

## Preliminary evidence for a role of the personality trait in visual perceptual learning



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### ABSTRACT

Recent research has shown that reinforcement can facilitate visual perceptual learning (VPL), but no study has examined the relations between individual differences in reinforcement sensitivity and VPL. This study tested the hypothesis that when monetary incentive was involved, the personality traits of harm avoidance and reward dependence (HA and RD, two measures of reinforcement sensitivity) would be linked to VPL performance. We trained two groups of subjects with a visual motion direction discrimination task for six days. The experimental group received monetary incentive feedback, whereas the control group received non-monetary feedback. As expected, the score of HA was negatively correlated with VPL for the experimental group, but not for the control group. RD was not a significant predictor. These results were discussed in terms of the role of non-perceptual factors such as reinforcement, personality, higher cognition, and motivation in VPL.

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### 1. Introduction

Organisms have an innate drive to maximize reward and minimize punishment (Daw & Frank, 2009). Therefore, reward and punishment can be used to reinforce learning. For decades, it has been generally assumed that the effects of reinforcement are limited to behavioral learning (Martin, 1963; Sigmund, Hauert, & Nowak, 2001; Stephens, 1933) and would not be relevant to visual perceptual learning (VPL) because VPL involves only the early stage of visual processing as shown in its specificity to the training location, feature, and eye (Bao, Yang, Rios, He, & Engel, 2010; Fahle & Morgan, 1996; Furmanski & Engel, 2000; Karni & Sagi, 1991; Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). Recent models, however, have suggested that VPL also depends on the modulation of later stages of processing (Bejjanki, Beck, Lu, & Pouget, 2011; Doshier, Jeter, Liu, & Lu, 2013; Petrov, Doshier, & Lu, 2005; Sasaki, Nanez, & Watanabe, 2010; Watanabe & Sasaki, 2015; Xiao et al., 2008; Yotsumoto & Watanabe, 2008; Zhang et al., 2010). For example, the reweighting model assumes that VPL occurs in the change of

read-out connections to the decision unit (Bejjanki et al., 2011; Doshier et al., 2013; Petrov et al., 2005). In consistent with this idea, neuroimaging studies have revealed that VPL involves higher decision-making brain regions (e.g., lateral intraparietal area and medial frontal cortex), suggesting the involvement of reinforcement learning in some VPL tasks (Kahnt, Grueschow, Speck, & Haynes, 2011; Law & Gold, 2009).

Indeed several studies have provided evidence for a role of reinforcement in VPL (Franko, Seitz, & Vogels, 2010; Seitz, Kim, & Watanabe, 2009; Seitz & Watanabe, 2003; Xue, Zhou, & Li, 2015). For example, participants deprived of food and water showed improved VPL for the trained stimuli paired with the liquid rewards (Seitz et al., 2009). Money, the typical reinforcement for human beings, has also been found to influence VPL with higher monetary reward leading to better VPL performance (Weil et al., 2010; Xue et al., 2015). Weil et al. (2010) further reported that monetary feedback increased brain activity in reward related areas (e.g. the striatum and frontal cortex). Moreover, monetary reinforcement has been shown to affect somatosensory processing, with bigger monetary feedback resulting in better performance and stronger brain activations compared to smaller monetary or performance (non-monetary) feedback (Pleger, Blankenburg, Ruff, Driver, & Dolan, 2008; Pleger et al., 2009). It is speculated that money (and other forms of reinforcement) triggers the reinforcement signals in the higher-level system, which then makes the sensory system more sensitive to stimuli and facilitates sensory

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learning (Sasaki et al., 2010; Seitz & Watanabe, 2005; Shibata, Sagi, & Watanabe, 2014; Watanabe & Sasaki, 2015). This speculation is supported by neuroimaging evidence of reinforcement-modulated activation in the visual cortex (Arsenault, Nelissen, Jarraya, & Vanduffel, 2013; Noudoost & Moore, 2011; Serences, 2008; Zaldivar, Rauch, Whittingstall, Logothetis, & Goense, 2014).

However, individuals vary in their sensitivity to reinforcement in the environment (Elliot, 2008). This raises a question: Does the effect of reinforcement in VPL vary across individuals? The traits of reinforcement sensitivity can be measured by two dimensions of the Temperament and Character Inventory (TCI) (Cloninger, Przybeck, Svrakic, & Wetzler, 1994). Harm avoidance (HA) represents behavioral inhibition in response to signals of punishment and reward dependence (RD) describes the importance of reward in behavioral maintenance. HA and RD have been found to be related to reinforcement learning in educational and industrial psychology (Elliot & McGregor, 1999; Elliot & Sheldon, 1997; Joyce et al., 2007; Pessoa, 2009; Roskes, Elliot, Nijstad, & De Dreu, 2013; Van Dijk, Seger-Guttman, & Heller, 2013).

