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Learning to discriminate the eye-of-origin during continuous flash suppression

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Abstract

Helmholtz asked whether one could discriminate which eye is the origin of one's perception merely based on the retinal signals. Studies to date showed that participants' ability to tell the eye-of-origin most likely depends on contextual cues. Nevertheless, it has been shown that exogenous attention can enhance performance for monocularly presented stimuli. We questioned whether adults can be trained to discriminate the eye-of-origin of their perceptions and if this ability depends on the strength of the monocular channels. We used attentional feed-forward training to improve the subject's eye-of-origin discrimination performance with voluntary attention. During training, participants received a binocular cue to inform them of the eye-of-origin of an upcoming target. Using continuous flash suppression, we also measured the signal strength of the monocular targets to see any possible modulations related to the cues. We collected confidence ratings from the participants about their eye-of-origin judgements to study in further detail whether metacognition has access to this information. Our results show that, even though voluntary attention did not alter the strength of the monocular channels, eye-of-origin discrimination performance improved following the training. A similar pattern was observed for confidence. The results from the feedforward attentional training and the increase in subjective confidence point towards a high-level decisional mechanism being responsible for the eye-of-origin judgements. We propose that this high-level process is informed by subtle sensory cues such as the differences in luminance or contrast in the two monocular channels.

KEYWORDS

attention, binocular vision, confidence, metacognition, utrocular discrimination

List of abbreviations: AIC, Akaike Information Criterion; b-CFS, breaking Continuous Flash Suppression; CFS, Continuous Flash Suppression; Cpd, cycles per degree; CR, Confidence Rating; RT, Reaction Time; Sd, standard deviation; UD, Utrocular Discrimination.

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1 | INTRODUCTION

Binocular vision is an essential part of visual perception, and the vast majority of neurons encoding visual information represent binocular information (Casagrande & Boyd, 1996; Hubel & Wiesel, 1968). However, at the very early stages of visual processing, monocular information is kept segregated in different channels: subcortical neurons (forming the pathways from the retinae to the primary visual cortex) respond only to the stimulation of a single eye (Casagrande & Boyd, 1996; Hubel & Wiesel, 1962 but see Maier et al., 2022 for a re-evaluation). Binocular integration begins at the level of the primary visual cortex (V1), where monocular neurons are organized in ocular dominance columns in layer IV and project to binocular neurons in layer III (Casagrande & Boyd, 1996; Hubel & Wiesel, 1968). Neurons from V1 layer III project to higher-order visual areas, so that, ascending the hierarchy, visual representations are binocular (Casagrande & Boyd, 1996). Hence, V1 is the last neural stage where information about eye-of-origin is preserved.

Intuitively, there is no obvious functional interest in keeping a trace of the eye-of-origin information for a given sensory signal once past the integration stage: most, if not all, of our everyday vision involves both eyes. However, if given the chance, would an observer be able to infer the eye-of-origin of a monocularly presented visual stimulus? This suggested ability to identify the eye-of-origin of a stimulus is called utrocular discrimination (Smith, 1945). A handful of studies on this topic suggest that on average people are unable to perform this task in various settings (Choe & Kim, 2022; Smith, 1945; Templeton & Green, 1968), contradicting studies (Blake & Cormack, 1979b; Enoch et al., 1969) are criticized to have external cues aiding people in their judgements (Barbeito et al., 1985; Ono & Barbeito, 1985). But can the ability to discriminate the eye-of-origin be trained? There are only a few studies to this day showing that under specific circumstances, feedback training, but not mere repetition, can improve the participants' accuracy on the utrocular discrimination task (Porac & Coren, 1984, 1986), although some studies found no improvement with training (Blake & Cormack, 1979a; Templeton & Green, 1968).

Here we investigate the effect of feedforward attentional training (a binocular cue informing of the eye-of-origin that is valid only 75% of the time) on utrocular discrimination. Our study aimed to understand (1) whether voluntary attention-based training can improve utrocular discrimination abilities, (2) whether the objective utrocular discrimination ability is reflected in subjective confidence judgements and (3) whether any

potential improvement in this ability depends on the signal strength of the monocular channels.

To assess utrocular discrimination, we used a dichoptic stimulation paradigm known as continuous flash suppression (CFS, Tsuchiya & Koch, 2005). The advantage of CFS is that it induces a rather long and constant suppression of a static target visual stimulus presented to one eye by a flashed high-contrast Mondrian mask presented to the other eye. At each trial, participants were required to report the location of the target visual stimulus as soon as it emerged from interocular suppression (breaking the CFS paradigm) and to guess the eye-of-origin of the target grating. The time it takes for the target to become visible (i.e. break suppression by the mask) during CFS is indicative of the strength of the target stimulus and can be taken as a proxy for the strength of the monocular channel that treats the target (but see Gayet et al., 2014; Moors et al., 2017; Stein & Sterzer, 2014, for post-perceptual effects). To gain more insight into whether the utrocular discrimination judgements are available for high-level processing, we also collected confidence ratings.

Our results show that feedforward attentional cue training improves the accuracy of eye-of-origin judgements but does not modulate the processing at the monocular level. Nevertheless, the notable improvement in discrimination and the increase in confidence after training both suggest that the eye-of-origin information is recoverable by higher-level processes and is most likely an inference based on subtle sensory cues.

