Tuned by experience: How orientation probability modulates early perceptual processing

CrossMark

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

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.

1. Introduction

We behave differently towards frequently occurring events than we do towards rarer ones. This 'probability effect' is typically demonstrated though 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, Jehee, & 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).

2.2. Stimuli

Stimulus locations and timings resembled those used in the Di Russo et al. (2002) study. Instead of checkerboard patterns, Gabors were used to allow for the orientation manipulation. The Gabors were oriented grayscale sine-wave gratings with a circular Gaussian mask (Fig. 1a), at 50% contrast, with an average measured luminance of 22 cd/mm^2. They had a spatial frequency of 4 cycles per degree of visual angle, and were presented on a grey background with a similar luminance of 23 cd/mm^2. When viewed from a distance of 60 cm, the Gabors subtended approximately 4 degrees of visual angle both vertically and horizontally. On any given trial, the center of the Gabor was located 4 degrees away from the center of the display, which was marked by a black fixation symbol. As with Di Russo et al. (2002), the four stimulus positions were centred along an arc that was located at a polar angles of 25° above and 45° below the horizontal meridian (see Fig. 1c). Lines, used as feedback and for participants to rotate to report their estimations, had a length of 4 visual degrees and always occurred in the same location as the Gabor for that trial.

Spatial Gabors were equally likely to appear in any one of the four locations surrounding the fixation symbol. *Collapsed across these four locations*, any orientation was equally likely. The critical manipulation was the occurrence-rate of the various *probability-location conjunctions*. Half the participants saw the conjunction depicted in Fig.1c: When a Gabor appeared on the top or bottom left, its orientation was more likely to be left-tilting, but this high-probability orientation was reversed if the Gabor appeared on the top or bottom right. Orientations were uniformly distributed across each quadrant, and were not shown at the exact cardinal orientations (0/90 degrees). High-probability orientations accounted for 80% of the trials. The lines in Fig.1c depict the distribution observed by the first participant. The location-orientation conjunctions were counterbalanced across participants.

Probability distributions were counterbalanced across participants and maintained within participants for both experimental sessions. For example, in every set of 20 trials there were 5 Gabors that appeared in the top-left location. Of these, 4 might be left-tilting while one was right-tilting (or vice versa). Participants were *not* informed about these probability distributions, and observed the same distribution across their two sessions. The first 20 trials of the first session, and the first 60 trials in the second session were practice trials which had uniformly distributed orientations.

Auditory feedback was given after each response to maintain motivation. A high pitched sound (http://www.freesound.org/people/HardPCM/sounds/32950/) was played if the participant made an angular error less than 12 degrees. A lower pitch (http://www.freesound.org/people/tombola/sounds/49219/) indicated an error greater than 12 degrees. Participants were not explicitly informed that 12 degrees was the error threshold.

2.3. Equipment

The experiment was programmed in Python using the PsychoPy library (Peirce, 2009). In both sessions, eyetracking was done using an Eyelink1000 recording the dominant eye at 2000 Hz and tracking both the pupil and corneal reflections. Participant head position was stabilized using a chin rest. Participants were instructed to fixate at the center of the screen and to avoid excessive blinking during stimulus presentations, but were free to blink or move their eyes prior to confirming the drift correction, during breaks or during responses. The task was gaze-contingent in that stimuli were not flashed until a central fixation (radius 0.5 visual angle) was

Fig. 1. Experiment paradigm. a) Behavioural session. A Gabor stimuli was shown in one of four equiprobable locations for 50 ms, followed by black screen for 500 ms, followed by an estimation response. Behavioral session trials (400 in total) always required this response. There was a variable ISI of 250–500 ms to the next Gabor. b) EEG session was similar to the behavioral session, except only 5% of the trials (3600 in total) required a response. Most of the time it was a 50 ms Gabor presentation with an ISI of 250–500 ms. c) Orientation probability distribution. In two locations orientations occurred in one quadrant four times more likely (high-probability: blue) than in the other (low-probability: red). The orientation probability was reversed in the other two locations. This location-orientation conjunction was counterbalanced across participants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detected. This was set-up so that all stimulus locations were always presented in roughly the same peripheral location retino-topically, and presumably involved a consistent pool of V1 neurons.

In the 2nd session, a BioSemi Active II system (64 channel) was used for the EEG recording. The electrode cap was placed according to the International 10–20 placement system. Additional electrodes were placed on the lateral side of each eye, inferior to each eye, and on each mastoid. EEG recording was done at 1024 Hz.

Participants sat approximately 60 cm from a 32 cm × 24 cm gamma-corrected CRT monitor that refreshed at 85 Hz (*mean* refresh time = 11.8 ms, *SD* = 0.5 ms). Prior to the task, participants were instructed to make their estimations of the Gabor orientations as accurately as they could. They were *not* told that they needed to be fast. Responses were made with a computer keyboard using their dominant hand.

2.4. Procedure

In the behavioral session (Fig. 1a), every trial consisted of a Gabor flash and a response. Participants were first given 20 practice trials in which the orientations occurred uniformly in orientation. These data were not included in the analyses. The behavioral session had 400 probability-manipulated trials, which were sectioned into two blocks with a break in-between. Drift corrections were done every 20 trials (approx. 1–2 min), and an eyetracker re-calibration was done after the break. This session took approximately 30 min.

In the EEG session (Fig. 1b), there were 60 practice trials with uniform orientations. This was followed by 3600 actual trials, which were sectioned into three blocks with breaks in-between. For this session, responses were required on only 5% of the trials (i.e. randomly chosen out of every 20-trial segment). This was done to maximize the number of stimulus presentations (and corresponding evoked potentials), and also to maintain parity with the Di Russo et al. (2002) study, where infrequent detection responses were required. Drift corrections were done after every 6th response (approx. 2–3 min), and an eyetracker re-calibration was done after each break. At the end of the main task, participants were given a short questionnaire to examine whether they could explicitly report the probability distribution of the orientations. While the whole session lasted approximately two hours, the experimental task only took approximately 50–60 min, the rest of the time taken for electrode placement/removal.

Each spatial Gabor flashed for approximately 50 ms (4 screen refreshes). If there was no response required, the next Gabor appeared between 250 and 500 ms after (contingent on participants' fixation still being centred). On response trials, following a 500 ms delay, a response line was drawn in the same spatial location as the last Gabor that had appeared. Participants made their estimations by rotating this line counter-clockwise or clockwise by pressing "Z" or "C" on a QWERTY keyboard. This rotation was at a maximum of 1 angular degree per frame refresh of the monitor. Participants pressed the "X" key to confirm their estimations. Once confirmed, the auditory feedback was given. On practice trials, a white feedback line with the actual orientation was displayed on top of the participant's response. This visual feedback was not given during the main trials. This response procedure was the same as Jabar and Anderson (2015).