The traits of reinforcement sensitivity have been associated with cognitive control and decision-making and their underlying brain regions such as the frontal cortex and insula (Cohen, Schoene-Bake, Elger, & Weber, 2009; Gardini, Cloninger, & Venneri, 2009; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003). Despite the strong evidence that reinforcement affects VPL and individuals vary in reinforcement sensitivity with consequences for learning performance, no study thus far has examined the role of reinforcement sensitivity in VPL. A study of the relationship between the personality traits of reinforcement sensitivity and VPL performance can further our understanding of VPL and its modeling. For example, its results could indicate whether VPL depends only on the early visual cortex or on both low- and high-level systems and whether VPL models need to include “soft wired” factors such as motivational and personal factors.

In the current study, we trained two groups of subjects with a visual motion direction discrimination task for six days. The experimental group received performance-dependent monetary incentive. To examine whether reinforcement sensitivity was particularly relevant to VPL when monetary incentive was involved, the control group received non-monetary feedback. The personality traits of HA and RD were measured with TCI (Cloninger et al., 1994). Based on the literature review described above, we hypothesized that (1) the monetary group would show better VPL performance than the non-monetary group because of the reinforcement value of money; (2) the personality trait of RD would be positively related to VPL performance because high RD individuals would be more sensitive to the reward in the task (i.e., triggering more activations in higher-level areas and releasing stronger reward signals, which could facilitate VPL (Seitz et al., 2009; Xue et al., 2015)); (3) the personality trait of HA would be negatively related to VPL performance because high HA individuals are sensitive to punishment (i.e., showing higher anxiety, fear and stress and reducing the activations of higher-level areas which would have a negative effect on learning (Bishop, Duncan, Brett, & Lawrence, 2004; Hare et al., 2008; Hermann et al., 2007)); and (4) the associations between personality traits and VPL performance would be stronger for the monetary condition than the non-monetary condition, again because of the reinforcement value of money.

## 2. Methods

### 2.1. Subjects

Eighty healthy college students were recruited in this study and seventy-four of them completed the whole experimental procedure.

One subject was removed from analysis because of the strongly deviant questionnaire score (more than three standard deviations from the group mean). The remaining seventy-three subjects were randomly assigned to two groups: the experimental group (monetary group,  $n = 40$ , 42.5% female, mean age = 22.9 years,  $SD = 2.6$ ) and the control group (non-monetary group,  $n = 33$ , 51.5% females, mean age = 23.4 years,  $SD = 2.7$ ). All subjects were naive to visual perceptual learning. They had normal or corrected-to-normal vision and reported no history of neurological problems. Informed consent was obtained from all subjects. Experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences.