2 | MATERIALS AND METHODS

2.1 | Participants

Sixty-one adult volunteers (mean = 27.1 years, *sd* = 6.0, 15 Males), including two of the authors, participated in the experiment. All participants were screened with ETDRS charts and the Ishihara Color Perception test to ensure normal or corrected-to-normal eyesight and good colour vision. Eleven participants were excluded from the analyses: three participants were excluded because of poor binocular fusion during the task and three participants were excluded because of unusually long suppression times (> 10 sec). Due to a programming error, the confidence judgements from two participants were not recorded so they were excluded from further analysis. Three more participants were excluded due to a high number of incorrect target localization trials, nearing chance level performance, indicating that they did not perform the task as instructed. The data from the remaining 50 participants (mean = 26.5 years, *sd* = 5.1,

14 Males) was analysed: 30 in the trained group (mean = 26.3 years, sd = 5.6, 10 Males) and 20 in the control group (mean = 26.8, sd = 4.4, 4 Males).

2.2 | Apparatus and Stimuli

The experiment was conducted in a dark and quiet room. A PC (Alienware Aurora R8, Alienware Corporation, Miami, Florida, USA) equipped with an NVIDIA graphics card (GeForce RTX2080, Nvidia Corporation, Santa Clara, California, USA) was used to generate visual stimuli in Matlab (R2020b, The MathWorks Inc., Natick, MA) with Psychophysics Toolbox 3 (Brainard, 1997).

Visual stimuli were presented dichoptically through a custom-built mirror stereoscope. A chin rest placed 57 cm from the screen was used to stabilize the participants' heads. The visual stimuli consisted of a sinusoidal grating (size: 1.7° , cpd: 3) oriented 45° clockwise (target), presented either 0.85° above or below the fixation dot and high-contrast, coloured and dynamic Mondrian-circle patterns contained in a square frame (mask, size 3.5°). The mask was flashed continuously at 10 Hz to achieve suppression of the target. The stimuli were displayed on an LCD monitor (BenQ XL2420Z 1920×1080 pixels, 144 Hz refresh rate, Tapei, Taiwan) on a uniform grey background (luminance: 110 cd/m², CIE $x = 0.305$, $y = 0.332$) in the central vision with a central red fixation point and a common square white frame to facilitate dichoptic fusion (Figure 1). Responses were recorded through the computer keyboard.

2.3 | Experimental procedure

We employed a between-participants design with two experimental groups: a trained group and a control group. For both groups, the experiment started with a practice block of five trials. The main body of the experiment consisted of 3 experimental blocks, each consisting of 100 trials. Participants in the trained group performed baseline, training and test blocks whereas participants in the control group performed a middle block that was identical to baseline and test blocks instead of the training block. Baseline and training blocks were separated by a 5-minute break, while a maximum of 2 minutes was allowed as a break between training and test blocks. Each block lasted for about 15 minutes on average. At the end of the baseline and test blocks, participants were asked if they used a particular strategy to answer the eye-of-origin question. Additionally, at the end of the experiment, they were asked if they thought their performance improved in the last block.

2.3.1 | Baseline and test blocks

The practice block and the baseline and test blocks followed the same procedure (Figure 1a). In the control group, the middle block also had the same structure. Each trial started with an empty squared frame to allow dichoptic fusion. When they achieved fusion, participants triggered the start of the visual stimulation with a key-press, initiating the presentation of the target and the

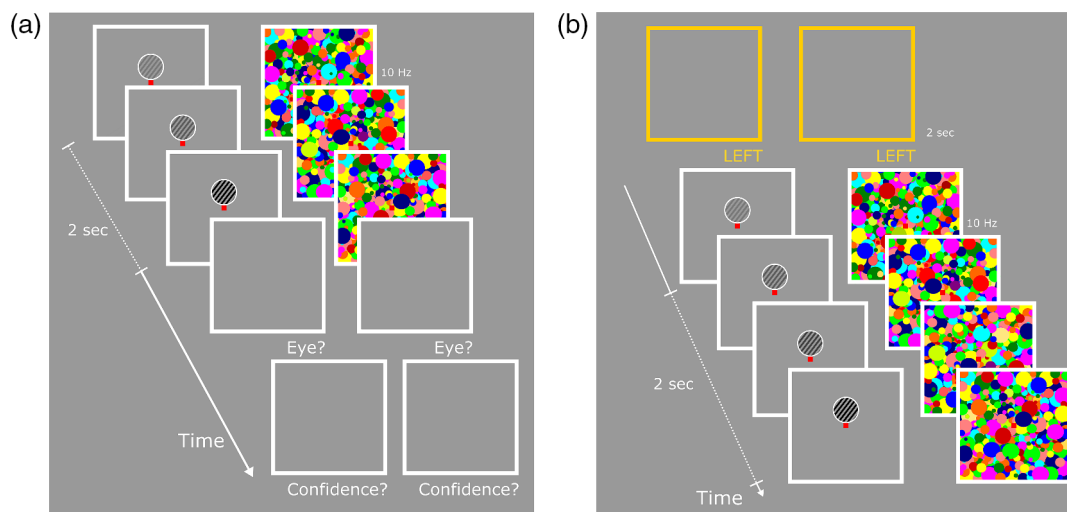


FIGURE 1 Experimental paradigm. (a) In the baseline and test blocks, participants saw a 10 Hz flashed Mondrian and a low contrast grating on each eye, including a red fixation dot in the middle of the frame, observed through a mirror stereoscope. The contrast of the grating was ramped up to 50% within 2 seconds. After the participants localized the grating, they answered two questions: "What is the eye-of-origin of the grating?" and "How confident are you in your answer?" (b) In the training block, participants first received a cue that was valid only 75% of the time, telling them which eye would be seeing the grating. They were then presented with the CFS stream and were instructed to localize the target grating as soon as they were able to see it.

mask on opposite eyes. They were instructed to report the location of the target via keypresses as soon as they saw it, even if only partially, i.e. when the target breaks suppression (target localization task). The target was presented either above (50% of trials) or below the central fixation point and participants used the up and down arrow keys accordingly to respond. The contrast of the target grating was ramped up linearly from 0% to 50% within the first 2 seconds in each trial to facilitate immediate suppression (Han et al., 2016; Tsuchiya & Koch, 2005). When participants did not press a key within the first 2 seconds, the target remained at 50% contrast until the keystroke. The physical locations (and therefore the eye of presentation) of the mask and the target on the screen were counterbalanced across trials.

