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Perceptual learning evidence for supramodal representation of stimulus orientation at a conceptual level

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ABSTRACT

When stimulus inputs from different senses are integrated to form a coherent percept, inputs from a more precise sense are typically more dominant than those from a less precise sense. Furthermore, we hypothesized that some basic stimulus features, such as orientation, can be supramodal-represented at a conceptual level that is independent of the original modality precision. This hypothesis was tested with perceptual learning experiments. Specifically, participants practiced coarser tactile orientation discrimination, which initially had little impact on finer visual orientation discrimination (tactile vs. visual orientation thresholds = 3:1). However, if participants also practiced a functionally orthogonal visual contrast discrimination task in a double training design, their visual orientation performance was improved at both tactile-trained and untrained orientations, as much as through direct visual orientation training. The complete tactile-to-visual learning transfer is consistent with a conceptual supramodal representation of orientation unconstrained by original modality precision, likely through certain forms of input standardization. Moreover, this conceptual supramodal representation, when improved through perceptual learning in one sense, can in turn facilitate orientation discrimination in an untrained sense.

1. Introduction

We perceive the world with multiple senses. When near-threshold stimulus inputs from difference senses are integrated to form a coherent percept, super-additivity often occurs as multimodal responses are larger than the linear sum of unimodal responses (Meredith & Stein, 1983; Stein & Stanford, 2008). At suprathreshold, multimodal integration appears to be a Bayesian process, in which inputs from each modality are weighted by their relative reliabilities before linear summation (Hillis, Watt, Landy, & Banks, 2004; Angelaki, Gu, & DeAngelis, 2009). In other words, more precise (lower threshold) unimodal inputs will carry more weight than less precise (higher threshold) unimodal inputs in multimodal integration, as evidenced in various psychophysical and neurophysiological observations (Welch & Warren, 1980; Ernst & Banks, 2002; Battaglia, Jacobs, & Aslin, 2003; Alais & Burr, 2004; Hillis et al., 2004; Gu, Angelaki, & DeAngelis, 2008). Moreover, task precision appears to affect the cross-modal transfer of perceptual learning, in that learning with a more precise modality transfers to a less precise one, but not vice versa. A famous example is that learning of auditory temporal interval discrimination transfers to visual temporal interval discrimination, but not in the opposite direction (Bratzke, Seifried, & Ulrich, 2012; McGovern, Astle, Clavin, & Newell, 2016).

Here we further hypothesized that basic sensory features, such as orientation, can be supramodal-represented at a higher conceptual level that is independent of original modality precision. Although the formation of such representation depends on unimodal inputs, inputs with different modality precisions can be standardized and thus represented equally. For example, visual and tactile orientation discrimination thresholds differ by several folds, but a supramodal representation of orientation could be independent of the threshold differences between two modalities. Some hints for this possibility is the report that sound motion can facilitate perceptual learning of visual motion direction (Seitz, Kim, & Shams, 2006), even if sound motion direction is apparently much coarser than visual motion direction. Moreover, this hypothesis can be extended to predict that when a conceptual supramodal representation is improved in precision through training at one modality, it would in turn improve sensitivity at a different modality, even if

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the inputs from the trained modality are coarser than those from the untrained one.

We used perceptual learning experiments to test this hypothesis. Tactile orientation discrimination is much less precise than visual orientation discrimination in terms of threshold. Therefore, tactile orientation learning is not expected to have a significant impact on visual orientation following the principle of precision-based Bayesian interaction. However, if there exists a conceptual supramodal representation of orientation, the modality precision differences of orientation inputs would not matter at this level. And if tactile learning can improve conceptual supramodal orientation representation, the latter would in turn improve visual orientation discrimination in principle.

Here by "in principle" we mean that such learning transfer may not automatically occur when conventional single training is administrated, as demonstrated by various specificities of perceptual learning. However, we can apply a double training design that has successfully abolished many forms of learning specificities in visual perceptual learning (Xiao et al., 2008; Zhang, Zhang, et al., 2010; Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Xiong, Zhang, & Yu, 2016), as well as in auditory (Xiong, Tan, Zhang, & Yu, 2019) and visuomotor learning (Yin, Bi, Yu, & Wei, 2016; Grzeczkowski, Cretenoud, Mast, & Herzog, 2019). Double training consists of training of the primary task (e.g., orientation discrimination), as well as a secondary functionally orthogonal task (e.g., contrast discrimination) at the transfer condition (e.g., an untrained orientation). The secondary training has little impact on the primary task by itself, but it lets the participants receive exposure of the transfer condition. This exposure would activate sensory neurons at the transfer condition, so that high-level conceptual learning can functionally connect to these neurons to enable learning transfer (Zhang, Zhang, et al., 2010; Solgi, Liu, & Weng, 2013; Zhang, Cong, Song, & Yu, 2013; Wang et al., 2016; Xiong et al., 2016). More details on double training can be found in Results and Discussion.

2. Methods

2.1. Participants

Forty-five right-handed college students (mean age = 21.1 years, about half female and half male) participated in the experiments. They had normal or correct-to-normal vision, normal tactile sensation, and no history of neurological diseases. They were naive to the purpose of the study and had no prior experience of psychophysical experiments. Informed written consent was collected from each participant before training. This project was approved by the Peking University Institutional Review Board, and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus and stimuli: Tactile

The tactile stimulus was presented using a custom-built device, which was able to vary the stimulus orientation at a resolution of 1°. The stimulus surface and the top of the presenting panel of the device were calibrated to be on the same level before the stimulus onset. A microcontroller (with an Arduino Board and Matlab programming) controlled vertical stimulus movement.

The stimulus was a 3D-printed dome-shaped plastic grating (Fig. 1A). The size of the grating was 20 mm in diameter, consisting of 2.00-mm wide parallel bars separated by 2.00-mm wide grooves (Fig. 1B). The grooves were sufficiently deep to prevent a participant's finger from contacting the bottom of the grating.

