

Correspondence

Task-specific transfer of perceptual learning across sensory modalities

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It is now widely accepted that primary cortical areas of the brain that were once thought to be sensory-specific undergo significant functional reorganisation following sensory deprivation. For instance, loss of vision or audition leads to the brain areas normally associated with these senses being recruited by the remaining sensory modalities [1]. Despite this, little is known about the rules governing crossmodal plasticity in people who experience typical sensory development, or the potential behavioural consequences. Here, we used a novel perceptual learning paradigm to assess whether the benefits associated with training on a task in one sense transfer to another sense. Participants were randomly assigned to a spatial or temporal task that could be performed visually or aurally, which they practiced for five days; before and after training, we measured discrimination thresholds on all four conditions and calculated the extent of transfer between them. Our results show a clear transfer of learning between sensory modalities; however, generalisation was limited to particular conditions. Specifically, learned improvements on the spatial task transferred from the visual domain to the auditory domain, but not *vice versa*. Conversely, benefits derived from training on the temporal task transferred from the auditory domain to visual domain, but not *vice versa*. These results suggest a unidirectional transfer of perceptual learning from dominant to non-dominant sensory modalities and place important constraints on models of multisensory processing and plasticity.

Forty volunteers participated in the experiment, with 10 participants

assigned to each of the four training conditions depicted in Figure 1A. In spatial tasks, participants had to judge which of two intervals contained the stimuli separated by the largest physical distance. In temporal tasks, participants had to judge which of two intervals contained the stimuli separated by the longest duration. Visual stimuli consisted of a pair of Gaussian blobs each presented for 200 ms. Auditory stimuli consisted of a pair of 100 ms white noise bursts convolved with a set of head-related transfer functions. Further information on the tasks and procedure can be found in the Supplemental Information.

On the first day of the experiment (pre-training session), we measured participants' thresholds on all four tasks using a staircase procedure. Participants were then randomly assigned to one task on which they trained for five days, with each training session consisting of six blocks of 50 trials. Finally, in a post-training session, we again measured participants' thresholds on all four tasks. All groups showed significant learning on their training task, with thresholds gradually decreasing over the course of the training period (see Supplemental Figure S1). To measure the extent of transfer between the different conditions for each observer, we calculated a threshold ratio for each condition by dividing thresholds measured in the post-training session by pre-training session thresholds (Figure 1B). Here, a value of one indicates no change in performance following training, while a value less than one indicates improved performance. As expected, the greatest performance improvements were seen in the trained condition for each group. In some, but not all, cases this improvement on the trained task generalised to the other sensory modality. Specifically, learned improvements in the spatial task transferred from the visual domain to the auditory domain (Figure 1B, yellow box), whilst benefits derived from training on the temporal task transferred from audition to vision (Figure 1B, red box). The converse pattern of transfer was not observed for either task (Figure 1B, blue and green boxes). This pattern of transfer was robust to the level of the single subject,

with all data points lying below the unity line in the yellow and red boxes of Figure 1C, indicating improved performance in the post-training session relative to the pre-training session.

Given the dominant status of vision in performing spatial judgments (for example [2]) and audition in performing temporal judgments (for example [3]), our data suggest that benefits derived from perceptual learning transfer from the dominant modality for a given task to the non-dominant modality, but not *vice versa*. To test this hypothesis, we combined data from the different training groups according to whether they trained in the dominant (visual spatial and auditory temporal conditions) or non-dominant modality (auditory spatial and visual temporal conditions) for a given task and tested whether these combined groups showed significant post-training improvements in the untrained modality with respect to baseline (threshold ratio = 1). While the combined dominant training group showed significant learning in the untrained modality ($t(19) = 11.01$, $p < 0.0001$), this was not the case for the non-dominant group ($t(19) = 0.15$, $p = 0.883$).

