

ORIGINAL RESEARCH PAPER

*J. Todd et al. / Neuroscience xxx (2018) xxx–xxx*Reprint of: Initial uncertainty impacts statistical learning in sound sequence processing[☆]Juanita Todd,^{*} Alexander Provost Lisa Whitson and Daniel Mullens*School of Psychology, University of Newcastle, Newcastle, Australia*

Abstract—This paper features two studies confirming a lasting impact of first learning on how subsequent experience is weighted in early relevance-filtering processes. In both studies participants were exposed to sequences of sound that contained a regular pattern on two different timescales. Regular patterning in sound is readily detected by the auditory system and used to form “prediction models” that define the most likely properties of sound to be encountered in a given context. The presence and strength of these prediction models is inferred from changes in automatically elicited components of auditory evoked potentials. Both studies employed sound sequences that contained both a local and longer-term pattern. The local pattern was defined by a regular repeating pure tone occasionally interrupted by a rare deviating tone ($p = 0.125$) that was physically different (a 30 ms vs. 60 ms duration difference in one condition and a 1000 Hz vs. 1500 Hz frequency difference in the other). The longer-term pattern was defined by the rate at which the two tones alternated probabilities (i.e., the tone that was first rare became common and the tone that was first common became rare). There was no task related to the tones and participants were asked to ignore them while focussing attention on a movie with subtitles. Auditory-evoked potentials revealed long lasting modulatory influences based on whether the tone was initially encountered as rare and unpredictable or common and predictable. The results are interpreted as evidence that probability (or indeed predictability) assigns a differential information-value to the two tones that in turn affects the extent to which prediction models are updated and imposed. These effects are exposed for both common and rare occurrences of the tones. The studies contribute to a body of work that reveals that probabilistic information is not faithfully represented in these early evoked potentials and instead exposes that predictability (or conversely uncertainty) may trigger value-based learning modulations even in task-irrelevant incidental learning. © 2017 IBRO. Published by Elsevier Ltd. All rights reserved.

Keywords: Auditory evoked potentials, Sequential learning, Predictive coding, Mismatch negativity, Primacy bias.

1. INTRODUCTION

Our auditory system is incredibly adept at learning any patterning within a sequence of sound (Cowan et al., 1993; Bendixen et al., 2007). Any form of regularity within a sequence is readily extrapolated into an inferred repetition, even without focused attention, and also during early stages of sleep (Loewy et al., 1996; Sculthorpe et al., 2009). In the auditory evoked potential literature this inference has been referred to as the formation of a “prediction model” referencing a memory-based anticipation of the most likely properties of sound to be encountered in a given context (Näätänen et al., 2001; Winkler, 2007).

This inference is further weighted by an estimate of “certainty” in the underlying prediction (Winkler, 2007; but see also Pouget, Drugomitsch, & Kepecs, 2016). In computational biology it has been presented in the Bayesian framework of predictive coding as an “internal model” referencing a “belief” about the most likely next-state of brain activation, with this belief weighted by the “precision” afforded by prior evidence (Friston, 2005; Garrido et al., 2009; Lieder et al., 2013a). The existence and updating of an internal model is indexed in measures of auditory evoked potentials.

When a sound matches the content of a currently active internal model the model precision estimate increments (Friston, 2005). This can be observed in changes in the evoked potential; principally in reduced negativity in the waveform recorded at fronto-centrally located scalp electrodes within 200 ms of sound onset and, at least in some cases, the emergence of an early positive component (Baldeweg, 2006). Both of these effects are amplified in the presence of further matches between model predictions and brain activation (in

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response to sensory input), and this progression is considered a quantification of model precision (for the term precision see [Baldeweg, 2006](#); [Garrido et al., 2008](#); [Lieder et al., 2013a, 2013b](#) and for terms strength or confidence see [Schröger, 2007](#); [Näätänen et al., 2011](#); [Winkler, 2007](#); [Winkler, 2009](#)). If there is a mismatch between the internal state caused by the incoming sound (often called a “sensory buffer”, [Winkler and Cowan, 2005](#)) and model prediction, the evoked potential is characterised by a large negativity peaking 100–200 ms from the deviation. This additional negativity (commonly known as mismatch negativity or MMN, see [Näätänen et al., 2011](#) for review) has been suggested to reflect a prediction-error being signalled ([Friston, 2005](#)). Prediction-errors are large if the internal model is associated with high precision, which occurs when there is low variance in the underlying repetition. For example, MMN to deviations from a repetitive pattern will be large when there are a large number of repetitions of the pattern between two successive deviations (e.g., [Shelley et al., 1999](#); [Sato et al., 2000](#)), and when the repetition is exact (as opposed to repetition with some variance, [Winkler et al., 1990](#); [Daikhin and Ahissar, 2012](#); [Garrido et al., 2013](#)). However, we have previously observed that the sound probabilities at sequence onset appear to exhibit a disproportionately strong influence over precision estimates ([Todd et al., 2011](#)). In analogy to other similar phenomena, we termed this effect “first-impression bias”. In psychology, “first impression” refers to the way in which future learning and memory can be anchored to the earliest experience in a given context. It is perhaps best known and documented in literature pertaining to how our beliefs about a person are heavily influenced by the first encounter (e.g., [Willis and Todorov, 2006](#)), but in the present study we demonstrate how first impressions affect many aspects of early automatic relevance-filtering processes.