After target localization, only the white frame was presented and the utrocular discrimination question (“Eye?”) appeared below it. Participants were asked to report the eye-of-origin for the target, i.e., which eye they thought was seeing the target, using left and right arrow keys corresponding to each eye (two-alternative forced choice, utrocular discrimination task). After this question, they were asked to rate their confidence level in their previous answer as 1 (guess at random), 2 (moderate confidence) or 3 (fairly high confidence). They had no time limitations or feedback for any of the questions.

2.3.2 | Training

Only the participants in the trained group performed this block. The training block was identical to the baseline and test blocks, with two exceptions. Firstly, at the beginning of each trial participants were presented with a cue (the word LEFT or RIGHT was written at the bottom right of the initial frame for 2 seconds) indicating the eye to which the target will be presented (Figure 1b). Secondly, there were no questions about the eye-of-origin or the confidence level. Cues were valid 75% of the time. Participants were instructed to orient their attention to the cued eye at the beginning of the block.

2.4 | Analyses

In all three experimental blocks, we recorded the suppression times (time from the beginning of the trial to the reported target perception). In the baseline and test blocks, we recorded the reaction times (time from the display of the utrocular discrimination question until participant response) for each trial along with the utrocular discrimination and confidence judgements. The recorded data were first preprocessed on Matlab (R2020b, The

MathWorks Inc., Natick, MA), and the statistical analyses were performed on R (R Core Team, 2023) using the lme4 package (Bates et al., 2015). The data from incorrect target localization trials (103 trials in total, 2.06 ± 2.57 trials per participant) were excluded from further analysis.

We used generalized linear mixed effects models to analyse our data. All models were built with a step-down approach where we aimed to maximize the random effects structure (Barr et al., 2013) without compromising model quality based on the Akaike information criterion (AIC), details reported below. For the model comparisons, the degrees of freedom and significance were estimated by likelihood ratio tests. Correlations were computed using Pearson’s correlation coefficient and *p*-values based on *t* statistics of Pearson’s product-moment correlation coefficient.

2.4.1 | Utrocular discrimination judgements

To understand the effect of training on utrocular discrimination (UD) judgements, we used a generalized linear mixed effects model in which we took into account the potential effects of group (trained or control), reaction times (RT, the time elapsed from the eye-of-origin question to eye-of-origin judgement) and confidence ratings (CR). This model was built to be informative of how the accuracy of utrocular discrimination judgements changes with training (from baseline to test block) and the participants’ level of confidence while taking the speed-accuracy trade-off into account. We centered the numerical variables by median and contrast-coded the categorical variables before entering them into the model. A generalized linear mixed effects model was preferred because of its capability to model binomial, imbalanced and repeated measures data. The full model was as follows:

$$\text{UD Accuracy} \sim (\text{Group} + \text{Block} + \text{CR} + \text{RT})^{\wedge 2} + (\text{RT} | \text{Participant})$$

where the family was specified as binomial with a logit link function and using the bobyqa optimizer. This model includes random intercepts and slopes. We included only two-way interactions between the fixed effects (symbol $\wedge 2$) to improve model convergence and interpretability.

To get parameter estimates for each fixed effect of interest, a reduced model where the fixed effect of interest is subtracted from the full model is compared to the full model.

For post hoc tests, we calculated the mean accuracy rate of each participant in the baseline and test blocks. Average accuracy in each of these blocks was tested

separately against the chance level (0.5) as well as against each other with a paired *t*-test (two-tailed, $\alpha = 0.05$) for each group separately. Multiple comparisons are corrected with the Holm-Bonferroni method.

2.4.2 | Confidence ratings

Once considered the contribution of confidence levels to the utrocular discrimination judgements and therefore evaluated the reliability of confidence judgements in the task, we performed an additional analysis to better understand the relationship between confidence ratings and accuracy. Specifically, we looked into the correlation between each participant's accuracy rate and confidence ratings in the baseline and test blocks separately.

2.4.3 | Reaction times

Reaction times were computed as the delay between the appearance of the eye-of-origin question and the response onset for each participant. The aforementioned generalized linear mixed effects model investigated the relationship between the reaction times and accuracy in the utrocular discrimination task.

2.4.4 | Suppression times

For each trial, the suppression time was defined as the time elapsed from the stimulus onset until the localization response of the participant, given that the localization task required the participants to see the target. For each participant, trials with suppression times lower than 500 ms or higher than mean + 4sd were also removed from the dataset to eliminate keypress errors and outlier suppression times (60 trials in total, 1.2 trials \pm 1.12 per participant).

To estimate the effect of cue validity on suppression times in the training block, we built a generalized linear mixed model. Because suppression time distributions are usually skewed (i.e. not Gaussian), we used a Gamma distribution, which adequately reflects the asymmetrical long tail usually observed in this type of data (Lo & Andrews, 2015; Palmer et al., 2011).

Our full model had the following structure:

$$\text{Suppression Time} \sim \text{Cue validity} + (\text{Cue validity}|\text{Participant})$$

where we adopted a Gamma distribution with a log link function. To get parameter estimates for the effect of

interest, a reduced model where cue validity is subtracted is compared to the full model.

