows normal procedural learning, has normal language and has normal visual discrimination. Consistent with the anatomical distribution of his brain damage, B. has a profound impairment of taste and smell perception (complete ageusia and anosmia; Welsh, K.A. & Damasio, A.R., *Neurology* (suppl. 1), 1988), fails completely to recognize familiar food items by their taste and is abnormally indiscriminate in what he ingests.

We prepared 2% aqueous solutions of saline and of sucrose to achieve a clear distinction between an aversive and a pleasant taste and offered them to B. as unknown beverages in randomized order. B. spontaneously drank either solution (19/19 trials for each solution). On all of the 19 saline trials, he showed a pleased facial expression and continued drinking until we asked him to stop (he demonstrated the same behavior on the 19 sucrose trials). We conducted the same experiment in five normal, age- and education-matched comparison participants, as well as eight brain-damaged comparison participants who, unlike B., did not have bilateral damage to insula. One of these (subject J.M.)[2] had extensive bilateral medial temporal damage including amygdala and hippocampus, rendering him also densely amnesic. A second had bilateral damage to orbitofrontal cortex, and the others had varied damage to parietal, temporal and occipital cortices. All of the comparison subjects, normal and brain-damaged, immediately recognized the saline on the 19 saline trials, found it aversive and spontaneously stopped drinking after the first sip. On the 19 sucrose trials, the comparison participants manifested behavior similar to B.'s (for example, by showing pleased reactions to the drink and continuing to drink the solution), and they always recognized it as sugar water. The accuracy with which normal and brain-damaged comparison subjects could identify both solutions was thus 100%. When asked to identify what he was drinking immediately after each of the 38 saline or sucrose trials, B. replied on every trial that the solution tasted 'like pop' and was 'delicious' (responses that he gives indiscriminately to most gustatory stimuli). In sum, unlike any comparison subject, his recognition of the stimuli was at chance.

In a follow-up to the above experiment, we offered B. and the normal participants 100% lime juice in seven trials. All five normal participants found the lime juice highly aversive and puckered their faces upon sampling it; none continued to drink it after the first sip. Subject B. drank eagerly and showed a pleased facial expression on all seven lime juice trials. Again, after each trial he indicated that the drink was 'delicious,' further demonstrating that his verbal responses, facial expressions and consumption behavior to gustatory stimuli presented in isolation are severely defective.

By contrast to the above impairments, B. exhibited a markedly reliable behavioral preference when offered a choice among stimuli. We presented subjects with two drinks, one sucrose and the other saline (the same solutions as above), side-by-side in two cups visually distinguishable by different added food colors to help subjects keep track of the solutions as they sampled them sequentially (red or green, colors that B. can distinguish, were paired with the solutions in counterbalanced order in order to help subjects keep track of which cup held which taste). On each of 19 trials, B. was encouraged to sample each of the two drinks, and then to drink from the one he preferred. To our surprise, he demonstrated a strong and immediate preference for sucrose over saline (18/19 trials). The normal and brain-damaged control participants showed the same behavior, preferring the sucrose solution on all 19 trials.

We performed six additional trials with B., again using the two-alternative format with colored solutions. On these trials, after B. had made his selection of the preferred beverage (he chose sucrose on all six trials), we urged him to sip the other drink. B. vehemently refused to drink the saline in this situation. Moreover, the order in which the stimuli were sampled did not affect his choice: if sampling sucrose after just having sampled saline, he would refuse to switch to drinking saline; if sampling saline after just having sampled sucrose, he immediately rejected the saline and asked for the sucrose. Although it remains an open question to what extent B.'s preference behavior was driven by a preference for sucrose, or by an aversion to the saline, the above observation suggests that both may contribute.

One possible interpretation of the findings thus far could be that B. had greatly reduced but not completely abolished sensitivity to taste,

[1]Department of Neurology and Neuroscience Graduate Program, The University of Iowa, 200 Hawkins Drive, Iowa City, Iowa 52242, USA. [2]Division of Humanities and Social Sciences, California Institute of Technology, Pasadena, California 91125, USA. Correspondence should be addressed to R.A. (radolphs@hss.caltech.edu).