### 2.2. Questionnaire

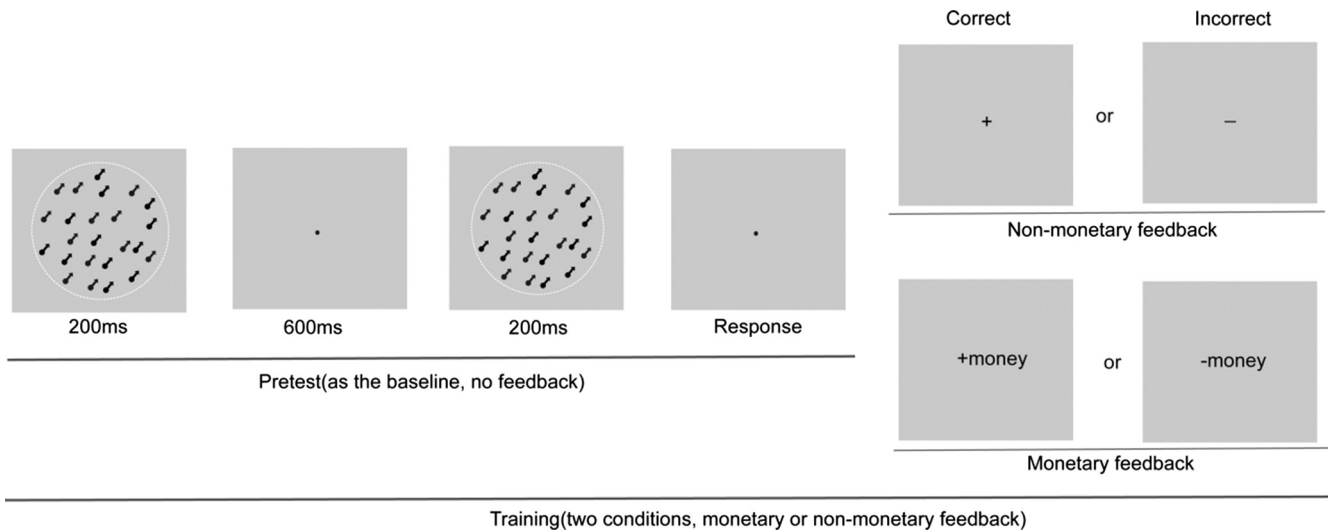
Reinforcement sensitivity was assessed using two dimensions (HA and RD) of the revised version of the Temperament and Character Inventory (TCI-R) (Cloninger, 1987; Cloninger et al., 1994). HA included four subscales: anticipatory worry & pessimism vs. uninhibited optimism (HA1, 11 items), fear of uncertainty (HA2, 7 items), shyness with strangers (HA3, 7 items), and fatigability & asthenia (HA4, 8 items). RD also included four subscales: sentimentality (RD1, 8 items), openness to warm communication vs aloofness (RD2, 10 items), attachment (RD3, 6 items), and dependence (RD4, 6 items).

### 2.3. Stimuli and apparatus

We used a classic visual motion direction discrimination task (Ball & Sekuler, 1982, 1987; Chen et al., 2015), in which two random-dot kinematograms (RDKs) were presented at fovea location (stimuli duration: 200 ms; interval duration: 600 ms). In each RDK, 400 black dots moved in the same direction within an  $8^\circ$  aperture on a gray background (dot diameter:  $0.1^\circ$ ; speed:  $10^\circ/s$ ). Subjects were asked to judge the direction of the second RDK relative to the first one (clockwise or counter-clockwise). Stimuli were presented on a gamma-corrected CRT monitor ( $1024 \times 768$  resolution at 85 Hz). Subjects viewed the stimuli from a distance of 57 cm. Their head position was stabilized using a head and chin rest. The monitor's mean luminance was  $59 \text{ cd/m}^2$ . Throughout the experiment, subjects were asked to fixate on a small black circle presented at the center of the visual stimuli (also the center of the monitor).

### 2.4. Procedure

Subjects first completed the TCI subscales mentioned before, followed by a pretest and six daily training sessions. In the pretest, all subjects performed the same motion direction discrimination task without any feedback (as the baseline). Each subject was randomly assigned two directions chosen from four directions:  $22.5^\circ$ ,  $67.5^\circ$ ,  $292.5^\circ$  and  $337.5^\circ$  (reference directions,  $0^\circ$  was the vertical direction in upper visual field and all four directions were in the upper visual field). The pretest included 12 blocks of 68 trials for each direction. In each trial, two displays of RDKs, with one in the reference direction and the other in the test direction (reference direction  $\pm$  offset direction), were separated by an interval. The offset direction in each trial was manipulated under a 2-down-1-up staircase rule. In total, 45 levels of offset direction were predetermined for later use in the staircase. These levels increased logarithmically from  $0.3^\circ$  to  $20^\circ$  (the greater the level, the bigger the offset direction, the easier the trial). The starting offset direction for each staircase was 2.5 times the expected threshold based on the results from a pilot testing. The initial step size for the staircase was 3 levels, and then decreased to 1 level after 3 reversals.



**Fig. 1.** Experimental protocol. All subjects went through the same pretest without feedback as the baseline. During training, experimental and control groups received monetary and non-monetary feedback respectively.

