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Reducing the size of the human physiological blind spot through training

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The physiological blind spot refers to a zone of functional blindness all normally sighted people have in each eye, due to an absence of photoreceptors where the optic nerve passes through the surface of the retina. Here we report that the functional size of the physiological blind spot can be shrunk through training to distinguish direction signals at the blind spot periphery. Training on twenty successive weekdays improved sensitivity to both direction and colour, suggesting a generalizable benefit. Training on one blind spot, however, did not transfer to the blind spot in the untrained eye, ruling out mediation via a generic practice effect; nor could training benefits be attributed to eye movements, which were monitored to ensure stable fixation. These data suggest that training enhances the response gains of neurons with receptive fields that partially overlap, or abut, the physiological blind spot, thereby enhancing sensitivity to weak signals originating primarily from within the functionally-defined region of blindness [1–3]. Our results have important implications for situations where localised blindness has been acquired through damage to components of the visual system [4,5], and support proposals that these situations might be improved through perceptual training [5–7].

We had 10 people train, for 20 consecutive weekdays, on a direction discrimination task concerning a drifting sinusoidal waveform presented in an annulus centered about the physiological blind spot in the stimulated eye (see Figure S1A and Supplemental Methods in the Supplemental Information for further details). Annulus size was manipulated according to an adaptive procedure to concentrate sampling at an annulus size promoting ~70% correct direction judgments. Prior to training participants completed baseline measures to map the location and extent of physiological blind spots in each eye (a perimetry task), in addition to measures of annulus size necessary to support ~75% correct task performance when discriminating either colour (red/green) or direction (left/right). Collectively, these measures were taken as functional estimates of the size of the physiological blind spot. Fixation was monitored on all experimental trials in all tasks via high-resolution eye tracking, and any trials with unstable fixation were excluded from analysis to ensure training benefits could not be attributed to eye movements (see Supplemental Methods for further details).

The results of a 3 (task – perimetry/motion/colour) x 2 (time – pre-training/post-training) repeated measures ANOVA test using data from the trained eye revealed a generalized reduction in the extent of the functionally-defined physiological blind spot. For these data, there was a main effect of time ($F_{1,9}$ = 20.54, p = 0.001), with larger blind spot estimates pre- (24 ± 1 dva^2) then post- (21 ± 1 dva^2) training. There was, however, no discernible interaction between time and task ($F_{2,18}$ = 1.52, p = 0.705); hence, these data suggest a generalized, statistically uniform, reduction in the extent of functionally defined blindness associated with the trained physiological blind spot. So training to discern direction of motion enhanced sensitivity to both colour and motion about the trained blind spot.

Apparent reductions in blind spot size could easily be explained if participants had either made more small eye-movements while supposedly fixating, or if they had fixated a position offset from the nominated fixation point post-training. Analyses of our data, however, revealed no relationship between training benefits and gaze changes — expressed either in terms of fixation instability (R^2 = 0.026; Figure S2A) or in terms of a gaze direction shift post-training (R^2 = 0.036 see Figure S2B). Data trends suggest greater reductions in blind spot size were associated with more precise and stable fixation — the opposite to that predicted if blind spot size reductions were due to eye movements. We stress, however, that there were no robust relationships between any eye movement metric and training benefits that could account for evident improvements post-training.

Further analyses suggested benefits were restricted to the trained eye. A 3 (task) x 2 (time) repeated measures ANOVA test of data from the untrained eye did not reveal a main effect of time ($F_{1,9}$ = 1.95, p = 0.196); hence, our data cannot be attributed to a generic practice effect that transferred to the untrained eye. Nor was there an interaction between time and task ($F_{2,18}$ = 0.64, p = 0.541), suggesting the lack of evident benefit in the untrained eye was not due to a subset of the three tasks failing to improve post-training.

To directly compare training benefits in the trained and untrained eyes, we calculated overall training benefit scores for each eye. These were given by post-training reductions in estimated physiological blind spot size averaged across each of our three tasks (perimetry, direction and colour discrimination). Analysis of these data revealed that training had resulted in a greater benefit in the trained (2.3 dva^2 ± 0.6) relative to the untrained eye (0.7 dva^2 ± 0.6; t_9 = 2.45, p = 0.037; Figure 1A, see also 1C,D). A final analysis suggested benefits in the trained eye manifested rapidly (Figure 1B). A one-phase decay function fit to functional estimates of the size of the physiological blind spot from direction judgments on sequential training days had a half-life of 2.64 training days, suggesting ~88% of the training benefit could be obtained after just 8 days of training.

