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Correcting misconceptions of tuning shifts in auditory cortex

Sirs

A specific memory trace (SMT) is an enduring neural record of a particular aspect of experience. We initiated receptive field analysis to determine whether associative learning produces SMTs in the primary auditory cortex, as indexed by modification of the neural representation of a signal stimulus (the conditioned stimulus or CS). A new paradigm, combining learning and sensory neurophysiology approaches, revealed tuning shifts that favour processing and representation of the CS. We claim that tuning shifts constitute SMTs because they are associative and specific; further, they are discriminative, become more specific over time (consolidation) and show long-term retention, as do memories[1]. The criticisms of Ohl and Scheich reflect assumptions of an archaic conception of memory traces and faulty analyses of the findings. A narrow minded view holds that memory traces can develop only in structures in which destruction produces behavioural impairments. They mistakenly attribute to us the claim that all auditory memory depends on tuning shifts in the auditory cortex and then attack this non-existent claim by recalling that cortical lesions do not prevent simple tonal conditioning. In contrast, contemporary conceptions of memory substrates acknowledge distributed storage. For tonal conditioning, specific receptive-field shifts also develop in all three nuclei of the medial geniculate body[2, 3, 4] and associative plasticity (not yet checked for specificity) develops in lower auditory structures[5], the amygdala[6] and the hippocampus[7]. A fundamental goal is to determine the relative contribution of all involved structures in the acquisition, storage and representation of experience, not which structure holds the entire memory. The view of Ohl and Scheich precludes the simultaneous development of SMTs sub-cortically and at cortical levels, where the information could be used more flexibly. We initially discussed the limitations of the auditory cortex lesion findings for SMTs[8] and recently provided a detailed analysis of the independence of auditory cortical SMTs from particular behavioural indices of learning[9]. Ohl and Scheich further erroneously assume that we hold that all cortical plasticity consists of tuning shifts, a position we did not present in our paper and have never held; the forms of cortical plasticity will vary depending on the challenges encountered and the solutions formulated. For example, if the relevant stimulus feature is tone repetition rate rather than acoustic frequency, then frequency tuning shifts are unlikely, but plasticity of tuning to temporal pattern might develop[10]. Ohl and Scheich claim that tonal conditioning produces "...an enhancement of contrast sensitivity..." because they found a relative decrease in response at the CS frequency rather than an increase and tuning shifts[11]. However, they used a training regimen in which subjects received as many as 30 tones, only one of which was paired with shock and they were unable to provide behavioral verification of CS-specific learning. If future use of this new task reveals what was learned, then this type of plasticity will simply join receptive field tuning shifts and expanded map representation, not replace them. Ohl and Scheich claim that tuning shifts reflect the use of biased criteria. In fact, we subtracted pre-training from post-training tuning curves and found CS-specific increases and tuning shifts[12]. This method would have revealed specific decreases, as it did for secondary auditory cortex[13]. The criterion to which they refer was instituted as a stringent test to eliminate potentially spurious findings, so the estimates of tuning shifts are conservative. Finally, their claim of bias can explain neither the replication of tuning shifts[14] and specific map expansions[15] reported by other laboratories, nor the positive relationship between the area of increased CS representation and correct performance[9], none of which involved the criterion they cite.

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