We looked into how suppression times evolve across the experimental blocks in the trained group by using a generalized linear mixed effects model. The model had the following structure:

$$\text{Suppression Time} \sim \text{Block} + (1|\text{Participant})$$

where we adopted a Gamma distribution with a log link function. We did not include random slopes per block per participant in order to reveal overall differences across blocks. We compared this model to a reduced model where the fixed effect of the block was left out.

3 | RESULTS

We investigated the effect of attentional training on utrocular discrimination (the ability to discriminate the eye-of-origin) in a breaking continuous flash suppression (b-CFS) paradigm (Figure 1a) in a group of 50 adult volunteers. Attentional training consisted of a cueing paradigm (75% of valid cues), indicating the eye-of-origin of the following target stimulus (Figure 1b). The utrocular discrimination task was performed before (baseline block) and after (test block) a 100-trial training block in the trained group. The participants in the control group did not undergo training, instead, they had three blocks of the utrocular discrimination task. We looked into how group (trained or control), training (block: baseline or test), confidence level and reaction times influence utrocular discrimination accuracy while controlling for participant-level effects by fitting a generalized linear mixed effect model to our data.

We found a main effect of group ($\chi^2[5] = 81.336$, $p = 4.407e-16$, delta AIC = -71, Figure 2a), indicating a difference in the utrocular discrimination accuracy in the trained and control groups. We also found a main effect of block ($\chi^2[5] = 177.31$, $p < 2.2e-16$, delta AIC = -167, Figure 2a), showing a difference between baseline and test blocks. Importantly, the interaction of group and block was also significant ($\chi^2(1) = 54.572$, $p = 1.499e-13$, delta AIC = -52, Figure 2a), pointing towards a different relationship between block and accuracy in the two groups, as visualized in Figure 2. In line with speed-accuracy trade-off, there was a main effect of reaction times ($\chi^2[5] = 12.778$, $p = 0.025$, delta AIC = -2) on utrocular discrimination accuracy, further manifesting itself as an interaction between block and reaction time ($\chi^2(1) = 6.788$, $p = 0.0091$, delta AIC = -4), as the reaction times show an overall decrease in the test block. There was no interaction

between group and reaction times ($\chi^2(1) = 1.169$, $p = 0.2796$, delta AIC = -1), showing that all participants had similar influences of reaction time. Confidence also proved to have a significant effect in explaining accuracy ($\chi^2[8] = 43.193$, $p = 8.078e-07$, delta AIC = -27, Figure 3a). The interaction of confidence and group ($\chi^2(2) = 22.728$, $p = 1.161e-05$, delta AIC = -18,

Figure 3a) was significant whereas confidence and block ($\chi^2(2) = 5.196$, $p = 0.07$, delta AIC = -1, Figure 3a) remained non-significant, indicating a difference in confidence-accuracy relationship in the two groups. Reaction times did not show a significant interaction with confidence ($\chi^2(2) = 3.989$, $p = 0.136$, delta AIC = 0).

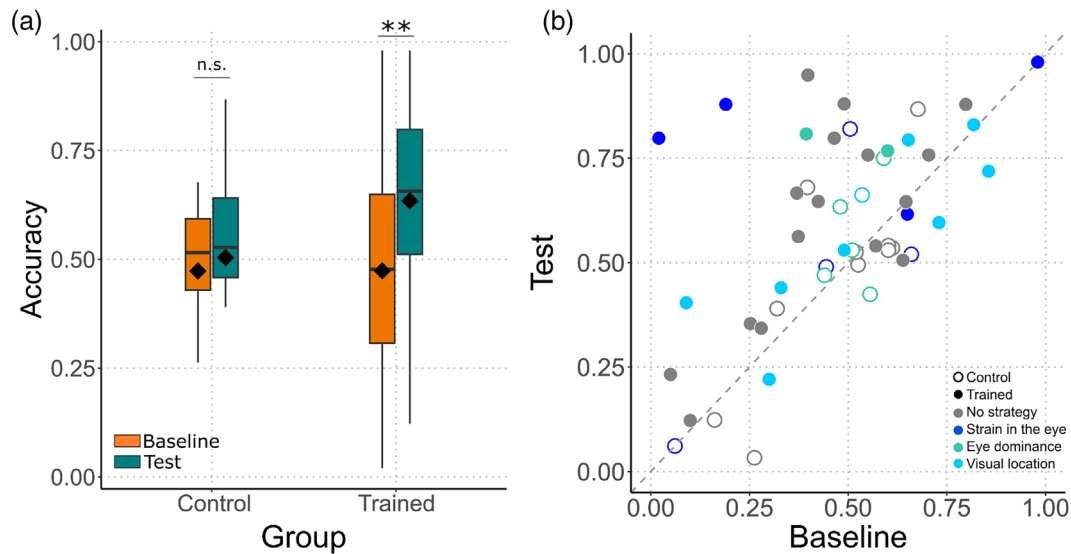


FIGURE 2 Results on utricular discrimination accuracy. (a) Utricular discrimination accuracy in baseline (orange) and test (dark cyan) blocks. The body of the box denotes the 25th to 75th percentiles. The whiskers cover minimum to maximum value range, excluding outliers. The dark grey line within the body is the median and the black diamond is the mean. ** denote $p < 0.01$. (b) Average accuracy for each participant in the baseline (x-axis) and test (y-axis) blocks. Filled symbols mark participants in the trained group whereas open symbols are for control participants. Participants who reported a strategy in utricular discrimination judgements are highlighted with different colours.

