

# Action video game play facilitates the development of better perceptual templates

Vikranth R. Bejjanki<sup>a,b,1</sup>, Ruyuan Zhang<sup>a,1</sup>, Renjie Li<sup>a</sup>, Alexandre Pouget<sup>a,c</sup>, C. Shawn Green<sup>d</sup>, Zhong-Lin Lu<sup>e</sup>, and Daphne Bavelier<sup>a,f,2</sup>

<sup>a</sup>Department of Brain and Cognitive Sciences and Center for Visual Science, University of Rochester, Rochester, NY 14627; <sup>b</sup>Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544; <sup>c</sup>Department of Basic Neurosciences, University Medical Center, University of Geneva, Geneva CH-1205, Switzerland; <sup>d</sup>Department of Psychology, University of Wisconsin–Madison, Madison, WI 53706; <sup>e</sup>Center for Brain and Cognitive Sciences and Department of Psychology, The Ohio State University, Columbus, OH 43210; and <sup>f</sup>Faculté de Psychologie et des Sciences de l'Éducation, University of Geneva, Geneva CH-1205, Switzerland

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**The field of perceptual learning has identified changes in perceptual templates as a powerful mechanism mediating the learning of statistical regularities in our environment. By measuring threshold-vs.-contrast curves using an orientation identification task under varying levels of external noise, the perceptual template model (PTM) allows one to disentangle various sources of signal-to-noise changes that can alter performance. We use the PTM approach to elucidate the mechanism that underlies the wide range of improvements noted after action video game play. We show that action video game players make use of improved perceptual templates compared with nonvideo game players, and we confirm a causal role for action video game play in inducing such improvements through a 50-h training study. Then, by adapting a recent neural model to this task, we demonstrate how such improved perceptual templates can arise from reweighting the connectivity between visual areas. Finally, we establish that action gamers do not enter the perceptual task with improved perceptual templates. Instead, although performance in action gamers is initially indistinguishable from that of nongamers, action gamers more rapidly learn the proper template as they experience the task. Taken together, our results establish for the first time to our knowledge the development of enhanced perceptual templates following action game play. Because such an improvement can facilitate the inference of the proper generative model for the task at hand, unlike perceptual learning that is quite specific, it thus elucidates a general learning mechanism that can account for the various behavioral benefits noted after action game play.**

action video games | perceptual templates | external noise method | learning | probabilistic inference

Playing action video games substantially improves performance in a range of attentional, perceptual, and cognitive tasks. In the case of attention, playing action video games has been shown to result in a variety of enhancements, such as a faster visual search rate, a reduction in the size of the attentional blink, better change detection, and an increase in the number of items that can be simultaneously tracked (1–3). These changes in attentional control are also accompanied by enhanced performance in visual tasks such as crowding acuity (4), backward masking (5), and contrast sensitivity (6), as well as by improved performance in high-level cognitive tasks such as mental rotation (7) and multitasking (8, 9). Such benefits even seem to carry over to real-world domains, because pilots and laparoscopic surgeons have been shown to outperform their peers after fast-paced, action-packed video game training (10–12). Together, these results suggest that action game play, unlike perceptual learning, which is usually specific to the learned task (13), may act to increase signal-to-noise ratio and facilitate improved distractor exclusion during perceptual processing (14), which is notable because such changes hold the potential to affect, for the better, a wide range of skills. Indeed, the importance of signal-to-noise ratio and distractor exclusion is highlighted by

multiple reports that indicate that reductions in these abilities might underlie a range of broad deficits, such as those seen with amblyopia (15–17), low vision (18), aging (19, 20), or dyslexia (21).

There are, however, no systematic studies of the mechanisms through which action video game play may lead to increased signal-to-noise ratio and to enhanced distractor exclusion. Here we make use of the perceptual template model (PTM) used previously to identify how attention (22) and perceptual learning (23) increase signal-to-noise ratio. Briefly, improvements in performance may result from a reduction in internal noise—for instance, by turning up the gain on the outputs of channels coding for signal-relevant information, or from a more systematic elimination of processing inefficiencies through the use of perceptual templates better-tuned to the task at hand. The PTM is ideally suited to distinguish between these two possibilities. By determining the signal strength necessary for participants to perform an identification task under different levels of image noise, also termed external noise, the PTM allows us to distinguish between a reduction in internal noise, which predicts performance improvements at low levels of external noise but not at high levels of external noise, vs. the development of better-tuned perceptual templates, which predicts an overall improvement in performance at all levels of external noise. The present study provides the first experimental evidence, to our knowledge,

## Significance

Recent advances in the field of learning have identified improvement of perceptual templates as a key mechanism underlying training-induced performance enhancements. Here, using a combination of psychophysics and neural modeling, we demonstrate that this mechanism—improved learning of perceptual templates—is also engaged after action video game play. Habitual action gamers or individuals trained to play action games demonstrate perceptual templates better tuned to the task and stimulus at hand than control groups, a difference shown to emerge as learning proceeds. This work further illustrates the importance of the development of improved perceptual templates as a mechanism mediating training and transfer effects and provides a novel account for the surprisingly broad transfer of performance enhancements noted after action game play.

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The authors declare no conflict of interest.

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<sup>1</sup>V.R.B. and R.Z. contributed equally to this work.

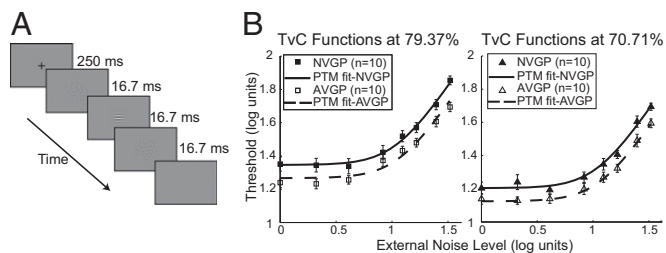
<sup>2</sup>To whom correspondence should be addressed. Email: Daphne.Bavelier@unige.ch.

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that playing action video games results in the use of improved perceptual templates. Furthermore, we show that the improved perceptual templates are not the result of direct “transfer” from action video games to the psychophysical tasks. Training on action video games does not endow players with better templates from the start of exposure to the perceptual task, unlike what is witnessed after perceptual learning of the same task, and unlike what would be predicted if video game training had resulted in a reduction in internal noise. Instead, action gaming seems to promote an enhanced ability to learn new templates (“learning to learn”), thereby providing direct support for a general mechanism that can account for the wide transfer of performance improvements noted after action game play. Specifically, such an improvement in action gamers’ ability to learn proper perceptual templates guarantees that they will represent and process task-relevant perceptual information more efficiently, while excluding task-irrelevant sources of variability.

## Results

**Experiment 1: Performance in External Noise in Action Video Game Players.** Expert action video game players (AVGPs) were compared with sex- and age-matched nonaction game players (NVGPs) as they performed an orientation identification task under varying levels of external noise as in ref. 24. AVGPs and NVGPs were chosen using overt recruitment and screening criteria identical to those used in our previous work (6). Each trial in the orientation identification task consisted of a Gabor signal frame presented between two external noise frames. The Gabor could be tilted 2° clockwise or counterclockwise from horizontal and participants had to indicate the orientation of the Gabor signal (Fig. 1A). The procedure and methods were similar to those of Lu and Doshier (24), with eight external noise contrast levels being used and the contrast of the Gabor signal being adaptively adjusted using interleaved staircases set to track the 79.37% and 70.71% threshold (see *Materials and Methods* and *Supporting Information* for further details). To improve our estimates of the thresholds, each participant carried out two runs of the task. Participants received auditory feedback on their performance. A 2\*2\*8\*2 ANOVA was performed with action game experience (AVGP/NVGP) as a between-subject factor; run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. Overall, AVGPs showed lower contrast thresholds than NVGPs

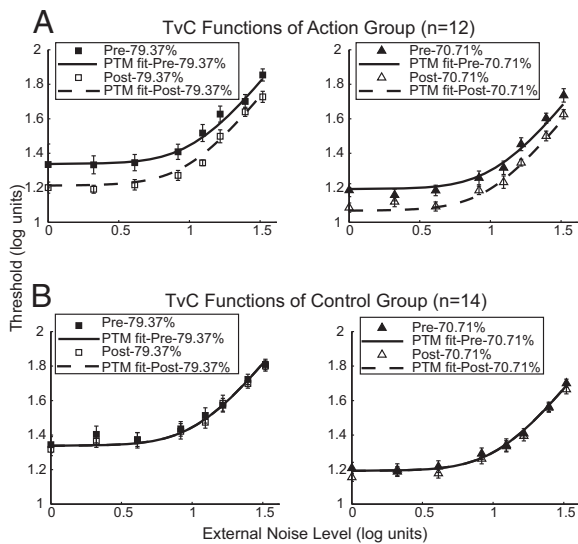


**Fig. 1.** AVGPs show improved performance in an orientation identification task. (A) An illustration of a typical trial. After a central fixation cross was presented, a Gabor signal frame appeared sandwiched between two external noise frames. Participants had to indicate the orientation of the Gabor signal, clockwise or counterclockwise from horizontal. (B) Signal contrast thresholds as a function of external noise contrast level (plotted in log-log units), at the two levels of performance, for AVGPs ( $n = 10$ ) vs. NVGPs ( $n = 10$ ). AVGPs showed overall lower signal contrast thresholds than NVGPs, indicating better performance in the task. The curves show the PTM fits and reveal a downward shift in the TvC curve from NVGPs to AVGPs, consistent with AVGPs’ developing a better perceptual template for the task. Error brackets are SEM.

( $F_{1,18} = 5.82$ ,  $P < 0.05$ ,  $\eta^2 = 0.24$ ), as shown in Fig. 1B (see *Supporting Information* for full statistics).

Although the analysis above indicates generally superior performance in AVGPs, it is insufficient to characterize the mechanisms that underlie the observed group differences and in particular to distinguish whether the improved performance observed in action game players was due to internal noise reduction or due to better-tuned perceptual templates. To clarify the exact source of the AVGP advantage, the PTM was used to fit the threshold vs. external noise contrast (TvC) data in each group (solid and dashed lines in Fig. 1B). We found that the improved performance in AVGPs was best fit (see *Supporting Information* for model-fitting details) with a combination of improved external noise exclusion (by 22%) and additive internal noise reduction (by 20%), resulting in a downward shift of the TvC curves across all levels of external noise—a pattern of results consistent with improved perceptual templates. Note that this pattern of results could, in principle, also be explained by a change in multiplicative internal noise in the PTM. However, the ratio of contrast thresholds between the two groups (AVGP/NVGP) was found to be similar at the two performance levels (79.37% and 70.71% accuracy) ( $1.26 \pm 0.03$  vs.  $1.22 \pm 0.02$ ), thereby ruling out multiplicative internal noise change, which would predict a greater ratio at the more stringent performance level (23). Instead, the near-uniform downward shift in TvC curves from NVGPs to AVGPs at both performance levels, indicating improved performance at all levels of external noise, is best explained by AVGPs’ developing better perceptual templates for this task (25).