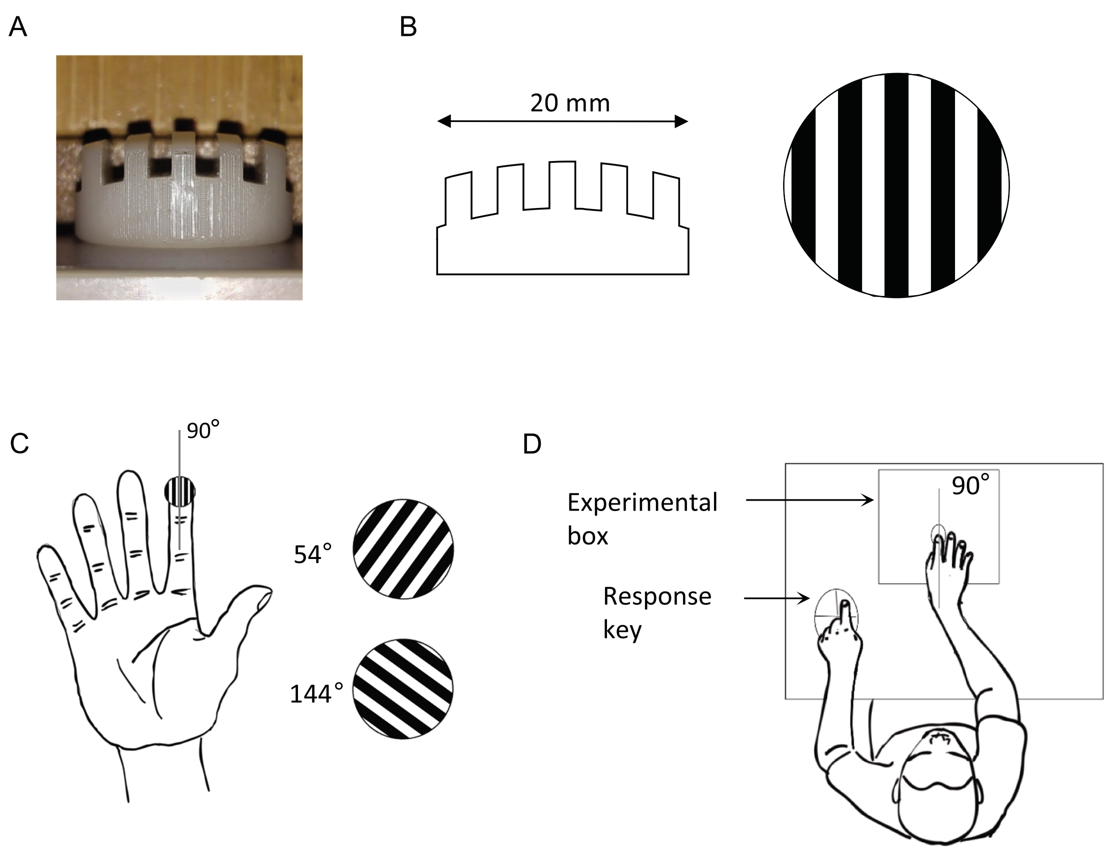

Fig. 1. The tactile stimulus and experimental settings. A. A dome-shaped 3D-printed plastic grating. B. The side (left) and top (right) views of the grating. C. The orientation along the index finger was defined as 90°. Two orthogonal orientations used in the experiments at 54° and 144° were also shown. D. A participant perceived the stimulus with the right index finger and responded with the left index finger by clicking the mouse buttons.

During a tactile orientation discrimination trial, the stimulus was presented to the right index finger that was fixed in position. The orientation along the index finger was defined as 90° (Fig. 1C). The blind-folded participants would respond with mouse clicks using their left index fingers (Fig. 1D).

2.3. Apparatus and stimuli: Visual

Visual stimuli were generated with PsychToolbox-3 (Brainard, 1997; Pelli, 1997) and presented on a 21-in Sony G520 CRT monitor (1024 × 768 pixels, 0.39 mm × 0.39 mm pixel size, 85 Hz frame rate, and 33.4 cd/m^2 mean luminance). The screen luminance was linearized by an 8-bit look-up table. The stimulus was viewed at a distance of 4 m through a circular opening (diameter = 17°) of the black cardboard that covered the rest of the monitor screen. A chin-and-head rest stabilized the head of the participant.

A Gabor stimulus (a Gaussian windowed sinusoidal grating) with a spatial frequency of 6 cycles/degree (cpd), standard deviation of 0.12°, contrast of 0.47, and phase randomized in every presentation, was used (Fig. 2B). The vertical orientation was regarded as being congruent to the tactile orientation along the index finger (90°). The Gabor was presented at the center of the screen.

2.4. Procedure

Tactile orientation discrimination thresholds were measured with a temporal two-alternative forced choice (2AFC) staircase procedure. In each trial, reference orientation and test orientation (reference + Δ orientation) were separately presented in two 2-s intervals in a random order. The inter-stimulus interval (ISI) was also 2 s (Fig. 2A). The participants judged which interval contained a more clockwise orientation, and for each response they received auditory and visual feedbacks (i.e., a beep for a wrong response, and a word "Correct" or "Wrong" on the screen). The reference orientation was either 54° or 144° (Fig. 1C). Every 10 trials was followed by a 10-s break to reduce index finger adaptation.

Visual orientation and contrast discrimination thresholds were also measured with a temporal 2AFC staircase procedure. In each trial, reference and test (reference + Δ orientation or Δ contrast) stimuli were separately presented in two 100-ms intervals in a random order, which were separated by a 500-ms ISI (Fig. 2B & C). The participants judged which interval contained a more clockwise orientation or a higher contrast. They received auditory feedback for each response. The reference orientation was either 54° or 144°, and the reference contrast was 0.47.

The Δ orientation or Δ contrast of each trial was controlled by a 3-down-1-up staircase, which resulted in a 79.4% convergence rate (Levitt, 1971). The step size of the staircase was 0.05 log unit. For tactile orientation discrimination, each staircase consisted of 60 trials. The geometric mean of the last six reversals was taken as the threshold. For visual orientation and contrast discrimination, each staircase consisted of four preliminary reversals and six experimental reversals. The geometric mean of the experimental reversals was taken as the threshold.

