

Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Predictive Coding: How Many Faces?

Clare E. Palmer and Antonella Macerollo

Sobell Department of Motor Neuroscience and Movement Disorders, UCL Institute of Neurology, London WC1N 3BG, United Kingdom
Review of Brodski, Paasch, et al.

Since von Helmholtz's (1867) supposition that the basis of perception is anchored in unconscious inference, it has been widely accepted that the brain uses a generative model to predict sensory input using learned statistical regularities about the world. Any discrepancy between these predictions and the sensory input produces a prediction error signal, which is then passed up the cortical hierarchy to update future expectations. In this way, the brain can highlight novel or surprising stimuli and efficiently allocate more resources when needed. Theoretically, our understanding of this predictive coding framework is extensive. However, empirical evidence highlighting the neural mechanisms that underlie the integration of prior information with sensory evidence is limited. In a recent study, Brodski, Paasch, et al. (2015) identified a neurophysiological correlate of prediction error during visual processing using a paradigm in which prior information was developed through lifelong experience.

Brodski, Paasch, and colleagues (2015) recorded magnetoencephalography from a sample of 48 subjects while the subjects completed a Mooney face-detection task. Subjects were presented with two-tone

stimuli of either faces or scrambled faces and instructed to identify the faces. Previous data have shown that accurate representations of two-tone objects can only be extracted if the objects are familiar (Moore and Cavanagh, 1998), and thus require combining stored information with sensory input to make inferences about what the visual stimuli represent. The authors highlight two lifelong priors that influence the ability to identify faces in this task: (1) an orientation prior, based on the tendency for faces to appear in an upright (UP) position; and (2) an illumination prior, based on the probability that a scene is normally lit from the top (TP). These priors were violated by using inverted faces (IN) and faces illuminated from the bottom (BT) to induce prediction errors. Thus stimuli fell into one of four categories in which none, one, or both priors were violated: UPTP, UPBT, INTP and INBT.

When priors were violated, reaction times (RT) increased and accuracy for correctly identifying faces decreased. Performance on the task worsened as more priors were violated, suggesting that prediction errors were successfully induced. In addition, the orientation effect caused greater behavioral disruption than the illumination effect.

There are two possible explanations for the greater effect of orientation than of illumination on subjects' behavior. First, there is a greater difference between the probability of seeing an upright face versus an inverted face than the probability of seeing a face lit from the top versus from the bottom. Thus, violation of the orien-

tation prior produces a greater prediction error and a greater disruption to RT and accuracy.

A second explanation expands upon this first hypothesis by accounting for the variability of the sensory input. It has been suggested that for a prediction error to be useful in updating future predictions, it must be precision-weighted, i.e., the influence of the error signal on updating future expectations is dependent on an estimate of the variability of the sensory input (Friston and Kiebel, 2009). The underlying principle is analogous to that of a *t* test: when comparing the mean of two samples, an estimate of the variance of each sample is essential for determining whether there is a significant difference between the measures. Likewise, an estimate of the variance of both the predicted and actual sensory input is essential to determine whether the difference between these signals is surprising, and thus meaningful. The behavioral results reported by Brodski, Paasch, et al. (2015) can be equally explained with regard to a precision-weighted prediction error signal. Prior experience of faces illuminated from above or below is highly variable among individuals and easily altered with experience, whereas faces are much less frequently viewed upside down. Therefore, it could be argued that changes in orientation have less variance and thus a higher precision than changes in illumination, which would lead to an increased prediction error signal for a violation of the orientation prior. Precision and prediction error cannot be dissociated within Brodski, Paasch, et al.'s (2015) current paradigm; therefore, it is difficult to conclude exactly what is causing the behav-

Received Aug. 17, 2015; revised Sept. 29, 2015; accepted Oct. 7, 2015.

C.E.P. is funded by a Wellcome Trust PhD studentship and is in the four-year PhD Programme in Neuroscience at UCL. A.M. is a PhD student at UCL and funded by the Medical Research Council.

The authors declare no competing financial interests.

Correspondence should be addressed to Clare E. Palmer, Sobell Department of Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London, London WC1N 3BG, UK. E-mail: clare.palmer.13@ucl.ac.uk.

DOI:10.1523/JNEUROSCI.3093-15.2015

Copyright © 2015 the authors 0270-6474/15/3514689-02\$15.00/0

ioral disruption and what the neurophysiological correlate of the behavior is signaling. Future research should aim to disambiguate these measures to determine the contribution of this proposed estimate of variance on the prediction error signal measured.

Because multiple studies have implicated gamma band activity (GBA) in the feedforward passing of prediction error (Arnal and Giraud, 2012; Bauer et al., 2014), Brodski, Paasch, et al. (2015) hypothesized that the deviation between the predicted and actual sensory input in their study would be associated with an increase in GBA in cortical areas in which this comparison takes place. This would be consistent with the common view that the neural signal should be positively correlated with the magnitude of the prediction error signal (Rao and Ballard, 1999). For example, the BOLD response decreases with repeated presentations of expected faces, and this is thought to reflect a reduction in the difference between the predicted and actual sensory information as the probability of the stimulus occurring increases and predictions become more accurate; consequently, when presented with an unexpected stimulus, there is an increase in the BOLD response (Summerfield et al., 2008). Indeed, Brodski, Paasch, and colleagues (2015) found that high-frequency GBA (68–144 Hz) was increased in early visual processing areas specialized for contour recognition when the orientation prior was violated and thus the stimuli were unexpected. In keeping with the temporal order in which facial stimuli are recognized, an increase in GBA in more frontal areas strongly involved in processing 3D shape occurred 40 ms later when the illumination prior was violated. Moreover, these increases in GBA positively correlated with RT. This fast-evoked gamma response is indicative of prediction error signaling described in canonical microcircuits by Bastos et al. (2012). It has been proposed that feedforward prediction errors received in granular layer 4 are transmitted to superficial pyramidal cells via high-frequency oscillations, such as gamma, and these cells send predictions carried by low-frequency oscillations, such as beta, alpha, or theta, in feedback connections to deep pyramidal cells. The findings of Brodski, Paasch, et al. (2015) provide further support for this hypothesis.