**Experiment 2: Performance in External Noise After Action Video Game Training.** To unambiguously establish the influence of action gaming in this finding, we conducted an intensive training study on a small sample of NVGPs. During training (50 h over 9 wk with 5–6 h/wk; see *Materials and Methods* and *Supporting Information* for details of the training procedure), participants in the experimental group (action-game trainees) were required to play action video games whereas those in the control group (control-game trainees) played commercially available, non-action video games. A fluid intelligence measure was administered at the start of the study to check that the two groups did not differ in fluid cognition ( $P > 0.4$ ). Furthermore participants were asked to fill out a “flow” questionnaire (26) to document their engagement with their assigned games and the two groups also did not differ on the flow scale ( $P > 0.7$ ). A few days before (pretest) and after (posttest) game training, participants in both groups carried out the same orientation identification task as described above. A 2\*2\*2\*8\*2 ANOVA was performed with group (action/control) as a between-subject factor; test (pre/post), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. Across all participants we found a significant interaction between test (pre/post) and group (action/control) ( $F_{1,24} = 8.66$ ,  $P < 0.01$ ,  $\eta^2 = 0.27$ ), indicating larger posttraining improvements in action-game trainees’ orientation identification performance, compared with control-game trainees (Fig. 2). Indeed, considering each group separately, action-game trainees showed significantly lower signal contrast thresholds after training ( $F_{1,11} = 21.46$ ,  $P < 0.001$ ,  $\eta^2 = 0.66$ ), reflecting improved performance, whereas control-game trainees showed no significant change in signal contrast thresholds after training ( $F_{1,13} = 0.57$ ,  $P = 0.46$ ,  $\eta^2 = 0.04$ ). In the action video game trainees PTM fits showed improvements in both external noise reduction (by 17%) and additive internal noise reduction (by 29%), which is again most consistent with the use of better perceptual templates after training. Conversely, the best-fitting PTM model showed no change in either internal noise or external noise reduction as



**Fig. 2.** Improved orientation identification performance as a result of action video game training (A) vs. control game training (B). Overall, action-trained participants ( $n = 12$ ) showed larger posttraining improvements in orientation identification performance than control trainees ( $n = 14$ ). Curves represent PTM fits and confirm improvements in external noise reduction and additive internal noise reduction consistent with the use of better perceptual templates after action game training.

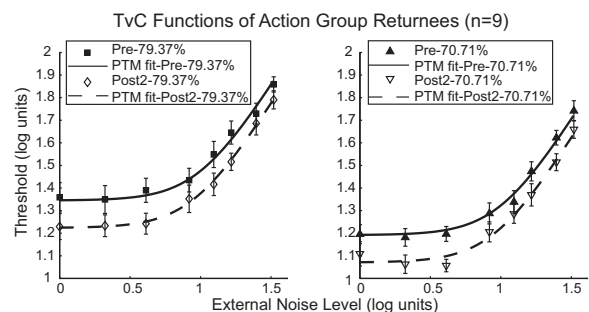
a result of training with control video games. Finally, the ratios between contrast thresholds at pre- and posttest remained relatively stable across the two performance levels ( $1.35 \pm 0.04$  at 79.37% correct vs.  $1.25 \pm 0.03$  at 70.71% correct), again rendering a change in multiplicative noise an unlikely mechanism. Taken together, these findings are best explained by action-trained participants' developing better perceptual templates for the task following training than participants trained with non-action video games, thereby providing compelling evidence for the direct effect of action video game play in improving the exclusion of both internal and external noise.

We also examined the extent to which the action-trained improvements were retained several months after the end of training. A subset of the control- and action-game-trained participants from the training study were brought back between 3 mo to 1 y after the end of the training and retested (post2) on the orientation identification task. A  $2 \times 2 \times 2 \times 8 \times 2$  ANOVA was performed with group (action/control) as a between-subject factor; test (pre/post2), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. The interaction between test (pre/post2) and group (action/control) was marginally significant and in the predicted direction ( $F_{1,14} = 3.25$ ,  $P = 0.09$ ,  $\eta^2 = 0.19$ ), indicating that action trainees continued to show improved performance in the task months to a year after training. A  $2 \times 2 \times 8 \times 2$  ANOVA considering only the data of action-game trainees verified significantly lower signal contrast thresholds at post2 than those observed before training ( $F_{1,8} = 21.64$ ,  $P < 0.01$ ,  $\eta^2 = 0.73$ ; Fig. 3), making it clear that the benefit from training on action games is long-lasting (see full statistics and further details in *Supporting Information*). Moreover, the ratio of contrast thresholds between pre and post2 did not change across the two performance levels ( $1.32 \pm 0.04$  at 79.37% correct vs.  $1.29 \pm 0.04$  at 70.71% correct), further ruling out any interpretation of the action trainees' performance improvement in terms of multiplicative noise changes. Fitting the data with the PTM confirmed that action-game-trained participants continued to show improvements in both additive

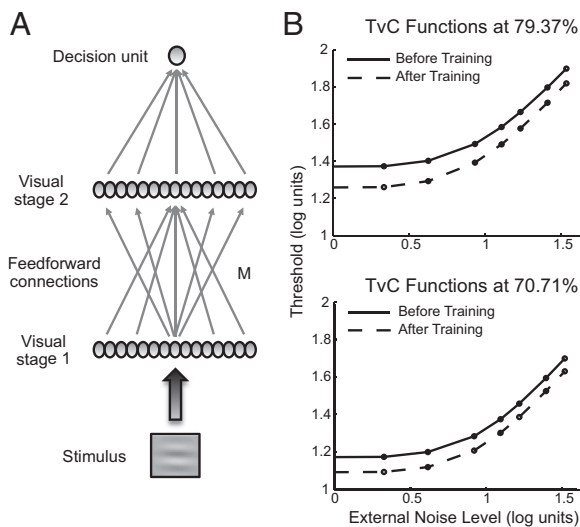
internal noise and external noise exclusion, thereby confirming that the improved perceptual templates developed as a result of action video game training were long-lasting.

**Neural Model: Exploring the Neural Basis of Action-Trained Improvements in Performance in External Noise.** Playing action video games leads to enhanced exclusion of both external and internal noise, the typical signature of improved perceptual templates according to the PTM. In this view, AVGPs are able to better tune their perceptual template for the task and stimuli at hand, and thus process task-relevant visual information more efficiently, while excluding task-irrelevant noise. To explore the neural implementation of this behavioral improvement, we adapted a recent probabilistic neural model of orientation selectivity (27) to our task and asked which types of network changes could best explain the effect of action game play (Fig. 4A). We simulated the network using stimuli similar to those used in our training study and obtained network TvC curves using an analytical approach combined with numerical simulations (as in ref. 27; see *Materials and Methods* and *Supporting Information* for further details). Action video game-induced changes in performance were well-modeled by changing the feed-forward connectivity between the visual stages in this network. A change in this single parameter led to a decrease in network signal contrast thresholds and a near-uniform downward shift in network TvC curves (Fig. 4B), as was observed in our behavioral data. Crucially, to obtain these results the feed-forward connections had to be changed in a manner that moved them closer to a matched filter for the stimulus. In a purely linear system such a move toward a matched filter would be mathematically equivalent to improving the perceptual template. However, because our network is nonlinear the equivalence with the perceptual template matching theory is only approximate. The uniform shift in network TvC curves nonetheless indicates that this is indeed a close approximation.

**Experiment 3: Dynamics of Perceptual Template Learning in AVGPs.** Although the results thus far indicate that action video game play results in better-tuned perceptual templates, it is unclear whether action gaming endows AVGPs with templates better tuned for the psychophysical task from the outset or whether action gaming instead results in an enhanced ability to rapidly learn perceptual templates tuned to the task at hand. The majority of the literature to date has treated the enhanced performance seen as a result of action video game experience as an example of direct transfer of learning—in other words, the skills and knowledge acquired during action video game play result in immediate benefits to performance when exposed to a new task. However, we have recently suggested (28) that the latter



**Fig. 3.** Action video game-induced improvements in performance were retained several months after training. A subset of action group participants ( $n = 9$ ) from the training study were brought back several months later and retested on the orientation identification task (post2). The curves represent PTM fits and confirm that action-trained participants continued to show improved perceptual templates several months after the end of training.



**Fig. 4.** Neural model of the improvements in orientation identification performance, observed as a result of action video game experience. (A) Schematic of the neural architecture used to simulate performance in the orientation identification task. The model consists of two visual stages, which simulate the representation and transmission of orientation information across neural layers, followed by a decoding stage that simulates the observer's decision about the target orientation. (B) Network TvC curves (solid and dashed lines) were obtained for the two performance levels used in the training study. Changing the feed-forward connections (M) between the visual stages of the network, in a manner that moved them closer to a matched filter for the stimulus, led to a decrease in the network signal contrast thresholds and a near-uniform downward shift in network TvC curves, as observed after action game play.

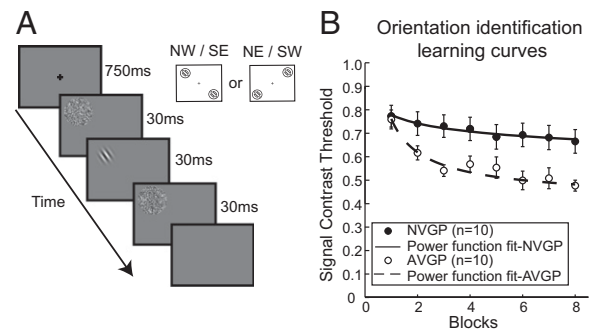
“learning to learn” hypothesis, and not direct transfer, may in fact underlie the AVGP advantage seen in many tasks. Under this hypothesis, when confronted with a new psychological task AVGPs are able to learn the specific statistics of the task more readily, thus developing better perceptual templates through their experience with the psychophysical task itself. This hypothesis has not been directly tested. Thus, we next exploited a well-studied perceptual learning paradigm (Gabor orientation identification with a fixed level of external noise) to test the hypothesis that AVGPs are able to learn task statistics faster than NVGPs.

Ten AVGPs and 10 NVGPs underwent eight sessions (across 2 d) of a Gabor orientation identification task (28), which was slightly different from that used in experiments 1 and 2 (Fig. 5A). The changes to the task (e.g., using a single fixed level of external noise, presenting the stimuli peripherally rather than centrally, using  $\pm 12^\circ$  away from reference angle; *Materials and Methods*) were made to maximize the ease with which the dynamics of learning can be tracked and thus group differences detected. Briefly, on each trial participants were presented with an oriented Gabor sandwiched between two external noise frames (Fig. 5A). The Gabor signal was presented at one of two peripheral spatial locations and in one of two possible orientations ( $12^\circ$  clockwise or counterclockwise from a fixed reference orientation, either  $-35^\circ$  or  $+55^\circ$ , the same procedure as in ref. 28). All parameters were counterbalanced and matched across groups. Participants indicated whether the Gabor was oriented clockwise or counterclockwise from the implicit reference angle, with auditory feedback being provided after each choice. The contrast of the Gabor on each trial was controlled by one of four independent, interleaved staircases (2/1 and 3/1 staircases for each of the two stimulus locations), with the final 75% contrast threshold being calculated by averaging across the four staircases.

Threshold data were entered into a 2 (group: AVGP/NVGP)  $\times$  8 (session: 1–8) ANOVA. Significant main effects of session ( $F_{7,126} = 13.42$ ,  $P < 0.001$ ,  $\eta^2 = 0.427$ ) and group ( $F_{1,18} = 7.54$ ,  $P < 0.05$ ,  $\eta^2 = 0.295$ ) were observed, indicating participants' contrast thresholds decreased as the task proceeded and that the contrast thresholds of AVGPs were overall lower than NVGPs. Most importantly, and consistent with the learning to learn hypothesis, a significant interaction was observed between group and session ( $F_{7,126} = 3.16$ ,  $P < 0.01$ ,  $\eta^2 = 0.149$ ). AVGP and NVGP thresholds were similar in the first session, but the performance of AVGPs improved more rapidly than that of NVGPs across subsequent sessions (Fig. 5B and *Supporting Information*). To better characterize differences in the dynamics of learning in the two groups, we then fit an elaborated power function to the threshold data, which allowed initial performance and rate of learning to be quantified for both groups (see details in *Supporting Information*). Again, consistent with the learning to learn hypothesis, in the best-fitting power function initial performance was roughly equivalent in AVGPs and NVGPs, but AVGPs showed a faster learning rate ( $P < 0.001$ ).