2.5. Experimental designs

Sequential and simultaneous double training designs were used (Xiao et al., 2008; Zhang, Zhang, et al., 2010). Sequential double training consisted of a tactile orientation training phase, including six staircases of tactile orientation discrimination training at one orientation per session for five daily sessions, and then a visual orientation exposure phase, including ten staircases of visual contrast discrimination at the same tactile-trained orientation per session for four daily sessions (Fig. 3). Simultaneous double training consisted of six staircases of tactile orientation discrimination training and ten staircases of visual contrast discrimination training at the same orientation in alternative blocks of trials for five daily sessions (Fig. 4). For both double training designs, there was an additional training phase in which visual orientation discrimination at the tactile-trained orientation was further practiced with ten staircases per session for 3–4 daily sessions.

Pre-training visual orientation discrimination thresholds at two reference orientations were measured in a counterbalanced order before double training, with each condition tested for six staircases. Then pre-training tactile orientation discrimination thresholds were tested only at the trained orientation for four staircases. Post-training visual and tactile thresholds were obtained with five visual staircases at two

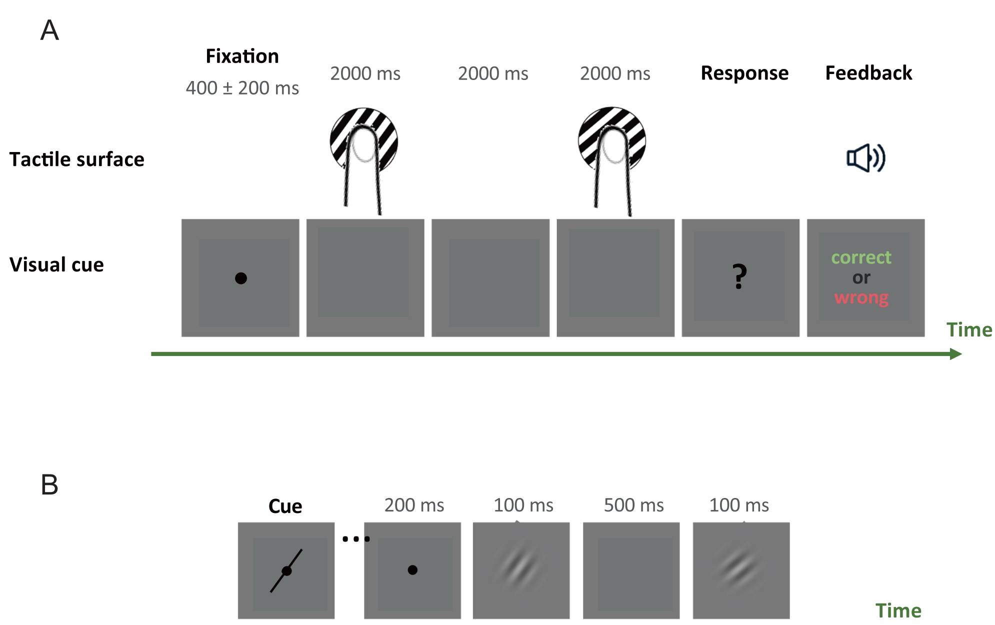

Fig. 2. Tactile and visual trials. A. In a tactile orientation discrimination trial, two stimuli were presented to the right index finger in two 2-s intervals, respectively, which were separated by a 2-s ISI. B. In a visual orientation discrimination trial, two stimuli were presented in two 100-ms intervals, respectively, which were separated by a 500-ms ISI. The orientation difference would be changed to contrast difference in a visual contrast discrimination trial.