For training, subjects were randomly assigned to either the experimental or the control group. Subjects were trained with one of the two directions they were assigned to during the pretest. Training consisted of a daily session (about 1 h) of 12 staircases of 68 trials. The starting offset direction for each staircase was 2.5 times the threshold (see the detail of how threshold calculated in the next paragraph) of the former session. For the control or non-monetary group, “+” or “-” would be presented at the end of each trial to indicate correct or incorrect response, respectively. For the experimental or monetary group, “+[money]” or “-[money]” would be presented after each trial to indicate how much money was given as a rewarded for a correct response or lost as a punishment for an incorrect response. The monetary value was based on how difficult the current trial relative to subject’s pretest threshold. The more difficult the trial was, the greater the reward or the less the punishment. Specifically, for trials with bigger offset direction than the threshold obtained from the pretest (i.e., very easy trials), the potential reward was 1 cent (RMB) and the potential punishment was 16 cents. For trials with the same or smaller offset direction than the pretest threshold, the amounts of potential reward and punishment were calculated as follows: reward = (pretest level – current level)/pretest level \* 15 + 1 for correct responses; punishment = 15 – (pretest level – current level)/pretest level \* 15 for incorrect responses. “15” was determined based on the results of the pilot study to ensure that the experimental group would obtain the same overall amount of money as the control group. The cumulative amount of money won was shown after each block. The experimental protocol was shown in Fig. 1.

Weibull functions were fit to the data pooled from all staircases at the training direction in the pretest and training sessions. Threshold was defined as the motion direction at which the best-fitting function estimated performance to be 82% correct. For each subject, the threshold of each day was then normalized by the initial threshold in the pretest as the performance for further calculation.

### 3. Results

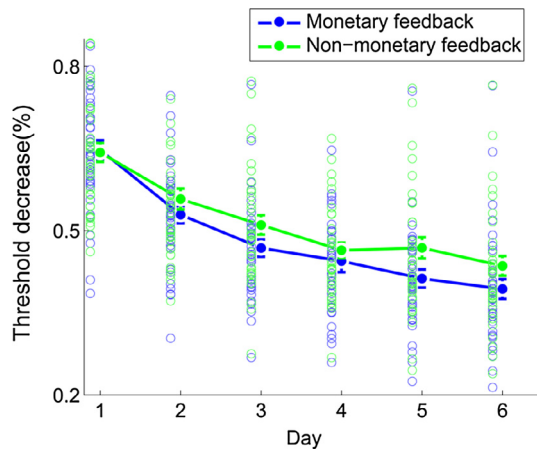
Fig. 2 shows the mean performance by group and training day. To test whether the two groups performed differently, a mixed 2 (groups) \* 6 (sessions) multi-factorial ANOVA was conducted. The

main effect of session was significant:  $F(3.546, 251.798) = 152.144$ ,  $p = 0.000$ , indicating significant training effects. The interaction between group and session was marginally significant:  $F(3.546, 251.798) = 2.250$ ,  $p = 0.072$ . The main effect of group was not significant:  $F(1, 71) = 2.448$ ,  $p = 0.122$ . However, simple effects analysis showed significant group differences for Day5 and marginally significant group differences for Day3 and Day6, favoring the experimental group.

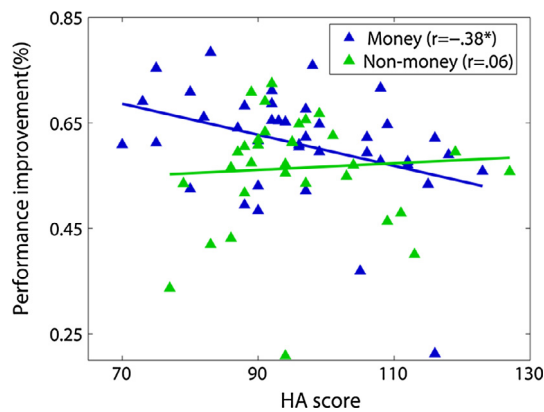
To examine the relationship between reinforcement sensitivity and the performance in VPL in the two groups, we conducted two sets of analyses. First, we calculated Pearson correlations between reinforcement sensitivity measures (HA and RD) and overall performance improvement across the whole training period in the two groups. There was no significant correlation between RD and performance improvement. HA had a significant negative correlation with performance improvement in the monetary group ( $p = 0.015$ , corrected  $p = 0.03$ ). Lower HA was associated with greater performance improvement. The corresponding correlation was not significant in the control group ( $p = 0.74$ ) (see Fig. 3). We further used the Fisher  $r$ -to- $z$  transformation and assessed the significance of the differences in correlations between the two groups using one-tailed  $t$  test (because of our specific directional hypothesis). There was a significant difference between the two correlation coefficients ( $p = 0.03$ , one-tailed).<sup>2</sup>