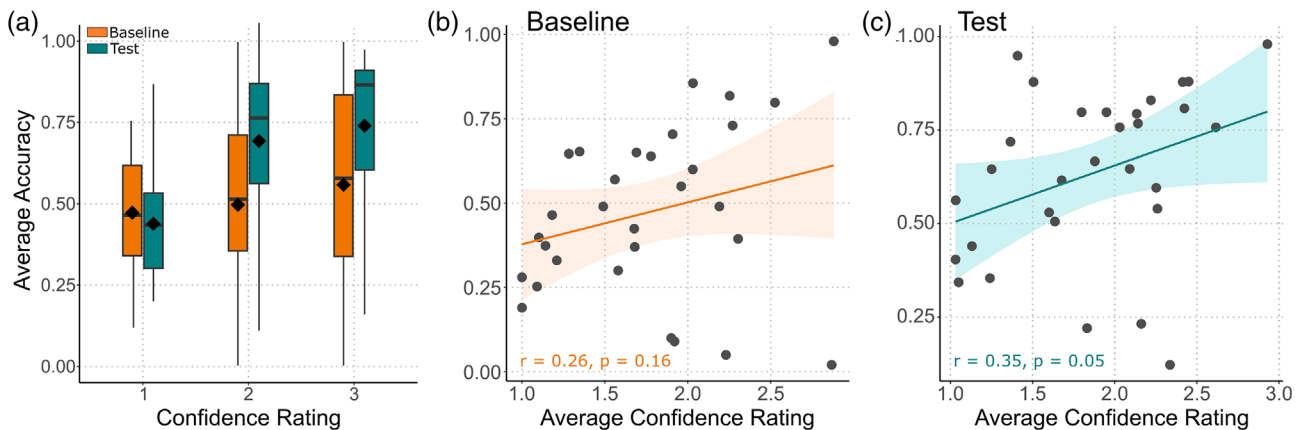


FIGURE 3 Results on confidence ratings in the trained group. (a) Mean accuracy in the utricular discrimination task in baseline (orange) and test (dark cyan) blocks, sorted according to confidence rating. The body of the box denotes the 25th to 75th percentiles. The whiskers cover minimum to maximum value range, excluding outliers. The dark grey line within the body is the median and the black diamond is the mean. The figure illustrates the group-level effect by grouping the trials according to confidence level, resulting in an uneven number of trials per participant and confidence level. We note that our generalized linear mixed-effects model analysis overcame this difficulty by considering trial-by-trial data points and individual participants as a random effect. (b) Correlation between average confidence rating and average accuracy per participant in the baseline block. (c) Correlation between average confidence rating and average accuracy per participant in the test block.

To verify the effect of training as an improvement in the eye-of-origin judgements, we computed the average accuracy in the blocks before and after training for the participants in the trained group. We found that, before training (baseline block) accuracy in the utrocular discrimination task did not differ from chance level (Mean accuracy = 0.47 ± 0.25 , $t[29] = -0.57$, $p = 0.57$, Cohen's $d = 0.10$, Figure 2a), indicating that, on average, observers were not able to discriminate the eye-of-origin of the target visual stimulus during CFS. However, after training (test block), the accuracy rate was significantly above the chance level (Mean accuracy = 0.63 ± 0.22 , $t[29] = 3.23$, $p = 0.003$, Cohen's $d = 0.59$, Figure 2a,c), showing a clear positive effect of training on utrocular discrimination judgements. Conversely, in the control group, the accuracy rates remain at chance level in both the baseline (Mean accuracy = 0.46 ± 0.16 , $t[19] = -0.86$, $p = 0.39$, Cohen's $d = 0.19$, Figure 2a) and the test (Mean accuracy = 0.48 ± 0.22 , $t[19] = -0.26$, $p = 0.79$, Cohen's $d = 0.06$, Figure 2a) blocks.

Participants were asked to report their response strategies for the utrocular discrimination at the end of each block. The overview of how various response strategies map onto task accuracy can be found in Figure 2b. The strain-in-the-eye cue stands out as leading to more correct responses together with eye dominance. Many participants tried to base their utrocular discrimination judgements on the knowledge of their dominant eye. However, this strategy did not prove reliable. We further looked into whether stronger eye dominance could lead to better utrocular discrimination accuracy. Specifically, we looked for a correlation between the average accuracy change from the baseline to the test block and the absolute difference in average suppression time between the right and left eye in the baseline block and found no correlation ($t = 0.88786$, $df = 28$, p -value = 0.3822, data not shown). Visual location (if the grating appears a little on the left or right from the centre) did not lead to a consistent performance among participants.

Some of the participants displayed either consistently low or consistently high performance already in the baseline block (Figure 2b). We reasoned that these participants were probably using some external cues to guide their utrocular discrimination judgements and hence were not exactly naive. To ensure that the effect of the training is not exclusively driven by these participants, we performed the previously explained analyses on a subset of our participants ($N = 39$), excluding the extreme performers (accuracy below 0.25 or above 0.75). The results from the subset of participants confirmed a main effect of group ($\chi^2[5] = 42.355$, $p = 4.992e-08$, delta AIC = -32.3) preserving the difference between the control and trained groups. The main effect of block ($\chi^2[5]$

= 69.034 , $p = 1.628e-13$, delta AIC = -159), as well as the interaction of group and block ($\chi^2(1) = 18.7$, $p = 1.53e-05$, delta AIC = -16.7), are still marked in this subset. We did not detect a main effect of reaction times ($\chi^2[5] = 7.628$, $p = 0.178$, delta AIC = 2.4), however, the interaction between reaction times and block was still detectable ($\chi^2(1) = 6.267$, $p = 0.0123$, delta AIC = -4.2), while the interaction of group and reaction time remained insignificant ($\chi^2(1) = 0.4192$, $p = 0.5173$, delta AIC = 1.6). The effect of confidence ($\chi^2[8] = 53.17$, $p = 9.996e-09$, delta AIC = -37.1) and the confidence-group interaction ($\chi^2(2) = 21.052$, $p = 2.683e-05$, delta AIC = -17) was also significant while the confidence-block ($\chi^2(2) = 4.3225$, $p = 0.1152$, delta AIC = -0.3) and confidence-reaction time ($\chi^2(2) = 0.0127$, $p = 0.9936$, delta AIC = 4) interactions remained insignificant.