Published online 12 June 2005; doi:10.1038/nn1489

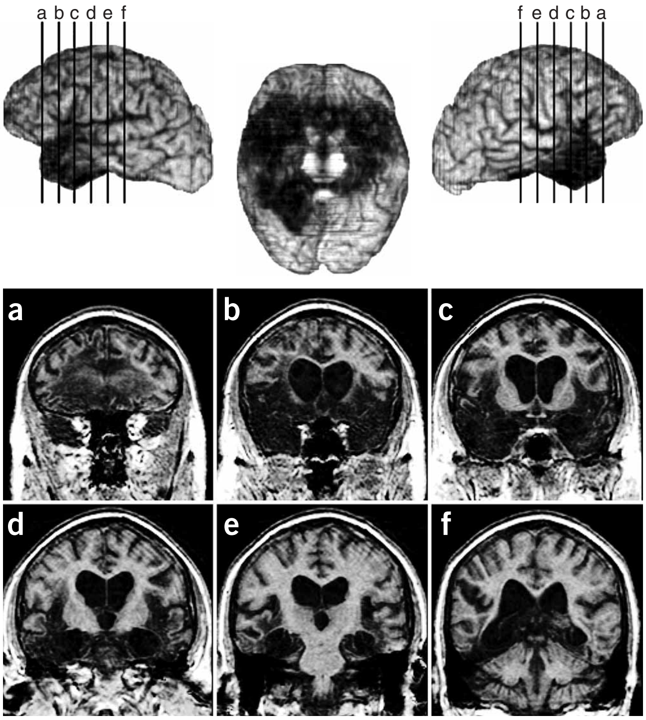

Figure 1 The brain of subject B. Shown are three-dimensional reconstructions of lateral (upper left and right) and ventral (upper middle) views of B.'s brain from magnetic resonance scans, indicating the extent of his brain damage in black. Coronal slices (lower panels) are indicated by the lettered vertical lines on the reconstructions. All participants had given informed written consent as approved by the Institutional Review Board of the University of Iowa.

and that it was easier to compare solutions presented pairwise than it was to recognize them in isolation. The data from the normal participants do not resolve this issue, because their scores were perfect in both experiments (100%). To clarify this issue, we carried out the above experiments once again in the five normal participants, but this time with taste stimuli that were so diluted (0.2% sucrose; 0.05% saline) that performance scores would not be at 100%. For the recognition experiment (ten trials), the five normal subjects obtained an overall score of 66% correct, indicating that, as expected, the weak solutions were more difficult to recognize than the strong solutions. For the preference experiment (ten trials), they also obtained an overall score of 66% correct. Thus there was no evidence to suggest that the recognition task is inherently more difficult than the preference task. We take these results to indicate that a difference in task difficulty was unlikely to have accounted for B.'s marked dissociation.

Although the dissociation we report appears robust, there remains some uncertainty about the sensory processing on which it is based. We verified in normal controls that the sucrose and saline could not be discriminated by smell alone (ten subjects performed at chance if allowed only to smell the stimuli), which together with B.'s previously reported anosmia rules out olfaction as a plausible modality. We also consider it unlikely that his discrimination was somatosensory, as the concentrations of sucrose and saline solutions were below the threshold normally necessary to induce trigeminal nerve activity. A final issue concerns the sensitivity of the taste recognition measures: it remains possible that more sensitive tasks, such as Likert ratings or receiver operating characteristic (ROC) curves of taste discrimination, could have demonstrated subtle residual abilities.

Strong preferences and strong aversions to taste are present at birth[3] and can be acquired within a single trial in conditioning experiments[4]. Gustatory pathways from the nucleus tractus solitarius via the parabrachial nucleus to the hypothalamus and thalamus, which are intact in subject B., must be capable of influencing preferences even without the assistance of structures normally involved in higher taste processing, such as the insula[5–7], regions of orbitofrontal cortex[8] and anterior temporal regions[9], which are damaged in B. Most critical appears to be the insular cortex, as it is damaged bilaterally in B. but not in any of the brain-damaged comparison subjects we tested. The dissociation is in line with a proposed distinction[10] between a ventral, limbic taste pathway that includes amygdala, hypothalamus and regions of the basal ganglia, which appears to be sufficient for basic behavioral taste discrimination[11], and a dorsal cortical pathway necessary for more complex taste processing and learning that involves insular cortex.

Of what is B. aware when he chooses sucrose over saline? When asked about his preferences, he was unable to give any additional information, other than stating that he liked the chosen solution better. We believe that he is aware of his preference of sucrose over saline, without awareness of the identity of either. That is, the taste comparison likely provides B. with an overt feeling that he would rather drink one solution than another, without any overt knowledge of the taste experiences that would normally provide the justification for this preference. The findings show that information that is meaningless for an isolated individual stimulus can yield relative values when the task is structured as a comparison involving multiple stimuli: in the latter case, the additional structure in the environment generates the marked dissociation we observed.

ACKNOWLEDGMENTS
Supported by US National Institute of Mental Health grant MH067681 and US National Institute of Neurological Disorders and Stroke grant P01 NS 19632.

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

Received 3 May; accepted 24 May 2005
Published online at http://www.nature.com/natureneuroscience/

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