

# Brain Plasticity Through the Life Span: Learning to Learn and Action Video Games

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## Keywords

transfer, generalization, probabilistic inference, cognitive control, resource allocation, knowledge, hierarchy, learning rules

## Abstract

The ability of the human brain to learn is exceptional. Yet, learning is typically quite specific to the exact task used during training, a limiting factor for practical applications such as rehabilitation, workforce training, or education. The possibility of identifying training regimens that have a broad enough impact to transfer to a variety of tasks is thus highly appealing. This work reviews how complex training environments such as action video game play may actually foster brain plasticity and learning. This enhanced learning capacity, termed learning to learn, is considered in light of its computational requirements and putative neural mechanisms.

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## INTRODUCTION

Human beings have a tremendous capacity to learn. And although there are unquestionably gradients in the ability to learn that arise as a function of intrinsic factors such as age and individual genetic propensities, nearly all humans demonstrate the ability to acquire new skills and to alter behavior given appropriate training. One common finding, however, is that the learning that emerges as a result of training is often quite specific to the trained stimuli, context, and task. Such specificity has been documented in every subfield of neuroscience that focuses on learning—e.g., motor learning (Shapiro & Schmidt 1982), expertise (Chase & Simon 1973), or memory (Godden & Baddeley 1975). In addition to being of theoretical interest, this fact is of great practical relevance in areas such as rehabilitation and education in

which the end goal necessarily requires that the benefits of learning extend beyond the confines of the particular training regimen. For instance, it is of little use for a patient with damage to the motor cortex to improve on reaching movements in therapy if it does not also improve their ability to reach for a bottle of milk in their refrigerator at home (Frey et al. 2011). Similarly, it is of limited benefit if pupils trained on one type of math problem are unable to solve similar problems when presented outside the classroom. Thus, for all practical purposes, the specificity that typically accompanies learning is a curse.

A crucial issue in the field of learning, therefore, concerns training conditions that result in observable benefits for untrained skills and tasks. A handful of behavioral interventions have recently been noted to induce more general learning than that typically documented in the learning literature. These learning paradigms are usually more complex than standard laboratory manipulations, reminiscent of the “enriched environment effects” seen in animal rearing (Renner & Rosenzweig 1987), and they typically correspond to real-life experiences, such as aerobic activity (Hillman et al. 2008), athletic training (Erickson & Kramer 2009), musical training (Schellenberg 2004), mind-body training (Lutz et al. 2008, Tang & Posner 2009), working memory training (Jaeggi et al. 2008, Klingberg 2010), and, the focus of this article, action video game training (Green & Bavelier 2003, Spence & Feng 2010). Here we first review the variety of tasks on which performance is enhanced as a result of action video game experiences. We then ask why action games might produce benefits on such a wide range of tasks. In particular, rather than hypothesizing that video games teach myriad individual specific skills (i.e., one for each laboratory test during which they have been shown to produce benefit), we instead consider the possibility that what video games teach is the capability to quickly learn to perform new tasks—a capability that has been dubbed “learning to learn” (Harlow 1949, Kemp et al. 2010).

The idea that the ultimate goal of training and education might be to enable learning to learn is not a new one. On the basis of his work on pairing tasks, in which training on task A may impact training on new task B, Thorndike & Woodworth (1901) observed, “It might be that improvement in one function might fail to give in another improved ability, but succeed in giving ability to improve faster” (p. 248). Around the same time, the educational psychologist Alfred Binet [1984 (1909)] described his classroom instructional goals by saying, “[O]ur first job was not to teach [the students] the things which seemed to us the most useful to them, but to teach them how to learn” (p. 111). To this end, Binet asked students to play games such as “statue,” wherein the students learned to stay focused, quiet, and still for long periods of time. Although no new academic concepts or facts were taught by these games, they allowed the children to develop skills, such as attention and control, that underlie the ability to learn in school. In the 1940s, Harlow (1949) outlined what he called “the formation of learning sets” wherein animals learned general rules, such as “win-stay, lose-switch,” that allowed them to quickly master new tasks that abided by this general rule. This work led Harlow to state, “The learning of primary importance to the primates . . . is the learning how to learn efficiently in the situations the animal frequently encounters” (p. 51). Despite this early interest in the topic, the factors that facilitate learning to learn and the computational principles on which it relies remain largely unexplored. Here we discuss these issues by anchoring our discussion in recent advances in the field of cognitive training through action video game play.

