



Tuned by experience: How orientation probability modulates early perceptual processing



Syaheed B. Jabar^a, Alex Filipowicz^{a,c}, Britt Anderson^{a,b,*}

^a Department of Psychology, University of Waterloo, 200 University Avenue West, Waterloo, ON N2L3G1, Canada

^b Centre for Theoretical Neuroscience, University of Waterloo, 200 University Avenue West, Waterloo, ON N2L3G1, Canada

^c Department of Neuroscience, University of Pennsylvania, Philadelphia, PA 19104, USA

ARTICLE INFO

Article history:

Received 12 February 2017

Received in revised form 20 June 2017

Accepted 19 July 2017

Number of reviewer = 2

Keywords:

Orientation probability

Visual perception

Attention

V1

C1

EEG

ABSTRACT

Probable stimuli are more often and more quickly detected. While stimulus probability is known to affect decision-making, it can also be explained as a perceptual phenomenon. Using spatial gratings, we have previously shown that probable orientations are also more precisely estimated, even while participants remained naive to the manipulation. We conducted an electrophysiological study to investigate the effect that probability has on perception and visual-evoked potentials. In line with previous studies on oddballs and stimulus prevalence, low-probability orientations were associated with a greater late positive 'P300' component which might be related to either surprise or decision-making. However, the early 'C1' component, thought to reflect V1 processing, was dampened for high-probability orientations while later P1 and N1 components were unaffected. Exploratory analyses revealed a participant-level correlation between C1 and P300 amplitudes, suggesting a link between perceptual processing and decision-making. We discuss how these probability effects could be indicative of sharpening of neurons preferring the probable orientations, due either to perceptual learning, or to feature-based attention.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

We behave differently towards frequently occurring events than we do towards rarer ones. This 'probability effect' is typically demonstrated through changes in reaction time and detection accuracy, either in simple detection tasks (Hon, Yap, & Jabar, 2013; Laberge & Tweedy, 1964; Miller & Pachella, 1973), or in visual-search tasks (Rich et al., 2008; Wolfe et al., 2007). Although the effect has been suggested to be due to decisional criterion shifts (e.g. Wolfe & Van Wert, 2010), probability effects have also been suggested to have a perceptual locus (e.g. Dykes & Pascal, 1981).

Supporting a perceptual locus are studies finding that probability affects the precision of perceptual estimation. By manipulating Gabor orientations, probable tilts are estimated both more quickly and with greater precision (Anderson, 2014). As with detection tasks, probability effects on precision developed quickly, and with participants remaining naive to the manipulation (Jabar & Anderson, 2015). While spatial exogenous cuing does result in a similar increase in orientation precision (Anderson & Druker, 2013), these effects are also likely independent from the effect of

orientation probability (Jabar & Anderson, 2017a). Orientation estimation precision is also not improved with *spatial* probability (Jabar & Anderson, 2017b), suggesting a separability of probability effects along feature vs. spatial lines, similar to the distinction made in the attention-literature (e.g. Carrasco, 2011).

We previously suggested that the mechanism driving orientation-probability effects is the selective tuning of orientation-selective neurons in the primary visual cortex (V1; Jabar & Anderson, 2015). This would be similar to how training monkeys with specific orientations affects the tuning width of V1 neurons preferring the trained orientation (Ringach, Hawken, & Shapley, 1997; Schoups, Vogels, Qian, & Orban, 2001). Axiomatically, selective orientation training is a manipulation of orientation-probability. This idea is also consistent with the suggestion that learnt likelihoods are reflected in the early phase of sensory processing (Summerfield & Egner, 2009), and that the site of plasticity must involve early cortical processing regions with narrow neural tuning (Gilbert, 1994).

An alternative account is that orientation probability is due to feature-based attention, although this is also thought to result in neural tuning (David, Hayden, Mazer, & Gallant, 2008; Ling, Jehes, & Pestilli, 2015; Paltoglou & Neri, 2012; Çukur, Nishimoto, Huth, & Gallant, 2013). For example, the pairing of an auditory

* Corresponding author at: Department of Psychology, University of Waterloo, 200 University Avenue West, Waterloo, ON N2L 3G1, Canada.

E-mail address: britt.anderson@uwaterloo.ca (B. Anderson).

cue with a particular orientation leads to both a decrease in fMRI activation and a concurrent increase in the sensory representation demonstrable by multi-voxel pattern analysis (Kok, Jehee, & de Lange, 2012). Presumably, even in the absence of an explicit cue, orientation probability could yield a similar pattern if it also produced neural sharpening. In contrast to the neural sharpening accounts of feature manipulations, space-based manipulations are thought to be more related to gain-mechanisms (Carrasco, 2011), such as increasing the input baseline of neural responses (Cutrone, Heeger, & Carrasco, 2014).

If orientation probability affects perception via sharpening the response profiles of neurons in early visual cortex, we should see both physiological changes in the early sensory systems tracking stimulus probability, and in behavioral measures of perceptual precision. By employing spatial gratings in varying visual field locations we can study the effects of orientation probability on early visual processing via the 'C1' ERP component. The C1 is an early visual evoked component that has a unique visual field-dependant phase reversal. For this reason it has often been proposed as an ERP reflecting V1 activity, and Di Russo, Martínez, Sereno, Pitzalis, and Hillyard (2002) used source localization methods to localize the C1 to the banks of the calcarine cortex. While a V1 source for the C1 has been traditional, some groups have more recently suggested that the C1 is less specific than V1 because forward-modelling suggests that either V2 and V3 might also result in the phase reversal property (Ales, Yates, & Norcia, 2010). However, the assumptions required for a V2/V3 C1 locus has been questioned, and also does not account for why there is a C1-V1 relation in primate neurophysiology (see Kelly, Schroeder, & Lalor, 2013).

