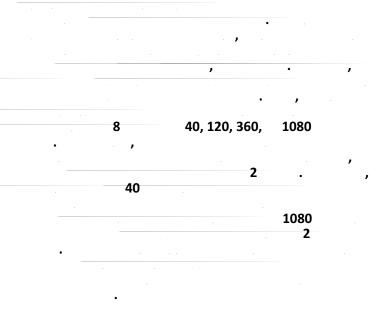
С

School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, People's Republic of China IDG/McGovern Institute for Brain Research, Peking University, Beijing, People's Republic of China Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, People's Republic of China

Department of Psychology, Tsinghua University, Beijing, People's Republic of China IDG/McGovern Institute for Brain Research, Tsinghua University, Beijing, People's Republic of China

School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, People's Republic of China IDG/McGovern Institute for Brain Research, Peking University, Beijing, People's Republic of China Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, People's Republic of China





The human brain can achieve long-term improvement in perceptual sensitivity as a result of learning (Fahle & Poggio, 2002). A prevailing view on this improvement is that "practice makes perfect," implying that tens of thousands of trials of training over days or weeks are necessary to induce substantial improvement in performance (Aberg et al., 2009; Banai & Lavner, 2014; Censor, Sagi, & Cohen, 2012; Chung, Levi, & Li, 2006; Husk, Bennett, & Sekuler, 2007; Sigman & Gilbert, 2000). However, several recent studies showed that a small amount of training was su cient to induce perceptual learning (Amar-Halpert et al., 2017; Hussain, Sekuler, & Bennett, 2009; Molloy et al., 2012). Hussain et al. (2009) examined the amount of practice needed to improve performance on texture and face identication. In a texture identication task, they found that 105 trials of practice on the rst day were required to enhance performance relative to the control group at the start of testing on the second day. In a face identi cation task, even only 21 trials of practice could enhance performance relative to the control group (Hussain et al., 2009). In a recent study

 $\sim$ 

 $\succ$ 



on texture discrimination learning (Amar-Halpert et al., 2017), participants underwent a practice for 252 trials on the rst day, and then they returned for 3 daily sessions with only ve near-threshold trials per session. Discrimination thresholds were measured on the rst day and the fth day. Intriguingly, such short training resulted in a remarkable learning e ect. Based on this nding, Amar-Halpert and colleagues proposed that learning was due to a memory reactivation mechanism.

It has been shown that training beyond a certain amount could not further bene t learning (Karni & Sagi, 1993; Savion-Lemieux, T., & Penhune, V. B., 2005). In a temporal-interval discrimination task, Wright and Sabin (2007) trained subjects for either 360 or 900 trials per day for 6 days. Signi cant learning occurred with both 360 and 900 training trials per day, and 900 training trials per day did not induce greater improvement relative to 360 training trials. Likewise, similar e ects were also observed with a mirror-reading letter task (Ofen-Noy, Dudai, & Karni, 2003), a visual texture discrimination task (Karni & Sagi, 1993), and an auditory identi cation task (Roth, 2005). Notably, overtraining could even be detrimental to the learning e ect already acquired (Ashley & Pearson, 2012; Censor, Karni, & Sagi, 2006; Mednick et al., 2002; Mednick, Arman, & Boynton, 2005; Ofen, Moran, & Sagi, 2007). Mednick et al. (2005) measured the performance on a texture discrimination task in three 1-hour sessions and found that the performance deteriorated steadily both within and across the rst two sessions. Because repeated within-day testing led to a retinotopically speci c decrease in performance, such perceptual deterioration is not simply due to general fatigue or boredom. Therefore, intensive training might lead to limited behavior improvement.

In this study, we aimed to investigate the relationship between daily training amount and behavioral improvement—how does the daily training amount modulate the magnitude and speci city of the perceptual learning e ect with a motion direction discrimination task? We were also interested in how long the modulation e ects could persist. Participants were trained for 40, 120, 360, or 1080 trials per day with a visual motion direction discrimination task. Threshold measurements were conducted before, one day after, and two weeks after eight training days at the trained direction and the untrained directions (30°, 60°, and 90° away from the trained direction).