2.5. Analysis

Behavioral and eye data were analyzed using the *R* statistical software package (*R* Development Core, 2016). EEG data was processed using EEGLAB (Delorme & Makeig, 2004). Angular errors for each response trial were calculated as the difference between the Gabor orientation and the orientation of the participants' estimates. Possible angular errors ranged from −90 (anti-clockwise error) to +90 (clockwise error) degrees. Due to the axial (half circular) nature of orientations, a +91 degree error wraps back as a −89 degree error. To look at the median error made, statistics were run on the *absolute values* of the estimation errors. Reaction time (RT) for each trial was taken as the time from when the response line appeared to when the orientation was confirmed. Time taken to initiate movement (IT), time taken to make movements after initiation (MT), initial rotation direction and number of direction switches (vacillations) per trial were also recorded. The analyses reported used the median across trials (timings are positively skewed), although using the mean gave the same results.

EEG recordings used a linked-mastoid reference, and a 50 ms window surrounding the onset of the stimulus (mean of −25 ms to 25 ms) was taken as the baseline voltage. Noisy electrodes, where the z-scored kurtosis across trials was 5 SD or greater (where most of the variance in the signal was the result of random large deviations), were removed and replaced by interpolation. Blink-contaminated trials were removed from analysis, as were trials where the electrode data where the average voltage was greater than the mean +/−2.5 SD of all trials. For the reported EEG analyses a low pass filter of 80 Hz was used. There was some contamination at 85 Hz, likely due to the refresh of the CRT monitor, and this was removed by an additional notch filter (a 1 Hz high pass with a 30 Hz low pass filter was also done, and led to the same results, and as such they are not reported here). This pre-processing preserved 85% of the trials.

For the C1 ERP component, presumed to originate in V1, and therefore reflecting the anatomy of striate cortex, upper-field stimuli should show a negative deflection while lower-field stimuli should show a positive deflection (see Fig.4a here, and Figs. 5 and 6 in Di Russo et al., 2002). The electrode used for calculating C1 amplitude was the electrode showing the maximal (or minimal) amplitude of all the electrodes posterior to Cz, within the 50–150 ms post-stimulus window. This was determined separately for each participant and for each of the four stimulus locations. This was done prior to the separation of high and low-orientation probability trials. We then used the maximum amplitude of the trial-averaged waveform within that 50–150 ms time window to determine the C1 amplitude for each trial-type. P300 amplitudes were determined similarly, but constrained to parieto-central electrodes with a positive deflection within the post-stimulus window of 250–500 ms.

3. Results

We first report the behavioral probability effects seen in the first session. Following that, we report the behavioral effects in the second (EEG) session, and then the effects of orientation probability on visual-evoked potentials.

3.1. Behavioral session

There was a significant effect of probability on RT, with high-probability orientations (*M* = 2027 ms, *SD* = 356 ms) being confirmed faster than low-probability orientations (*M* = 2083 ms, *SD* = 381 ms), (*t*(19) = 2.27, *p* = 0.035). This RT effect could either be due to the time required to initiate movements (IT) or the time required to complete moving the dial once movement had started (MT). ITs were significantly affected by probability (Fig. 2a), with high-probability orientations (*M* = 746 ms, *SD* = 107 ms) initiated more quickly than low-probability orientations (*M* = 766 ms, *SD* = 112 ms), (*t*(19) = 4.57, *p* < 0.001). Of the 20 participants, 17 showed this effect (Fig. 2a). There was no effect on MT between
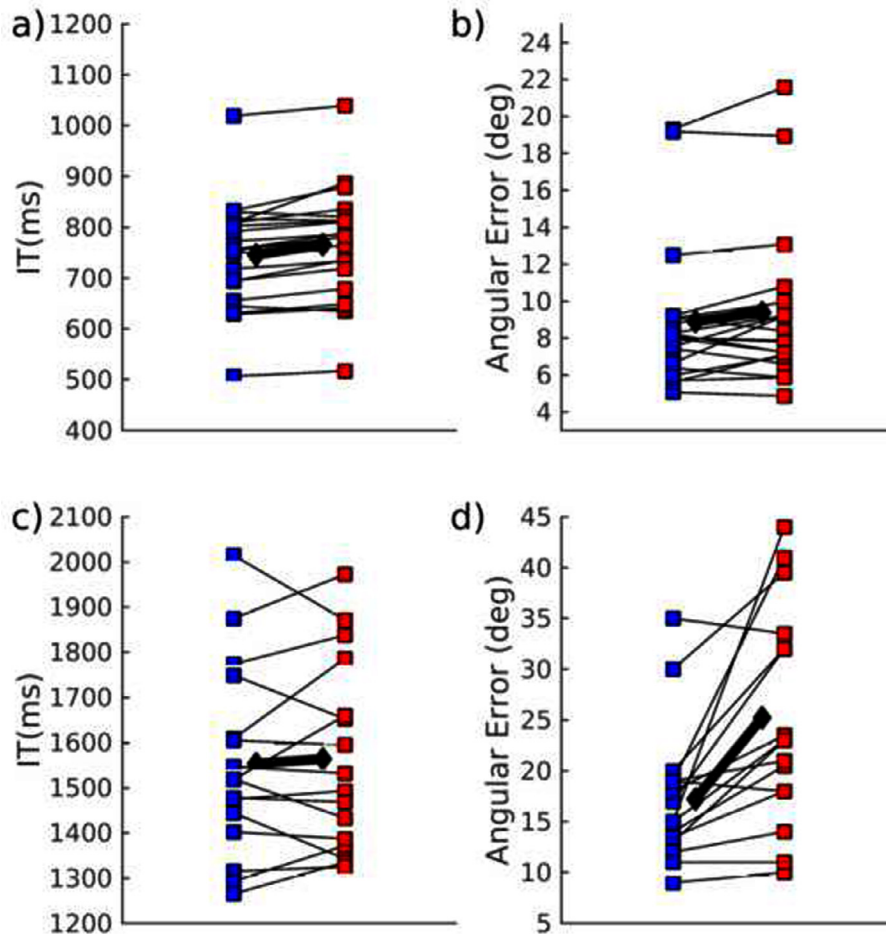
Fig. 2. Behavioural results. a) Initiation times in the first session across subjects (separate lines). The solid black line represents the mean across subjects. b) Median absolute angular errors in the first session. c) Initiation times in the second session. d) Median absolute angular errors in the second session. High-probability orientations: blue; low-probability ones: red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

high-probability ($M = 1281$ ms, $SD = 292$ ms) and low-probability orientations ($M = 1317$ ms, $SD = 318$ ms), ($t(19) = 1.56$, $p = 0.135$). Vacillations, that is the average number of direction switches participants made in their response in a trial, was also not significantly different between high-probability ($M = 0.11$, $SD = 0.08$) and low-probability tilts ($M = 0.13$, $SD = 0.10$), ($t(19) = 1.37$, $p = 0.187$).