Another interesting feature of the C1 component is the suggestion that it indicates feed-forward processing only. With a peak latency between 90 and 110 ms the C1 has been felt to occur too early for significant top-down trial-specific modulation, unlike the P1, a later visual ERP (Di Russo, Martinez, & Hillyard, 2003). In addition, *endogenous* manipulations of *spatial* attention affect the P1 but not the C1 (Clark & Hillyard, 1996; Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Di Russo et al., 2003). However, the feed-forward only claim for the C1 is not universally accepted, and some recent data challenge this claim (for a review see Rauss, Schwartz, & Pourtois, 2011). For example, Kelly, Gomez-Ramirez, and Foxe (2008) found that endogenous manipulation of spatial attention *did* affect both the C1 and P1. Studies on the effects of *feature*-attention on these ERP components are considerably scarcer, although it seems that at least the P1 is affected. For example, when participants are instructed to attend to red instead of green stimuli, P1 is amplified, even if the stimuli appeared in an unattended *location* (Zhang & Luck, 2009).

There is also some disagreement about the *direction* of the effects different manipulations may have on the C1 potential. Kelly et al. (2008) reported that endogenous spatial attention *increased* C1 amplitude, consistent with a spatial gain mechanism. Also consistent with a gain mechanism, Bao, Yang, Rios, He, and Engel (2010) and Zhang, Li, Song, and Yu (2015) found increases in C1 amplitude for learned orientations in perceptual learning tasks. However, data from other perceptual learning experiments have shown decreased early visual activity to learned orientations. Gratton (1997) demonstrated this with optical imaging, and Pourtois, Rauss, Vuilleumier, and Schwartz (2008) found *reduced* C1 amplitudes. These findings are more consistent with a neural sharpening mechanism similar to that seen in monkeys undergoing long term orientation discrimination training (Ringach et al., 1997; Schoups et al., 2001). These mixed results emphasize the need to carefully consider both the type of training and the experimental paradigm when interpreting effects (Hung & Seitz, 2014).

While our hypothesis that orientation probability effect are due to V1 sharpening is inspired by the perceptual learning studies done in monkeys (where direct neural recordings were possible; Ringach et al., 1997; Schoups et al., 2001), it is important to note that our task is in fact a probability manipulation and is procedurally distinct in many ways from traditional perceptual learning paradigms. In common perceptual learning paradigms either a single orientation is shown repeatedly in a predictable fashion (e.g. Ringach et al., 1997; Schoups et al., 2001) or only a pair of distinct orientations are possible one of which has the higher exposure rate (Bao et al., 2010; Zhang et al., 2015). Perceptual learning studies also usually involve a training period that spans several sessions and may go on for days or even weeks. In our probability task the orientations were not 'trained', but rather a subset of possible orientations were biased, and this was generally undetectable by our participants. Our probability effects develop quickly, within a single behavioral session (e.g. Jabar & Anderson, 2015, 2017b), faster than the typical perceptual learning experience.

Probability effects also persist despite orientations being biased in a location-contingent manner. In contrast, retinotopic transfer has been noted with perceptual learning, suggesting a top-down influence on the visual cortices (Zhang, Xiao, Klein, Levi, & Yu, 2010). Therefore, while our hypotheses regarding the direction of the effect we expected to see on the amplitude of the C1 were motivated by results from the perceptual learning literature, the specific interest of our study was to examine the C1 effects associated with a probabilistic paradigm, a paradigm where orientations are biased rather than 'trained'.

In summary, the behavioral results of manipulating orientation probability suggest perceptual effects (Jabar & Anderson, 2015, 2017a, 2017b). This raises the possibility of an early visual locus for the effect of orientation probability. While the principal electrophysiological focus of stimulus probability has most often been the decision-related P300 (e.g. Rohrbaugh, Donchin, & Eriksen, 1974; Bledowski et al. 2004; Polich, 1990), we hypothesized that early visual cortical potentials could also show orientation probability effects and that based on orientation training experiments in monkeys that the nature of the effects would be decreases in waveform amplitudes.

2. Methods

Since the 'C1' ERP component is the key variable of interest, the current study broadly replicated the design of Di Russo and colleagues (2002) while introducing the probability manipulation and estimation task employed in Anderson (2014) and Jabar and Anderson (2015), Jabar and Anderson (2017a).

2.1. Participants

Twenty paid participants were recruited from the University of Waterloo (10 females, 10 males). 18 were right-handed and 2 were left-handed. Participant ages ranged from 19 to 49 (median = 24). All participants had normal or corrected-to-normal vision, and did not declare any auditory deficits or any past neurological conditions/concussions. Informed consent was obtained. This study was approved by the University's Office of Research Ethics, and work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Participants came in for two sessions (first behavioral; second behavioral and EEG). Both sessions were always completed in the same week (Monday-Friday), with the majority having 2 or 3 days between sessions. Participants were asked to refrain from alcohol consumption for 24 h prior to the 2nd (EEG) session, and to maintain their regular caffeine habits. Participants were paid 25 dollars for their involvement (one 30 min session and one 2 h session).

Download English Version:

<https://daneshyari.com/en/article/5705850>

Download Persian Version:

<https://daneshyari.com/article/5705850>

[Daneshyari.com](https://daneshyari.com)