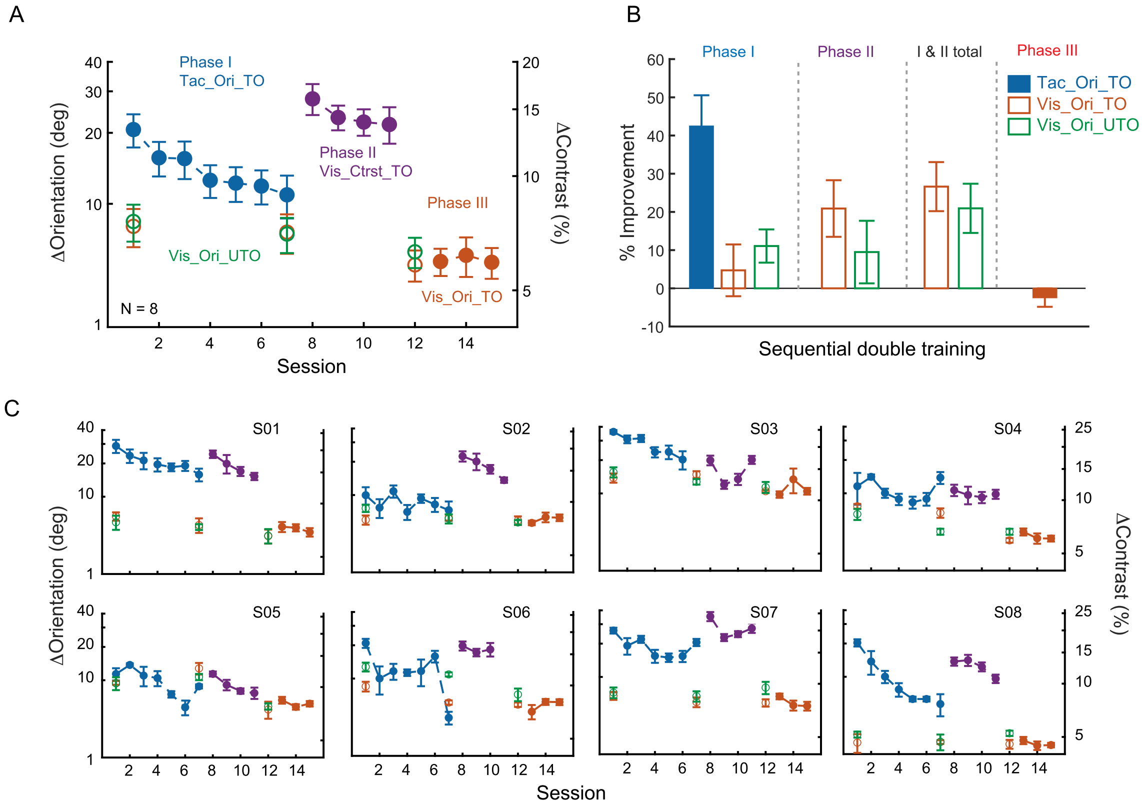

Fig. 3. Sequential double training. A. Double training consisted of initial tactile orientation discrimination training at 54°/144° (Tac_Ori_TO, Phase I) and later contrast discrimination training at the tactile-trained orientation (Vis_Ctrst_TO, Phase II). The tactile-to-visual learning transfer was tested at the trained (Vis_Ori_TO) and an untrained orthogonal orientation (Vis_Ori_UTO) after Phases I and II. The participants further practiced visual orientation discrimination at the tactile-trained orientation in Phase III. B. A summary of learning and transfer effects. C. Individual data. TO: Trained orientation. UTO: Untrained orientation. Error bars represent ±1 SEM.

orientations and four tactile staircases at the trained orientation, respectively, after the first phase of sequential double training (i.e., first post-training thresholds, Fig. 3A), or after simultaneous double training (Fig. 4A). The second post-training visual thresholds after the second phase of sequential double training were obtained with five visual staircases at each reference orientation. More details on experimental designs can be found in the Results section.

2.6. Statistical analysis

Data were analyzed with JASP 0.14.0. The learning and transfer effects were measured by the percent threshold improvement from pre- to post-test sessions, which was calculated with the equation $(\text{threshold}_{pre} - \text{threshold}_{post})/\text{threshold}_{pre} \times 100\%$. Unless otherwise specified, a two-tailed paired *t*-test was performed for single comparisons of threshold changes, and a mixed-design ANOVA with Bonferroni correction was performed for multiple comparisons.

To reduce the impact of procedural learning, the first staircase was excluded and the geometric mean of the subsequent four staircases was taken as the pre-training threshold of visual orientation discrimination. The post-training threshold was averaged over all five staircases. For continued practice of visual orientation discrimination after double training, the geometric mean of all ten staircases on the last day was taken as the post-training threshold.

3. Results

3.1. Tactile-to-visual orientation learning transfer: Sequential double training

Eight participants first practiced tactile orientation discrimination for five sessions at one of two orthogonal orientations (54° or 144°). The pre-training tactile orientation thresholds were 20.7 ± 3.3°, about 3 times as high as pre-training visual orientation thresholds at 7.8 ± 0.9° ($t_7 = 4.27, p = 0.004$; LogBF = 2.66). Training reduced tactile thresholds to 12.1 ± 2.3° by 41.8 ± 8.1% ($t_7 = 5.18, p = 0.001$; LogBF = 3.52) (Fig. 3A, Phase I). After tactile training, visual orientation discrimination thresholds were reduced by 2.7 ± 6.9% ($t_7 = 0.39, p = 0.707$; logBF = −1.03) at the tactile-trained orientation and 12.4 ± 4.5% ($t_7 = 2.73, p = 0.029$; LogBF = 1.04) at the untrained orientation, which were not significantly different from each other ($t_7 = 1.74, p = 0.126$; LogBF = 0.03). Later the first control experiment would indicate that these visual improvements were not significantly different from the test–retest effects (Fig. 5A). Therefore, tactile orientation learning appeared to be modality specific. (Note: Here the pre-training visual orientation thresholds with the Gabor stimulus were around 8°, which was similar to those in an earlier paper of ours when the same Gabor stimulus was used (Zhang, Zhang, et al., 2010). In another paper of ours using hard-edged gratings, the foveal orientation threshold before training was lower at 3–4° (Zhang, Xiao, Klein, Levi, & Yu, 2010)).

However, on the basis of our previous perceptual learning studies (Xiao et al., 2008; Zhang, Zhang, et al., 2010; Xiong et al., 2016), we hypothesized that this modality specific observation did not necessarily mean that tactile orientation learning was not transferable to visual orientation. That is, orientation learning could be supramodal and thus