For average (absolute) angular errors (Fig. 2b) participants showed smaller errors in the behavioral session when compared to the behaviour measured in the EEG task. For the behavioral session alone, there was a marginal effect of orientation probability on precision (Fig. 2b), with high-probability orientations ($M = 8.90$ deg, $SD = 3.91$ deg) being associated with smaller errors than low-probability orientations ($M = 9.39$ deg, $SD = 4.19$ deg), ($t(19) = 2.04$, $p = 0.055$).

3.2. Behavioral effects in the EEG session

Two participants' data was removed because of noisy EEG signals. These participants' data were left out from the behavioral analysis to show that the trends observed were due to the remaining 18 participants that contributed to the EEG data. Unlike in the 1st session, there were no demonstrable effect of orientation probability on any aspect of reaction time (all $ps > 0.05$). Of interest is that the ITs (Fig. 2c) for the high ($M = 1554$ ms, $SD = 199$ ms) and low-probability orientations ($M = 1564$ ms, $SD = 198$ ms) were significantly longer than in the behavioral session, (both $ps < 0.001$). This suggests that participants found the unpredictable, irregular

behavioral assessments in the EEG session to be more difficult than the consistent behavioral probes used in the 1st session. This is supported by the precision differences (Fig. 2d). Error magnitude was greater in the EEG session (both $ps < 0.05$) than in the 1st session. However, in the EEG session the benefit of probability on precision was significant with high-probability orientations ($M = 17.2$, $SD = 6.40$) being more precisely-estimated than low-probability orientations ($M = 25.2$, $SD = 10.24$), ($t(17) = 4.13$, $p < 0.001$), and 15/18 participants showing this direction of benefit.

Participants completed an open-ended post-experiment questionnaire after the second session. Two participants mentioned being aware of a probability manipulation, neither of whom described it accurately. One participant mentioned that things that looked like '/' were more likely (which was incorrect, because they did not note the location-contingency). When participants were directly asked whether they noticed that some orientations were more likely in certain locations, they expressed either surprise or confusion. This lack of explicit awareness was also seen in our previous studies.

3.3. Effects of orientation probability on early visual-evoked potentials

An overview of the electrode data and the visual-evoked potentials at each stimulus location is given in Fig. 3. The 'C1' component was identified based on a visual field location dependent phase reversal (Fig. 4a) that matched with the findings of Di Russo and colleagues (2002). Latencies were also comparable (Fig. 3;
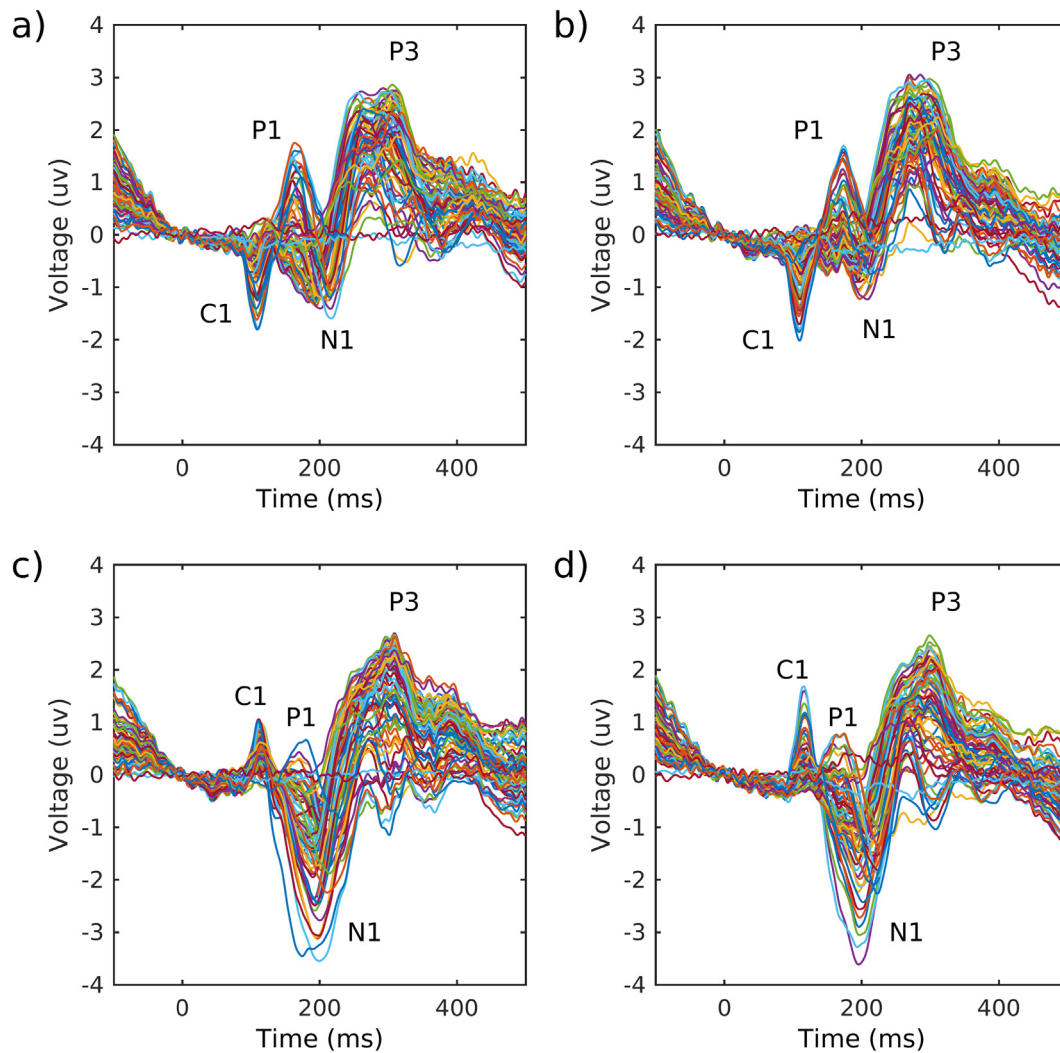
Fig. 3. Averaged waveforms across trials for each visual field. Lines indicate different electrodes. The top-left panel represents the top-left visual field, etc. Labels indicate where the components of interest are.

M = 109 ms) with that study, which is not surprising given the procedural similarities. Similar to the Di Russo et al. (2002) study, this component was maximally located at PO3/PO4, ipsilateral for the upper field stimuli and contralateral for the lower field stimuli (reflected in the topographies in Fig. 4a). This was mostly consistent across participants. Two participants demonstrated a slight shift in how far lateralized the target electrodes were, PO7/PO8 were the maximal electrodes instead of PO3/PO4. Two other participants showed a slightly more posterior distribution, O1/O2 instead of PO3/PO4.