Second, we also analyzed the data by splitting the subjects into high and low levels of reinforcement sensitivity and conducted 2 (monetary vs. non-monetary groups) \* 2 (high vs. low levels in RD or HA) ANOVAs. For RD, the main effect of group was marginally significant,  $F(1, 69) = 3.31$ ,  $p = 0.073$ , with the monetary group performing better than the non-monetary group. The main effect of RD and the interaction between group and RD were not significant:  $F(1, 69) = 0.90$ ,  $p = 0.35$  and  $F(1, 69) = 0.55$ ,  $p = 0.46$ , respectively. For HA, the main effect of group was marginally significant as found for the analysis for RD. The main effect of HA was not significant:  $F(1, 69) = 0.236$ ,  $p = 0.628$ , whereas the interaction between

<sup>2</sup> For readers interested in the relationship between HA and the performance in VPL in other days, we also did the daily analysis. Results showed that there were significant or marginally significant negative correlations between HA and subjects’ VPL performance for Day2 ( $p = 0.008$ ), Day4 ( $p = 0.055$ ) and Day5 ( $p = 0.086$ ). The respective correlations for the control group were not significant. Further Fisher  $r$ -to- $z$  transformation and assessment showed there were significant or marginally significant differences between correlation coefficients of experimental and control groups for Day1 ( $p = 0.02$ ), Day2 ( $p = 0.004$ ) and Day4 ( $p = 0.10$ ).



**Fig. 2.** Threshold decrease in VPL during six training days relative to pretest in the two conditions. Error bars represent the standard error of the mean across subjects.



**Fig. 3.** Scatter plots of correlations between HA and performance improvement in VPL in the two conditions. (Note: \* $p < 0.05$ .)

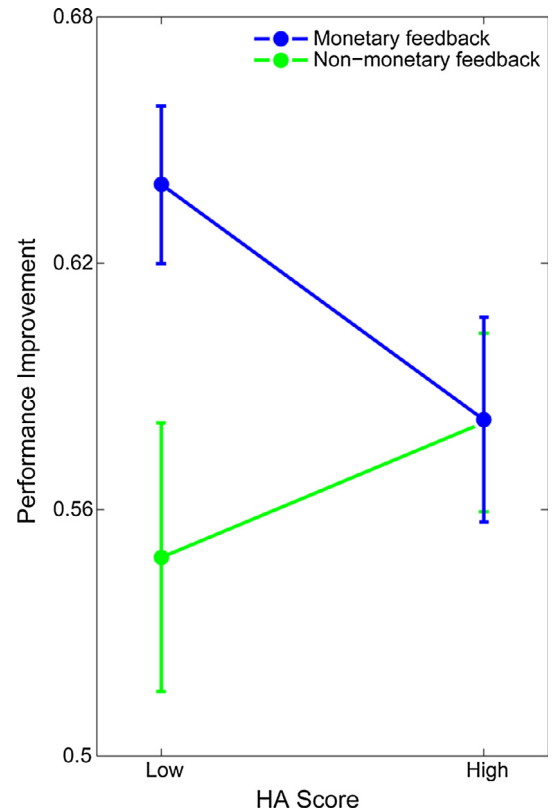
group and HA was marginally significant,  $F(1, 69) = 3.21$ ,  $p = 0.078$ . Fig. 4 shows the mean scores. Simple effects analysis showed that low-HA individuals had marginally greater performance improvement than the high-HA individuals in the monetary group ( $p = 0.08$ ), but not in the non-monetary group ( $p = 0.42$ ).

#### 4. Discussion

The purpose of the current study was to investigate whether personality traits relevant to reinforcement sensitivity were associated with VPL when monetary incentive was involved. It was found that when monetary incentive was involved, the personality trait of harm avoidance (HA) was negatively related to subjects' performance and the negative association was marginally stronger in the monetary condition than the non-monetary condition. No significant result was found for the other personality trait, reward dependence (RD).

Several previous studies have documented the effect of money on VPL (Weil et al., 2010; Xue et al., 2015) as well as somatosensory processing (Pleger et al., 2008, 2009). Consistent with these results, we found that the monetary feedback group showed greater improvement in performance than the non-monetary group. We interpret this result as money's role in triggering more reinforcement signals that enhance the sensitivity of the visual system and hence facilitate VPL.