## Discussion

Through a series of experiments and modeling work, we show here that action video game play results in enhanced perceptual templates and does so by facilitating the rapid learning of task-relevant statistics. The PTM framework we use here is closely related to the inference process implemented in the neural network presented (27). In this view, the nervous system represents probability distributions over task-relevant variables, which are initially inferred from sensory measurements. For instance, during orientation identification this would involve inferring a probability distribution over orientation from the retinal image (29). Such probability distributions can be inferred by inverting the generative model of the sensory data—the probabilistic model of how an image is generated given an orientation. Our data support the hypothesis that action video game training



**Fig. 5.** AVGPs show faster learning in an orientation identification task. (A) An illustration of a typical trial. After a central fixation cross was presented, a Gabor signal frame appeared in one of two peripheral locations and was sandwiched between two external noise frames. Participants had to indicate the orientation of the Gabor signal, clockwise or counterclockwise from an implicit reference angle ( $-35^\circ$  or  $55^\circ$ ). Reference angles and locations of stimuli (northeast/southwest quadrants or northwest/southeast quadrants; see inset) were counterbalanced across participants and matched between groups. (B) Signal contrast thresholds as a function of learning sessions for AVGPs ( $n = 10$ ) vs. NVGPs ( $n = 10$ ). Both groups showed comparable performance at the outset of the task but as learning proceeded the two groups' performance gradually diverged, with AVGPs eventually showing lower signal contrast thresholds overall than NVGPs, indicating better performance by the end of the task. The curves show the elaborated power function fits to the data and reveal a markedly faster learning rate for the AVGPs in comparison with the NVGPs, consistent with AVGPs' more rapidly developing a better perceptual template for the task at hand. Error brackets are SEM.

generally improves the ability to learn such task-relevant generative models. This learning to learn hypothesis stands in contrast to the proposal that the knowledge acquired during action video game experience provides direct and immediate benefits. We further show through neural simulations that the outcome of such learning can be understood as modifying the feed-forward connections between the visual processing stages in the model, so as to more closely match the stimulus, or equivalently improve the quality of inference during orientation identification (27).

The present experiments take advantage of the external noise method to document for the first time to our knowledge better perceptual templates after action video game play. Based on simulations within a neural model we have previously argued that playing action video games improves the probabilistic inference performed by neural circuits, without affecting internal noise, which in the parlance of signal detection theory translates to an increase in the signal at the decision stage with no change in the noise (30). However, until now, there was no experimental evidence that action video game play did so, because the decision-making task used in this previous work did not allow us to distinguish between internal noise reduction and better-tuned perceptual templates. Experiments 1 and 2 resolve this issue by showing that, at least in the case of orientation selectivity, the behavioral improvement triggered by action video game training is due to improved perceptual templates. Furthermore, experiment 3 documents for the first time, to our knowledge, a faster rate of perceptual learning in AVGPs than in NVGPs, a main prediction of the learning to learn account. The ability to more quickly learn task-relevant statistics allows action gamers to better infer the proper generative model for the task at hand, which in turn results in improved inference about task-relevant variables and enhanced perceptual sensitivity and/or reliability. Such a general learning mechanism, unlike the usually task-specific improvements following perceptual learning, can account for the wide range of behavioral benefits noted after action game play. Thus, AVGPs may not be endowed with better vision, better task-switching abilities, or better attentional tracking abilities per se, but instead they benefit from having the ability to quickly learn on the fly the diagnostic features of the tasks they face so as to readily excel on them.

## Materials and Methods

**Ethics Statement.** All experimental protocols were approved by the Research Subjects Review Board at the University of Rochester. Informed written consent was obtained from all participants. None of these experiments has been previously reported in the literature.

### Experiment 1: Performance in External Noise in AVGPs.

**Participants.** Ten male NVGPs (age range 21–25 y old, mean age 22.7 y) and 10 male AVGPs (age range 20–25 y old, mean age 22.3 y) participated in this experiment. All participants had normal or corrected-to-normal vision, provided informed written consent, and were paid \$8 per hour. AVGPs and NVGPs were chosen using overt recruitment and screening criteria identical to those used in our previous work (6). Although overt recruitment may reflect population bias or trigger Hawthorne-type effects in the recruited groups (31), the rationale for overt recruitment is threefold. First, covert recruitment is extremely costly because AVGPs and NVGPs represent respectively only 5–10% of the population each. Thus, to enroll 10 AVGPs and 10 NVGPs as we did here, through covert recruitment, we would have to enroll about 200 subjects, rather than 20, incurring a cost in subject fee and staff that is hard to motivate given the two other shortcomings discussed next. Second, several studies have used covert recruitment and have replicated the findings observed with overt recruitment; for example, Dye et al. (32) covertly enrolled more than 100 children and confirmed the effects of action video game play on attentional skills. Third, comparisons involving an expert population are always weakened by the possibility that expertise may have arisen from a preselection bias, rather than vice versa. For instance, participants who develop better perceptual templates on the fly may just be more likely to play action video games. Consideration of this and other similar biases calls for training studies, in which participants are randomly

assigned to at least two active training protocols, as was done in experiment 2 of the current study.

**Stimuli and procedure.** The stimuli and task were similar to those used in Lu and Doshier (24), except that the size ( $1.5 \times 1.5^\circ$ ), degree of tilt ( $\pm 2^\circ$ ), and reference angle (horizontal reference) were different. A typical trial is shown in Fig. 1A. Eight external noise contrast levels (0, 2.1, 4.1, 8.3, 12.4, 16.5, 24.8, and 33%) were used in an interleaved fashion, and for each level of external noise two interleaved staircase procedures were used, with step sizes of 10% of the current contrast level, so as to converge upon two different levels of performance—79.37% and 70.71% correct—corresponding to a three-down-one-up or a two-down-one-up staircase, respectively. Signal contrast threshold was defined as the mean of all of the reversals, excluding the first four. For each three-down-one-up staircase there were 100 trials and for each two-down-one-up staircase there were 80 trials, leading to a total of 1,440 trials per session. To improve our estimates, each participant carried out two such sessions in a row, for a total duration of 1.5 h.

### Experiment 2: Performance in External Noise After Action Video Game Training.

**Participants.** NVGPs (selected using the same video game experience criterion as in experiment 1 above) were recruited to participate in this training experiment and divided randomly into an action-trained group and a control-trained group. The final sample of participants included 12 action group participants (9 males and 3 females, 20–28 y old, mean age 23.9 y) and 14 control group participants (5 males and 9 females, 20–28 y old, mean age 22.6 y). Note that a few other participants had to be excluded owing to an inability to carry out the tasks, play the games, or comply with the training schedule ([Supporting Information](#)).

**Video game training procedure.** For both groups, training consisted of playing two games for a total of 50 h (25 h per game). Participants were allowed to play for a maximum of 2 h per day and a maximum of 10 h per week and were required to finish the 50 h of training in no more than 9 wk. Participants in the action group played *Unreal Tournament 2004* (Epic Games) in “Death Match” mode, during the first 25 h and *Call of Duty 2* (Activision) during the second 25 h. Participants in the control group played *The Sims 2* (2004, Electronic Arts Inc.) for the first half of training and *Restaurant Empire* (2003, Enlight Software Ltd.) for the second half of training.

**Stimuli and procedure for pre- and posttest tasks.** Participants were tested a few days before and a few days after the training period (designated as pretest and posttest, respectively) on the same orientation identification under external noise task as that used in experiment 1.

**Further tests.** All participants were asked to fill out a “flow” questionnaire as defined by Csikszentmihalyi (26) to confirm that participants in both groups were equally engaged with their assigned games. We did not, however, administer a direct test of participants’ expectation to excel, leaving open the possibility that, despite equal engagement of the two groups with their respective training games, action trainees may have expected to benefit more. In addition, all participants were administered the Raven Advanced Progressive Matrices (RAPM) at pre- and posttest to ensure that participants across groups did not a priori differ significantly in fluid intelligence and that both training regimens led to comparable effects on fluid intelligence. We found no significant differences between the two groups on either measure (see [Supporting Information](#) for further details).

**Evaluating long-term retention of action-trained improvements in performance.** A subset of the participants (nine action group participants and seven control group participants) who completed the training study were brought back to the laboratory a few months after the end of their training. All of the participants confirmed resuming their pretest habits and thus engaging in almost no video game play at the end of their 50 h of training. They were again tested (designated as posttest2) on the orientation identification under external noise task used in the pretest and posttest (see main text and Fig. 3 for results from action group returnees and [Supporting Information](#) for results from control group returnees).

### Neural Model: Exploring the Neural Basis of Action-Trained Improvements in Performance in External Noise.

We adapted a recent probabilistic neural model of orientation selectivity (27) to our task and asked which type of network changes could best explain the performance improvements observed with action-trained participants.

**Stimulus design.** Network simulations were run using stimuli similar to those used in experiments 1 and 2 (described above). Each stimulus image consisted of a centrally presented oriented Gabor signal that was tilted  $\pm 2^\circ$  around the horizontal reference and extended over  $2.3 \times 2.3^\circ$  of visual angle. Noise gray level values, corresponding to the eight external noise levels used in the training study, were added to the signal gray level values on a pixel-by-pixel basis to generate the noise-injected image.

**Network architecture.** The network model, adapted from Bejjanki et al. (27), consists of two visual processing stages that simulate the representation and transmission of orientation information across neural layers, followed by a decoding stage that simulates the observer's decision about the target orientation. The first visual stage simulates the processing of stimulus information early in the visual system akin to the retina and the lateral geniculate nucleus. The input layer includes uncoupled grids of ON and OFF center ganglion cells modeled as difference-of-Gaussian filters, which are driven by the noisy stimulus image. The output of each filter is passed through a smooth nonlinearity and used to drive cells in visual stage 1, which includes uncoupled, spiking neurons generating Poisson spikes. The output spikes from stage 1 cells are pooled using oriented Gabor function receptive fields, the orientations of which are uniformly distributed along a circle. This pooled output is then used as input to the second visual stage, which simulates a cortical visual area such as V1. This visual stage 2 represents an orientation hypercolumn—a set of neurons with receptive fields centered at the same spatial location but with different preferred orientations—of Linear Nonlinear Poisson (LNP) neurons, coupled through lateral connections. The final stage of the network, which simulates the decision stage, includes a single unit, with connections to each of the cells in visual stage 2, which takes as input the activities of stage 2 units and which gives as output an estimate of the orientation of the stimulus. Although the format of the representations considered in the present neural implementation corresponds to early visual stages of processing, we are not in a position to determine whether these may correspond to the actual processing levels at which action game play acts. Rather, the goal of this neural implementation is to demonstrate how changes in feed-forward connectivity, as information travels from one visual area to another, naturally give rise to enhanced perceptual templates, by allowing improved probabilistic inference.

**Computing orientation identification performance and deriving TvC curves.** As in Bejjanki et al. (27), we use a recently derived analytic expression for linear Fisher information in a population of LNP neurons with a fixed decoder, to compute the Fisher information, and hence the identification threshold, at the decision stage in response to a given stimulus. We compute Fisher information at the decision stage using stimuli with 17 signal contrast levels—10, 12, 14, 16, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 80, and 90%—and with the eight levels of external noise used in our behavioral experiments. We

then derive network TvC curves by computing an iso-information contour, for a value of information that is equivalent to the percent correct criterion used in the behavioral experiments (computed via signal detection theory), through the resulting information matrix (see *Supporting Information* and ref. 27 for further details).

### Experiment 3: Dynamics of Perceptual Template Learning in AVGPs.

**Participants.** Ten NVGPs (six male and four female; 19–31 y old, mean age 25.1 y) and 10 AVGPs (seven male and three female; 18–26 y old, mean age 20.1 y) participated in the experiment. All participants were chosen using similar procedures and screening criteria as those used in experiment 1. None had participated in experiments 1 or 2.

**Stimuli and procedures.** The stimuli and task were similar to those used in Jeter et al. (28), except that only the high noise contrast (33%) and low precision ( $\pm 12^\circ$ ) stimuli were used. A typical trial is illustrated in Fig. 5A. On each trial, stimuli were presented in the periphery at one of two locations (in the northeast or southwest quadrants for half the participants and in the northwest or southeast quadrants for the other half; Fig. 5A, *Inset*). The reference orientation ( $-35^\circ/+55^\circ$ ) and the diagonal in which the stimuli were located (northeast or southwest quadrants/northwest or southeast quadrants) were randomly assigned to each subject and counterbalanced and matched across groups. Each participant carried out a total of eight sessions (four sessions per day over 2 d) with 312 trials per session. In each session, four randomly interleaved staircases—two-up-one-down and three-up-one-down for each of the two stimulus locations—were used. Signal contrast thresholds were estimated by averaging all of the reversals in each staircase, except the first three reversals. Overall contrast thresholds for each participant were then computed by averaging the thresholds across all four staircases, thereby converging to the 75% correct threshold.

