NeuroImage 167 (2018) 224–236

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

# Predictability of what or where reduces brain activity, but a bottleneck occurs when both are predictable☆

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ARTICLE INFO

*Keywords:*
Uncertainty
Prediction
Statistical learning
Predictive coding
Disorder
Entropy

ABSTRACT

Detecting regularities in the sensory environment licenses predictions that enable adaptive behaviour. However, it is unclear whether predictions about object category, location, or both dimensions are mediated by overlapping systems, and relatedly, whether constructing predictions about both category and location is associated with processing bottlenecks. To examine this issue, in an fMRI study, we presented participants with image-series in which non-deterministic transition probabilities enabled predictions about either the location of the next image, its semantic category, both dimensions, or neither (the latter forming a “no-regularity” random baseline condition). Speaking to a common system, all three predictable conditions resulted in reduced BOLD activity in four clusters: left rostral anterior cingulate cortex; bilateral putamen, caudate and thalamus; right precentral gyrus, and left visual cortex. Pointing to a processing bottleneck, in some regions, a significant interaction between the two factors was found whereby category-predictable series were associated with lower activity – but only when location regularity was absent. Finally, category regularity decreased activation in areas of the ventral visual stream and semantic areas of lateral temporal cortex, and location regularity decreased activation in a dorsal fronto-parietal cluster, long implicated in the endogenous control of spatial attention. Our findings confirm and expand a role for dACC/dmPFC and striatum in monitoring or responding to uncertainty in the environment and point to a limited capacity bottleneck when multiple predictions are concurrently licensed.

## Introduction

Humans excel at detecting regularities. They can detect patterns matching chaotic (non-random) processes, differentiate fractal dynamics across multiple time scales, and recognize subtle interactions between multiple variables (Lewicki et al., 1992; Smithson, 1997; Stephen and Dixon, 2011). This ability develops early (e.g., Saffran et al., 1996) and applies to both visual and non-visual input (for review, see Conway et al., 2009). Moreover, the ability to recognize temporally unfolding regularities or patterns in the sensory environment offers multiple advantages: it allows prediction when regularities exist, or conversely, an increased emphasis on bottom-up processing when the environment lacks regularity.

Much of the neurobiological research to date has focused on brain regions whose activity tracks regularity of simple visual or auditory streams. This work has linked several brain regions to the processing of regularity, including lateral and dorso-medial prefrontal cortex (dmPFC; Behrens et al., 2007; Huettel et al., 2005), hippocampus (Bornstein and Daw, 2012; Harrison et al., 2006; Strange et al., 2005), posterior parietal sulcus (Huettel et al., 2005; Nastase et al., 2014), anterior cingulate cortex (ACC; Harrison et al., 2011; Nastase et al., 2015) and lateral temporal regions (e.g., Bischoff-Grethe et al., 2000; Tobia et al., 2012a, 2012b; Tremblay et al., 2013).

While the use of simple tonal or visual series has proved effective for identifying mechanisms by which regularities are coded or deployed for purposes of prediction, these paradigms have not examined an important use of environmental regularities: making predictions about semantic features and location of elements in the environment that have yet to appear. In particular, it is unclear whether contexts that allow for joint predictions about the *location and identity* of future stimuli involve those neural systems engaged when only location or identity are predictable. It is also unclear whether the ability to predict both dimensions is associated with a processing bottleneck. As we review in detail below, there are two views on this issue. One view posits that separate systems code for different dimensions of the environment (location, visual features, etc'; see Keele et al., 2003), and that these systems operate in parallel to

☆ This research has received funding from the European Research Council under the 7th Framework Starting Grant Program [ERC-STG #263318] to Uri Hasson.
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https://doi.org/10.1016/j.neuroimage.2016.06.001
Received 26 February 2016; Received in revised form 31 May 2016; Accepted 1 June 2016
Available online 3 June 2016

encode location and category information (what appears where). On the other, a single core fronto-parietal system mediates anticipation of future locations and identity (Egner et al., 2008).

To address these issues, we conducted an fMRI study in which participants observed series of images that were drawn from four semantic categories and presented at four screen locations. The four types of series were constructed so that the transition structure allowed for predictions about *i*) just the location of the next image, *ii*) just its category, *iii*) both dimensions (dual regularity), or *iv*) neither dimension (the latter forming the "no-regularity" baseline condition). We examined activity in the baseline no-regularity condition vis-à-vis activity in the other three conditions, where predictions regarding location, category, or both were licensed. This allowed for identification of neural systems sensitive to statistical regularities in these domains and second, identification of systems where the ability to predict both location and category produced activation patterns consistent with a processing bottleneck. From the perspective of experimental design, a bottleneck in predictive processing would appear as an interaction between the levels of location and categorical predictability. If the two dimensions were tracked by independent systems, those would show main effects of regularity in the categorical and location domains. However, if the two systems are integrated or interact with each other, then the level of location regularity should affect the expression of categorical predictability or vice-versa. This interaction may be expressed in different forms and we were particularly interested to see if there would be brain areas where the dual regularity condition was associated with higher activity than both the location- and category-regularity conditions.