The confidence-group interaction likely reflects that in the control group, as performance remained at a chance level, the participants were not able to give reliable confidence judgements. Whereas in the trained group, participants were able to form more informed confidence judgements in the test block. This is seen by the improvement in the confidence-accuracy relationship after training in the trained group: while before training confidence ratings did not correlate with utrocular discrimination accuracy across participants (Pearson's $r = 0.26$, $p = 0.16$, BF = 0.92, Figure 3b), after training, a trend towards correlation was observed ($r = 0.35$, $p = 0.05$, BF = 1.87, Figure 3c). The control group, on the other hand, did not show a correlation between confidence ratings and utrocular discrimination accuracy in the baseline (Pearson's $r = -0.20$, $p = 0.38$, BF = 0.64, data not shown) or the test block (Pearson's $r = -0.23$, $p = 0.31$, BF = 0.70, data not shown). We should note that a confidence-accuracy relationship at the group level informs only modestly on the actual metacognitive ability of the individual participants, as participants' average confidence ratings might be subject to biases (a participant could have low confidence on average, despite being good at discriminating between correct and wrong answers). For this reason, it is important to consider within-participants patterns instead.

No difference in suppression times between baseline (mean suppression time = 5.19, sd = 1.64) and test blocks (mean suppression time = 5.42, sd = 1.95) was observed ($t[49] = 0.48$, $p = 0.563$, Cohen's $d = 0.06$) in the b-CFS paradigm (Figure 4a). To investigate whether voluntary attention cued to one or the other eye could change the signal strength at the monocular level in the trained group, we looked into the effect of cue validity on suppression times in the training block using a generalized linear mixed effects model analysis. We did not find a main effect of cue validity ($\chi^2(1) = 0.011$, $p = 0.97$,

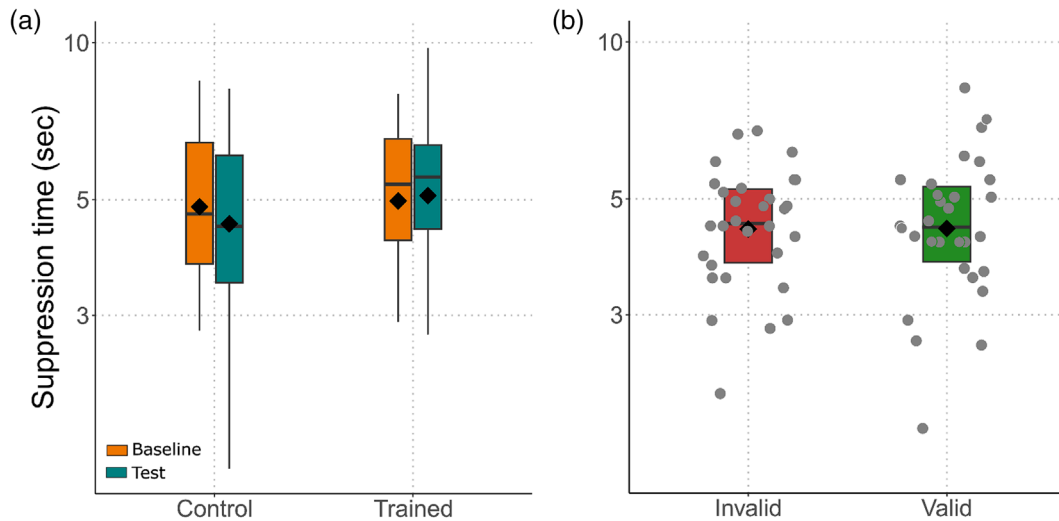


FIGURE 4 Results on suppression times. (a) Suppression times in baseline (orange) and test (dark cyan) blocks in the trained and control groups. The body of the box denotes the 25th to 75th percentiles. The whiskers cover minimum to maximum value range, excluding outliers. The dark grey line within the body is the median and the black diamond is the mean. (b) Suppression times for invalid (red) and valid (green) cue trials in the training block. Boxplot representations are the same as in (a), each point represents individual data.

delta AIC = 2, Figure 4b), suggesting that the training did not modulate the strength of monocular channels (mean suppression time = 4.87 [valid], 4.81 [invalid]; sd = 1.41 [valid], 1.14 [invalid]). Noticing that suppression times during the training have lower means, we looked into the effect of the block on suppression times in the trained group alone. Given the skewed distribution of suppression times, we opted for a generalized linear mixed effects model analysis. We found a main effect of block ($\chi^2(2) = 82.662$, $p = 2.2e-16$, delta AIC = -64). To further look into this effect, we performed paired t -tests to examine whether there are significant differences between the baseline, training and test blocks. The difference between baseline and training was insignificant ($t[29] = 1.32$, $p = 0.19$, Cohen's $d = 0.24$) while test block and training block showed a slight difference ($t[29] = 2.08$, $p = 0.04$, Cohen's $d = 0.38$), although this p -value did not survive the multiple comparisons (Bonferroni-Holm adjusted $p = 0.09$). This suggests that while there can be suppression time differences between blocks, the effects are not uniform across all blocks and participants.