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# Supporting Information

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## SI Note 1: Experimental Procedures

### Experiment 1: Performance in External Noise in AVGPs.

**Participants.** All 10 male NVGPs and 10 male AVGPs who participated in this experiment had normal or corrected-to-normal vision as measured with the logarithmic visual acuity chart “2000” (Early Treatment for Diabetic Retinopathy Study). All participants provided informed written consent and were paid \$8 per hour.

Participants completed the same video game playing questionnaire, aimed at establishing their video gaming history in the 12 mo before testing, as in ref. 1. Participants who reported playing at least 5 h of action video games per week during the past year were classified as AVGPs. Qualified action video games included first-person and third-person shooter games such as *Unreal Tournament*, *Counter Strike*, *Halo*, *Call of Duty*, and so on. Participants who had little to no action video game experience (less than 1 h per week) during the past year were classified as NVGPs; note that most NVGPs did play other kinds of games, such as board games, puzzle games, card games, strategy games, or social games.

**Stimuli and procedure.** Stimuli were displayed on a ViewSonic Graphics Series G225f CRT monitor with 1,024 × 768 pixel resolution and 120-Hz refresh rate, driven by a Mac OS X 10.4.11 system. A video switcher was used to combine two 8-bit output channels of the graphics card so that the display system could produce gray levels with 14 bits of resolution (2). Participants were tested in a dark room, with the mean display luminance set to 58 cd/m<sup>2</sup>, and viewing distance set to 59 cm. Monitor gamma was calibrated by fitting the best power function to the measured luminance level (Minolta Chromameter, CS-100) of 10 different gray-level settings (from 0 to 240) of the monitor (full field).

The stimuli and task were similar to those of Lu and Doshier (3), except that the size (1.5 × 1.5°), degree of tilt (±2°), and reference angle (horizontal) were different. The stimuli were Gabor signals. The luminance distribution of the Gabor signal is described by the following equation:

$$L(x, y) = l_0 * (1.0 + c \sin(2\pi f(x \cos(\theta) + y \sin(\theta)))) * \exp(-(x^2 + y^2)/2\sigma^2),$$

where  $\theta = \text{rad}(0^\circ \pm 2)$ ,  $l_0$  is the background luminance,  $f = 2$  cycles/degree is the center spatial frequency of the Gabor signal,  $\sigma = 0.375^\circ$  is the SD of the Gabor's circular Gaussian envelope, and peak contrast  $c$  was determined by the adaptive staircase procedures (described below). External noise images consisted of pixels with contrasts independently drawn from an identical Gaussian distribution. To increase the noise energy in the task-relevant spatial frequency channels, external noise images were filtered by a band-pass filter with spatial frequencies ranging from one octave below to one octave above the spatial frequency of the Gabor signals. The sizes of both the Gabor signals and the external noise images, in terms of visual angle, were set to 1.5 × 1.5°.

A typical trial is shown in Fig. 1A of the main text. After a central fixation cross was presented for 250 ms a Gabor signal frame was presented, sandwiched between two external noise frames, for 16.7 ms per frame. The Gabor signal was tilted 2° clockwise or counterclockwise from 0°, with participants indicating the orientation of the Gabor—clockwise or counterclockwise from horizontal—using a key press. Participants received auditory feedback on their performance. Eight external noise contrast levels (0, 2.1, 4.1, 8.3, 12.4, 16.5, 24.8, and 33%) were used in an interleaved fashion, and for each level of external noise two interleaved staircase procedures were used, with step sizes of 10% of the

current contrast level, so as to converge upon the 79.37% or 70.71% signal contrast threshold (a three-down-one-up or a two-down-one-up staircase, respectively). Signal contrast threshold was defined as the mean of all of the reversals, excluding the first four. For each three-down-one-up staircase there were 100 trials and for each two-down-one-up staircase there were 80 trials, leading to a total of 1,440 trials per session. To improve our estimates, each participant carried out two such sessions in a row for a total duration of 1.5 h.

### Experiment 2: Performance in External Noise After Action Video Game Training.

**Participants.** Thirty-six NVGPs (selected using the same video game experience criterion as in experiment 1 above) were initially recruited to participate in this training experiment and were divided randomly into an action group and a control group. However, not all recruited participants completed all parts of the experiment. The final sample included 12 action group participants (9 males and 3 females, 20–28 y old, mean age 23.9 y) and 14 control group participants (5 males and 9 females, 20–28 y old, mean age 22.6 y). Excluded participants included five female participants in the action group and two male participants in the control group who dropped out early during the video game training phase (described below) because of motion sickness or an inability to comply with the demanding schedule of the training, one male participant who was excluded from the control group owing to an inability to perform the noise-exclusion task at pretest, and two female participants who were excluded from the action group because one never learned to play the second action game used in the training study and the other did not conform to the prescribed schedule of training.

**Video game training procedure.** For both groups training consisted of playing two games for a total of 50 h (25 h per game). During the first 25 h of training, participants in the action group played the game *Unreal Tournament 2004* (Epic Games) in “Death Match” mode, where the goal is for the player to kill as many of the computer-controlled characters as possible while minimizing the number of deaths for the player-controlled character. During the second half of training (next 25 h of training), the action game trainees were switched to a second game, *Call of Duty 2* (Activision). This game places the player in fictionalized World War II combat situations, with the primary goal again being to kill as many computer-controlled characters as possible while minimizing deaths for the player-controlled character. Subjects were retested on all levels of *Unreal Tournament 2004* at the end of training to assess improvement in skill.

Participants in the control group played *The Sims 2* (2004, Electronic Arts Inc.) for the first half of training and *Restaurant Empire* (2003, Enlight Software Ltd.) for the second half of training. *The Sims 2* is a simulation-style game, wherein the player takes complete control over the simulated daily life of a character, from everyday activities (eating, bathing, etc.) to going to work, managing relationships with other characters, getting married, having and raising children, and eventual old age. As characters are added to the household the player takes control of those characters as well. *Restaurant Empire* is also a simulation-style game, wherein the player takes complete control of the simulated operation of restaurants, from developing recipes and menus to decorating restaurants, handling customers, and joining cooking competitions.

The training games for both the action and the control groups covered the entire display screen (visual angle of ~15° high × 18°

wide). Each group was requested to log their performance regularly (control game: accumulated wealth; experimental game: ratio of kills to death). In addition, because the action games did not control player advances in a systematic fashion, action group participants were required to reach a ratio of two kills for one death before they could advance to a harder level. This ensured that players progressed through the game smoothly, thereby avoiding long periods of frustration because the game became too hard or boredom because the game became too easy. This was not an issue with the control game, which progressed automatically through increasingly advanced situations.

**Stimuli and procedure for pre- and posttest tasks.** Participants were tested a few days before and a few days after the training period (designated as pretest and posttest, respectively) on the same orientation identification under external noise task as that used in experiment 1.

In addition, all participants were asked to fill out the “flow” questionnaire as defined by Csikszentmihalyi (4) after every 10 h of video game training, as well as after the pre- and posttest. This allowed us to assess participants’ engagement with the training games at different times during training. We were especially interested in determining whether the two training games were equally engaging. The specific questionnaire we used included 36 questions, covering four domains (enjoyment, attention, reward, and confidence). Participants answered each question by selecting one of five answers that ranged from “strongly disagree” to “strongly agree,” scoring 1–5, respectively.

**RAPM.** All participants were administered the RAPM at pretest to ensure participants across groups were matched in fluid intelligence, because differences in such aspects of intelligence have previously been related to differences in performance on perceptual tasks (5, 6). Raven scores, at pretest, were comparable between the two groups [mean score for AVGPs = 30 and mean score for NVGPs = 28.6,  $t(20) = 0.85$ ,  $P = 0.41$ , two-tailed], indicating matched fluid intelligence across the two groups. Note that the exact same RAPM test was also administered at posttest. Both groups improved by a comparable amount from pre- to posttest [from a mean of 30–32.8 for AVGPs and from a mean of 28.6–29.4 for NVGPs,  $F(1,20) = 5.31$ ,  $P = 0.03$ ,  $\eta^2 = 0.21$ ; no group effect, no interaction]. This pattern likely reveals a change in participants’ familiarity with the specific test items, rather than a true change in fluid intelligence (7, 8).

Finally, various pilot data were also collected from different subsets of the participants used here. All pilot experiments were administered after participants had completed the reported orientation identification task. One set of participants was tested on two visual working memory tasks, a task-switching paradigm, a speeded response time task, and visual tests focusing on center-surround interactions. A different set of participants was tested on a go/no-go task, the Posner letter identity task, a numerosity estimation task, an exogenous attention task, and an inhibition of return paradigm. The aim of these pilot experiments was to refine paradigms testing these various constructs in subsequent studies and will not be further discussed here.

### Evaluating Long-Term Retention of Action-Trained Improvements in Performance (Posttest2).

**Participants.** Out of the nine action group participants and seven control group participants who were brought back to the laboratory a few months after the end of their training some had been trained 3 mo before, whereas others had been trained more than 1 y before (action-trained: five 3 mo, four more than 1 y; control-trained: three 3 mo, four more than 1 y). This schedule is a consequence of in-laboratory training studies’ being extremely time-intensive for participants. Accordingly, training studies are run only during the summer, so as to not interfere with participants’ academic performance. This training study was run over two consecutive summers, yet posttest2 for all participants occurred

at one point in time. Hence, some participants were run 3 mo after their last session (i.e., those subjects that had done the study during the previous summer) and others more than a year (i.e., those subjects that had done the study during the summer before that). This is also a way for us to check the durability of the effects over a relatively long time period. Participants were asked about their video game habits in the intervening period between the training study and the current test. All of the participants reported going back to their pretest habits in terms of video game play.

**Stimuli and procedure.** All of the participants were again tested (designated as post2-test) in the same orientation identification under external noise task as that used in experiments 1 and 2.

### Experiment 3: Dynamics of Perceptual Template Learning in AVGPs.

**Participants.** All 10 NVGPs and 10 AVGPs who participated in this experiment had normal or corrected-to-normal vision, provided informed written consent, and were paid for their participation. All participants were selected using the same video game experience criterion as in experiment 1 above.

**Stimuli and procedure.** Stimuli were displayed on a Mitsubishi color graphic monitor (Diamond Pro-2070SB) with 1,024 × 768 pixel resolution, 85-Hz refresh rate, 22 inches in size and at a viewing distance of 58 cm. Subjects’ head position was stabilized using a chin and forehead rest. The stimuli and task were identical to those used in Jeter et al. (9), with the exception that only the high noise contrast (33%) and low precision ( $\pm 12^\circ$ ) stimuli were used. Signal frames included a Gabor signal (subtending  $3 \times 3^\circ$  visual angle, orientation  $\pm 12^\circ$  around a reference angle of  $-35^\circ$  or  $55^\circ$ , spatial frequency = 2 cycles/degree and SD of the spatial Gaussian envelope  $\sigma = 0.4^\circ$ ). External noise frames included a noise patch, identical in size to the Gabor signal, made up of individual  $2 \times 2$  pixel noise elements, with the contrast levels for the noise elements being drawn from a Gaussian distribution centered at the background luminance value and with an SD of 0.33 of 100% contrast. The Gabor signal and external noise patches were presented in the visual periphery (eccentricity =  $5.67^\circ$ ) at one of two locations (in the northeast or southwest quadrants for half the participants and in the northwest or southeast quadrants for the other half). The reference orientation and the locations in which the stimuli were presented were randomly assigned to each subject and counterbalanced and matched across groups.