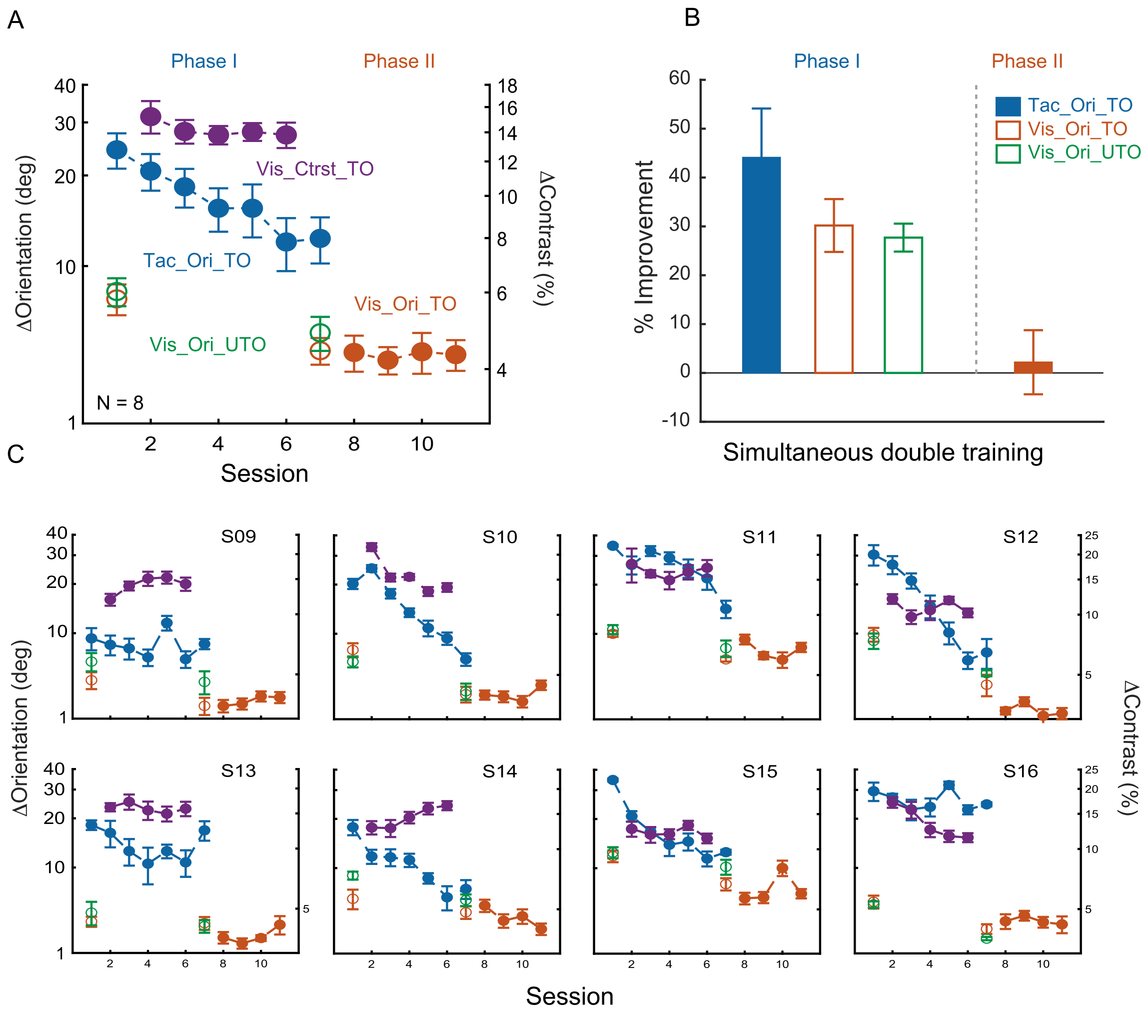

Fig. 4. Simultaneous double training. A. Simultaneous double training consisted of tactile orientation training (Tac_Ori_TO) and visual contrast training at the same orientation (Vis_Ctrst_TO) in alternating blocks of trials. The transfer of learning was tested for visual orientation at tactile-trained (Vis_Ori_TO) and untrained orientations (Vis_Ori_UTO). Visual orientation discrimination at the tactile-trained orientation was further practiced for 4 sessions. B. A summary of learning and transfer effects. C. Individual data. TO: Trained orientation. UTO: Untrained orientation. Error bars represent ±1 SEM.

completely transferable, but the cross-modal learning transfer might have been hindered by some non-learning factors. Nevertheless, the specificity could be overridden by double training (see Discussion).

To examine the possible tactile-to-visual learning transfer with double training, the same participants received exposure to the visual orientation by further practicing visual contrast discrimination at the tactile-trained orientation. After this exposure, which alone would have little impact on visual orientation thresholds (see Fig. 6 for a second control), visual orientation thresholds were improved at the tactile-trained orientation by 20.9 ± 7.4%, and at the orthogonal orientation by 9.5 ± 8.2% (Fig. 3A, Phase II). The total improvement of visual orientation discrimination after double training was 25.1% ± 6.4% ($t_7 = 2.35$, $p = 0.006$; LogBF = 2.35) at the tactile-trained orientation and 21.7% ± 6.9% at the orthogonal orientation ($t_7 = 3.14$, $p = 0.016$; LogBF = 1.49). The two improvements were not significantly different from each other ($t_7 = 0.58$, $p = 0.579$; LogBF = -0.95), suggesting possible orientation unspecific tactile-to-visual transfer of orientation learning, which would be confirmed by the simultaneous double training experiment (Fig. 4) and a third control (Fig. 7) later.

To test whether the learning transfer had maximized after double training, the participants further practiced visual orientation discrimination at the tactile-trained orientation for three sessions. This direct visual orientation training produced no significant threshold change (−3.5 ± 2.2%; $t_7 = -1.64$, $p = 0.146$; LogBF = −0.13) (Fig. 3A, Phase III). Therefore, the tactile-to-visual learning transfer after sequential double training was complete, and further visual orientation training was unnecessary.

3.2. Tactile-to-visual orientation learning transfer: Simultaneous double training

Our previous studies have shown that simultaneous double training is also able to enable learning transfer (Xiao et al., 2008; Zhang, Zhang, et al., 2010). The simultaneous procedure has an additional advantage: it excludes the possibility that the learning transfer could result from two pretests in sequential double training (before Phases I & II in Fig. 3A). Eight new participants practiced tactile orientation discrimination and visual contrast discrimination in alternating blocks of trials for five sessions (Fig. 4A, Phase I). This simultaneous double training improved tactile orientation discrimination by 44.1 ± 10.0% ($t_7 = 4.39$, $p = 0.003$; LogBF = 2.78). It also improved untrained visual orientation discrimination at the tactile-trained orientation by 30.2 ± 5.4% ($t_7 = 5.58$, $p < 0.001$; LogBF = 3.87) and the orthogonal orientation by 27.7 ± 2.9% ($t_7 = 9.68$, $p < 0.001$; LogBF = 6.72). Again, there was no significant difference of visual improvements at tactile-trained and orthogonal orientations ($t_7 = 0.59$, $p = 0.575$; LogBF = −0.95), consistent with earlier sequential double training results. Continued training of visual orientation discrimination at the tactile-trained orientation failed to further