Our work assumes that environmental statistics are vital information for systems that mediate predictive coding – a computation in which systems associated with higher level functions generate predictions about expected environmental states – that is, construct a model of expected neural activity in low-level sensory regions (Friston, 2009; Grossberg, 2009; Rao and Ballard, 1999; Summerfield and Egner, 2009). Satisfied – i.e., correct – predictions are associated with reduced prediction errors, and lower activity in sensory regions (Feldman and Friston, 2010; Kok et al., 2012). Predictions may be instantiated and evaluated via interactions between frontal regions and sensory systems (Bar et al., 2006; Summerfield et al., 2006), or via interactions between sensory regions (den Ouden et al., 2009). A representation of stimulus regularity can license predictions about what is likely to appear where. This not only speeds up orientation towards, but also improves the identification of, a future stimulus via pre-sensitization of systems that code for its expectation. (e.g., Esterman and Yantis, 2010). The predictive coding framework makes well-defined hypotheses about the impact of statistically induced predictions regarding location and identity. However, as we detail below, it leaves open the *neurobiological question* of whether the potential to anticipate both location and category is associated, at any level, with increased difficulty as compared to conditions where only one of the dimensions is predictable.

With respect to location regularities, it has been shown that individuals are highly sensitive to them (Marcus et al., 2006; Walthew and Gilchrist, 2006). They respond faster to targets appearing in more predictable locations, either because these target locations have higher marginal frequencies (Geng and Behrmann, 2002, 2005; Jones and Kaschak, 2012) or because they are linked to stronger transition probabilities (Remillard, 2003, 2009). We therefore expected that being able to predict location transitions would serve as an endogenous cue, resulting in increased activity in regions associated with recruitment and directing of spatial attention, specifically the bilateral intraparietal sulcus and the frontal eye fields (see Corbetta and Shulman, 2002, and also Szczepanski and Kastner, 2013, for recent review). At the same time, the greater proportion of correct predictions should translate in reduced activity in visual cortex when location is predictable (~V1; Kok et al., 2012).

In addition, we studied the impact of regularities governing the semantic categories from which visual images were drawn. This examination was more exploratory, since there is little if any prior work that informs this issue. Individuals are sensitive to the presence of fixed sequences of images drawn from basic-level categories (Brady and Oliva, 2008; Goschke and Bolte, 2012), but whether this extends to stochastic contexts has not been examined. As far as regions that might be sensitive to category in the context of visual regularity, prior results point to lateral occipital cortex and the fusiform. These regions show stronger repetition-suppression effects when repetitions are more predictable, which has been taken to suggest they mediate anticipatory predictions (Mayrhauser et al., 2014; Summerfield et al., 2008). Importantly, reduced activity in these regions likely also reflects long-term familiarity with the stimuli (i.e., not solely a visual representation) as the pattern of repetition suppression in the fusiform depends on stimulus familiarity (Henson et al., 2000). We thus hypothesized that being able to make category-level predictions would result in reduced activity across the lateral occipital cortex and fusiform. We note that our paradigm evaluated whether predictions could be made on the abstract level (of category, not specific tokens) as in our study all images were unique and presented once, making it impossible to predict the specific feature of the next image.

As mentioned above, some have argued that coding for multiple input streams relies on separate systems (e.g., Keele et al., 2003), whereas others have suggested that anticipating location and identity relies on a single system (e.g., Egner et al., 2008). Current approaches to statistical learning are similarly concerned about whether the capacity to learn the statistics of an input stream is mediated by a single, modality-general system, or carried out by additional more modality-specific systems (Frost et al., 2015). Our own prior work on this matter, which manipulated regularities in auditory-only or visual-only streams, showed that separate systems might be involved (Nastase et al., 2014). In support of the separate-system view, work that examined sequential (as opposed to statistical) learning suggested that the coding of two sequence streams does not accrue additional costs (quantified behaviorally) beyond what is necessary to code for a single dimension (Mayr, 1996). This supports the modular approach, in which separate processes code the regularity of different stimuli dimensions (see Goschke and Bolte, 2012; Mayr, 1996, for supportive behavioral data). Such findings have been interpreted within a framework in which sequential structures in different stimuli dimensions are processed by different modules (Keele et al., 2003). Consistent with this view, Bubic et al. (2011) found that different neural systems are involved in evaluating predictions regarding object identity, location, and presentation time. Other studies have shown that odd-ball (unexpected) auditory or visual events produce patterns corresponding to surprise or prediction error in respective sensory cortices (Kok et al., 2012; Mustovic et al., 2003; Todorovic et al., 2011).

However, an alternative viewpoint emerges from neuroimaging work that suggests that predictions are mediated by a single fronto-parietal system that codes for both stimulus features and stimulus locations. For example, Egner et al. (2008) manipulated the validity of cues in a cue-target paradigm and found that more informative cues evoked higher activity in fronto-parietal regions, not only when cues informed about a future location, but also when they informed about a specific visual feature of the to-be presented item. Similarly, Cristescu et al. (2006) studied responses to cues that predicted either the semantic category of a to-be-presented word or its spatial location, and the authors identified a similar network to that reported by Egner et al. (2008), with greater activity for diagnostic cues.

Thus, in the current study we hypothesized that *i*) predictable location streams would be associated with reduced metabolic demands seen in lower BOLD signal (prediction-related saving) in visual cortex as compared to the no-regularity baseline, *ii*) that predictable category streams would result in reduced BOLD activity in lateral occipital cortex and fusiform, *iii*) that location regularity could produce increased activity in fronto-parietal systems linked to valid cuing. Finally, we did not have a precise prediction regarding the dual regularity condition. On the one hand, the increased predictability in that condition within both streams, should produce reduced activity when compared to baseline, if only because the location dimension itself is easier to track. On the other hand,