A typical trial is shown in Fig. 5A of the main text. After a central fixation cross was presented for 750 ms (the onset of each trial was signaled by an auditory tone), a Gabor signal frame was presented sandwiched between two external noise frames (30 ms per frame), leading to temporal integration of the Gabor signal with the external noise patches. Participants were tasked with indicating the orientation of the Gabor—clockwise or counterclockwise around the reference angle—using a key press. Auditory feedback was provided after the participants’ choice. Each participant carried out a total of eight sessions, four sessions per day over 2 d, with 312 trials per session. In each session, four randomly interleaved staircases—two-up-one-down and three-up-one-down staircases for each of the two stimulus locations—were used. Signal contrast thresholds were estimated by averaging all of the reversals in each staircase, excluding the first three reversals. Overall contrast thresholds for each participant were then computed by averaging the thresholds across all four staircases, thereby converging to the 75% correct threshold. In the first session, staircases quickly hovered around a signal contrast of about 0.77 for NVGP and AVGPs (Fig. S3). In subsequent sessions, to achieve efficient estimation, initial signal contrast levels for the two 2/1 and the two 3/1 staircases were computed by averaging the estimates from the corresponding 2/1 and 3/1 staircases from the immediately preceding session.



## SI Note 2: Overview of the PTM

**The PTM.** Limited by nonlinear signal transduction as well as by many sources of variability, such as intrinsic stimulus variability, receptor sampling error, variability in neural responses, and loss of information during neural transmission, human perception exhibits many inefficiencies. Since the 1950s, sensory psychologists have adopted the equivalent input noise method, used by electrical engineers (10) to measure the intrinsic noise of amplifiers, to characterize the limiting noise in perceptual processes (11–15). In a typical application, this method systematically adds increasing amounts of external noise to the signal stimulus and observes how threshold (i.e., signal stimulus energy required for an observer to maintain a predetermined performance level) depends on the amount of external noise (Fig. S1). This threshold vs. external noise contrast (TvC) function can then be used to specify the sources of perceptual limitations in an observer model, which maps external stimuli to internal perceptual representations and predicts human performance using a decision process such as signal detection theory.

A number of components, derived from both sensory psychology and physiology, have been used to construct observer models, including a perceptual template, a nonlinear transducer, additive noise, multiplicative noise, and a decision rule (13, 14, 16–18). For example, internal additive noise is associated with absolute thresholds in perceptual tasks and internal multiplicative noise is associated with Weber's law behavior of the perceptual system. In the PTM (Fig. S2), perceptual inefficiencies are attributed to three limitations: internal additive noise, internal multiplicative noise, and perceptual templates (imperfectly) tuned to the target stimuli. Lu and Dosher (19) carried out an extensive analysis of all of the major existing observer models, including a linear amplifier model (13), a multiplicative noise model (20), and a multiplicative noise plus uncertainty model (17). The classical observer models are reduced cases of the PTM. The PTM accommodates all of the known standard properties of data in the equivalent input noise literature, as well as providing the best qualitative and quantitative account of a range of particular data sets.

The central idea behind the PTM is that of a filter or template through which the signal is passed so as to optimize pattern recognition; the efficiency of that filter is under the control of five main components (Fig. S2): (i) a contrast gain to the signal  $\beta$  that is normalized relative to its gain to the external noise, (ii) a nonlinear transducer function that raises its input to the  $\gamma^{\text{th}}$  power, (iii) a Gaussian-distributed internal multiplicative noise term with mean 0 and SD proportional to  $(N_m \times)$  the contrast energy in the input stimulus, (iv) a Gaussian-distributed additive internal noise term with mean 0 and "constant" SD  $N_a$ , and (v) a decision process. In the PTM, accuracy of perceptual task performance is indexed by  $d'$  (18, 19):

$$d' = \frac{(\beta c)^{\gamma}}{\sqrt{N_{\text{ext}}^{2\gamma} + N_m^2 [N_{\text{ext}}^{2\gamma} + (\beta c)^{2\gamma}] + N_a^2}} \quad [\text{S1}]$$

For a given performance level,  $d'$ , we can solve Eq. S1 to express threshold contrast  $c_t$  as a function of external noise ( $N_{\text{ext}}$ ) in log form:

$$\log(c_t) = \frac{1}{2\gamma} \log \left( (1 + N_m^2) N_{\text{ext}}^{2\gamma} + N_a^2 \right) - \frac{1}{2\gamma} \log \left( 1/d'^2 - N_m^2 \right) - \log(\beta). \quad [\text{S2}]$$

**Mechanisms of Performance Improvement.** In signal processing there are three ways to improve signal-to-noise ratio: amplification,

improved filtering, and modified gain control. Similar principles of contrast gain, retuning of cellular signal selectivity, and reduced contrast gain have also been demonstrated in single-unit neurophysiology (21). Motivated by the principles in signal processing and neurophysiology, Lu and Dosher (22) developed a theoretical framework based on the PTM to distinguish three mechanisms underlying performance improvements (22). Stimulus enhancement acts by multiplying the contrast of the input stimulus by a factor greater than 1, which is mathematically equivalent to internal additive noise reduction. The behavioral signature for this mechanism is performance improvement (reduced thresholds) in the region of low to zero external noise (Fig. S2B). Because it affects both the signal and the external noise in the input stimulus in the same way, this mechanism does not affect performance in high external noise conditions. External noise exclusion improves performance by focusing perceptual analysis on the appropriate temporal duration, spatial region, and/or content characteristics of the signal stimulus. This focus serves to eliminate/admit external noise from further processing. The behavioral signature for this mechanism is performance improvements in the region of high external noise (Fig. S2C). Internal multiplicative noise reduction reduces a noise source that is proportional to the energy in the input stimulus. The mechanism produces a behavioral signature of performance improvements in both high and low levels of external noise (Fig. S2D). Improved perceptual template, or what has been termed *reweighting*, results in a combination of reduced additive internal noise and improved external noise exclusion. This also has the behavioral signature of performance improvements in both high and low levels of external noise. It corresponds to the use of a more closely matched filter to the signal (Fig. S2). Finally, measuring TvC functions at two or more criterion performance levels makes it possible to resolve the individual contribution of each mechanism in situations where more than one mechanism may be operative (23).

In the PTM, performance improvements across groups, or time, are respectively modeled by multiplying  $N_a$  by a factor  $A_a < 1.0$  for better stimulus enhancement,  $N_{\text{ext}}$  by a factor  $A_f < 1.0$  for better external noise exclusion, and  $N_m$  by factor  $A_m < 1.0$  for reduced internal multiplicative noise. If all three mechanisms are operative, the contrast threshold vs. external noise function for a PTM becomes

$$\log(c_t) = \frac{1}{2\gamma} \left\{ \log \left[ (1 + A_m^2 N_m^2) A_f^{2\gamma} N_{\text{ext}}^{2\gamma} + A_a^2 N_a^2 \right] - \log \left[ \frac{1}{d'^2} - A_m^2 N_m^2 \right] \right\} - \log(\beta), \quad [\text{S3}]$$

where  $c_t$  denotes the predicted contrast threshold,  $N_{\text{ext}}$  is the SD of external noises,  $d'$  is the perceptual sensitivity of the observer, corresponding to the thresholds in the two-alternative forced-choice task. Note that both reduced internal multiplicative noise and better perceptual templates predict a downward shift of the whole function. However, as shown in Dosher and Lu (23), whereas a perceptual template change predicts a ratio of contrast threshold between the compared conditions to be similar across performance levels (79.37% and 70.71% accuracy), a reduction in multiplicative noise predicts a greater ratio at the more stringent performance level (79.37%).

The external noise approach has been used to characterize mechanisms of performance improvements and decrements in a wide range of applications, including attention (22, 24), perceptual learning (25–29), adaptation (30), amblyopia (31, 32), perceptual interaction (33), dyslexia (34), and visual memory (35). In many cases, a pure mechanism of stimulus enhancement/diminution or external noise exclusion/admittance has been identified, with mixtures of these two mechanisms also being observed in

some instances. The internal multiplicative noise reduction/increase mechanism has not been found empirically.

### SI Note 3: Data Analysis

**Experiment 1: Performance in External Noise in AVGPs.** An omnibus  $2 \times 2 \times 8 \times 2$  ANOVA was performed with action game experience (AVGP/NVGP) as a between-subject factor; run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. As expected, significant effects of external noise level [ $F(7,126) = 260.41, P < 0.001, \eta^2 = 0.94$ ] and performance level [ $F(1,18) = 284.07, P < 0.001, \eta^2 = 0.94$ ] were observed, indicating lower signal contrast thresholds at low external noise levels and at the easier performance criterion level. No main effect of runs was observed [ $F(1,18) = 1.82, P = 0.19, \eta^2 = 0.09$ ], nor did run interact with any other variable (all  $P > 0.05$ ). Importantly, AVGPs showed overall lower contrast thresholds than NVGPs [ $F(1,18) = 5.82, P < 0.05, \eta^2 = 0.24$ ], indicating better performance in that group (Fig. 1B in the main text). No other significant effect or interaction was observed (all  $P > 0.05$ ).

**Fitting the PTM.** Signal contrast thresholds across the eight external noise levels and two performance levels, for both AVGPs and NVGPs, were fit with the PTM to derive TvC curves for both groups (see ref. 19 for a review describing the PTM model and refs. 22 and 25 for studies describing the use of PTM models in capturing the mechanisms underlying performance changes owing to training or attention). In the PTM, performance improvements can be attributed to one or more of three noise reduction mechanisms: improved external noise exclusion, improved internal additive noise reduction, and improved internal multiplicative noise reduction. As discussed in SI Note 2 above, the signature of an improved perceptual template is a combination of reduced internal additive noise and improved external noise exclusion, with the ratio of contrast thresholds between the conditions under consideration being similar across performance levels (that is, across the 79.37% and 70.71% accuracy levels in our study).

We compared the results obtained by fitting eight models, ranging from no change in any of the three noise-reduction mechanisms in AVGPs to the full model with changes in all three noise-reduction mechanisms in AVGPs. As discussed above, the full model then consists of four shared parameters ( $\beta$ , Nm, Na, and  $\gamma$ ) across the two groups and three AVGP-specific noise parameters  $A_f$ ,  $A_a$ , and  $A_m$ . To find the best-fitting model, we compare nested models in a model lattice. The comparisons are not strictly independent. The logic is the same as in stepwise regression, where comparing models with more and more regressors is not considered as involving independent comparisons. The model with the least number of parameters that was still statistically equivalent to the model in which all changes were allowed was considered to be the best-fitting model (see ref. 3 for a similar approach). Model fitting was carried out using a least-square method, and an  $F$  test over nested models was used to compare the different models. Formally, the  $F$  test can be described as

$$F(df_1, df_2) = \left[ \frac{(r_{full}^2 - r_{reduced}^2)}{df_1} \right] / \left[ \frac{(1 - r_{full}^2)}{df_2} \right],$$

where  $df_1 = k_{full} - k_{reduced}$ , and  $df_2 = N - k_{full}$ .  $N$  is the number of predicted data points (i.e., 32 eight external noise levels  $\times$  two levels of performance  $\times$  two groups) and  $k_s$  is the number of parameters in each model.

The best-fitting model was the model with a combination of increased additive internal noise reduction and improved external noise exclusion in AVGPs. This model has six parameters, four shared between AVGPs and NVGPs ( $\beta$ , Nm, Na, and  $\gamma$  values),

and two AVGP-specific noise values,  $A_f$  and  $A_a$ . With six parameters and  $r^2 = 98.89\%$ , this reduced model was statistically equivalent to the full model with all noise parameters changed [ $F(1,25) = 0.00, P = 0.99$ ] and was significantly better than the model with no noise parameters changed [ $F(2,26) = 69.92, P < 0.01$ ], the model with external noise exclusion only [ $F(1,26) = 41.69, P < 0.001$ ], and the model with internal additive noise reduction only [ $F(1,26) = 54.81, P < 0.001$ ]. The results of the model fitting are plotted in Fig. 1B of the main text (fit lines). In addition, the model with only a multiplicative noise change provided a significantly worse fit ( $r^2 = 98.03\%$ ) than the full model [ $F(2,25) = 9.68, P < 0.001$ ]. Because multiplicative noise reduction predicts a larger improvement at the 79.37% than at the 70.71% accuracy level, but an improved perceptual template does not, we computed the ratios of contrast thresholds at each accuracy level (23). Crucially, the ratios of contrast thresholds between AVGPs and NVGPs were not significantly different at the two performance levels:  $1.26 \pm 0.03$  at 79.37% correct vs.  $1.22 \pm 0.02$  at 70.71% correct. These results make multiplicative noise change an unlikely mechanism underlying the improvements in AVGPs (23) and instead support the improved perceptual template as the mechanism underlying the performance differences between the two groups.