Functional regions of blindness selectively shrunk through training in this study were caused by an absence of retinal photoreceptors. This dictates that the mechanism underlying improved performance must be an enhanced sensitivity to stimulation at the periphery of the physiological blind spots. Similar training could shrink regions of localized blindness acquired from

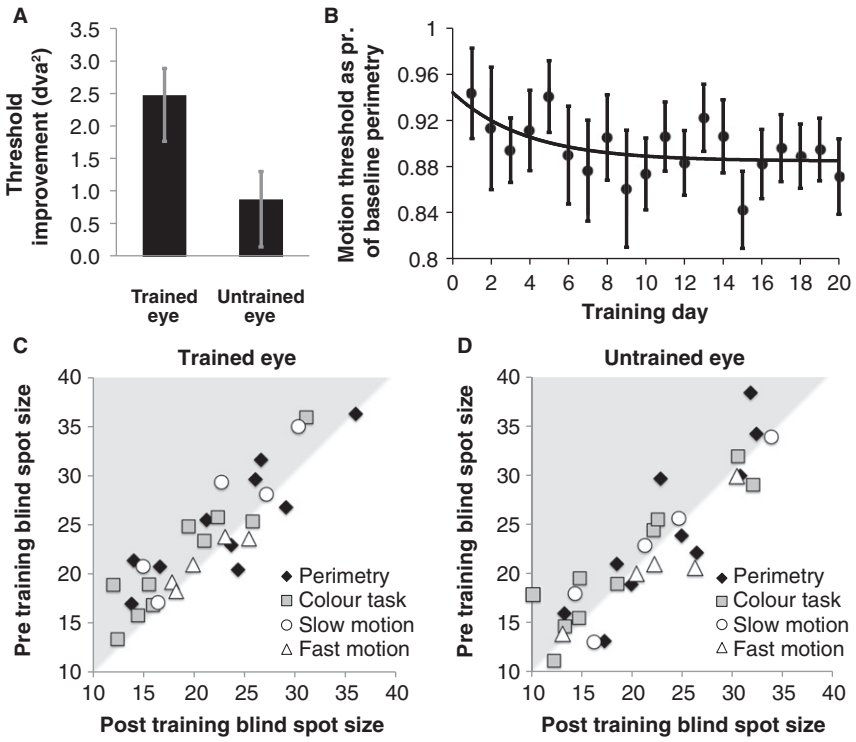

Figure 1. Experimental results.
(A) Reductions in estimates of functionally-defined physiological blind spots, averaged across experimental task (perimetry, motion discriminations and colour discriminations). Data are shown for trained and untrained eyes. (B) Estimates of size thresholds for annuli to support successful direction discriminations, expressed as a proportion of the perimetry determined baseline estimate of the size of the physiological blind spot. Data are expressed as a function of training day. There is an initial reduction in size threshold estimates as a function of training day, which asymptotes after ~10 days of training, as indicated by a best-fit single phase decay function. In both plots error bars depict +/- 1 SEM. (C) Blind spot size before and after training, for all participants in each of the three tasks, within the trained eye. Points falling in the shaded region of the graph represent a reduction in blind spot size after training. (D) As in C, but for the untrained eye.

damage to components of the human visual system. Conceptually, it should not matter if a region of blindness has been acquired through a pathological process, or if it exists due to the normal architecture of vision. The functionally defined region of blindness should be susceptible to shrinkage through training that enhances sensitivity to weak signals near or within the site of blindness.

Arguably, the scope for improved sensitivity from perceptual training might be greater in cases of acquired localised blindness, relative to the reductions about physiological blind spots that we have induced. This is likely due to the presence of residual, trainable architecture in cases of acquired localised blindness [1–3,8–10], which are absent at the optic disc.

Our data are ambiguous in terms of whether training benefits arise from mechanisms receiving monocular input from regions abutting the trained blind spot, or from binocularly activated mechanisms. To investigate this issue future experiments will need to assess sensitivity in the non-trained eye for input coinciding with the location of the trained blind spot. It is also worth noting that our participants were trained on one of two speeds, and data trends suggest the slower of the two was more efficacious — but this requires confirmation.

Overall, our data show that the extent of functional blindness associated with physiological blind spots can be reduced through training. This corroborates prior suggestions that perceptual training can be used to reduce the extent of localized blindness resulting from pathology [5–7]. Moreover, we have identified a readily available context wherein such training protocols might be optimized.

SUPPLEMENTAL INFORMATION

Supplemental information including experimental procedures, figures, individual subject data, and additional discussion can be found online at http://dx.doi.org/10.1016/j.cub.2015.07.026.

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