4 | DISCUSSION

Our study investigated whether adults could be trained to discriminate the eye-of-origin of their perception and if so, whether this improvement is related to monocular signal strength. In addition, we examined if the participants had metacognitive access to their performance on the utrocular discrimination task by collecting confidence ratings. Our results show that feedforward voluntary

attentional training improves the accuracy of utrocular discrimination but does not change the signal strength at the monocular level. Furthermore, the effect of the training is most likely manifest in the higher-level decisional processes, as supported by participants' confidence ratings. Helmholtz proposed that our ability to discriminate the eye-of-origin of our visual perception, called utrocular discrimination, depends on external cues and learned interpretation rather than on an intrinsic distinction of the eye-of-origin label (von Helmholtz, 1962). Our results support Helmholtz's proposition that utrocular discrimination depends on learned interpretation rather than an intrinsic eye-of-origin label.

Previous studies have provided mixed results for utrocular discrimination performance at baseline (Blake & Cormack, 1979b; Enoch et al., 1969; Schwarzkopf et al., 2010; Smith, 1945; Templeton & Green, 1968) and the effect of feedback training (Blake & Cormack, 1979a; Porac & Coren, 1984, 1986). Attentional cueing paradigms for utrocular discrimination remain largely underexplored with only one study finding no improvement in target discrimination following an eye-of-origin cue without any tests on utrocular discrimination ability (Kimchi et al., 1995). A few studies investigated the interplay between attention and eye-of-origin information. One study found that visual search is impossible for a target solely defined by eye-of-origin, suggesting that attention cannot be voluntarily directed to a single eye (Wolfe & Franzel, 1988). However, Zhaoping (2008) showed that exogenous attention can nevertheless be directed to monocular channels: participants performed better when the target stimulus was an ocular singleton in a visual search

task. Later on, Zhang et al. (2012) showed that voluntarily attending to a monocular cue, without awareness of its eye-of-origin, actually strengthens the signals of other stimuli presented to the same eye. A recent study by Kim and Chong (2022) has found that a monocular cue to capture exogenous attention leads to performance improvements in an orientation discrimination task and subjective visual awareness rating. Although these studies propose a role for eye-based attention in improving performance, these results could be also explained by interocular divisive normalization, rather than eye-based attention, according to a model of interocular suppression proposed by Li et al. (2015).

In our training paradigm, we used a feedforward training method to incite our participants to direct their attention to a single eye. It has been shown that in bottom-up capture of attention, invalid cues lead to longer reaction times, showing a facilitating role of attention (Posner, 1980). Top-down attention leads to differences in reaction times in valid and invalid cues in a similar vein (Carrasco, 2011). We, therefore, used a binocular cue to avoid any bottom-up capture of attention and to focus on whether directing attention voluntarily to a single eye is possible. If the participants were able to orient their attention according to the cue they received, we would observe a difference in suppression times between valid and invalid cues, as an invalid cue would require orienting attention to the wrong eye and hence prolong suppression. This cue manipulation enabled us to see if the training operated on the monocular signal level. Our results, however, show no difference in suppression times due to voluntary attention. This could be interpreted as additional support for the lack of eye-based attention in interocular suppression. We observe, nevertheless, an improvement in utrocular discrimination performance following the training.

The lack of difference in suppression times between valid and invalid cues as well as before and after training suggests that the strength of the monocular channels is not the basis for the utrocular discrimination decision. Nevertheless, the improvement in accuracy demonstrates that the training has a positive influence on eye-of-origin judgements despite no feedback being provided during the baseline and test blocks. Our paradigm prompted the subjects to pay attention to their sensory states during training. Although they had no feedback on the accuracy of their eye-of-origin judgements otherwise, during training, they were 75% of the time provided with a valid cue informing them of the eye-of-origin. By paying close attention to differences in their sensations when the target was on their left vs. right eye, they showed a good improvement in their performances after training. Since there is no evidence that this improvement is a result of a modulation of the strength of monocular channels, we

suggest that the participants acquired a higher-level inferential skill such as the discrimination of subtle sensory differences between the two eyes, e.g., luminance, contrast and convergence. The cue provided at the beginning of each trial during the training block could have taken on the role of feedback, enforcing the discrimination in the sensory states of the participants, thereby facilitating learning. A 100% valid cue could have boosted learning, however, including 25% invalid trials was crucial in clarifying the role of attention on the monocular signal strength and its contribution to utrocular discrimination judgements. Using a subset of trials with invalid cues allowed us to rule out an imbalance in signal strength induced by voluntary attention and provided us with stronger evidence for contextual learning.

Further support for higher-level learning comes from the confidence ratings. The confidence ratings of the participants increased in line with their utrocular discrimination skills after the training. Previous work found metacognition to reflect certain fluctuations in accuracy following the orienting of attention (Denison et al., 2018; Recht et al., 2021, 2023). However, given that suppression times remained relatively immune to the validity of the attentional cue during training, it is likely that both discrimination ability and metacognition emerged from sensory heuristics built beyond the attentional state itself. Notably, despite often adequate trial-by-trial confidence judgements post-training, most participants were unable to report any deliberate strategy for their utrocular discrimination judgements and were unsure if their performances improved globally. This result fits nicely with a recent line of investigations considering how 'local' confidence relates to more 'global' estimates of performance over many trials (Lee et al., 2021; Rouault et al., 2019) and suggests some sort of dissociation between local and global confidence during utrocular discrimination.

If the participants did not gain explicit knowledge of their accuracy on the eye-of-origin judgements but got better regardless, then what could be the cue that was reinforced with the training? The literature on utrocular discrimination provides us with some candidates: visual location, strain-in-the-eye, luminance difference and eye dominance (Ono & Barbeito, 1985). We asked each of our participants to report if they based their judgements consistently on any characteristics of the stimuli or their own sensations. Nine participants reported using visual location, eight participants expressed strain-in-one-eye and seven others based their judgements on the inferences from their eye dominance (Figure 2b). Visual location, in our setting, was not a reliable cue. The visual location of the stimulus was dependent on the convergence point of the eyes and how well the mirrors of the stereoscope were aligned. Even though at the start of each trial we

ensured stable fusion by aligning the bars on the two frames projected to the two eyes, minor changes in convergence could still lead to a slight shift in position for the target grating (deviation to the left or right). However, since the visual location of the grating did not depend on the eye-of-origin but on the mirror angle and/or convergence, using this cue did not lead to consistently good performance.