### Experiment 2: Performance in External Noise After Action Video Game Training.

**Orientation identification task.** A  $2 \times 2 \times 8 \times 2$  ANOVA was performed with group (action/control) as a between-subject factor; test (pre/post), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. No main effect of run was observed [ $F(1,24) = 1.41, P = 0.25, \eta^2 = 0.06$ ], nor did run interact with any other factor (all  $P > 0.05$ ). Main effects of external noise level [ $F(7,168) = 414.22, P < 0.001, \eta^2 = 0.95$ ], performance level [ $F(1,24) = 297.34, P < 0.001, \eta^2 = 0.93$ ], and test [ $F(1,24) = 15.65, P < 0.001, \eta^2 = 0.40$ ] were observed, indicating the expected effects of lower thresholds at low external noise levels and for the less demanding performance level, as well as at posttest. Crucially, a test (pre/post)  $\times$  group (action/control) interaction was found [ $F(1,24) = 8.66, P < 0.01, \eta^2 = 0.27$ ], indicating larger improvement in contrast thresholds between pre- and posttest in action trainees than in control trainees. Finally, a weak group  $\times$  external noise level interaction [ $F(7,168) = 2.35, P < 0.05, \eta^2 = 0.09$ ] indicated an overall advantage throughout the whole experiment in the action group at low external noise levels. No other effects were observed (all  $P > 0.05$ ).

The significant test  $\times$  group interaction led us to separately analyze action and control trainees' performance in the task. For each group, a  $2 \times 2 \times 8 \times 2$  ANOVA was performed with test (pre/post), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors and log signal contrast threshold as the dependent variable. For control trainees there was no effect of run [ $F(1,13) = 0.23, P = 0.64, \eta^2 = 0.02$ ], nor did this factor interact with any other (all  $P > 0.1$ ). Main effects of external noise level [ $F(7,91) = 184.50, P < 0.001, \eta^2 = 0.93$ ] and performance level [ $F(1,13) = 149.90, P < 0.001, \eta^2 = 0.92$ ] were observed. No other interactions were significant (all  $P > 0.3$ ). Importantly, there was no effect of test (see Fig. 2B in the main text), indicating no reliable change in performance from pre- to posttest [ $F(1,13) = 0.57, P = 0.46, \eta^2 = 0.04$ ].

For the action group, there was no effect of run [ $F(1,11) = 1.83, P = 0.20, \eta^2 = 0.14$ ], nor did this factor interact with any other factor (all  $P > 0.1$ ). Main effects of external noise level [ $F(7,77) = 237.11, P < 0.001, \eta^2 = 0.96$ ] and performance level [ $F(1,11) = 165.61, P < 0.001, \eta^2 = 0.94$ ] were observed. Crucially, a main effect of test was observed (see Fig. 2A in the main text), reflecting a lower signal contrast threshold and therefore improved

performance at posttest relative to pretest [ $F(1,11) = 21.46, P < 0.001, \eta^2 = 0.66$ ]. The effect of test marginally interacted with performance level [ $F(1,11) = 5.12, P = 0.045, \eta^2 = 0.32$ ], indicating a different magnitude of improvement at the two levels of task performance with greater improvement at the hardest level. No other effect was observed (all  $P > 0.1$ ).

**Fitting the PTM.** Signal contrast thresholds in both pretest and posttest, across the eight external noise levels and two performance levels, for the control and action groups were then fitted with the PTM. The lack of difference between control and action groups at pretest [ $F(1,24) = 0.01, P = 0.93, \eta^2 = 0.00$ ] led us to constrain  $\beta$ , Nm, Na, and  $\gamma$  (a subset of PTM parameters) to be the same across the two groups. Control and action groups' data in both pre- and posttests were then fitted simultaneously forcing the same  $\beta$ , Nm, Na, and  $\gamma$  parameters but allowing changes in the three noise-reduction mechanisms separately for each group, to capture the impact of the type of game training. This generated 64 models that range from changes in all three noise-reduction mechanisms for both groups to no change in noise reduction in either group. The model with the smallest number of parameters changed that was still statistically equivalent to a model with all parameters changed was defined as the best model fit. The model that assumed increased internal additive noise reduction and improved external noise exclusion in the action group, and no change in noise reduction in the control group, after training, provided the best fit. With six parameters and  $r^2 = 98.60\%$ , this model is statistically equivalent to the most saturated model with all noise parameters changed [ $F(4,54) = 1.50, P = 0.22$ ] and is significantly better than the model with no change in noise parameters [ $F(2,58) = 108.54, P < 0.001$ ], the model with external noise exclusion only [ $F(1,58) = 120.14, P < 0.001$ ], and the model with internal noise reduction only [ $F(1,58) = 44.33, P < 0.001$ ]. In addition, the model with only multiplicative noise change provided a significantly worse fit ( $r^2 = 97.90\%$ ) than the full model [ $F(5,54) = 7.20, P < 0.001$ ]. Results from these model comparisons therefore support improved perceptual templates in action video game trainees, rather than an alternative explanation such as a change in multiplicative noise. Indeed, a change in multiplicative noise predicts greater pre- to posttraining contrast threshold ratio at the 79.37% performance level than at the 70.71% performance level. This was not reliably observed in our data ( $1.35 \pm 0.04$  at 79.37% correct vs.  $1.25 \pm 0.03$  at 70.71% correct), thereby further reinforcing improved perceptual templates as the most likely mechanism underlying improved performance of action trainees. The results of the model fitting are plotted in Fig. 2 of the main text (fit lines).

**Game training results.** To quantitatively assess how participants improved their game play as a result of training, several measures were used.

For the action games, kills and deaths in each block were used to calculate a skill metric  $S = ([\text{Kills} - \text{Deaths}]/[\text{Kills} + \text{Deaths}])$ . The S score was measured at all six levels of difficulty at pretraining, after 25 gaming hours (after *Unreal Tournament* training) and posttraining (hours 49 and 50 of game training). As with the control game, we compared pre- and posttraining S scores. The S scores at all of the difficulty levels increased from 0.65 (level 1), 0.58 (level 2), 0.35 (level 3),  $-0.07$  (level 4),  $-0.45$  (level 5), and  $-0.61$  (level 6) to 0.94 (level 1), 0.84 (level 2), 0.75 (level 3), 0.42 (level 4), 0.08 (level 5), and  $-0.11$  (level 6). Increases were observed for all participants and at all levels of difficulty, indicating generally improved performance with training.

For the control games, money accumulated was a reliable measure because it increases with positive actions such as making good recipes or adding a member to the household and decreases with negative actions such as burning down one's restaurant or having a character die due to neglect. All participants showed an accelerating increase in accumulated wealth over the course of training, indicating an improvement in game performance with

training. The time course of the accumulation was well fit by a linear function: For *The Sims2*, wealth =  $(4,919 * \text{training hour}) + 110, r^2 = 98.05\%$ ; for *Restaurant Empire*, wealth =  $(30,757 * \text{training hour}) - 6,020, r^2 = 96.23\%$ . Taken together, these results demonstrate that both groups showed improvement in their respective training tasks.

In addition, it is worth noting that the control group trainees managed an average of three different characters during their first 25 h of training and an average of four different restaurants during their second 25 h of training. Thus, the control-group trainees played/managed on average 3.5 times as many characters/restaurants, had more variable goals, and were exposed to more diversity in their environment than the action-group trainees. We chose to keep the action game trainees at a disadvantage for these factors to ensure that the amount of stimulating situations encountered could not easily explain any improvements in the action group, beyond what is seen with the control group.

**Flow measure.** To investigate whether action and control games were similarly engaging, flow scores at hours 20 (toward the end of game 1) and 50 (after game 2) were compared across action and control groups (Fig. S3). On average, participants in both groups showed a high degree of engagement (the higher the flow, the greater the engagement) with their assigned games. A 2\*2 ANOVA was performed with group (action/control) as a between-subject factor, order (first/second) as a within-subject factor, and flow score as the dependent variable. Although the mean flow score was slightly larger for the control trainees than for the action trainees, we found no significant effect of group [ $F(1,24) = 2.32, P = 0.16, \eta^2 = 0.08$ ] or order [ $F(1,24) = 0.38, P = 0.54, \eta^2 = 0.02$ ], nor did we find a significant group  $\times$  test order interaction [ $F(1,24) = 0.12, P = 0.73, \eta^2 = 0.01$ ]. Thus, better performance in the action-trained group cannot be attributed to greater engagement with their assigned game.

#### Evaluating Long-Term Retention of Action-Trained Improvements in Performance.

**Orientation identification task.** A 2\*2\*2\*8\*2 ANOVA was performed using the pretest and post2-test data for the subset of participants that were brought back to the laboratory, with group (action/control) as a between-subject factor; test (pre/post2), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable. Main effects of test [ $F(1,14) = 24.06, P < 0.001, \eta^2 = 0.63$ ], performance level [ $F(1,14) = 257.47, P < 0.001, \eta^2 = 0.95$ ], and external noise level [ $F(7,98) = 318.19, P < 0.001, \eta^2 = 0.96$ ] were observed and, more relevant to our aim, a marginally significant interaction between pre/post2 and group [ $F(1,14) = 3.25, P = 0.09, \eta^2 = 0.19$ ] was noted. In addition, we also noted an interaction between performance level and external noise level [ $F(7,98) = 2.47, P < 0.05, \eta^2 = 0.15$ ], indicating a greater difference in contrast thresholds between the two performance levels at low than at high external noise levels, and an interaction between external noise level and group [ $F(7,98) = 3.51, P < 0.01, \eta^2 = 0.20$ ]. Across all test sessions the action group showed lower contrast thresholds at low external noise levels than the control group, but no difference between the two groups was noted at high external noise levels. Finally, unlike any of the previous results, run was seen to interact with several factors, leading to triple and quadruple interactions (all  $P$  at 0.05 level), which are difficult to interpret.

Because the pre/post2  $\times$  group interaction was only marginally significant [ $F(1,14) = 3.25, P = 0.09, \eta^2 = 0.19$ ], we confirmed the presence of a test effect within the action group. A 2\*2\*8\*2 ANOVA using the pretest and post2-test data for the subset of action group participants that were brought back to the laboratory, with test (pre/post2), run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors and log signal contrast threshold as the

dependent variable, confirmed a main effect of test [ $F(1,8) = 21.64, P < 0.01, \eta^2 = 0.73$ ; see Fig. 3 in the main text], indicating that the action video game-induced improvements in performance were retained several months after training. As expected, main effects of external noise level [ $F(7,56) = 178.85, P < 0.001, \eta^2 = 0.96$ ] and performance level [ $F(1,8) = 105.58, P < 0.001, \eta^2 = 0.93$ ] were also observed, indicating lower thresholds at low external noise levels and for the less-demanding performance level, as expected. No other main effect or interactions were significant (all  $P > 0.3$ ). To better characterize performance improvements of action trainees across the different tests, we further examined how their performance changed between posttest (immediately after training) and post2-test (several months after the end of training) compared with between pre- and posttest (immediately before and after training). Because a smaller group of subjects participated in post2 compared with the initial pre/post tests (experiment 2, discussed above),  $2 \times 2 \times 8 \times 2$  ANOVAs were again performed with tests (pre/post or post/post2) as a between-subject factor; run (first/second), external noise level (eight levels), and performance level (79.37% and 70.71%) as within-subject factors; and log signal contrast threshold as the dependent variable, for the subset of action trainees that were brought back to the laboratory. We confirmed that even with this restricted group of participants the main effect of test was significant between pre- and posttest [ $F(1,8) = 20.47, P < 0.01, \eta^2 = 0.72$ ], but it was not between post- and post2-test [ $F(1,8) = 0.24, P = 0.64, \eta^2 = 0.03$ ], thereby suggesting that the observed improvements of action returnees in post2 most likely occurred while they trained on the action game, and that these improvements were retained after the end of training, between post- and post 2-test.