## BENEFITS OF ACTION VIDEO GAME EXPERIENCE

An overview of the existing literature on action video game (one specific subgenre of video game) play indicates performance benefits after action game play in many domains typically thought of as distinct. This breadth is particularly notable and runs counter to the predomi-

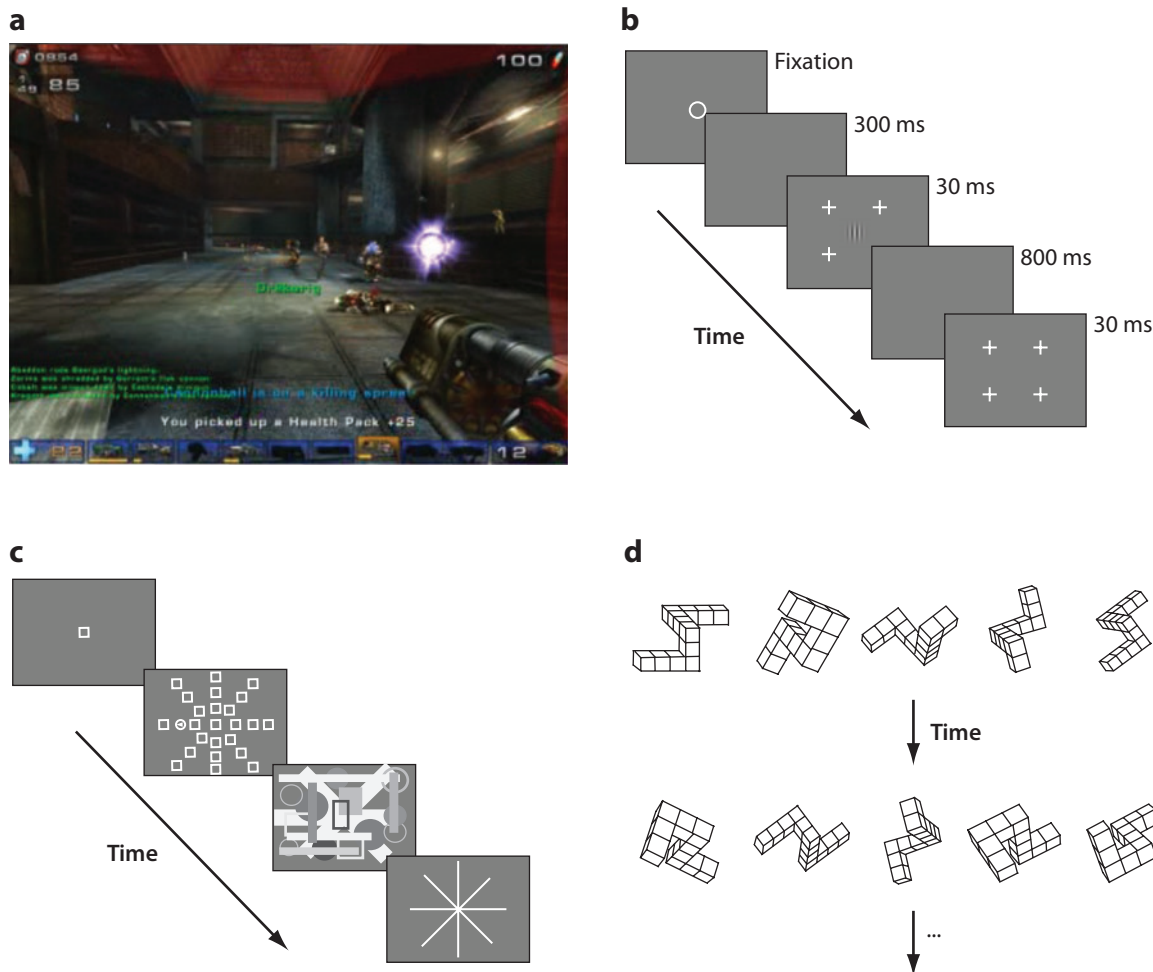
nant pattern of results in the learning literature, wherein training facilitates the trained task but typically leads to little benefit to other, even related tasks. In the case of video game training, the transfer of learning takes place between tasks and environments that have different goals and feel. Most laboratory tasks on which avid action video game players (VGPs) are tested involve simple stimuli and highly repetitive choices, making for a rather dull environment. In sharp contrast, action video games include complex visual scenes, an enthralling feel, and a wide variety of goals at different timescales (from momentary goals such as “jump over the rock” to game-long goals such as “rescue the princess”) (see **Figure 1**). Although it seems reasonable to expect VGPs to show transfer across a broad range of similar games (e.g., first-person shooters or third-person shooters), the fact that VGPs best their nonaction game-playing peers (NVGPs) on standard laboratory tests that are quite dissimilar to video games begs further investigation.