Having replicated the key behavioral effects of orientation probability, we turn to the key issue of the effects of orientation probability on early perceptual processing. There was a significant effect of orientation probability on the C1 amplitude that was consistent across participants (Fig. 5b/c). The absolute amplitude of the C1 was significantly larger for the low-probability orientations than for the high probability orientations in *both* the upper-visual field stimuli (−2.95 vs. −2.35, $t(17)$ = 3.89, p = 0.001) and the lower-field stimuli (2.35 vs. 2.01, $t(17)$ = 3.84, p = 0.001).

Because there are four times as many high-probability trials as there were low-probability ones, sub-sampling was carried out to rule out the C1 effects as being simply due to differences in the volume of data. Because each participant only did 720 low probability trials across the four locations, in each run an equivalent number of high probability trials were randomly selected for comparison instead of the full 2880 trials. EEG analysis was otherwise the same as before (the same electrodes were used to measure the C1 amplitude, etc). This sampling was done 10,000 times and in most cases, there was a significant (p < 0.05) difference in amplitudes between high and low probability trials. For the upper field, the mean t-value across these comparison was 3.91 (SD = 0.72), with only 58 out of 10,000 cases failing the p < 0.05 cutoff. For the lower field, the mean t-value across this sub-sampling was 3.80 (SD = 0.77), with only 82 out of 10,000 cases failing the p < 0.05 cutoff.

3.4. Repetition suppression

To address the possibility of repetition suppression being a factor, repeats of high-probability orientations were examined. Trials of high-probability orientations that repeated, but at different locations, had the same C1 amplitudes as when high probability orientations repeated at the same visual field location (ps > 0.05). Furthermore, when stimuli that repeated locations and were of similar orientations (within 20 degrees) were removed from the analyses (approximately 10% of trials), the C1 probability-based modulation remained, and was significant, in both the upper and lower visual fields (ps < 0.001).
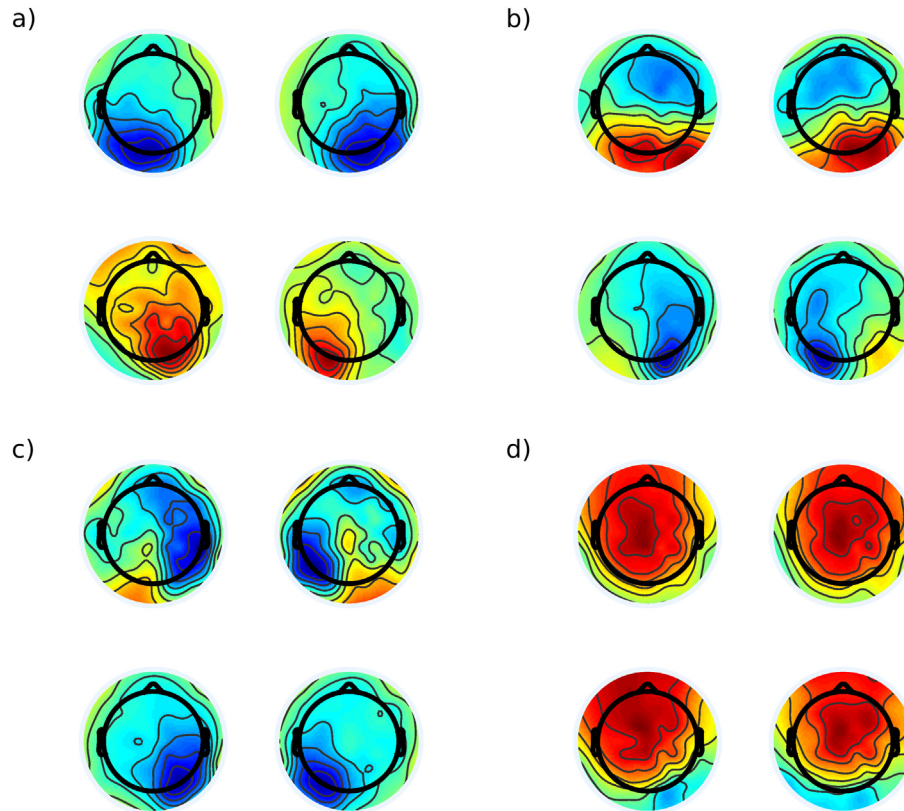
Fig. 4. Scalp topographies. a) C1 distribution. Because the visual field in which the stimuli appears affects the direction of the C1, depicted is the average topography at 109 ms post-stimulus at the corresponding location (top-left panel represents stimuli presented in the top-left, etc). b) P1 distribution at 165 ms. Note that for the P1 in the lower fields, the positive peak was occluded by the concurrent N1, see Fig. 3. c) N1 distribution at 200 ms. d) P300 distribution at 295 ms. Red = positive, blue = negative. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
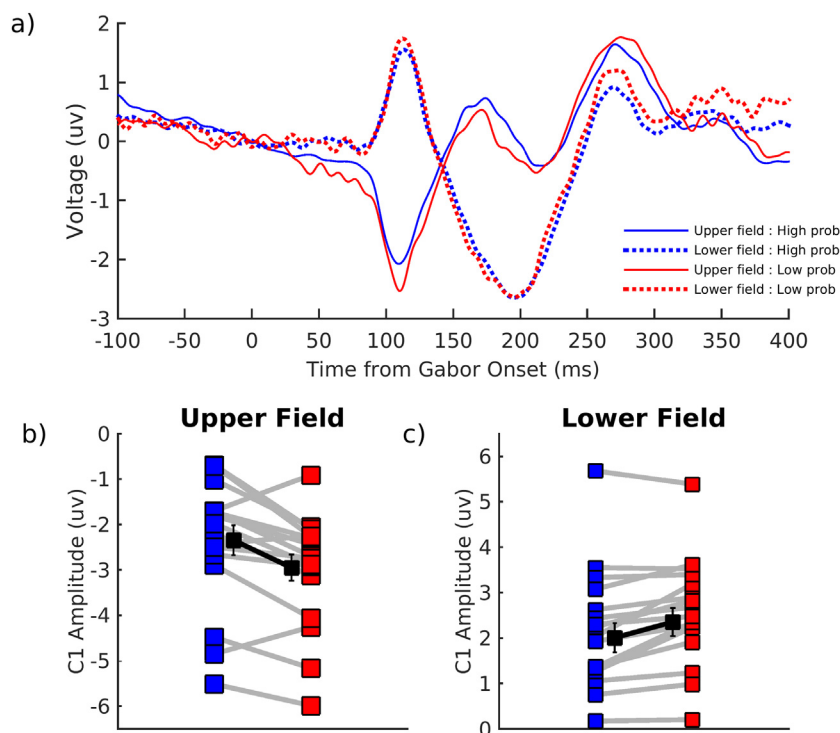
Fig. 5. C1 analysis. C1s were calculated at the posterior electrodes that showed the maximum deflection at the 50–150 ms time window, at each stimulus location. Left/right visual fields were collapsed. Deflections (at fig about 100 ms) are positive for upper-field stimuli (solid lines) and negative for lower-field stimuli (dotted lines), and split across high (blue) and low (red) probabilities. a) Average C1 wave across subjects. b) C1 amplitudes across subjects (separate lines) by probability, for upper-field stimuli. The solid line reflects the means across subjects. c) Same as previous panel, but for lower-field stimuli. C1 probability effects were consistent in both fields, with the amplitude of the low-probability trials being larger (direction is flipped due to the field-dependant nature of C1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Effects of orientation probability on P1 and N1

Because the P1 and N1 are modulated in spatial cuing tasks (e.g. Clark & Hillyard, 1996), we investigated whether our probability manipulations affected these 'attentional' components in the same way.