For completeness, we report the  $2 \times 2 \times 8 \times 2$  ANOVA, with pre- and post2-test data, performed on the subset of control-trained participants that were brought back to the laboratory. The main effect of test (pre/post2) was almost significant [ $F(1,6) = 5.71, P = 0.054, \eta^2 = 0.49$ ; see Fig. S4], owing mainly to an improvement from pretest to post2 at low levels of external noise, an effect that was not noted between pre- and posttest in the larger sample of control-trained participants. Main effects of external noise level [ $F(7,42) = 162.85, P < 0.001, \eta^2 = 0.96$ ] and performance level [ $F(1,6) = 226.05, P < 0.001, \eta^2 = 0.97$ ] were also observed. Unlike any of the previous results, run was seen to interact with several factors (all  $P = 0.05$ ), with the meaning of such interaction remaining difficult to interpret. As we did for action trainees, pre- and posttest changes were explored separately from post- and post2-test changes in the small group of control trainees that returned for post2-test. The same  $2 \times 2 \times 8 \times 2$  ANOVAs as performed with the action group trainees above showed no significant test effect between pre- and posttest [ $F(1,6) = 0.42, P = 0.54, \eta^2 = 0.07$ ] and showed a marginally significant effect between post- and post2-test [ $F(1,6) = 3.89, P = 0.10, \eta^2 = 0.07$ ]. Thus, the improvements in low noise observed in control returnees at post2 most likely occurred between post and post2-test, with performance remaining stable between pre- and posttest. Why performance improved at low noise levels between posttest and post2-test remains unclear because all subjects reported having stopped playing video games after the end of their training.

**Fitting the PTM.** The data from the control and the action returnees at pretest and post2-test was fitted with the PTM model. Action and control returnees showed a significant noise  $\times$  group interaction [ $F(7,98) = 2.40, P < 0.05, \eta^2 = 0.15$ ] in their pretest data, suggesting different patterns of pretest performance in the subset of participants that were brought back to the laboratory. This fact, combined with the very different pattern of changes across pre-, post-, and post2-test in each group of returnees led us to fit each group's data separately by keeping the  $\beta$ , Nm, Na, and  $\gamma$  parameters (a subset of PTM parameters; see ref. 3) for

each group constant from pre- to post2-test and considering the full range of models, from no change in noise reduction in either group in post2 to a change in all three noise parameters in post2. The procedure for model fitting and selection was identical to that described above. The model-fitting results for the action group are plotted in Fig. 3 of the main text (fit lines) and the results for the control group are plotted in Fig. S4 (fit lines).

For the action group, the model that assumes improvements in internal additive noise reduction and external noise exclusion at post2 provided the best fit. Specifically, in comparison with the pretest, the best-fitting model assumed a 17% improvement in external noise exclusion and a 28% increase in internal noise reduction in post2. With six parameters and  $r^2 = 99.25\%$ , this model is statistically equivalent to the most saturated model with all noise parameters changed [ $F(1,25) = 0.34, P = 0.57$ ] and is significantly better than the model with no change in noise parameters [ $F(2,26) = 97.07, P < 0.001$ ], the model with external noise exclusion only [ $F(1,26) = 99.15, P < 0.001$ ], and the model with internal noise reduction only [ $F(1,26) = 38.83, P < 0.001$ ]. The model with only a multiplicative noise change ( $r^2 = 98.26\%$ ) provided a significantly worse fit than the most saturated model [ $F(2,25) = 16.89, P < 0.001$ ]. These model comparison results help reject a multiplicative noise change explanation and are in accordance with the finding of comparable contrast ratio at 79.37% performance level ( $1.32 \pm 0.04$ ) and at 70.71% performance level ( $1.29 \pm 0.04$ ). Together, as in experiments 1 and 2, these results support improved perceptual templates as the most likely mechanism underlying the observed improvements in action trainees and show that this improvement is maintained for several months after the end of training.

For the control group, the model that assumes an improvement in internal additive noise reduction at post2 provided the best fit. Specifically, in comparison with the pretest, the best-fitting model assumed a 19% improvement in internal noise reduction in post2, with no change in external noise exclusion. With five parameters and  $r^2 = 97.86\%$ , this model is statistically equivalent to the most saturated model with all noise parameters changed [ $F(2,25) = 0.36, P = 0.70$ ] and is significantly better than the model with no change in noise parameters [ $F(1,27) = 24.60, P < 0.001$ ] and fits the data better than the model that assumes improvement in external noise exclusion alone ( $r^2 = 96.38\% < r^2 = 97.86\%$  of best-fitting model). Moreover, the model with only a multiplicative noise change ( $r^2 = 97.19\%$ ) provided a significantly worse fit than the most saturated model [ $F(2,25) = 4.39, P < 0.05$ ], providing no support for the multiplicative noise model. Indeed, we did not observe a greater contrast ratio at the 79.37% performance level ( $1.14 \pm 0.04$ ) than at the 70.71% performance level ( $1.16 \pm 0.04$ ), as predicted by the multiplicative noise model. Improved internal noise reduction is the most likely mechanism underlying the improvements observed in the control group trainees at post2-test. It remains unclear why we observe internal noise reduction between the end of training and retest at post2 in controls trainees, whereas in action trainees we see performance changes only during the training period and these changes are best accounted for by a change in perceptual template.

### Experiment 3: Dynamics of Perceptual Template Learning in AVGPs.

**Orientation identification learning task.** A  $2 \times 8$  ANOVA was performed on the contrast thresholds across the eight sessions, with group (AVGPs/NVGPs) as a between-subject factor and session (1–8) as within-subject factor. Main effects of session [ $F(7,126) = 13.42, P < 0.001, \eta^2 = 0.427$ ] and group [ $F(1,18) = 7.54, P < 0.05, \eta^2 = 0.295$ ] indicated significant learning effects on this orientation identification task and generally lower contrast thresholds in AVGPs compared with NVGPs. Most importantly, a significant interaction between session and group indicated that the two groups differed across learning sessions [ $F(7,126) = 3.16, P < 0.01, \eta^2 = 0.149$ ]. Post hoc tests confirmed comparable

performance across the two groups in the first session [ $F(1,18) = 0.05$ ,  $P = 0.825$ ,  $\eta^2 = 0.003$ ; Fig. S5] but lower signal thresholds in AVGPs in subsequent learning sessions (all  $P < 0.05$ ; all  $P$  corrected for multiple comparison with the Sidak correction).

**Fitting the elaborated power function.** Contrast thresholds across the eight learning sessions were fit with an elaborated power function  $c(t)$  with three free parameters: (i)  $\alpha$ , baseline contrast; (ii)  $\lambda$ , incremental threshold; and (iii)  $\rho$ , learning rate. Formally, the power function can be written as

$$c(t) = \lambda(t)^{-\rho} + \alpha,$$

where  $t$  is the learning session. For the two groups of subjects, the complete model has six parameters (one  $\lambda$ ,  $\rho$ , and  $\alpha$  per group). The model that postulates no change between the two groups has three parameters ( $\lambda$ ,  $\rho$ , and  $\alpha$ ), because it assumes that  $\lambda$ ,  $\rho$ , and  $\alpha$  are the same across the two groups. Between the fully saturated model and the no-change model, a lattice of models with different numbers of parameters was explored. Similar to the PTM fitting procedure, goodness of fit was measured by the  $r^2$  statistic, and a model lattice consisting of eight models, ranging from the no-change model to the fully saturated model, was used to select the best-fitting model based on the following  $F$  test:

$$F(df_1, df_2) = \left[ \frac{(r_{full}^2 - r_{reduced}^2) / df_1}{(1 - r_{full}^2) / df_2} \right].$$

The model that had the smallest number of parameters and was statistically equivalent to the complete model was defined as the best-fitting model (9). The number of predicted data points in this case was 16 (2 groups  $\times$  8 time points).

The model that assumed that only the learning rate  $\rho$  differed between the two groups provided the best fit. With four parameters and  $r^2 = 97.45\%$ , this model is statistically equivalent to the full model [ $F(2,10) = 0.54$ ,  $P = 0.60$ ] and is significantly better than the model with no change between groups [ $F(1,12) = 297.27$ ,  $P < 0.001$ ]. Furthermore, it fits the data better than the model that assumes only baseline contrast  $\alpha$  changes ( $r^2 = 86.97\% < r^2 = 97.45\%$  of best-fitting model), as well as the model that assumes only incremental threshold  $\lambda$  changes ( $r^2 = 90.73\% < r^2 = 97.45\%$  of the best-fitting model).

#### SI Note 4: Neural Model

We adapted a recent probabilistic neural model of orientation selectivity (36) to our task and asked which type of network changes could best explain the performance improvements observed as a result of action video game training.

**Stimulus Design.** Network simulations were run using stimuli similar to those used in our behavioral experiments (described above). Each stimulus image included an oriented Gabor signal that was tilted  $\pm 2^\circ$  around the horizontal reference, and was created by assigning grayscale values to image pixels, according to the following function:

$$Z(x,y) = z_0 * (1.0 + c \cos(2\pi f(x \cos(\theta) + y \sin(\theta)))) * \exp(-(x^2 + y^2) / 2\sigma^2),$$

where  $\theta = \text{rad}(0^\circ \pm 2)$ ,  $z_0$  is the background grayscale value,  $f = 2$  cycles/degree is the center spatial frequency of the Gabor signal,  $\sigma = 0.375^\circ$  is the SD of the Gabor's circular Gaussian envelope, and  $c$  is the maximum contrast of the Gabor signal, as a proportion of the maximum achievable contrast. The Gabor signal extended over  $2.3 \times 2.3^\circ$  of visual angle and was rendered on a  $23 \times 23$  pixel grid. In addition, as in ref. 36, each stimulus image was padded with extra pixels (10 pixels at each end), set to the background value, to eliminate possible edge effects.

Pixel gray levels for the external noise were drawn from a Gaussian distribution with mean zero and SD depending on the experimental condition. As in our behavioral experiments, we used eight levels of external noise in which the SD of the distribution was varied as a proportion of the maximum achievable contrast. The effective noise contrast levels used were 0.005, 2.1, 4.1, 8.3, 12.4, 16.5, 24.8, and 33%. Each noise element included a single pixel and the noise gray level values were added to the stimulus gray level values on a pixel-by-pixel basis to generate the noise-injected image.

#### Network Model of Orientation Selectivity.

**Network architecture.** For a complete description of the network architecture and the response properties of units in each stage of the network, the reader is referred to Bejjanki et al. (36). There are two points to note regarding the current implementation. First, the behavioral task used here differed from the task simulated previously by Bejjanki et al. (36) in two major ways: (i) The Gabor patch appeared in central vision rather than in peripheral vision and (ii) the Gabor orientation and tilt to identify were different. As such, in adapting the model to the current task, some baseline network parameters were changed so as to match network performance to the pretest performance of our behavioral participants. These parameters were then fixed and the minimal number of parameter changes necessary to capture the action video game-induced improvements in behavior was explored. All relevant parameters and their values are described in the following sections. Second, a note of caution is necessary about the hypothesized neural locus of action game-induced improvements in human participants. Although we show that the behavioral improvements observed as a result of action video game experience can be captured in our neural implementation by changing the pattern of thalamo-cortical feed-forward connections, we do not intend to claim that this is the specific neural locus of action game-induced improvements in human participants. Rather, as described in the main text, our intent here is to show using a biologically realistic neural model of orientation selectivity that improving the quality of the inference during the processing of perceptual information results in improved behavioral performance, in line with the improvements observed as a result of action game training. Ultimately, the precise neural locus of action game-induced improvements in performance is likely to depend on the specific task used, the sensory modalities involved, and the nature of feedback and training received by gamers. Irrespective of the precise locus of the changes, however, we argue that playing action video games leads to improved performance by changing the pattern of feed-forward connections between neural layers so as to instantiate improved probabilistic inference.