Fifty-nine subjects (21 males) participated in the study. Their ages ranged from 18 to 28. All subjects

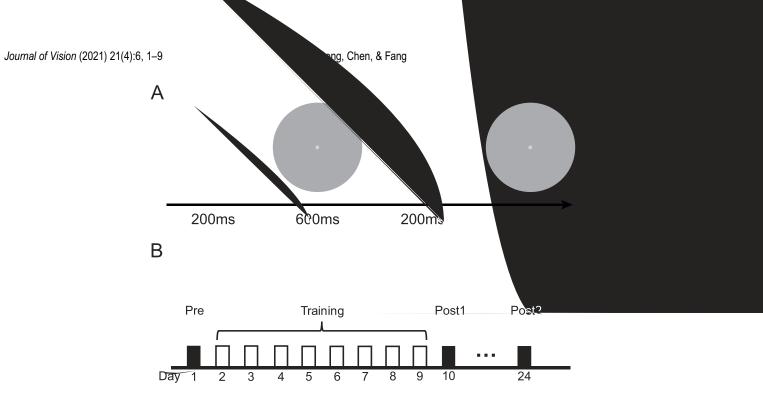
were naïve to the purpose of the study and had never participated in any perceptual learning experiment before. They were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. They gave written, informed consent in accordance with the procedures and protocols approved by the human subject review committee of Peking University. This study adhered to the Declaration of Helsinki.

Similar to our previous study (Chen et al., 2015), visual stimuli were random-dot kinematograms (RDKs) with 100% coherence (Figure 1A). All dots in a RDK moved in the same direction (luminance:  $3.76 \text{ cd/m}^2$ ; diameter:  $0.1^\circ$ ; speed:  $10^\circ$ /sec). At any one moment, 400 dots were visible within an 8° circular aperture. The dots were presented against a gray background (luminance:  $19.8 \text{ cd/m}^2$ ). The visual stimuli were presented on an IIYAMA HM204DT 22-in monitor, with a spatial resolution of  $1024 \times 768$  and a refresh rate of 60 Hz. Subjects viewed the stimuli from a distance of 60 cm. Their head was stabilized using a head and chin rest.

Fifty-nine subjects were randomly assigned into four training groups (= 12, 11, 12, and 12), respectively and a control group (= 12). Four training groups underwent four phases (Figure 1B): pretraining test (Pre), motion direction discrimination training, post-training test 1 (Post1), and post-training test 2 (Post2). The control group only underwent Pre, Post1, and Post2. Pre and Post1 took place on the days immediately before and after training, and Post2 took place 2 weeks after training.

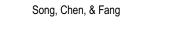
During the training phase, each subject underwent eight daily training sessions to perform a motion direction discrimination task at a direction of  $\theta$ , which was chosen randomly from eight directions: 22.5°, 67.5°, 112.5°, 157.5°, 202.5°, 247.5°, 292.5°, and 337.5° (0° was the rightward direction) at the beginning and was xed for all the sessions. For the four training groups, a daily training session consisted of 1, 3, 9, and 27 QUEST (Watson & Pelli, 1983) staircases of 40 trials, corresponding with 40, 120, 360, or 1080 trials, respectively. In a trial, two RDKs with motion directions of  $\theta + \Delta \theta/2$  and  $\theta - \Delta \theta/2$  were presented successively for 200 ms each and were separated by a 600-ms blank interval. The temporal order of these two RDKs was randomized. Subjects were asked to make a two-alternative forced-choice judgment of the direction of the second RDK relative to the rst one (clockwise or counterclockwise). Informative feedback was provided

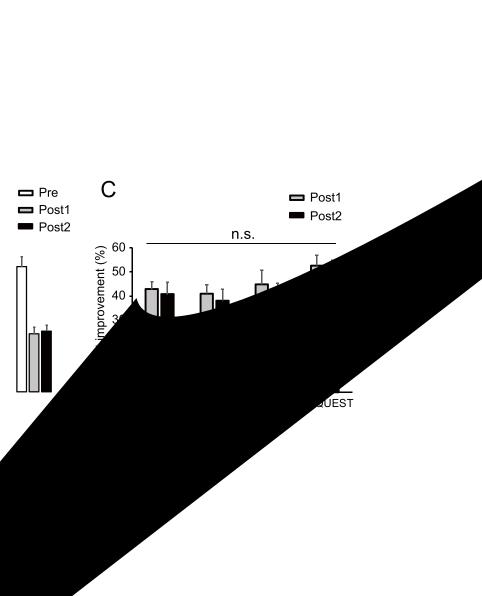
2



В

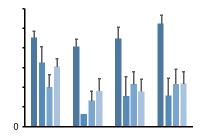
Threshold(°)





ed from jov.arvojournals.org on 04/13/2021

ſ



signi cant, (3, 43) = 2.383, < 0.1. The main e ect of test was not signi cant, (1, 43) = 1.035, = 0.315, and the interaction between test and training amount was not signi cant either, (3, 43) = 0.242, = 0.867. Then, we made comparisons between training amount conditions at Post1 and Post2. Planned -tests showed that the group receiving 27 QUEST staircases training per day exhibited stronger speci city than the group receiving 1 QUEST staircase training per day at Post1, (22) = -2.779, < 0.01, and Post2, (22) = -1.929, < 0.05. Our results demonstrated that less training led to less speci city or more transfer, and the characteristic lasted for at least two weeks.