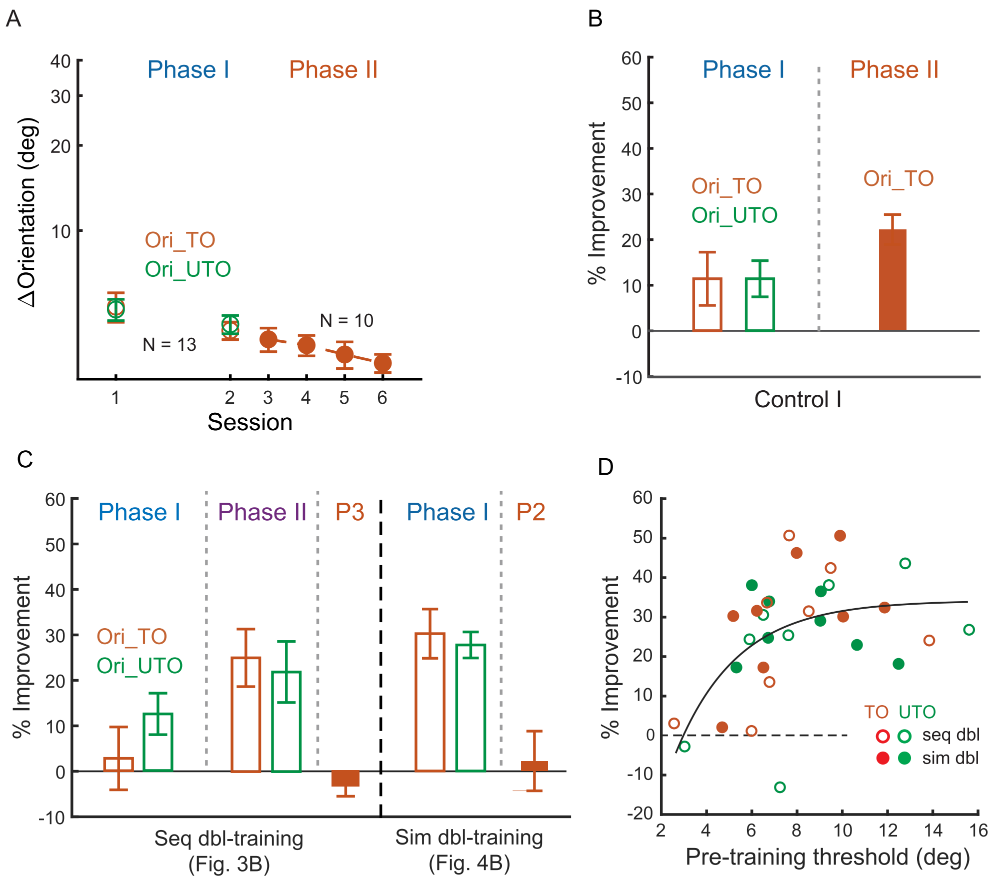

Fig. 5. Control I: The test–retest effects. A. Thresholds of visual orientation discrimination were tested and retested after 5 days with no actual training conducted (Phase I). Ten of 13 participants then continued to practice visual orientation discrimination at one orientation (Ori_TO) for 3 more sessions (Phase II). B. A summary of test–retest effects and further orientation training effects. C. Visual orientation improvements after each training phase in sequential double training (replotted from Fig. 3B) and simultaneous double training (replotted from Fig. 4B). D. Individual visual orientation improvements at the tactile trained and untrained orientations after double training as a function of the pre-training threshold. TO: Trained orientation. UTO: Untrained orientation. Error bars represent ±1 SEM.

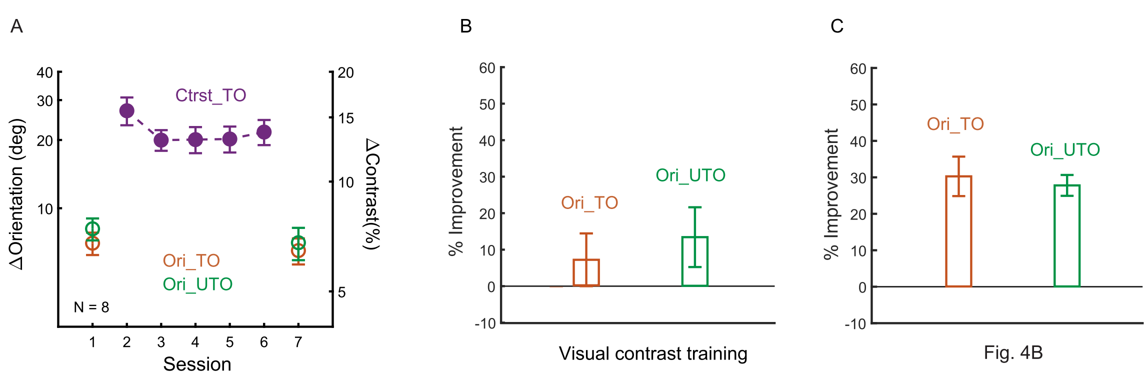

Fig. 6. Control II: The effects of contrast training alone on visual orientation discrimination. A. The impacts of contrast training on visual orientation discrimination at the contrast trained orientation (Ori_TO) and untrained orthogonal orientation (Ori_UTO). B. A summary of visual orientation improvements. C. Visual orientation improvements after simultaneous double training (replotted from Fig. 4B). TO: Trained orientation. UTO: Untrained orientation. Error bars represent ±1 SEM.

boost the performance (2.2 ± 6.6%, $t_7 = 0.33$, $p = 0.748$; LogBF = −1.04) (Fig. 4A, Phase II). Therefore, simultaneous double training also enabled complete tactile-to-visual transfer of orientation learning.

3.3. *Control experiment I: test–retest effects*

We ran three control experiments to examine whether the double training results could have alternative explanations.

The first control measured the test–retest effects to answer two questions: Whether tactile orientation learning was truly modality specific initially, and whether the double training effects could be explained by the test–retest effects. Visual orientation thresholds at 54° and 144° were measured and remeasured with a 5-day gap in thirteen participants with no actual orientation training performed. The test–retest effects amounted to reductions of orientation thresholds by 11.3 ± 5.0% at 54° ($t_{12} = 2.28$, $p = 0.041$; LogBF = 0.62) and 11.3 ± 4.0% at 144° ($t_{12} = 2.85$, $p = 0.015$; LogBF = 1.45) (Fig. 5A, B, Phase I).