In our data, there was a positive peak for both upper/lower visual fields in the 140–180 ms time range (Figs. 3 & 4b). We looked at the electrodes showing maximal activity in this range, and found that this 'P1' was *not* significantly modulated by orientation probability in either the upper field (high: 1.17 vs. low: 2.19, $t(17) = 1.50$, $p = 0.152$) or the lower field (high: 1.38 vs. low: 1.65, $t(17) = 1.61$, $p = 0.125$). Removing 'repeats' did not change the outcome of the analyses. Also, note that the trend for the data is in the opposite direction to that found by Clark and Hillyard (1996) for attended stimuli.

A negative dip for both upper/lower visual fields occurred in the 170–230 ms time range (Figs. 3 & 4c). We looked at the electrodes showing maximal (negative) activity in this range, and found that this 'N1' was *not* significantly modulated by orientation probability in either the upper field (high: -1.09 vs. low: -0.58, $t(17) = 1.10$, $p = 0.288$) or the lower field (high: -0.93 vs. low: -1.02, $t(17) = 1.09$, $p = 0.293$). For neither the N1 (*mean* = 200 ms) nor the P1 (*mean* = 165 ms) was the peak latency modulated by orientation probability (all *ps* > 0.05).

3.6. Time course of the C1 effect

Since the probability effect has to be acquired during the exposure to the trials, we were interested in looking at how quickly the C1 effect might occur. The 3600 trials were separated into 6 bins of 600 trials. Each bin therefore had 120 low-probability trials, with 30 in each of the four locations. Left/right amplitudes were averaged to obtain the mean amplitude for the upper and lower visual fields. Paired t-tests revealed a significant C1 probability effect (high - low probability) for the 2nd to 6th bins for lower visual field and all bins for the upper visual field (*ps* < 0.05, see Fig. 6). The 1st bin in the lower field had a marginal probability effect, $t(17) = 1.92$, $p = 0.071$.

In the lower visual field, the C1 amplitudes for the low-probability trials was consistent and not significantly different across any bins (*ps* > 0.05). This was the same in the upper visual field as well, suggesting that C1 amplitudes relating to the low-probability events are unchanging. This was a different case for the high-probability trials. The C1 in the 1st bin for the lower field was significantly more positive (*M* = 2.47, *SD* = 0.80) than in the 2nd bin (*M* = 2.19, *SD* = 0.94), $t(17) = 2.52$, $p = 0.022$. There was no difference across the 2nd to 6th bins (all pairwise comparisons, *ps* > 0.05). This trend was repeated in the upper field, where the 1st bin had a significantly more negative C1 (*M* = -2.46, *SD* = 0.81) than the 2nd bin (*M* = -2.06, *SD* = 0.95), $t(17) = 4.49$, $p < 0.001$. Again, there was no difference across the 2nd to 6th bins (all pairwise comparisons, *ps* > 0.05).

3.7. Effects of orientation probability on P300

The P300 is a late parietocentral component (Figs. 3 & 4d) that shows a greater magnitude when targets are unexpected (Bledowski et al. 2004). We explored whether our orientation probability manipulation affected this component. We found that this late positive component was maximal over the Pz electrode for most participants. The effect of orientation probability on P300 magnitude was not significant for the upper visual field ($t(17) = 0.46$, $p = 0.649$), but was significant (Fig. 7c) for the lower visual field ($t(17) = 2.63$, $p = 0.018$), with low-probability orientations having the larger P300 (Low probability: *M* = 3.29,
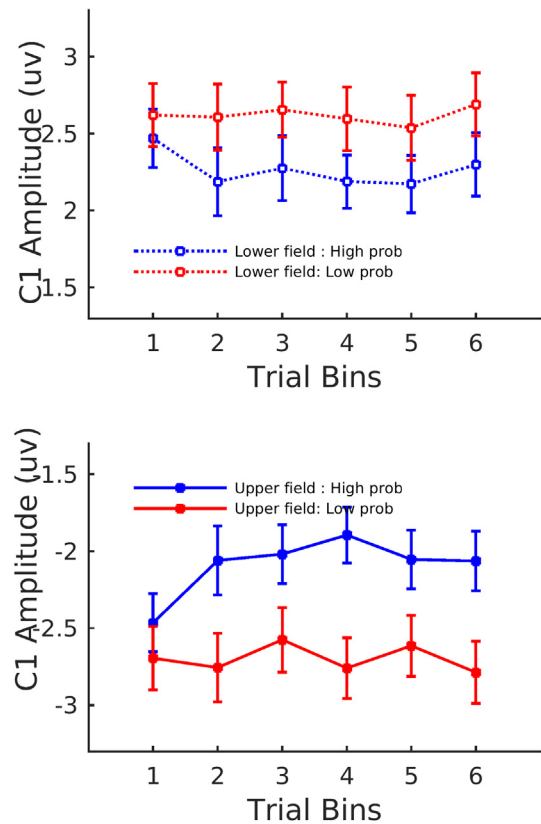
Fig. 6. Time course analysis. The 3600 trials each participant went through was segmented into 6 bins, and the average C1 evoked potential per condition for each bin was calculated. The top panel depicts the lower visual field, and the bottom panel depicts the upper visual field. High-probability = blue, low-probability shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

SD = 1.59; High probability: *M* = 2.96, *SD* = 1.69). There was no significant probability effect on (peak) latency (*M* = 295 ms) in either field (*ps* > 0.05).

We also examined if C1 and P300 amplitudes were related. The data presented in Fig. 5b/c and 7b/c were recast into a separate analysis, which revealed that the C1-P300 correlation was significant for *both* the upper ($r = -0.55$, $p < 0.001$) and lower visual fields ($r = 0.52$, $p = 0.001$). The direction of the correlation is reversed because the phase of the C1 reverses for lower and upper visual field stimulus presentations (Fig. 8).