It remains unclear to what extent the performance improvements in the trained and untrained directions are due to a test-retest e ect occurring at Pre, Post1, and Post2. To quantify the test-retest e ect, we collected data from a control group, which only underwent Pre, Post1, and Post2. Relative to Pre, the percent improvements averaged across the four directions were 3.095%, one-sample -test (47) = 0.656, = 0.515, at Post1 and 18.116%, (47) = 4.401, < 0.001, at Post2. Notably, the improvements at the untrained direction at Post2 were largely due to the test-retest e ect.

In this study, we examined the relationship between daily training amount and two visual learning outcomes: the improvement at the trained feature, and the transfer e ect to the untrained features. We found that (1) a small daily training amount of 40 trials was su cient to induce a signi cant behavioral improvement; no further improvement was observed in groups with larger daily training amounts and (2) the group with the smallest daily training amount exhibited the largest transfer e ect. These e ects persisted up to 2 weeks after training. These ndings shed light on determining the training amount in practical application and help to better understand the role of training amount in some key ideas such as consolidation-reactivation, transfer, and stabilization in learning.

Traditional perceptual learning studies have hundreds or even thousands of training trials per day. Here we show that only 40 trials of daily practice were enough to trigger an improvement comparable to 1080 trials of daily practice. This nding supports a memory-reactivation framework for perceptual learning. Throughout multiple training sessions, the learning e ects gained from individual training sessions transform from short- to long-term memory via a process named consolidation (McGaugh, 2000; Wright & Sabin, 2007). After the initial memory consolidation has been established, brief reactivations may trigger reconsolidation-like processes to improve the existing perceptual memory (Amar-Halpert et al., 2017; Bang et al., 2018). Amar-Halpert et al. (2017) have shown that decreasing the standard training amount (from 252 trials to 5 trials) on day 2 to day 4 led to no change in the overall learning e ect. However, further decreasing the training from a standard to a small amount on day 1 led to a signi cant decrease in the overall learning e ect. In the present study, all the subjects underwent a pretest of 400 trials for each condition, which established the new memory. After that, 40 trials of daily training were su cient to reactivate the memory for reconsolidation. Our results indicate that motion perceptual learning, as a speci c kind of procedural memory, might function via a consolidation-reactivation mechanism.

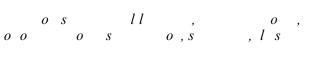
In contrast, overtraining might be detrimental to perceptual learning, which was referred to as perceptual deterioration (Mednick et al., 2002, 2005). Induced by too much training, perceptual deterioration is possibly due to sensory adaptation (Censor et al., 2006), strengthening less e cient neuronal connections and accumulating noise in the brain network (Censor & Sagi, 2008), or changes in the ability for attention to selectively enhance the responses of low-level sensory neurons (Mednick et al., 2005). In our studala50(studehe)-0547: deteriora tlle1.2(y)-301.1(th (Lengyel & Fiser, 2019). In the present study, stimuli variation was introduced at the pretest and post-test stages, and was kept constant across the groups. This test gave subjects a su cient amount of training (400 trials for each direction) over a relatively broad feature space (four motion direction with 0°, 30°, 60°, and 90° o set from the trained direction). During 8 training days, subjects received training on a speci ed motion direction with a near-threshold variation. Note that we used continuous staircases for each training day; except for the rst staircase, each staircase started with the threshold derived from the preceding staircase. Our training protocol resembles the single prolonged staircase used in Hung and Seitz (2014) and other perceptual learning studies (Jehee et al., 2012; Schoups et al., 1995). Therefore, by increasing the training amount, we increased the number of near-threshold trials. Because such training over-represents a particular feature in the space, increasing the daily training amount leads to over tting and greater speci city. Consistent with Hung and Seitz (2014), our results showed that prolonged training at threshold a ects transfer in perceptual learning. It is worth mentioning that the account of stimuli variation and speci city in perceptual learning is reminiscent of Eleanor Gibson and James Gibson's ecological approach to perception, which suggested more variability led to a more general learning result (Gibson & Gibson, 1955). The 1 QUEST group might undergo a larger variation, therefore showing more transfer than the 27 QUEST group.