To answer the first question, a mixed-design ANOVA compared the current test–retest effects to reductions of visual orientation thresholds after tactile orientation training (Phase I in Fig. 3, replotted here in Fig. 5C), with Experiment as a between-subject variable and Orientation (54° and 144°) as a within-subject variable. The ANOVA outputs indicated no significant main effects of Experiment ($F_{1,\ 19} = 0.307$, p = 0.586; LogBF = −0.571) and Orientation ($F_{1,\ 19} = 3.081$, p = 0.095; LogBF = −0.558), confirming initial modality specificity of tactile orientation learning.

To answer the second question, another mixed-design ANOVA compared the current test–retest effects to visual orientation threshold

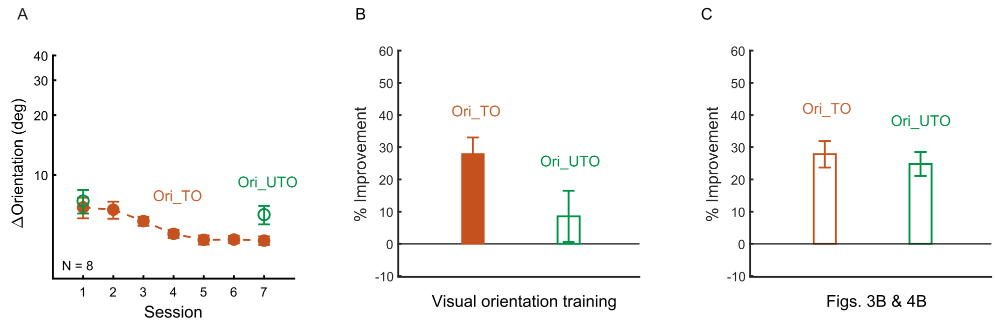

Fig. 7. Control III: Orientation specificity in visual orientation learning. A. Visual orientation discrimination was trained at one orientation (Ori_TO) and the transfer was tested at an untrained orthogonal orientation (Ori_UTO). B. A summary of training and transfer effects. C. Combined visual orientation improvements after sequential and simultaneous double training from Fig. 3B & Fig. 4B. TO: Trained orientation. UTO: Untrained orientation. Error bars represent ±1 SEM.

reductions after sequential and simultaneous training, with Experiment (test–retest, seq dbl_training, and sim dbl_training) as a between-subject variable and Orientation (54° and 144°) as a within-subject variable. The ANOVA outputs indicated a significant main effect of Experiment ($F_{2,\ 26} = 3.907$, p = 0.033; LogBF = 0.905) and an insignificant main effect of Orientation ($F_{1,\ 26} = 0.696$, p = 0.412; LogBF = −1.056). Further contrast analysis indicated that the test–retest effects were significantly different from visual orientation improvements after simultaneous double training ($t_{26} = 2.654$, p = 0.013) and after combined sequential and simultaneous double training ($t_{26} = 2.694$, p = 0.012), but not after sequential double training ($t_{26} = 1.823$, p = 0.080).

We made extra effort to address the insignificant difference between the test–retest effects and the sequential double training effects. Besides the comparison of performance improvements with different training conditions, a complementary method to examine whether double training effects could be accounted for by the test–retest-effects was to evaluate whether there would be further training effects after retests, as further direct orientation training after double training had shown no additional benefits (Phase III in Fig. 3A & Phase II in Fig. 4A, replotted here in Fig. 5C). Ten of the thirteen observers after the retests continued to practice visual orientation training at one orientation, which improved orientation discrimination by 21.8 ± 3.1% ($t_9 = 6.69$, $p < 0.001$; LogBF = 5.75). A one-way ANOVA compared the visual orientation training effects after the retests here and after sequential and simultaneous training, which suggested a significant main effect ($t_{23} = 10.304$, p < 0.001; LogBF = 3.971). Further contrast analysis suggested that the orientation training effects after the retests were significantly different from those after sequential double training ($t_{23} = 3.298$, p = 0.003), as well as after simultaneous double training ($t_{23} = 4.260$, p < 0.001). Therefore, the overall outcomes of above two lines of data analysis supported the conclusion that the test–retest effects could not fully explain the complete tactile-to-visual orientation learning transfer after sequential and simultaneous double training.

Earlier studies reported that the amount of perceptual learning is correlated to the pre-training threshold (Fahle & Henke-Fahle, 1996; Wong, Peters, & Goldreich, 2013; Yehezkel, Sterkin, Lev, Levi, & Polat, 2016; Lengyel & Fiser, 2019). We found that this correlation could partially explain why sequential double training produced less visual orientation improvements than did simultaneous double training (Fig. 3A). When individual improvements were plotted against pre-training visual orientation thresholds, the relationship could be described with an exponential function: $y = 0.35 - 0.97 \times \exp(-0.36x)$ ($R^2 = 0.301$, Fig. 5D). More specifically, there were more data points that were near or below the zero improvement line with sequential than with simultaneous double training (4:1), and these data points tended to be associated with lower initial thresholds.

3.4. Control II: the effects of visual contrast training on visual orientation discrimination

A second control experiment examined whether the secondary contrast training in double training could alone account for improved visual orientation discrimination. Eight new participants practiced contrast discrimination at 54° or 144° for five sessions, which produced insignificant changes of visual orientation discrimination at the contrast trained orientation by 7.0 ± 7.2% ($t_7 = 0.97$, $p = 0.195$; LogBF = −0.72) and the orthogonal orientation by 13.3 ± 8.2%, ($t_7 = 1.63$, $p = 0.148$; LogBF = −0.14) (Fig. 6).

A mixed-design ANOVA compared current orientation threshold changes to those after simultaneous double training (Fig. 4A, phase I), with Experiment (sim dbl-training and current contrast training) as a between-subject variable and Orientation (54° and 144°) as a within-subject variable. The ANOVA outputs indicated a significant main effect of Experiment ($F_{1,\ 14} = 5.054$, p = 0.041; LogBF = 0.68) and an insignificant main effect of Orientation ($F_{1,\ 14} = 0.431$, p = 0.522; LogBF = −0.93). Therefore, contrast training per se cannot fully explain the visual orientation improvements with double training.

