Action video game play facilitates the development of better perceptual templates

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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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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. 1*A*). The procedure and methods were similar to those of Lu and Dosher (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 ($F_{1,18} = 5.82$, $P < 0.05$, $\eta^2 = 0.24$), as shown in Fig. 1*B* (see *Supporting Information* for full statistics).

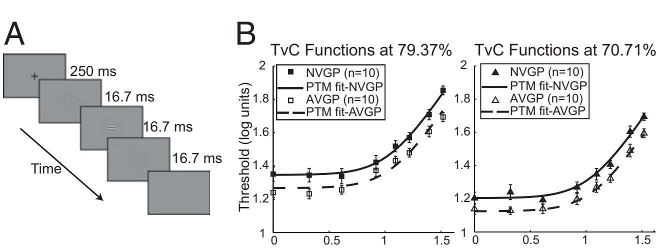

Fig. 1. AVGPs show improved performance in an orientation identification task. (*A*) An illustration of a typical trial. After a central fixation cross was presented, a Gabor signal frame appeared sandwiched between two external noise frames. Participants had to indicate the orientation of the Gabor 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.

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. 1*B*). 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 ± 0.03 vs. 1.22 ± 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, nonaction 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

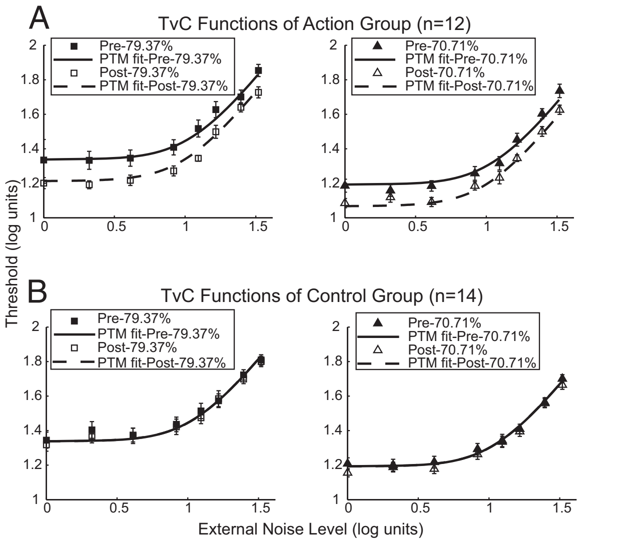

Fig. 2. Improved orientation identification performance as a result of action video game training (*A*) vs. control game training (*B*). Overall, action-trained participants (n = 12) showed larger posttraining improvements in orientation identification performance than control trainees (n = 14). Curves 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 ± 0.04 at 79.37% correct vs. 1.25 ± 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*2*2*8*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*2*8*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 ± 0.04 at 79.37% correct vs. 1.29 ± 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. 4*A*). 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. 4*B*), 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

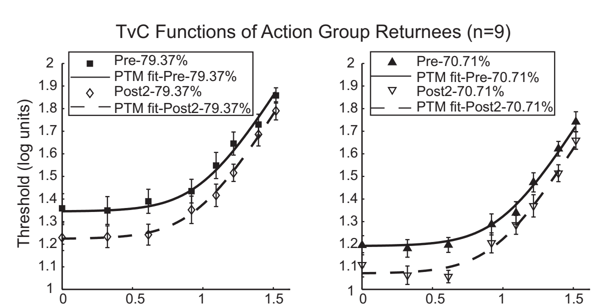

Fig. 3. Action video game-induced improvements in performance were retained several months after training. A subset of action group participants (n = 9) from the training study were brought back several months later and retested on the orientation identification task (post2). The curves represent PTM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

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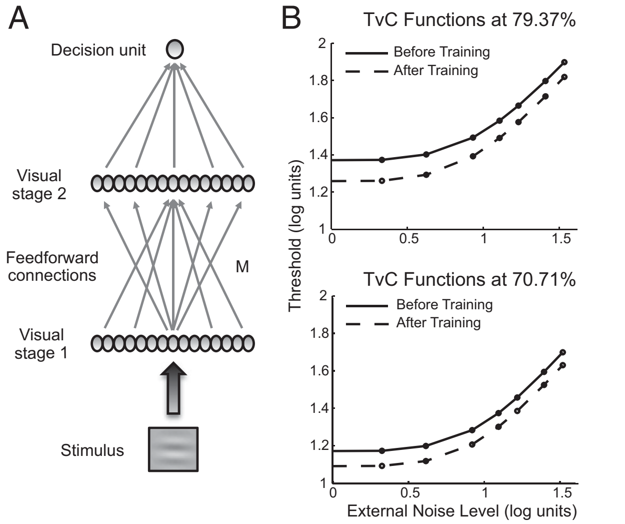

Fig. 4. Neural model of the improvements in orientation identification performance, observed as a result of action video game experience. (*A*) Schematic of the neural architecture used to simulate performance in the orientation identification task. The model consists of two visual stages, which simulate 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 NVPGs 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. 5*A*). The changes to the task (e.g., using a single fixed level of external noise, presenting the stimuli peripherally rather than centrally, using ±12° 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. 5*A*). The Gabor signal was presented at one of two peripheral spatial locations and in one of two possible orientations (12° clockwise or counterclockwise from a fixed reference orientation, either −35° or +55°, 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) × 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. 5*B* 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

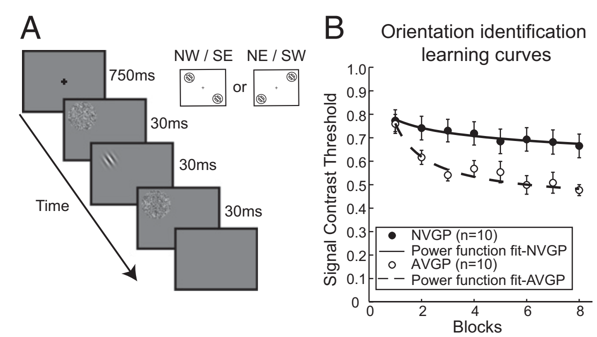

Fig. 5. AVGPs show faster learning in an orientation identification task. (*A*) An illustration of a typical trial. After a central fixation cross was presented, a Gabor signal frame appeared in one of two peripheral locations and was sandwiched between two external noise frames. Participants had to indicate the orientation of the Gabor signal, clockwise or counterclockwise from an implicit reference angle (−35° or 55°). 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 Dosher (24), except that the size ($1.5 \times 1.5°$), degree of tilt ($\pm 2°$), and reference angle (horizontal reference) were different. A typical trial is shown in Fig. 1*A*. 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 $\pm 2°$ around the horizontal reference and extended over $2.3 \times 2.3°$ 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.

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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 (±12°) stimuli were used. A typical trial is illustrated in Fig. 5*A*. 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. 5*A*, *Inset*). The reference orientation (−35°/+55°) 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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