4. Discussion

Probability effects were apparent in behaviour and were similar to the findings from our previous studies (Anderson, 2014; Jabar & Anderson, 2015, 2017a, 2017b). In the behavioral session, initiation times (IT) were consistently shorter for high-probability tilts. The probability effect on IT was probably not seen in the EEG session as that task was significantly harder with continuous rapid flashing of stimuli, and had unpredictable, irregular behavioral probes. Most likely the probability effect showed up more strongly in IT as compared to precision in the 1st session because, it being the easier task, participants managed to encode the stimulus fully in most instances. The time to fully encode was affected by probability in this case. Importantly though, there was a behavioral effect for trials in the EEG session with a clear probability effect on the angular errors: high-probability orientations were estimated more precisely.
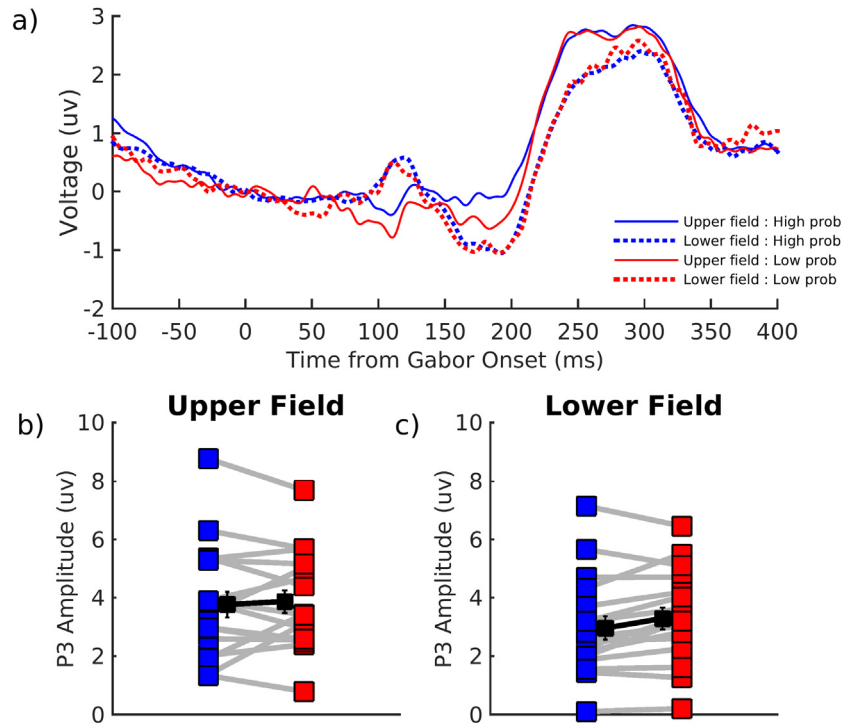
Fig. 7. P300 analysis. P300s were calculated at the parieto-central electrodes showing maximum deflection at the 300–500 ms time window, at each stimulus location. a) Average P300 wave across subjects for upper (solid) and lower-field (dotted) stimuli, across high (blue) and low (red) orientation probability. b) P300 amplitudes across subjects (separate lines) by probability, for upper-field stimuli. Sold line reflects the means across subjects. c) Same as previous panel, but for lower-field stimuli. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
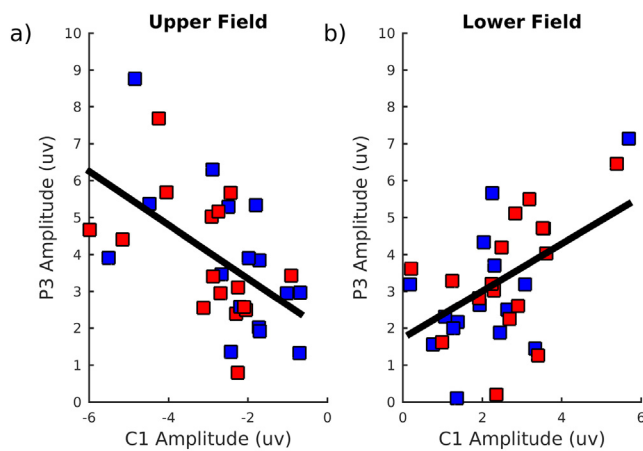
Fig. 8. C1-P300 correlations. Amplitudes shown in Figs. 5b/c and 7b/c were recast as scatter plots. Significant correlations were found in both the a) upper and b) lower visual fields. Note that directions are reversed due to C1 directions depending on the field location. High-probability = blue, low-probability shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To evaluate early visual processes as a locus of this benefit we focused on the 'C1' ERP component that has been source-localized to the primary visual cortex (Di Russo et al., 2002). In our study, we also found an early C1 component that was topographically centred on the posterior parietal/occipital scalp area. In addition to replicating Di Russo and colleagues' findings we also show that the C1 component is modulated by orientation probability: C1 amplitudes were *smaller* for the high-probability orientations as compared to the low-probability ones. Further, the time-course analysis (Fig. 6) would suggest that this effect is due to a

quick reduction in the C1 amplitudes for the high probability trials, detectable within about 600 trial exposures (approximately 7–8 min in-task), and possibly plateauing within about 1200 trial exposures. This matches data from previous studies (e.g. Jabar & Anderson, 2015) suggesting that perceptual effects due to probabilistic manipulations arise quickly.

The current study neither cued nor biased space. All locations were equiprobable but it was the *orientation-location conjunction* that was biased. Effects from this manipulation have been demonstrated to be distinct from spatial cuing (Jabar & Anderson, 2017a) and from spatial probability (Jabar & Anderson, 2017b). This is likely why the effects observed in this study are in contrast to those found with spatial attention, which either find no effect of spatial probability on C1 (Clark & Hillyard, 1996; Di Russo, Martinez, & Hillyard, 2003), or that the cued space has a greater C1 (Kelly et al., 2008).

One account of our orientation probability effects would be to regard them as a form of expectation or top-down attention. But if this account is adopted, then it would imply that attentional effects for features are based on neural tuning (David et al., 2008; Ling et al., 2015; Paltoglou & Neri, 2012; Çukur et al., 2013), whereas feature-based attention has been suggested to involve *both* gain and tuning mechanisms (Ling, Liu, & Carrasco, 2009). While cuing of orientations do lead to reduced activity and sharper representations in V1 (Kok et al., 2012), attending to features has also been demonstrated to increase P1 ERPs (Zhang & Luck, 2009), which we do not find with our task.

As an alternative to a top-down feature-based attention account, we have previously hypothesized (Jabar & Anderson, 2015, 2017a, 2017b) that more frequent presentations of some orientations result in changes to the tuning widths of orientation-selective neurons in V1, similar to how orientation training in macaques leads to adaptive-tuning (e.g. Ringach et al., 1997), but on a much shorter time scale. While the source of the C1 potential

could be V2/V3 (Ales et al., 2010), it is known that both cuing of orientations (Kok et al., 2012) and perceptual training (Ringach et al., 1997; Schoups et al., 2001) affect V1, making that the more likely locus in our opinion. Perhaps this modulation in V1 is mediated by recurrent local connections such as are the basis for the learning and adaptation effects seen in the Teich and Qian (2003) computational model of V1. Probable stimuli could "train" neurons with the result that tuning curves sharpen. Sensory neural tuning would offer a dynamic mechanism for our adaptations to uncertain and statistically non-stationary environments (Yaeli & Meir, 2010). Such arguments have been also made before for the auditory domain (Dean, Harper, & McAlpine, 2005) and visual (retina) domains (Hosoya, Baccus, & Meister, 2005).