**Visual stage 1.** As in Bejjanki et al. (36), the input layer consists of an array of ON center-surround cells and an array of OFF center-surround cells, each of which contains 529 units arranged in a  $23 \times 23$  grid. The firing rate of a cell at location  $(x, y)$  is given by

$$r_{ON}(x,y) = G[r_{baseline} + r_{center}(x,y) - r_{surround}(x,y)]$$

$$r_{OFF}(x,y) = G[r_{baseline} - r_{center}(x,y) + r_{surround}(x,y)],$$

where with  $\alpha = \{\text{center, surround}\}$ ,

$$r_\alpha(x,y) = q(c) K_\alpha \left( \int_{-\frac{w}{2}}^{\frac{w}{2}} \frac{1}{\sqrt{2\pi\sigma_\alpha^2}} e^{-\frac{(x-x')^2}{2\sigma_\alpha^2}} dx' \right) \left( \int_{-\frac{l}{2}}^{\frac{l}{2}} \frac{1}{\sqrt{2\pi\sigma_\alpha^2}} e^{-\frac{(y-y')^2}{2\sigma_\alpha^2}} dy' \right).$$

The new parameters used were  $\sigma_{center} = 0.12^\circ$ ,  $\sigma_{surround} = 0.5^\circ$ ,  $K_{center} = 18$ ,  $K_{surround} = 21$ ,  $r_{baseline} = 15$  Hz, and  $q(c)$  is given by

$$q(c) = \left( \frac{\beta [\log(c)]^2}{c} \right) \text{ with } \beta = 0.1.$$

**Visual stage 2.** The stage 2 layer contains 1,024 neurons, which as in Bejjanki et al. (36) are modeled as LNP units. Specifically, each stage 2 cell is modeled as a single point process and the input–output relationship in the cell is composed of three distinct operations: (i) a linear step where the input spike trains, both feed-forward and recurrent, are linearly combined to obtain a “membrane potential proxy,” (ii) a nonlinear step where the membrane potential proxy is passed through a static nonlinearity to generate the instantaneous probability that it emits a spike, and (iii) a Poisson step where the instantaneous spike probability is used to generate Poisson spikes. These spikes are in turn transmitted to all of the other stage 2 cells through lateral connections, thereby influencing the postsynaptic cells’ membrane potential proxies at the next time step.

As in Bejjanki et al. (36), we model the receptive field of each cell in visual stage 2, with respect to visual stage 1, using a Gabor function  $gab(x, y, \theta)$  defined as

$$gab(x, y, \theta) = e^{-\left[ \frac{c_x^2}{2\sigma_x^2} + \frac{c_y^2}{2\sigma_y^2} \right]} \cos(2\pi k C_x),$$

where

$$\begin{aligned} C_x &= x \cos \theta + y \sin \theta \\ C_y &= y \cos \theta - x \sin \theta. \end{aligned}$$

The strength of each connection was set to  $\alpha * |gab(x, y, \theta)|^2$ . The new baseline parameters used were  $\sigma_x = 0.25$ ,  $\sigma_y = 0.3$ ,  $k = 1.45$ , and  $\alpha = 0.55$ .

As in Bejjanki et al. (36), we implement full lateral connectivity with the strength of the connection between two cells  $x$  and  $y$ , with preferred orientations  $P_x$  and  $P_y$  (in radians), given by

$$W(x, y) = \frac{G_w}{N_{out}} \left[ e^{K_e(\cos(P_y - P_x) - 1)} - A_i e^{K_i(\cos(P_y - P_x) - 1)} \right] + DC_w.$$

The new baseline parameters used were  $K_e = 0.5$ ,  $K_i = 0.25$ ,  $DC_w = -2.0$ ,  $G_w = 1$ , and  $A_i = 0.4$ .

**Decision stage.** The final stage of the network involves connections from all stage 2 cells to a single decision unit that outputs an estimate for the orientation of the stimulus (clockwise or counter clockwise around horizontal, for example). As in Bejjanki et al. (36), we used a linear classifier as the decoder in our network, which was optimized for the before-training network condition and then kept constant across all network manipulations.

**Computing Orientation Discrimination Performance and Deriving TvC Curves.** As in Bejjanki et al. (36), we compute the orientation discrimination performance of our network, when presented with the noisy oriented Gabor stimuli (described above), by estimating Fisher information, an information-theoretic quantity that directly predicts performance in discriminations tasks. Re-

cently, we have derived an analytic expression for the linear Fisher information in a population of LNP neurons driven to a noise-perturbed steady state, with network properties similar to those of the network used here (37). Linear Fisher information is the fraction of Fisher information that can be recovered by a locally optimal linear estimator—in practice, it has been found to provide a tight bound on total Fisher information, both in simulations (38) and in vivo (39). This expression, when applied to a network with a fixed decoder, can be written as

$$I(W_{dec}) = \frac{(W_{dec}^T \mu')^2}{W_{dec}^T \Gamma W_{dec}},$$

where

$$\begin{aligned} \mu' &= (D^{-1} - W)^{-1} M h' \\ \Gamma &= (D^{-1} - W)^{-1 T} [M \Gamma_{hh} M^T + D^{-1} G D^{-1}] (D^{-1} - W)^{-1}. \end{aligned}$$

$W_{dec}$  represents the fixed pattern of connection weights from stage 2 to the decision stage,  $W$  represents the matrix of stage 2 recurrent connections,  $M$  represents the matrix of stage 1 – stage 2 feed-forward connections,  $h$  represents the mean input firing rates from stage 1,  $\Gamma_{hh}$  represents the covariance matrix of the input firing rates from stage 1,  $G$  is a diagonal matrix whose entries give the mean response of the LNP neurons, obtained from the nonlinear function that transforms the membrane potential proxy  $u(t)$  to the firing rate for the LNP neurons, and  $D$  is a diagonal matrix that gives the derivative or slope of the activation function  $G$  of the stage 2 neurons at steady state.

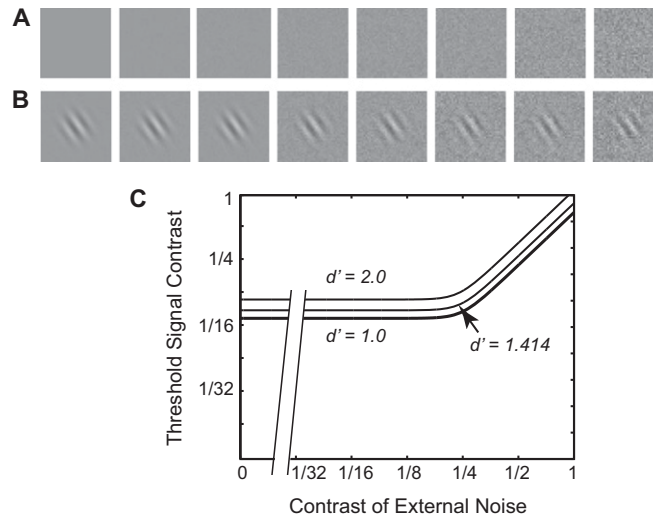
Using the above expression allows us to compute the Fisher information, and hence the discrimination threshold, at the decision stage in response to a given stimulus. We compute Fisher information at the decision stage using stimuli with 17 signal contrast levels (10, 12, 14, 16, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 80, and 90%) and with the eight levels of external noise used in our behavioral experiments. We then derive network TvC curves by computing an iso-information contour for a value of information that is equivalent to the percent correct criterion used in the behavioral experiments (computed via signal detection theory), through the resulting information matrix (see ref. 13 for further details). We can now examine the influence of changes in network parameters on these network TvC curves in an effort to model the neural basis for the action-trained improvements in performance.

**Modeling Action-Trained Improvements in Performance.** As discussed in the main text (Fig. 4), action video game-induced changes in performance were captured in our model by making changes only to the feed-forward connectivity between stage 1 and stage 2. A change in this single network parameter led to a decrease in network signal contrast thresholds and a nearly uniform downward shift in network TvC curves (Fig. 4B), similar to those observed in our behavioral experiments. The specific network parameter values that led to the reported results are listed in Table S1.

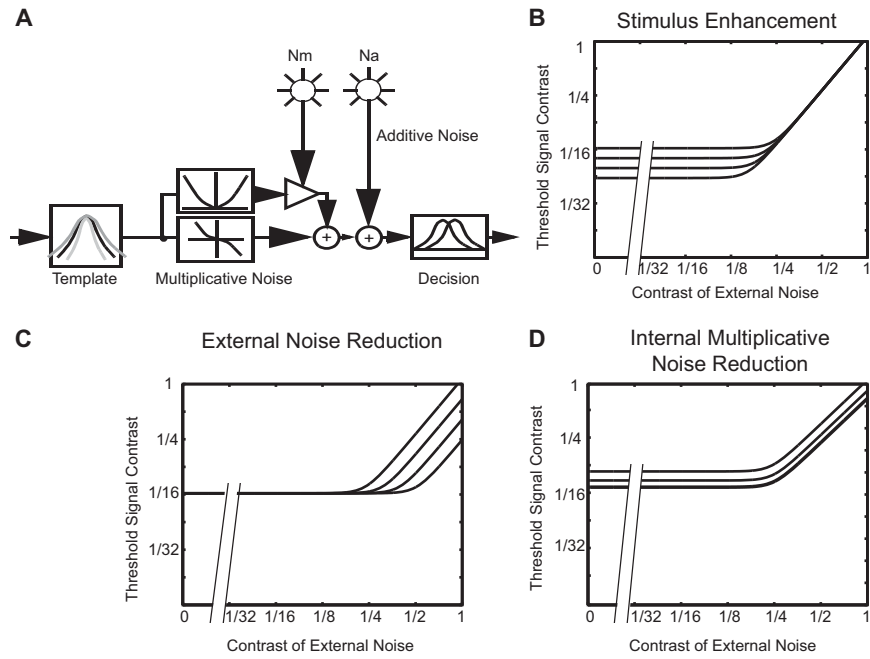
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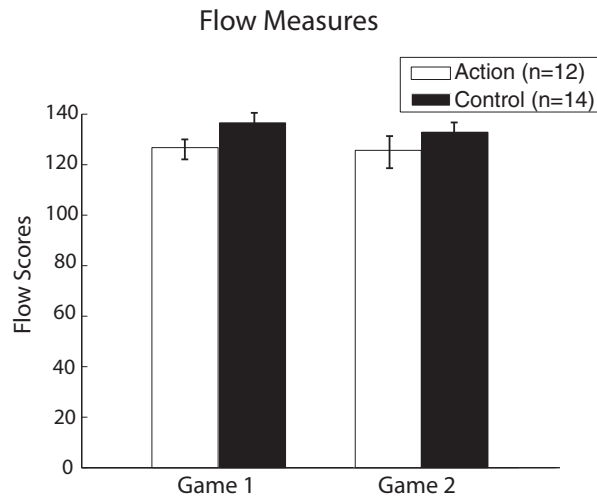
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**Fig. S1.** The external noise method. (A) From left to right, external noise images with increasing contrast. (B) A signal Gabor patch embedded in increasing levels of external noise. (C) The signal contrast required to maintain threshold performance at three criterion performance levels as functions of external noise contrast.



**Fig. 52.** The PTM. (A) A schematic of the components included in the PTM. (B–D) Behavioral signatures of three mechanisms of performance improvements and decrements.



**Fig. 53.** Flow measures. Mean “flow” scores computed for the action ( $n = 12$ ) and control ( $n = 14$ ) groups, after 20 h (toward the end of game 1) and 50 h (after game 2) of game training. Participants in both groups displayed high flow scores, and although the control trainees tended to exhibit greater flow, this difference was not statistically significant ( $P = 0.16$ ).