Perceptual learning with ne feature discrimination tasks usually results in high speci city and less transfer (e.g., Liu, 1999; Shiu & Pashler, 1992). Liu (1999) reported that, although learning in a motion discrimination task with a 3° directional di erence was strongly speci c to the training direction, learning transferred to new motion directions with an 8° directional di erence. The idea that training precision modulates the degree of transfer in perceptual learning has been suggested in earlier psychophysical studies (Ahissar & Hochstein, 1997; Jeter et al., 2009) and is recently modeled using a deep neural network (Wenliang & Seitz, 2018).

In addition, our present ndings provided the rst piece of evidence for the long-term modulation e ect of training amount on speci city, which persisted for at least 2 weeks after training. Future studies are needed to evaluate how the degree of transfer was modulated under di erent manipulations of the stimuli variations, such as changing the range of stimuli in the feature space, changing the probability distribution of stimuli (e.g., the ratio between the training amount of the trained and untrained features), and changing the time point the variation is presented (e.g., early, middle, or late training phase).

Training with a small daily amount provides a promising alternative protocol for perceptual learning

studies in the future. When deciding on the training amount in practice, the following factors should be taken into consideration. (1) Generalization. Based on the current and previous learning studies with a motion or orientation discrimination paradigm, a larger daily training amount leads to less transfer to the untrained feature or spatial location. If one aims to induce a learning e ect highly speci c to the trained feature for a baseline control, a classical training paradigm with hundreds or thousands of daily training trials would be required. Otherwise, fewer trials (e.g., 40 trials or 5 trials in the middle phase of learning in Amar-Halpert et al. [2017]) in a daily session may be a choice for e ciency. (2) Stability. According to the hyperstabilizes account of overlearning, the learning e ect becomes less susceptible to interference with an increasing daily k0 Tc 70TJ 1.090il1 4 TD -&



## Α

Supported by the National Natural Science Foundation of China (31930053, 31671168, 31421003, and 31971031), Beijing Municipal Science and Technology Commission (Z181100001518002), and Beijing Academy of Arti cial Intelligence (BAAI).

## Commercial relationships: none.

Corresponding authors: Fang Fang and Nihong Chen. Email: ang@pku.edu.cn, nihongch@tsinghua.edu.cn. Address: School of Psychological and Cognitive Sciences, Peking University, Beijing 100871, People's Republic of China.

Aberg, K. C., Tartaglia, E. M., & Herzog, M. H. (2009). Perceptual learning with Chevrons requires a minimal number of trials, transfers to untrained directions, but does not require sleep. so
s , 49(16), 2087–2094.

- Ahissar, M., & Hochstein, S. (1997). Task di culty and the speci city of perceptual learning. *38* (6631), 401–406.
- Amar-Halpert, R., Laor-Maayany, R., Nemni, S., Rosenblatt, J. D., & Censor, N. (2017). Memory reactivation improves visual perception. *os , 20*(10), 1325–1328.
- Ashley, S., & Pearson, J. (2012). When more equals less: Overtraining inhibits perceptual learning owing to lack of wakeful consolidation. *o s o o l o d o l s*, *2* 9(1745), 4143–4147.
- Banai, K., & Lavner, Y. (2014). The e ects of training length on the perceptual learning of time-compressed speech and its generalization. *o l o o s l o o , 13* (4), 1908–1917.
- Bang, J. W., Shibata, K., Frank, S. M., Walsh, E.
  G., Greenlee, M. W., Watanabe, T., ... Sasaki,
  Y. (2018). Consolidation and reconsolidation
  share behavioural and neurochemical mechanisms. *o* , 2(7), 507–513.
- Censor, N., Karni, A., & Sagi, D. (2006). A link between perceptual learning, adaptation and sleep. *s o s* , *4* (23), 4071–4074.
- Censor, N., & Sagi, D. (2008). Bene ts of e cient consolidation: Short training enables long-term

resistance to perceptual adaptation induced by intensive testing. *s o s , 48*(7), 970–977.