Although we think that the data from this study provides strong evidence for an early visual locus of the probability effect, it is possible that there might be other effects in addition to what we demonstrate here. Ghose, Yang, and Maunsell (2002), found that perceptual learning only produced weak reductions in V1 activity, and other studies, while confirming V1 effects for perceptual learning, have found V1 effects to be smaller than changes in V4 (e.g. Raiguel, Vogels, Mysore, & Orban 2006; Yang & Maunsell, 2004). It could be that V4 modulations are downstream effects from initial changes in V1. Alternatively, V4 involvement could be taken as evidence for top-down control which trickles down to V1. The presence of retinotopic transfer in perceptual learning tasks (Zhang et al., 2010; Hung & Seitz, 2014) supports a top-down account. Perhaps a combination of prolonged training and predictable stimuli enables participants to explicitly expect the stimuli, something which our participants in our probability task did not demonstrate a capability for.

Probability effects could also go beyond visual processing. The other component we looked at was the late parietocentral positive component, the 'P300', which traditionally has been studied in the context of oddball paradigms. Although the component has been more studied in the auditory domain (Polich, 1990; Sutton, Braren, Zubin, & John, 1965), it has also been linked to the detection of rare visual events. Source-modelling suggests a source of either parietal and inferior temporal cortices or the insula/frontal cortices, depending on the specific sub-component (P3a/P3b; Bledowski et al. 2004). Although one might therefore expect the P300 to be modulated by our probability manipulations, this effect was weak compared to the C1. One potential reason could be that P300s seem to be more susceptible to modulation when stimulus intervals are long (Strüber & Polich, 2002), and the ISIs in the current task were very short. It could also be that P300s are more clearly modulated by 'oddballs' which are not simply low-probability, but explicitly surprising events (Mars et al., 2008; Teigen & Keren, 2003). In our case, low-probability orientations were less frequent, but not necessarily "surprising".

Could repetition suppression or habituation be the explanation for probability effects on precision and C1 modulation? While it is generally true that more probable events will result in more repetitions, true repeats were rare in our study because there were four equiprobable target locations, and the high-probability orientations was counterbalanced across them. Across locations, a high-probability tilt of 45 degrees is as likely to be followed by a high-probability tilt of 135 degrees as being followed by another 45 degree tilt. Comparing high-probability orientations that repeated location to those that those did not revealed no differences between C1 amplitudes. This may be because trials of repeated high probability are usually different angles as the range of possible orientations for the high probability quadrant spans 90 degrees. Even when 'repeats' of similar orientations were left out of the analysis, there was still a significant probability-based modulation of the C1 component: In prior studies, when repeats were left out of the analyses, effects on perceptual precision still remain

(e.g. Jabar & Anderson, 2015). From an electrophysiological perspective, one would also think that if repetition-based habituation was the reason for the C1 differences, the same difference should be present in the P300 components (Ravden & Polich, 1998); however, the upper visual field P300s failed to show a difference between high and low probability orientations. We propose that the more likely explanation for orientation probability effect is the adaptive-tuning observed in prior primate long-term training studies (e.g. Ringach et al., 1997; Schoups et al., 2001; Yaeli & Meir, 2010).

What we have demonstrated is that probability effects are accompanied by processing changes in early visual cortices. We have not eliminated other processing levels as likewise being affected by stimulus probability. And with conditions as complex as acquired badminton experience affecting C1 amplitudes (Jin et al., 2010), it seems likely that probability effects are mediated at multiple levels all working to link neural tuning to decisions. Probabilistic information for features might tune relevant perceptual channels, which then affect decision-making (Eckstein, Peterson, Pham, & Droll, 2009).

Assuming that the P300 also reflects decision-making processes (Rohrbaugh et al., 1974; Wang, Zheng, Huang, & Sun, 2015), our finding of a C1-P300 correlation can link early perceptual modulation to later decision-making processes. Alternatively, the causal direction might be reversed: The C1 might be the result of a top-down modulation that acts across the experimental block (e.g. Zhang et al. 2015). However, ERP amplitudes are variable across individuals, and while this C1-P300 relation leads to interesting hypotheses, the current study is not able to test this idea, and it remains a topic for further exploration. At the very least, it should be clear that probability does affect early perception, and any mechanistic explanation of probability should take this into account.

References

Ales, J. M., Yates, J. L., & Norcia, A. M. (2010). V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *Neuroimage, 52*, 1401–1409.

Anderson, B. (2014). Probability and the changing shape of response distributions for orientation. *Journal of Vision, 14*(15), 1–11.

Anderson, B., & Druker, M. (2013). Attention improves perceptual quality. *Psychonomic Bulletin & Review, 20*, 120–127.

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *The Journal of Neuroscience, 30*, 15080–15084.

Bledowski, C., Prvulovic, D., Hoechstetter, K., Scherg, M., Wibral, M., Goebel, R., et al. (2004). Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging study. *The Journal of Neuroscience, 24*, 9353–9360.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research, 51*, 1484–1525.

Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *Journal of Cognitive Neuroscience, 8*, 387–402.

Çukur, T., Nishimoto, S., Huth, A. G., & Gallant, J. L. (2013). Attention during natural vision warps semantic representation across the human brain. *Nature Neuroscience, 16*, 763–770.

Cutrone, E. K., Heeger, D. J., & Carrasco, M. (2014). Attention enhances contrast appearance via increased input baseline of neural responses. *Journal of Vision, 14*, 16–19.

David, S. V., Hayden, B. Y., Mazer, J. A., & Gallant, J. L. (2008). Attention to stimulus features shifts spectral tuning of V4 neurons during natural vision. *Neuron, 59*, 509–521.

Dean, I., Harper, N. S., & McAlpine, D. (2005). Neural population coding of sound level adapts to stimulus statistics. *Nature Neuroscience, 8*, 1684–1689.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods, 134*, 9–21.

Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95–111.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 486–499.

Dykes, J. R., & Pascal, V. (1981). The effect of stimulus probability on the perceptual processing of letters. *Journal of Experimental Psychology: Human Perception and Performance, 7*, 528.

Eckstein, M. P., Peterson, M. F., Pham, B. T., & Droll, J. A. (2009). Statistical decision theory to relate neurons to behavior in the study of covert visual attention. *Vision Research, 49*, 1097–1128.

Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology, 87*, 1867–1888.

Gratton, G. (1997). Attention and probability effects in the human occipital cortex: An optical imaging study. *NeuroReport, 8*, 1749–1753.