3.5. Control III: orientation specificity in visual orientation learning

The tactile-to-visual transfer of orientation learning was orientation-unspecific (Figs. 3 and 4). In contrast, foveal orientation learning is known to be specific to the trained orientation under conventional single training (Fahle, 1997; Zhang, Zhang, et al., 2010). It is thus necessary to examine whether the tactile-to-visual learning transfer merely reflected some general procedural learning, or real orientation learning. This was achieved by testing whether the amount of learning transfer was comparable to that via direct orientation training, and whether direct orientation learning with the current stimulus condition was orientation specific. As a third control experiment, we had eight new participants practice visual orientation discrimination at 54° or 144°, and measured the pre- and post-training thresholds at both trained and orthogonal orientations (Fig. 7). Training improved visual orientation discrimination by 27.9 ± 5.1% ($t_7 = 5.45$, p < 0.001; LogBF = 3.76) at the trained orientation, but it failed to do so at the untrained orthogonal orientation (8.5 ± 8.0%, $t_7 = 1.07$, $p = 0.320$; LogBF = −0.64).

A mixed-design ANOVA compared the current orientation improvements at the trained and untrained orientations and the improvements at two corresponding orientations after double training (data from sequential and simultaneous double training experiments were pooled here to increase the statistical power; Fig. 7C), with Experiment (current and combined seq/sim dbl-training) as a between-subject variable and Orientation (trained and untrained) as a within-subject variable. The ANOVA outputs indicated no significant main effect of Experiment ($F_{1,\ 22} = 1.585$, p = 0.221; LogBF = −0.364) but a significant main effect of Orientation ($F_{1,\ 22} = 9.897$, p = 0.005; LogBF = 0.789) and a significant interaction of Experiment and Orientation ($F_{1, 22} = 5.368$, $p = 0.030$; LogBF = 1.082). Post hoc comparisons further revealed a significant difference of orientation improvements between the trained orientation and the orthogonal orientation in the current control condition ($t = 3.345$, $p = 0.018$ after Bonferroni-Holm correction). These results thus confirmed that the tactile-to-visual orientation learning transfer after double training and the direct orientation training effects were comparable, and that the direct orientation training effects were orientation specific, which ruled out the possibility that the tactile-to-visual transfer of orientation learning merely reflected general procedural learning.

4. Discussion

This study demonstrates complete tactile-to-visual transfer of orientation learning with double training, even if initial tactile orientation thresholds are three times as high as visual orientation thresholds and tactile orientation learning is initially modality specific. Moreover, cross-modal transfer of orientation learning is orientation unspecific, in contrast to orientation specific learning within the same sensory modality.

The complete cross-modal learning transfer suggests that stimulus orientation can be supramodally represented regardless of respective modality precision. The 3:1 ratio of pre-training tactile and visual orientation thresholds implies that the standard deviation of the tactile orientation input distribution is 3 times of that of the visual orientation input distribution. It is therefore difficult for the supramodal orientation representation to represent two distributions by their raw values. One simple solution is to transform the two distributions by statistical standardization, so that they are equally represented according to the standard scores. We regard this standardized orientation representation as conceptual supramodal representation.

Our previous double training studies have suggested that perceptual learning improves conceptual representation of a visual stimulus feature because learning transfers regardless of the physical appearances, underlying neuronal encoders, and precisions of the stimuli (Wang et al., 2016; Xie & Yu, 2019). The current results further demonstrate that this conceptual perceptual learning also occurs at a supramodal level. Perceptual learning may reweight the standardized distributions of stimulus inputs to improve the sensitivity. Various reweighting models have been proposed to explain perceptual learning (Dosher & Lu, 1998; Law & Gold, 2009; Sotiropoulos, Seitz, & Seriès, 2011; Dosher, Jeter, Liu, & Lu, 2013). Our double training results over the years suggest that perceptual learning is more than reweighting the sensory inputs for better matching them to a rigid stimulus template, as implied in various reweighting models. Rather it is at an abstract and conceptual level that perceptual learning improves the readout of standardized stimulus inputs. This learning process, being non-specific to stimulus location, orientation, motion direction, physical appearance, precision, etc. (Xiao et al., 2008; Zhang, Zhang, et al., 2010; Zhang & Yang, 2014; Wang et al., 2016; Xie & Yu, 2019), and now sensory modality, is highly efficient and versatile.

It is intriguing to ask why initially modality specific perceptual learning becomes transferrable after double training. Previously we have reported that location and orientation specificity can be abolished when the transfer location or orientation is activated with either bottom-up stimulation or top-down attention (Xiong et al., 2016). This study and additional ERP evidence (Zhang et al., 2013) suggest that learning specificity may result from a lack of functional connections from high-level learning to sensory inputs associated with untrained retinal location or orientation. The same reasoning may apply to current modality specificity of orientation learning because the visual modality was neither stimulated nor attended during tactile orientation learning. It is double training that overrides these specificity-related factors and connects supramodal orientation learning to the untrained visual modality to enable learning transfer.

Back to multisensory integration introduced at the beginning of this paper, future experiments may elucidate how the improved conceptual supramodal representation of a stimulus feature would influence multisensory integration in a top-down manner. That is, how double training, which improves performance in both trained and untrained modalities, would improve subsequent multisensory integration. Future experiments may also study whether conceptual supramodal representation could be improved without unimodal training. This may be achieved by having the participants practice to discriminate the difference between a tactile orientation and a visual orientation. This potential cross-modal learning would provide useful insights into the interactions between a supramodal stimulus concept and unimodal stimulus inputs.

Author contributions

C. Yu and L. H. Chen conceived and designed the study. D. Z. Hu and K. Wen collected data, C. Yu and D. Z. Hu performed data analysis. C. Yu, L. H. Chen, and D. Z. Hu wrote the manuscript. All authors approved the final version of the manuscript for submission.

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