Our results further showed that HA was negatively associated with VPL when monetary incentive was involved (i.e., higher HA,



**Fig. 4.** Performance improvement of low and high HA individuals in VPL in the two conditions. Error bars represent the standard error of the mean across subjects.

lower VPL performance). HA is the tendency to learn to avoid punishment (Cloninger, 1987) and is characterized by easy induction of negative emotions (i.e., fear and anxiety). High HA has been linked to psychiatric disorders such as anxiety and mood disorders (Blairy et al., 2000; Kusunoki et al., 2000; Smith, Duffy, Stewart, Muir, & Blackwood, 2005; Starcevic, Uhlenhuth, Fallon, & Pathak, 1996). At the brain level, HA has been correlated with the structure and function of brain areas related to emotion and decision making, including the insular, amygdala, frontal, and parietal cortices (Buckholz et al., 2008; Gardini et al., 2009; Paulus et al., 2003; Westlye, Bjornebekk, Grydeland, Fjell, & Walhovd, 2011). In the context of this study, we speculated that high HA produced negative emotions such as anxiety, fear, and stress, which would tax cognitive regulation, reduce top-down control, and prevent VPL (Bishop et al., 2004; Hare et al., 2008; Hermann et al., 2007). Our results suggest that VPL is subject to modulation by a combination of factors such as reinforcement (involving motivation) and personality traits. It should be noted that one previous study found that the negative emotion of stress as well as the trait of anxiety did not affect performance on a visual texture discrimination task (Aberg, Clarke, Sandi, & Herzog, 2012). However, in that study, the negative cue was exposed after (not during) the training, which might have attenuated the effect. Future research should directly examine the effect of the timing of negative cues.

The current study did not find any relationship between the personality trait of RD (reward dependence) and VPL performance, perhaps because all subjects were well compensated in the monetary incentive group, which might have produced a ceiling effect. Future research should adjust the reward levels to test this speculation.

One limitation of this study should be mentioned. The monetary group used graded feedback whereas the non-monetary group used binary feedback. This difference in feedback might have

contributed to the condition difference in VPL performance. Previous studies have compared the effects of various feedbacks on VPL (Aberg & Herzog, 2012; Herzog, Ewald, Hermens, & Fahle, 2006; Herzog & Fahle, 1997, 1999; Liu, Doshier, & Lu, 2014; Petrov, Doshier, & Lu, 2006), but the graded and binary feedback. In motor learning, one study revealed the same effect of the binary and graded feedback (Galea, Mallia, Rothwell, & Diedrichsen, 2015). Future research may consider using multiple '+'s or '-'s to indicate difficulty levels in the non-monetary condition.

To our knowledge, this is the first study to report a relationship between a personality trait and VPL. Our study has two implications for VPL research. First, our results supported the VPL models that incorporate the higher cognition brain areas (Doshier et al., 2013; Sasaki et al., 2010; Watanabe & Sasaki, 2015). Second, our results showed that motivational and personality factors needed to be considered when attempting to optimize VPL.