Gilbert, C. D. (1994). Early perceptual learning. *Proceedings of the National Academy of Sciences, 91*, 1195–1197.

Gonzalez, C. M. G., Clark, V. P., Fan, S., Luck, S. J., & Hillyard, S. A. (1994). Sources of attention-sensitive visual event-related potentials. *Brain Topography, 7*, 41–51.

Hon, N., Yap, M. J., & Jabar, S. B. (2013). The trajectory of the target probability effect. *Attention, Perception, & Psychophysics, 75*, 661–666.

Hosoya, T., Baccus, S. A., & Meister, M. (2005). Dynamic predictive coding by the retina. *Nature, 436*, 71–77.

Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience, 34*, 8423–8431.

Jabar, S. B., & Anderson, B. (2015). Probability shapes perceptual precision: A study in orientation estimation. *Journal of Experimental Psychology: Human Perception and Performance, 41*, 1666–1679.

Jabar, S. B., & Anderson, B. (2017a). Orientation probability and spatial exogenous cuing improve perceptual precision and response speed by different mechanisms. *Frontiers in Psychology, 8*, 183.

Jabar, S. B., & Anderson, B. (2017b). Not all probabilities are equivalent: Evidence from orientation versus spatial probability learning. *Journal of Experimental Psychology: Human Perception and Performance, 43*, 853–867.

Jin, H., Xu, G., Zhang, J. X., Ye, Z., Wang, S., Zhao, L., et al. (2010). Athletic training in badminton players modulates the early C1 component of visual evoked potentials: A preliminary investigation. *International Journal of Psychophysiology, 78*, 308–314.

Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2008). Spatial attention modulates initial afferent activity in human. *Cerebral Cortex, 18*, 2629–2636.

Kelly, S. P., Schroeder, C. E., & Lalor, E. C. (2013). What does polarity inversion of extrastriate activity tell us about striate contributions to the early VEP? A comment on Ales et al. (2010). *Neuroimage, 76*, 442–445.

Kok, P., Jehee, J. F., & de Lange, F. P. (2012). Less is more: expectation sharpens representations in the primary visual cortex. *Neuron, 75*, 265–270.

Laberge, D., & Tweedy, J. R. (1964). Presentation probability and choice time. *Journal of Experimental Psychology, 68*, 477–481.

Ling, S., Jehee, J. F., & Pestilli, F. (2015). A review of the mechanisms by which attentional feedback shapes visual selectivity. *Brain Structure and Function, 220*, 1237–1250.

Ling, S., Liu, T., & Carrasco, M. (2009). How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Research, 49*, 1194–1204.

Mars, R. B., Debener, S., Gladwin, T. E., Harrison, L. M., Haggard, P., Rothwell, J. C., et al. (2008). Trial-by-trial fluctuations in the event-related electroencephalogram reflect dynamic changes in the degree of surprise. *The Journal of Neuroscience, 28*, 12539–12545.

Miller, J. O., & Pachella, R. G. (1973). Locus of the stimulus probability effect. *Journal of Experimental Psychology, 101*, 227–231.

Paltoglou, A. E., & Neri, P. (2012). Attentional control of sensory tuning in human visual perception. *Journal of Neurophysiology, 107*, 1260–1274.

Peirce, J. W. (2009). Generating stimuli for neuroscience using psychopy. *Frontiers in Neuroinformatics, 2*, 1–8.

Polich, J. (1990). P300, probability, and interstimulus interval. *Psychophysiology, 27*, 396–403.

Pourtois, G., Rauss, K. S., Vuilleumier, P., & Schwartz, S. (2008). Effects of perceptual learning on primary visual cortex activity in humans. *Vision Research, 48*, 55–62.

Core Team, R. (2016). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. URL http://www.R-project.org/.

Raiguel, S., Vogels, R., Mysore, S. G., & Orban, G. A. (2006). Learning to see the difference specifically alters the most informative V4 neurons. *The Journal of Neuroscience, 26*, 6589–6602.

Rauss, K., Schwartz, S., & Pourtois, G. (2011). Top-down effects on early visual processing in humans: A predictive coding framework. *Neuroscience & Biobehavioral Reviews, 35*, 1237–1253.

Ravden, D., & Polich, J. (1998). Habituation of P300 from visual stimuli. *International Journal of Psychophysiology, 30*, 359–365.

Rich, A. N., Kunar, M. A., Van Wert, M. J., Hidalgo-Sotelo, B., Horowitz, T. S., & Wolfe, J. M. (2008). Why do we miss rare targets? Exploring the boundaries of the low prevalence effect. *Journal of Vision, 8*, 11–17.

Ringach, D. L., Hawken, M. J., & Shapley, R. (1997). Dynamics of orientation tuning in macaque primary visual cortex. *Nature, 387*, 281–284.

Rohrbaugh, J. W., Donchin, E., & Eriksen, C. W. (1974). Decision making and the P300 component of the cortical evoked response. *Perception & Psychophysics, 15*, 368–374.

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature, 412*, 549–553.

Strüber, D., & Polich, J. (2002). P300 and slow wave from oddball and single-stimulus visual tasks: Inter-stimulus interval effects. *International Journal of Psychophysiology, 45*, 187–196.

Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences, 13*, 403–409.

Sutton, S., Braren, M., Zubin, J., & John, E. R. (1965). Evoked-potential correlates of stimulus uncertainty. *Science, 150*, 1187–1188.

Teich, A. F., & Qian, N. (2003). Learning and adaptation in a recurrent model of V1 orientation selectivity. *Journal of Neurophysiology, 89*, 2086–2100.

Teigen, K. H., & Keren, G. (2003). Surprises: Low probabilities or high contrasts? *Cognition, 87*, 55–71.

Wang, L., Zheng, J., Huang, S., & Sun, H. (2015). P300 and decision making under risk and ambiguity. *Computational Intelligence and Neuroscience*. e108417.

Wolfe, J. M., Horowitz, T. S., Van Wert, M. J., Kenner, N. M., Place, S. S., & Kibbi, N. (2007). Low target prevalence is a stubborn source of errors in visual search tasks. *Journal of Experimental Psychology: General, 136*, 623.

Wolfe, J. M., & Van Wert, M. J. (2010). Varying target prevalence reveals two dissociable decision criteria in visual search. *Current Biology, 20*, 121–124.

Yaeli, S., & Meir, R. (2010). Error-based analysis of optimal tuning functions explains phenomena observed in sensory neurons. *Frontiers in Computational Neuroscience, 4*, 130.

Yang, T., & Maunsell, J. H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience, 24*, 1617–1626.

Zhang, G. L., Li, H., Song, Y., & Yu, C. (2015). ERP C1 is top-down modulated by orientation perceptual learning. *Journal of Vision, 15*, 8–10.

Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience, 12*, 24–25.

Zhang, T., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research, 50*, 368–374.