Prediction in vision - elements of predictive coding in awake and anaesthetized primates

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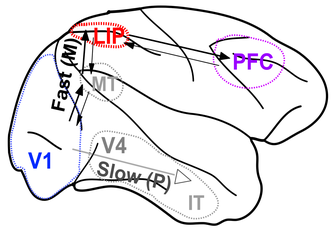
INTRODUCTION

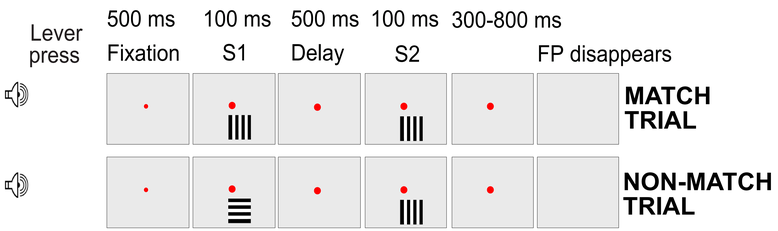
Theory of predictive coding suggests that higher-order cortical areas supply expectation signals based on prior sensory experience to sensory areas at early stages of processing, e.g. primary visual cortex (V1). We tested the presence of such feedback by comparing responses obtained from awake behaving and anaesthetized macaques.



METHODS

Fixation task

Each trial consisted of a pair of gratings of either the same orientations (match) or of orthogonal (non-match) gratings. The second grating in all pairs had the same orientation, so the differences of the responses to identical (second) stimuli could be attributed to expectations based on past sensory experience.



Trial probability

expected	unexpected
80% MATCH	20% NON-MATCH
80% NON-MATCH	20% MATCH

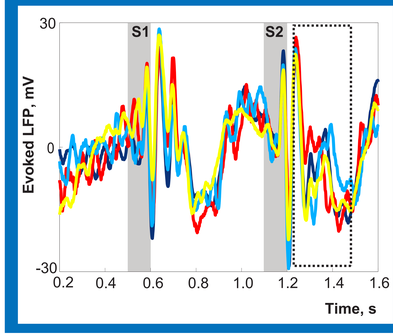
We manipulatedthe expectation by altering the probability of match and non-match trials within a block of trials, by having blocks with either 80% match and 20% non-match or 80% non-match and 20% match trials. Local field potentials (LFP) were recorded from 28 V1 intracortical sites in the awake and 16 sites in a macaque under isoflurane and nitrous oxide anaesthesia, which supresses activity in higher cortical areas. In the awake monkey, recordings were also made from V1-matching receptive fields of 2 areas of dorsal visual stream: lateral intraparietal (LIP) and dorsolateral prefrontal (dlPFC) cortices to study information transfer along the dorsal stream in predictive coding.

RESULTS

V1 lfp response amplitude

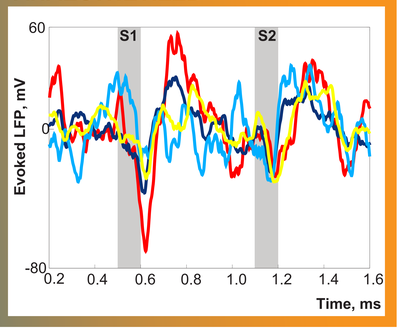
80% expected non-match / 20% unexpected match — 80% expected match / 20% unexpected non-match

AWAKE



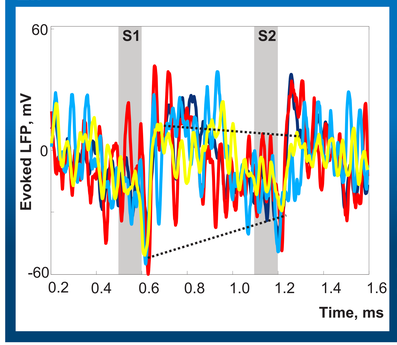
In the awake macaque, we found that in a 400 ms interval from the second stimulus onset, the unexpected grating pairs led to a significant change of the LFP amplitude in 24 out of 28 V1 recordings (Wilcoxon rank sum test, the amplitude change was considered significant at $p<0.05$ for comparing LFP amplitude in the unexpected condition to each of the 2 common conditions over the same interval). In contrast, no significant expectation effects were found under anaesthesia (0/16, using the same analytic approach).