- Censor, N., Sagi, D., & Cohen, L. G. (2012). Common mechanisms of human perceptual and motor learning. *s os , 13*(9), 658–664.
- Chen, N., Bi, T., Zhou, T., Li, S., Liu, Z., & Fang, F. (2015). Sharpened cortical tuning and enhanced cortico-cortical communication contribute to the long-term neural mechanisms of visual motion perceptual learning. *o* , *115*, 17–29.
- Chung, S. T. L., Levi, D. M., & Li, R. W. (2006). Learning to identify contrast-de ned letters in peripheral vision. *s o s , 4* (6–7), 1038–1047.
- Fahle, M., & Poggio, T. (Eds.). (2002).lL. Cambridge, MA: MIT Press.
- Fox, O., Karni, A., & Adi-Japha, E. (2016). The consolidation of a motor skill in young adults with ADHD: Shorter practice can be better. *s lo l s l s*, *51 52*, 135–144.
- Frangou, P., Emir, U. E., Karlaftis, V. M., Nettekoven, C., Hinson, E. L., Larcombe, S., ... Kourtzi, Z. (2019). Learning to optimize perceptual decisions through suppressive interactions in the human brain. *Co* o s, 10(1), 474.
- Gibson, J. J., & Gibson, E. J. (1955). Perceptual learning: Di erentiation or enrichment? *s d o l , 2*(1), 32–41.
- Goldhacker, M., Rosengarth, K., Plank, T., & Greenlee, M. W. (2014). The e ect of feedback on performance and brain activation during perceptual learning. *s o s , 99*, 99–110.
- Hung, S.-C., & Seitz, A. R. (2014). Prolonged Training at Threshold Promotes Robust Retinotopic Speci city in Perceptual Learning. *o l o os , 34*(25), 8423–8431.
- Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2007). Inverting houses and textures: Investigating the characteristics of learned inversion e ects. s os, 4 (27), 3350–3359.
- Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2009). How much practice is needed to produce perceptual learning? *s o s , 49*(21), 2624– 2634.
- Hussain, Z., Bennett, P. J., & Sekuler, A. B. (2012). Versatile perceptual learning of textures after variable exposures. *s o s , 1*, 89–94.
- Jehee, J. F. M., Ling, S., Swisher, J. D., van Bergen, R. S., & Tong, F. (2012). Perceptual learning selectively re nes orientation representations in early visual cortex. *o l o os , 32* (47), 16747–16753.

- Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines speci city of perceptual learning. *o l o s o* , *9*(3), 1–1.
- Jeter, Pamela E., Dosher, B. A., Liu, S.-H., & Lu, Z.-L. (2010). Speci city of perceptual learning increases with increased training. *s o s , 50*(19), 1928–1940.
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *, 3* 5(6443), 250–252.
- Lengyel, G., & Fiser, J. (2019). The relationship between initial threshold, learning, and generalization in perceptual learning. *o l o s o , 19*(4), 28.
- Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *o so o l o so so , 9* (24), 14085–14087.
- Liu, L., Kuyk, T., & Fuhr, P. (2007). Visual search training in subjects with severe to profound low vision. *s o s , 4*, 2627–2636.
- McGaugh, J. L. (2000). Memory—A century of consolidation. , 28 (5451), 248–251.
- Mednick, S. C., Arman, A. C., & Boynton, G. M. (2005). The time course and speci city of perceptual deterioration. *o so o l o so so o j 102*(10), 3881–3885.
- Mednick, Sara C., Nakayama, K., Cantero, J. L., Atienza, M., Levin, A. A., Pathak, N., ... Stickgold, R. (2002). The restorative e ect of naps on perceptual deterioration. *os* , 5(7), 677–681.
- Molloy, K., Moore, D. R., Sohoglu, E., & Amitay, S. (2012). Less is more: Latent learning is maximized by shorter training sessions in auditory perceptual learning. *Lo*, (5), e36929.
- Ofen, N., Moran, A., & Sagi, D. (2007). E ects of trial repetition in texture discrimination. *s o s , 4* (8), 1094–1102.
- Ofen-Noy, N., Dudai, Y., & Karni, A. (2003). Skill learning in mirror reading: How repetition determines acquisition. *Co s , 1* (2), 507–521.
- Polat, U. (2009). Making perceptual learning practical to improve visual functions. *s o s , 49*(21), 2566–2573.
- Robertson, E. M. (2018). Memory instability as a gateway to generalization. *Lo do* , *1* (3), e2004633.
- Roth, D. A.-E. (2005). A latent consolidation phase in auditory identic cation learning: Time in the

awake state is su cient. L & o , 12(2), 159-164.

- Savion-Lemieux, T., & Penhune, V. B. (2005). The e ects of practice and delay on motor skill learning and retention. *l s , 1 1*(4), 423–431.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation speci city and monocularity. *o l o s d o , 483*(3), 797–810.
- Shibata, K., Sasaki, Y., Bang, J. W., Walsh, E. G., Machizawa, M. G., & Tamaki, M., . . .Watanabe, T. (2017). Overlearning hyperstabilizes a skill by rapidly making neurochemical processing inhibitory-dominant. *os* , 20(3), 470–475.
- Shiu, L.-P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *o* & *s o s s*, *52*