

following trial based on a violation of a negative association compared with that of a positive association. This result was mirrored in the pattern of activation of right dorsolateral prefrontal cortex (DLPFC) in response to unpredictable trials.

The study therefore demonstrates that DLPFC activation during expectancy violation is sensitive to the nature of the change in contingency. This is very

important for a couple of reasons. Firstly, it reinforces hypotheses that DLPFC activation in cases of expectancy violation is not merely a 'rarity-' or 'error-detector', as the nature of the violation of learned associations in each session was not constant, and the error rate across the different conditions was comparable. Secondly, the fact that DLPFC activation was predictive of behavioural change

provides an insight into how this brain area might be involved in learning and behavioural flexibility.

1 Fletcher, P.C. *et al.* (2001) Responses of human frontal cortex to surprising events are predicted by formal associative learning theory. *Nat. Neurosci.* 4, 1043–1048

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Priming: a tool for imaging

The ultimate goal of neuroimaging research must be to localize cortical function at the level of neural machinery at which these functions operate. A recent study by Naccache and Dehaene shows how the incorporation of a well established psychological phenomenon – behavioural priming – into fMRI paradigms, can heighten sensitivity to cognitive processes of interest¹. In a typical priming experiment, the subject is exposed first to one stimulus (the prime), then to another (the target). Subjects perform a constant task with respect to the target, regardless of the prime. If the prime and target stimuli are related in a cognitively meaningful way, the effect of the prime on the task of interest can be measured by comparing the reaction times to the target in the presence or absence of the prime.

This robust psychological phenomenon appears to have a neural correlate: brain activity as a result of priming can be measured by single-cell recording studies and by imaging studies. In the simplest case, where the prime and target are simply the same stimulus, repeated, specific cortical regions show suppression of activity, even when the two stimuli are varied in size, or are made to differ conceptually rather than physically. Naccache and Dehaene set out to establish whether this 'repetition suppression' could also be achieved using subliminal priming. In an fMRI experiment, during scanning subjects made a left or right button press to indicate whether a target number was larger or smaller than five. The target was preceded by a masked prime – a number presented either in the same or a different notation from the target (e.g. 'eight' rather than '8'). The numerical value of the prime could be identical or non-identical to the target. Areas of the brain involved in coding numerical quantity were expected to show

repetition suppression to numerically identical prime–target pairs but not to non-identical, congruent pairs.

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Behavioural analysis of the data revealed, as expected, a facilitation of reaction time with numerically identical primes relative to non-identical, congruent primes, even though the primes were not consciously seen by the subjects. Crucially, the facilitation was just as great when prime–target pairs were presented in different notations, suggesting that the priming occurred at an abstract level of representation. fMRI analysis identified the intraparietal sulci bilaterally as the only regions to show reduced activation for numerically identical (relative to non-identical) prime–target pairs, independent of notation. Putting aside the conceptual relevance of this finding for models of number processing, the finding is of extreme methodological significance. The demonstration that repetition suppression can be measured when the subject has no awareness of the distinction between

repeated and non-repeated stimuli suggests that repetition suppression is a robust phenomenon, which cannot be ascribed merely to strategic or attentional factors that might be operating when the prime is available to conscious awareness.

Repetition priming is a rare example of a psychological phenomenon that has a direct neural correlate in the brain. In addition, both priming and repetition suppression appear to be generalizable: behavioural priming occurs at many different psychological levels (object identification, orthographic and phonological processing, semantic word processing) and the neural signature of repetition suppression has been observed in a variety of cortical regions (occipito-temporal, temporal, frontal). Taken together, priming and repetition suppression would therefore seem to represent a fruitful new strategy for brain imaging.

1 Naccache, L. and Dehaene, S. (2001) The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb. Cortex* 11, 966–974

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