ANAESTHETIZED



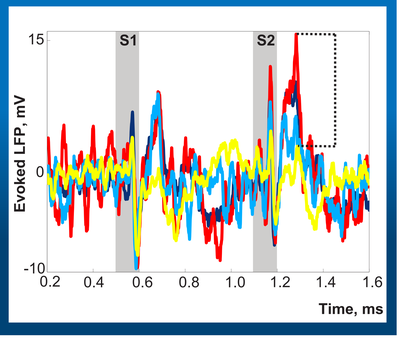
LIP and dlPFC lfp response amplitudes in awake behaving monkey

LIP

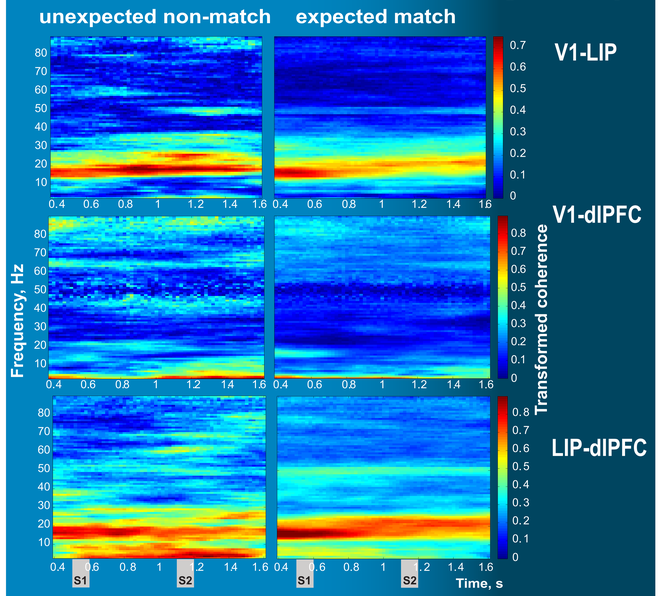


The most prominent LFP amplitude effect in area LIP was the suppression of response to common stimuli, with the peak-to-peak amplitude of the response to S2 being dramatically reduced in all recordings. In dlPFC, we observed an amplification of the difference in response to common and novel stimuli: in 5/7 recordings LFP amplitude was decreased in the expected match condition and enhanced in one or both non-match conditions.

dlPFC



Local field coherence, awake behaving monkey



LFP-coherence was calculated for all 3 pairs of recording sites (V1-LIP, LIP-PFC and V1-PFC), and the differences between condition assessed using the Aversen statistical technique to multiple comparisons across frequencies (multitaper spectral estimations implemented in Matlab-based Chronux toolbox, http://chronux.org/, calculated within 800 ms interval from 250 ms from S1 onset to 450ms from S2 onset, 3 orthogonal Slepian taper functions and a time bandwidth product of 2).
We observed increased gamma coherence for the unexpected conditions in V1-LIP pairs, decreased theta to low alpha coherence for the expected match condition in LIP-PFC pairs and enhancement of the beta-low gamma coherence occurring only in the unexpected nonmatch condition in V1-PFC pair.

CONCLUSION

- Primary visual cortex and the dorsal visual stream areas LIP and dlPFC demonstrate involvement in predictive coding.
- Magnification of the difference between LFP responses to the most expected and the most unexpected stimuli was observed along the dorsal stream, with LIP mostly involved in the suppression of the response to the expected stimuli while dlPFC also showed increased separation of unexpected and expected stimuli. Therefore dlPFC seems to be able to detect novelty.
- Coherence analysis demonstrated the involvement of gamma frequency oscillation in the transfer of the error signal between V1 and the higher order areas of the dorsal visual stream. Suppression of the expected response is associated with the loss of low frequency coherence between LIP and dlPFC.
- V1 is affected by both expectation and repetition, but effects of expectations are eliminated by anaesthesia.

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