Seven other participants used their knowledge of their dominant eye to infer that when the target broke suppression in a shorter amount of time, it was on their dominant eye. Figure 2b shows that, as it is not possible to accurately estimate the differences in suppression times in the order of milliseconds, this strategy proves inefficient in the baseline block. The two participants reporting this strategy in the trained group abandoned it after the training block and showed an improvement in their performance. Additional analysis looking into the relationship between the degree of eye dominance and utrocular discrimination accuracy further demonstrated that eye dominance does not serve as a cue for the eye-of-origin discrimination.

The remaining eight participants indicated that during dichoptic stimulation, they felt a strain in one of their eyes, i.e., one of the eyes felt “heavier”, or “more stimulated” than the other. These participants in the trained group, except for one of them, outperformed most other participants in the test block. In CFS, one eye is necessarily more stimulated than the other. It is therefore conceivable that participants who are susceptible to sensing this difference in stimulation will approximate ceiling performance in utrocular discrimination. Earlier studies on utrocular discrimination found better than chance level performance when a single eye was stimulated at a time (Blake & Cormack, 1979b; Enoch et al., 1969; Schwarzkopf et al., 2010; Smith, 1945). Additional studies finding better performance were also criticized for providing extraneous cues such as luminance differences (Barbeito et al., 1985; Ono & Barbeito, 1985; Templeton & Green, 1968). We argue that this strengthens the case that during training, participants are most likely implicitly learning subtle sensory cues such as differences in contrast, luminance or colour. In our experiments, participants were at chance level for the utrocular discrimination judgements at baseline and the control group did not improve with mere repetition. This result may argue against the luminance or stimulation differences being the main contributor to utrocular judgements. Our interpretation is that even if the participants do not have enough sensitivity to this discrepancy at the beginning, during the training they become sensitized to the differences in stimulation in their two eyes and therefore improve their eye-of-origin judgements.

A study by Baker (2017) shows that even though the subjects are unable to reliably report the eye-of-origin of their perception, this information is decodable from EEG activity. This shows that despite being lost to awareness in later stages of processing, the eye-of-origin information is embedded deeply enough in the cortical hierarchy so that the eye-of-origin signal is systematically decodable from brain activity. Baker (2017) further found that this decoding performance is not explained by eye dominance, a result supporting our analyses that stronger eye dominance does not lead to better utrocular discrimination. Another study by Schwarzkopf et al. (2010) found that overall activation in V1, measured by fMRI, is distinct for separate stimulation of the two eyes. The authors propose that this response difference can be a basis for inferring the eye-of-origin of a stimulus. Our paradigm stimulated both eyes at the same time, rendering the differences in activation a more complex cue due to interocular suppression. Song et al. (2024) propose that in interocular suppression, ocular opponency neurons receive inputs from monocular ones and fire when the excitatory drive of the fellow eye is larger than the other, and inhibit the other eye. This mechanism could provide a more elaborate measurement of activation differences between the two eyes. High-level processes, in theory, could be reading out this information and using it to make a utrocular discrimination judgement. Alternatively, Li et al. (2015) suggest an interocular division weight difference between the two eyes as one of the determining factors of interocular suppression. Although their model does not encompass continuous flash suppression, our findings fit this framework. As Li et al. (2015) proposed, we also did not find an eye-based attention effect in our experiment, despite an improvement in eye-of-origin judgements. By presenting both eyes with different stimuli and changing the target-eye and mask-eye on trials, the imbalance in stimulation and difference in the normalization weight could have led to a high-level learning in the readout of these resulting weights of the stimuli in interocular suppression and thus be associated to the eye-of-origin information during the training block. Our results emphasize the need for the involvement of high-level signals as the control group, despite having similar stimulation conditions, did not show an improvement in utrocular discrimination accuracy.

5 | CONCLUSION

Our results indicate that utrocular discrimination is indeed dependent on learned interpretation and advance the state of the art by showing that voluntary attention-based training can improve this ability. We show that the

improvement in this task does not necessarily depend on the strength of monocular channels. The results from the feedforward attentional training and the increase in confidence ratings point towards a high-level decisional mechanism being responsible for the eye-of-origin judgements. We propose that this high-level process is informed by subtle sensory cues such as the differences in luminance or contrast in the two monocular channels. The impact of the training duration on the effect or how long the effect lasts was not in the scope of our study but both these questions paved the way for future research. Further studies ensuring minimal differences in visual stimulation of the two eyes and no cues from the visual location can advance our understanding of what precisely contributes to the eye-of-origin judgements.

AUTHOR CONTRIBUTIONS

IDS: formal analysis, investigation, project administration, software, visualization, writing – original draft, writing – review & editing.

SR: conceptualization, methodology, project administration, formal analysis, software, visualization, writing – review & editing.

CL: conceptualization, funding acquisition, methodology, project administration, software, supervision, writing – review & editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.16373>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Open Science Framework at <https://doi.org/10.17605/OSF.IO/FN5QU>.

ETHICS STATEMENT

The local ethics committee (Comité d'éthique de la Recherche de l'université Paris Descartes, CER-PD:2019-16-LUNGHI) approved the experimental protocol and the study was conducted in accordance with the Declaration of Helsinki (DoH-Oct2008). Each participant gave

their written informed consent and received a financial compensation amounting to 10€ per hour.

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