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## References

- Aberg, K. C., Clarke, A. M., Sandi, C., & Herzog, M. H. (2012). Trait anxiety and post-learning stress do not affect perceptual learning. *Neurobiology of Learning and Memory*, *98*, 246–253.
- Aberg, K. C., & Herzog, M. H. (2012). Different types of feedback change decision criterion and sensitivity differently in perceptual learning. *Journal of Vision*, *12*.
- Arsenault, J. T., Nelissen, K., Jarraya, B., & Vanduffel, W. (2013). Dopaminergic reward signals selectively decrease fMRI activity in primate visual cortex. *Neuron*, *77*, 1174–1186.
- Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, *218*, 697–698.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*, 953–965.
- Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*, 15080–15084.
- Bejjanki, V. R., Beck, J. M., Lu, Z. L., & Pouget, A. (2011). Perceptual learning as improved probabilistic inference in early sensory areas. *Nature Neuroscience*, *14*, 642–648.
- Bishop, S., Duncan, J., Brett, M., & Lawrence, A. D. (2004). Prefrontal cortical function and anxiety: Controlling attention to threat-related stimuli. *Nature Neuroscience*, *7*, 184–188.
- Blairy, S., Massat, I., Staner, L., Le Bon, O., Van Gestel, S., Van Broeckhoven, C., ... Mendlewicz, J. (2000). 5-HT<sub>2a</sub> receptor polymorphism gene in bipolar disorder and harm avoidance personality trait. *American Journal of Medical Genetics*, *96*, 360–364.
- Buckholtz, J. W., Callicott, J. H., Kolachana, B., Hariri, A. R., Goldberg, T. E., Genderson, M., ... Meyer-Lindenberg, A. (2008). Genetic variation in MAOA modulates ventromedial prefrontal circuitry mediating individual differences in human personality. *Molecular Psychiatry*, *13*, 313–324.
- 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. *Neuroimage*.
- Cloninger, C. R. (1987). A systematic method for clinical description and classification of personality variants. *Archives of General Psychiatry*, *44*, 573–588.
- Cloninger, C. R., Przybeck, T., Svrakic, D. M., & Wetzel, R. D. (1994). *The temperament and character inventory (TCI): A guide to its development and use*. St Louis, MO: Center for Psychobiology of Personality, Washington University.
- Cohen, M. X., Schoene-Bake, J. C., Elger, C. E., & Weber, B. (2009). Connectivity-based segregation of the human striatum predicts personality characteristics. *Nature Neuroscience*, *12*, 32–34.
- Daw, N. D., & Frank, M. J. (2009). Reinforcement learning and higher level cognition: Introduction to special issue. *Cognition*, *113*, 259–261.
- Doshier, B. A., Jeter, P., Liu, J., & Lu, Z. L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences USA*, *110*, 13678–13683.
- Elliot, A. J. (2008). *Handbook of avoidance and approach motivation*. New York: Psychology.
- Elliot, A. J., & McGregor, H. A. (1999). Test anxiety and the hierarchical model of approach and avoidance achievement motivation. *Journal of Personality and Social Psychology*, *76*, 628–644.
- Elliot, A. J., & Sheldon, K. M. (1997). Avoidance achievement motivation: A personal goals analysis. *Journal of Personality and Social Psychology*, *73*, 171–185.
- Fahle, M., & Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. *Current Biology*, *6*, 292–297.
- Franko, E., Seitz, A. R., & Vogels, R. (2010). Dissociable neural effects of long-term stimulus-reward pairing in macaque visual cortex. *Journal of Cognitive Neuroscience*, *22*, 1425–1439.
- Furmanski, C. S., & Engel, S. A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. *Vision Research*, *40*, 473–484.
- Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. *Nature Neuroscience*, *18*, 597–602.
- Gardini, S., Cloninger, C. R., & Venneri, A. (2009). Individual differences in personality traits reflect structural variance in specific brain regions. *Brain Research Bulletin*, *79*, 265–270.
- Hare, T. A., Tottenham, N., Galvan, A., Voss, H. U., Glover, G. H., & Casey, B. J. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. *Biological Psychiatry*, *63*, 927–934.
- Hermann, A., Schafer, A., Walter, B., Stark, R., Vaill, D., & Schienle, A. (2007). Diminished medial prefrontal cortex activity in blood-injection-injury phobia. *Biological Psychology*, *75*, 124–130.
- Herzog, M. H., Ewald, K. R., Hermens, F., & Fahle, M. (2006). Reverse feedback induces position and orientation specific changes. *Vision Research*, *46*, 3761–3770.
- Herzog, M. H., & Fahle, M. (1997). The role of feedback in learning a vernier discrimination task. *Vision Research*, *37*, 2133–2141.
- Herzog, M. H., & Fahle, M. (1999). Effects of biased feedback on learning and deciding in a vernier discrimination task. *Vision Research*, *39*, 4232–4243.
- Joyce, P. R., McKenzie, J. M., Carter, J. D., Rae, A. M., Luty, S. E., Frampton, C. M., & Mulder, R. T. (2007). Temperament, character and personality disorders as predictors of response to interpersonal psychotherapy and cognitive-behavioural therapy for depression. *British Journal of Psychiatry*, *190*, 503–508.
- Kahnt, T., Grueschow, M., Speck, O., & Haynes, J. D. (2011). Perceptual learning and decision-making in human medial frontal cortex. *Neuron*, *70*, 549–559.
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences USA*, *88*, 4966–4970.
- Kusunoki, K., Sato, T., Taga, C., Yoshida, T., Komori, K., Narita, T., ... Ozaki, N. (2000). Low novelty-seeking differentiates obsessive-compulsive disorder from major depression. *Acta Psychiatrica Scandinavica*, *101*, 403–405.
- Law, C. T., & Gold, J. I. (2009). Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nature Neuroscience*, *12*, 655–663.
- Liu, J., Doshier, B., & Lu, Z. L. (2014). Modeling trial by trial and block feedback in perceptual learning. *Vision Research*, *99*, 46–56.
- Martin, B. (1963). Reward and punishment associated with the same goal response: A factor in the learning of motives. *Psychological Bulletin*, *60*, 441–451.
- Noudoost, B., & Moore, T. (2011). Control of visual cortical signals by prefrontal dopamine. *Nature*, *474*, 372–375.
- Paulus, M. P., Rogalsky, C., Simmons, A., Feinstein, J. S., & Stein, M. B. (2003). Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *Neuroimage*, *19*, 1439–1448.
- Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences*, *13*, 160–166.
- Petrov, A. A., Doshier, B. A., & Lu, Z. L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, *112*, 715–743.
- Petrov, A. A., Doshier, B. A., & Lu, Z. L. (2006). Perceptual learning without feedback in non-stationary contexts: Data and model. *Vision Research*, *46*, 3177–3197.
- Pleger, B., Blankenburg, F., Ruff, C. C., Driver, J., & Dolan, R. J. (2008). Reward facilitates tactile judgments and modulates hemodynamic responses in human primary somatosensory cortex. *Journal of Neuroscience*, *28*, 8161–8168.
- Pleger, B., Ruff, C. C., Blankenburg, F., Kloppel, S., Driver, J., & Dolan, R. J. (2009). Influence of dopaminergically mediated reward on somatosensory decision-making. *PLoS Biology*, *7*, e1000164.
- Pourtois, G., Rauss, K. S., Vuilleumier, P., & Schwartz, S. (2008). Effects of perceptual learning on primary visual cortex activity in humans. *Vision Research*, *48*, 55–62.
- Roskes, M., Elliot, A. J., Nijstad, B. A., & De Dreu, C. K. (2013). Time pressure undermines performance more under avoidance than approach motivation. *Personality and Social Psychology Bulletin*, *39*, 803–813.
- Sasaki, Y., Nanez, J. E., & Watanabe, T. (2010). Advances in visual perceptual learning and plasticity. *Nature Reviews Neuroscience*, *11*, 53–60.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, *483*(Pt 3), 797–810.
- Seitz, A., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, *9*, 329–334.
- Seitz, A. R., Kim, D., & Watanabe, T. (2009). Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron*, *61*, 700–707.
- Seitz, A. R., & Watanabe, T. (2003). Psychophysics: Is subliminal learning really passive? *Nature*, *422*, 36.
- Serences, J. T. (2008). Value-based modulations in human visual cortex. *Neuron*, *60*, 1169–1181.
- Shibata, K., Sagi, D., & Watanabe, T. (2014). Two-stage model in perceptual learning: Toward a unified theory. *Annals of the New York Academy of Sciences*, *1316*, 18–28.

- Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, *52*, 582–588.
- Sigmund, K., Hauert, C., & Nowak, M. A. (2001). Reward and punishment. *Proceedings of the National Academy of Sciences USA*, *98*, 10757–10762.
- Smith, D. J., Duffy, L., Stewart, M. E., Muir, W. J., & Blackwood, D. H. (2005). High harm avoidance and low self-directedness in euthymic young adults with recurrent, early-onset depression. *Journal of Affective Disorders*, *87*, 83–89.
- Starcevic, V., Uhlenhuth, E. H., Fallon, S., & Pathak, D. (1996). Personality dimensions in panic disorder and generalized anxiety disorder. *Journal of Affective Disorders*, *37*, 75–79.
- Stephens, J. M. (1933). Punishment and reward in learning. *Science*, *78*, 60.
- Van Dijk, D., Seger-Guttman, T., & Heller, D. (2013). Life-threatening event reduces subjective well-being through activating avoidance motivation: A longitudinal study. *Emotion*, *13*, 216–225.
- Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*, 197–221.
- Weil, R. S., Furl, N., Ruff, C. C., Symmonds, M., Flandin, G., Dolan, R. J., ... Rees, G. (2010). Rewarding feedback after correct visual discriminations has both general and specific influences on visual cortex. *Journal of Neurophysiology*, *104*, 1746–1757.
- Westlye, L. T., Bjornebekk, A., Grydeland, H., Fjell, A. M., & Walhovd, K. B. (2011). Linking an anxiety-related personality trait to brain white matter microstructure: Diffusion tensor imaging and harm avoidance. *Archives of General Psychiatry*, *68*, 369–377.
- Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, *18*, 1922–1926.
- Xue, X., Zhou, X., & Li, S. (2015). Unconscious reward facilitates motion perceptual learning. *Visual Cognition*, *23*, 161–178.
- Yotsumoto, Y., & Watanabe, T. (2008). Defining a link between perceptual learning and attention. *PLoS Biology*, *6*, e221.
- Zaldivar, D., Rauch, A., Whittingstall, K., Logothetis, N. K., & Goense, J. (2014). Dopamine-induced dissociation of BOLD and neural activity in macaque visual cortex. *Current Biology*, *24*, 2805–2811.
- Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience*, *30*, 12323–12328.