Chem. Senses 30 (suppl 1): i228–i229, 2005 doi:10.1093/chemse/bjh197

Temporal Characteristics of Human Taste Judgements as Calibrations for Gustatory Event-related Potentials and Gustatory Magnetoencephalographs

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Key words: evoked potential, reaction time, MEG, GEM, ERP, gustatory

Introduction

Activity in the central nervous system (CNS) constantly fluctuates. CNS changes that are potential responses to sensory stimulation must occur before an observable external outcome of the stimulation. If the external change is an overt, measurable behavior, then the time interval between a controlled stimulus and the behavior is a reaction time (RT) (Halpern, 1986, 1991, 1994). Human RT can be used to predict when relevant changes in human CNS activity in response to a specified controlled stimulus will occur. Therefore, human RT both indicate the time after stimulus onset (latency) when relevant human CNS changes should be found and provide a means of excluding CNS changes for which the latency is too long.

Human gustatory RT require controlled stimuli with known arrival times, concentration profiles and durations. They can be provided by rapidly changing from a carrier liquid (solvent only) to a stimulus liquid (solvent plus solute), both delivered at a fixed flow rate and temperature over a consistent and limited area of the human tongue for predetermined durations and then rapidly changing back to the carrier liquid (e.g. Kelling and Halpern, 1983, 1987, 1988). Physical measurements at the tongue of concentration changes over time provide calibration of stimulus duration and concentration profile. Effects of the rapid change events on RT are identified by 'changing' from carrier liquid to carrier liquid, thus controlling for responses to alterations in liquid flow. If subjects are asked to respond only to taste changes and are given identified practice trials during which there is, or is not, a change from carrier liquid to stimulus liquid and back to carrier liquid, then reports of a change in taste during unidentified simple taste reaction time (RT_s) control trials average <10%; error rates are higher for brief duration stimulus trials, but fall below 10% for durations >100 ms (Kelling and Halpern, 1987). RT responses may require movement of a button or lever, or a spoken word; in some instances, a computer display gives feedback. All timing accuracy can be at the millisecond level.

CNS measurements

A number of non-invasive techniques for measurement of CNS activity are available. In many cases there is a reciprocal relationship between precision of time registration and degree of spatial location or representation of the structural aspects of CNS regions. Two approaches with relatively high temporal resolution are evoked potentials, also known as event-related-potential (ERP) recording and magnetoencephalography (MEG; see Plattig, 1991; Näätänen *et al.*, 2002). MEG has a better spatial resolution (Endo *et al.*, 1999).

ERP

In a comparison of ERP and MEG, the gustatory evoked potentials (GEP) included a positive-going change (P1) with a mean latency of 127 ms, a negative going change at 263 ms (N1) and a second (and sustained for ~200 ms) positive-going potential at 432 ms (P2) (Mizoguchi *et al.*, 2002). All three GEP latencies were less than the 446 ms mean human simple taste reaction time (RT_s) to 500 mM NaCl presented under similar conditions (Kelling and Halpern, 1987). However, because one subject in the Kelling and Halpern (1987) study had a RT_s of 283 ms, it may be that P2 and perhaps N1 denoted some cortical processing of the gustatory input. Mizoguchi *et al.* (2002) reached a similar conclusion based upon relations between N1, P2 and responses simultaneously recorded using MEG. On the other hand, the latencies of P1, N1 and P2 were all briefer than the mean complex taste reaction times (RT_C) of 600 ms or more associated with taste quality identifications (RT_{Ci}) (Yamamoto and Kawamura, 1981, 1984; Halpern, 1986, 1991). This might imply that the degree of cortical processing that was indicated by N1 and P2 of the measured GEP (Mizoguchi *et al.*, 2002), although perhaps more than sufficient for $RT_{s,}$ may not have been at the level of RT_{Ci}.

MEG

Measurements of changes in cortical magnetic fields (MEG) evoked by sensory stimulation provide ms timing and high spatial resolution, as studies of relationships between visual RT and CNS preparatory motor activity have demonstrated (e.g. Endo *et al.*, 1999). There appears to be less distortion than with ERP (Murayama *et al.*, 1996). MEG recordings in gustatory areas of the CNS have been done using either electrical stimulation of the tongue (see Frank and Smith, 1991) or with flowing tastants. For electrical stimulation of the tongue (electrogustometry) with currents that evoked reports of taste but not irritation (Yamamoto *et al.*, 2003) the latency for MEG responses was considerably longer than that produced by flowing tastants (Mizoguchi *et al.*, 2002) and longer than many GEM (see below). This raises questions about the use of electrogustometry.

Both MEG responses to flowing tastants (GEM) and RT_s have been examined in a number of studies (e.g. Kobayakawa *et al.*, 1996; Saito *et al.*, 1998). GEM onset latencies and RT_s were correlated. One possible issue is the extent to which the 1 M NaCl that was used might have been both a trigeminal and a gustatory stimulus and therefore elicited chemesthetic (Bryant and Silver, 2000) as well as taste responses. This probably did not affect the GEM data because the onset latency did not change with NaCl concentration.

A later study (Yamamoto *et al.*, 2000) with flowing tastants observed GEM to tastants but no responses to flow of H_2O. Furthermore, after subjects chewed a taste-modifier that results in humans perceiving citric acid as sweet ('miracle fruit'), the GEM latency for citric acid approached that for sucrose. These data provided strong support for interpretation of the MEG data as GEM, apparently with little or no contamination from chemesthetic input.

A series of studies illuminated GEM latency differences between several cortical gustatory areas (Kobayakawa *et al.*, 1999; Saito *et al.*, 2000; Mizoguchi *et al.*, 2002). It is possible that the 1 M NaCl that was used may have been both a gustatory and a chemesthetic stimulus, but the saccharin and the lower NaCl concentrations that were employed were likely to be only taste stimuli. Latencies ranged from a few hundred to >1000 ms. The shorter GEM latencies were similar to those reported in pervious investigations. The later GEM latencies, which were found in regions other that primary gustatory areas, may have been associated with CNS processing related to the taste quality or intensity judgements which subjects were asked to report after each recording. This series of studies is important because they suggest that sequential cortical processing of gustatory input can be studied using GEM and related to perceptual and cognitive judgements more demanding than RT_s.

In general, the ERP and GEM studies have focused on RT_s. Since this represents only the earliest and perhaps least sophisticated level of gustatory processing, it would be valuable for future studies to be designed such that RT_C for taste quality and intensity, as well as gustatory time-intensity and time-quality tracking, can be related to measures of gustatory ERP and to GEM.

Acknowledgements

I thank P. Halpern, S. Saito and the anonymous referee for helpful recommendations on earlier drafts of this manuscript.

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