While some previous studies have shown that improvements in temporal interval discrimination can generalise from one sensory modality to another ([4,5], but see [6]), to our knowledge this is the first study to show that benefits derived from training on a spatial task in the visual domain transfer to the auditory domain. Moreover, by examining spatial and temporal tasks in a single study, our results reveal that the asymmetric transfer of perceptual learning between sensory modalities, previously reported for temporal interval discrimination [4], may be a general principle of crossmodal plasticity. One possible explanation for this asymmetry is that unisensory input is outsourced to task-appropriate sensory systems, irrespective of which sense delivered the information [7]. For instance, auditory cortex might encode temporal information from multiple modalities with incoming visual input automatically converted into an auditory representation (e.g. [8]). If this were the case, however, training with visual stimuli would also be expected to recruit and improve

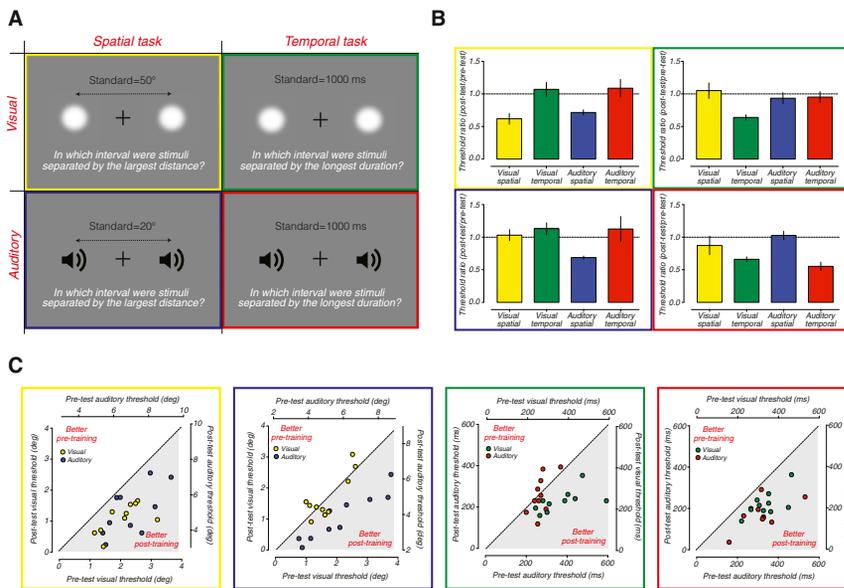


Figure 1. Experimental paradigm and transfer of improvements between tasks. (A) Participants were randomly assigned to a spatial or temporal task, which could be performed visually or aurally. In spatial tasks, participants had to judge which of two intervals contained the stimuli separated by the largest distance. In temporal tasks, participants had to judge which of two intervals contained the stimuli separated by the longest duration. Participants trained on their assigned task with feedback for five days. (B) Before and after training, discrimination thresholds were measured on all four tasks. Data are expressed as threshold ratios calculated by dividing post-training thresholds by pre-training thresholds, such that values less than one indicate improved performance. All groups showed improvement on their trained task; however, transfer was limited to specific conditions. Participants trained on the spatial task in the visual domain improved on the auditory spatial task (see blue bar in yellow box), while those trained on the temporal task in auditory domain improved on the visual temporal task (see green bar in red box). The converse pattern of transfer in each condition was not observed. (C) Transfer effects were robust to the level of individual participants. Each box plots pre-training thresholds as a function of post-training thresholds for the trained task and the same task performed in the other sensory modality. In the yellow and red boxes, all blue and green data points fall below the unity line, respectively.

the mechanism responsible for time estimation, meaning that we might expect bidirectional transfer of learning between the senses. Rather, our data support the idea of crossmodal sensory calibration [9], in which the most accurate sense for a given task calibrates the other sense. Within this framework, an improved representation in the dominant, ‘calibrating’ sense would lead to a knock-on benefit for the other sense. Moreover, this model predicts that training on a task with the non-dominant sense would lead to modality-specific learning effects, a prediction consistent with our findings.

While this theory provides a framework for understanding our behavioural effects, further work is required to elucidate how exactly an improved spatial representation in vision leads to an improvement in the auditory representation. For instance, how does improved spatial information

in the visual domain, which is encoded primarily in retinotopic coordinates, affect the auditory representation of space derived from interaural time and level differences? Another interesting line of inquiry would be to investigate how the transfer effects we observe are related to effects from multisensory learning paradigms, in which training with multisensory stimulation facilitates unisensory learning (see [10] for a review). For example, it may be that the size of the benefit derived from multisensory learning is contingent on the sense used to perform the task in the test session and whether this task involves a temporal or spatial judgement.

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures, experimental procedures and further details of results, and can be found with this

article online at <http://dx.doi.org/10.1016/j.cub.2015.11.048>.

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