The first impression bias has been observed in protocols that include a simple sound sequence that contains patterns that alternate on different timescales (the “multi-timescale paradigm”, [Frost, Winkler, Provost & Todd, 2016](#); [Todd et al., 2011, 2013, 2014a, 2014b](#); [Mullens et al., 2014, 2016](#)). In these experiments there are only two sounds in the sequence and these sounds exchange roles as a common repeating “standard” defining the local pattern ($p = 0.875$), and rare pattern deviation or “deviant” ($p = 0.125$) that differs physically from the other tone (hereafter referred to as *context A*). The local pattern alters at regular intervals when the roles of the sounds exchange (probabilities invert, *context B*), and these exchanges happen at regularly timed intervals creating a second-order (or superordinate) pattern embodied in the length of sequence blocks. The context change from A to B is abrupt and the former deviant starts repeating, generating a sequence of prediction-errors. These error signals are rapidly suppressed (within as few as 2–3 repetitions) as a new internal model is formed ([Bendixen et al., 2008](#); [Sams et al., 1983](#)). This reflects a locally dynamic predictive system keeping the auditory system adaptive and current. However, it has long been

known that local probabilities are not the only influence on MMN amplitude to the deviant sounds (e.g., [Horvath et al., 2001](#)). One of the key findings in the multi-timescale paradigm is that the amplitude of MMN to the rare sounds is differently affected by local stability in the underlying pattern in context A and B ([Todd et al., 2014a, 2014b](#)). MMN to the sound-type that is rare in context A (the “first-deviant”) is large at the beginning of sequence blocks and stays large into the second-half of blocks. In contrast, MMN to the sound that becomes deviant in context B (the “second-deviant”) is very small at the beginning of blocks and increases in amplitude into the second-half of blocks.

In previous papers we have suggested that the different pattern of MMN amplitude in context A and B reflects a lasting first impression based on the initial sound probabilities (e.g., [Todd et al., 2014a, 2014b](#); [Mullens et al., 2016](#)). We have proposed that high precision is assigned to the internal model for the repetitious sound in context A, specifying the behaviour of the sound that is first encountered as common and predictable. There is little value in updating this model, as its precision is already high (i.e., it is akin to a strong belief that is resistant to counter-evidence). In contrast, the auditory system has little information about the deviant in context A (the first-deviant) because this tone is rare (improbable in the context) and the timing of its occurrence cannot be accurately anticipated. MMN evoked in context A to this rare sound is large throughout blocks because the active internal model for context A is held with high precision producing large error signals when predictions are violated. When context B begins, the high precision for the internal model of context A may explain why the MMN evoked to the deviant in context B is small initially, but then later increases as evidence accumulates that the roles of the two sounds are reversed in the new context.

Although first-impression biases have been replicated a number of times, the analysis of effects on ERP responses has only produced significant order effects on the evoked potential to the rare deviant. However, the hypothesis put forward to explain the bias would predict that we might also see order effects on the responses to the repetitious sounds if we examine the data most likely to show the effects. Models of learning predict that with higher uncertainty about an event, learning about this event becomes fast (for confirmation in an animal model, see [Dayan and Jyu, 2003](#); [Pearce and Hall, 1980](#)). In the multi-timescale paradigm, uncertainty about an event should be associated with more readiness to update the internal model in the face of new evidence. As noted above, at the point of role reversal, there is higher uncertainty associated with the sound that has been rare before, because the brain cannot anticipate when it will occur. Before the role reversal (in context A), the sound elicits a prediction-error signal, and when the context shifts from A to B, there is a sudden increase in the frequency of prediction errors as this sound starts to repeat and a new model needs to be built. The mechanisms of new model formation have been studied in depth by [Moran et al. \(2013\)](#) in pharmacological studies employ-

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