In contrast to Brodski, Paasch, et al.'s (2015) findings regarding increases in GBA, several studies have found that increasing prediction error signals are associated with neural signal suppression. When macaque monkeys are trained to

recognize novel geometric stimuli, the incidence of neurons with receptive fields for these specific complex objects increases as they become more familiar (Logothetis et al., 1995); this is in contrast to the repetition suppression effect of the BOLD response described above. In addition, increased GBA over the occipital cortex has been found for familiar versus novel stimuli (Herrmann et al., 2004). However, these paradoxical findings may be reconcilable. Brodski, Paasch, et al. (2015) identified two opposing changes in GBA when the illumination prior was violated: an increase in GBA in the superior frontal gyrus, medial frontal cortex, and anterior cingulate cortex (as described above) at 120 ms poststimulus presentation; and a decrease in GBA in the right supramarginal gyrus and inferior temporal gyrus, a later part of the ventral stream, at 135 ms and 310 ms poststimulus presentation. In these later negative peaks, faces illuminated from the top, rather than the bottom, showed higher gamma power compared with baseline.

The authors suggest the contradicting decrease in GBA for the violated illumination prior may reflect an attentional mechanism to identify the mnemonic representation of the more familiar stimulus according to the attention to memory hypothesis (Wagner et al., 2005). However, the difference in familiarity between upright and inverted faces is far greater than that of faces illuminated from above and below; therefore, if this were the case, there should be a greater decrease in GBA for the orientation contrast (not found) and even more for faces versus scrambled faces (results not reported).

An alternative role of this attentional mechanism may be to alter the precision-weighting of the prediction error. It has been proposed that attention can modulate the synaptic gain of superficial pyramidal cells in a top-down manner. These cells are thought to report prediction errors and thus modulating the cells' sensitivity could increase the precision of the prediction error (Friston et al., 2015). Increased GBA to faces illuminated from the top may reflect a positive modulation of precision such that these prediction errors have more influence over future predictions than those from faces illuminated from below. We can only postulate that the reason this effect was not found for the orientation contrast is because here the prediction error may be more obvious and immediate and thus not require attentional modulation. Future experiments specifically designed to investigate

how this attentional modulation of precision may be implemented in the brain are necessary to test this hypothesis.

Brodski, Paasch, and colleagues (2015) highlight that the integration of prior information with sensory input occurs at multiple time points and in a distributed network throughout the brain. In this highly powered study, the authors demonstrate that, within the same frequency, oscillations in different areas may be working in parallel to modulate this integration process. However, their findings emphasize the need to design experiments in which each component of this process can be truly disambiguated so that we can identify the neural mechanisms underlying all faces of predictive coding.

References

- Arnal LH, Giraud AL (2012) Cortical oscillations and sensory predictions. *Trends Cogn Sci* 16:390–398. [CrossRef Medline](#)
- Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ (2012) Canonical microcircuits for predictive coding. *Neuron* 76:695–711. [CrossRef Medline](#)
- Bauer M, Stenner MP, Friston KJ, Dolan RJ (2014) Attentional modulation of alpha/beta and gamma oscillations reflect functionally distinct processes. *J Neurosci* 34:16117–16125. [CrossRef Medline](#)
- Brodski A, Paasch GF, Helbling S, Wibral M (2015) The faces of predictive coding. *J Neurosci* 35:8997–9006. [CrossRef Medline](#)
- Friston K, Kiebel S (2009) Predictive coding under the free-energy principle. *Philos Trans R Soc Lond B Biol Sci* 364:1211–1221. [CrossRef Medline](#)
- Friston KJ, Bastos AM, Pinotsis D, Litvak V (2015) LFP and oscillations—what do they tell us? *Curr Opin Neurobiol* 31:1–6. [CrossRef Medline](#)
- Herrmann CS, Lenz D, Junge S, Busch NA, Maess B (2004) Memory-matches evoke human gamma-responses. *BMC Neurosci* 5:13. [CrossRef Medline](#)
- Logothetis NK, Pauls J, Poggio T (1995) Shape representation in the inferior temporal cortex of monkeys. *Curr Biol* 5:552–563. [CrossRef Medline](#)
- Moore C, Cavanagh P (1998) Recovery of 3D volume from 2-tone images of novel objects. *Cognition* 67:45–71. [CrossRef Medline](#)
- Rao RP, Ballard DH (1999) Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat Neurosci* 2:79–87. [CrossRef Medline](#)
- Summerfield C, Trittschuh EH, Monti JM, Mesulam MM, Egner T (2008) Neural repetition suppression reflects fulfilled perceptual expectations. *Nat Neurosci* 11:1004–1006. [CrossRef Medline](#)
- von Helmholtz H (1867) *Handbuch der physiologischen optik*. Leipzig: Voss.
- Wagner AD, Shannon BJ, Kahn I, Buckner RL (2005) Parietal lobe contributions to episodic memory retrieval. *Trends Cogn Sci* 9:445–453. [CrossRef Medline](#)