## Vision

Action video game play enhances the spatial and temporal resolution of vision as well as its sensitivity (Green et al. 2010). For example, when asked to determine the orientation of a T that is flanked by distracting shapes above and below, VGPs can tolerate the distractors being nearer to the T shape while still maintaining a high level of accuracy (Green & Bavelier 2007). Such capacity to resolve small details in the context of clutter, also called crowding acuity, is thought of as a limiting property of spatial vision and is often compromised in low-vision patients who complain that the small print of newspapers is unreadable because letters are unstable and mingle into one another (Legge et al. 1985). In addition, the enhancements noted in this ability as a result of action video game play occur both within and outside the typical eccentricities of game play, a finding that stands in contrast to the bulk of the perceptual learning literature, which finds that learning is typically specific to the trained retinal location.

**VGP:** action video game player

**NVGP:** nonaction-video game players



**Figure 1**

Action video game play (*a*) bears little resemblance in terms of stimuli and goals to perceptual, attentional, or cognitive tasks at which VGPs are found to excel in the laboratory (*b*: contrast sensitivity, *c*: visual search, *d*: mental rotation). This raises the question of why action video game play enhances such a varied set of skills.

Along with this improvement in spatial resolution, enhanced temporal resolution of vision as a result of action game experience has also been noted. VGPs show, for example, significant reductions in backward masking (wherein a display of interest is more difficult to see if it is quickly followed by another display) as compared with NVGPs. This difference suggests a change in the dynamics of the visual system: VGPs can resolve events at a higher temporal frequency (Li et al. 2010). Although backward

masking, which is believed to reflect limitations on cortical processing, is improved in VGPs, this is not true of forward masking (wherein the masking display precedes the display of interest), which is believed to reflect mostly limitations of early, retinal factors. As we discuss below, these results are consistent with the view that action video game play retrains cortical networks such that each layer of the processing hierarchy makes better use of the information it receives from earlier layers, rather than

changing the nature of the early sensory input (e.g., altering the optics of the eye).

Finally, a third aspect of vision found to be enhanced in VGPs is contrast sensitivity, or the ability to detect small changes in levels of gray. Although this effect appears across spatial frequencies, it is particularly pronounced at intermediate spatial frequencies (Li et al. 2009). Thus, contrary to the folk belief that screen time is bad for eyesight, action video game play appears to enhance how well one sees. Video game training, therefore, may become a powerful tool to improve eyesight in situations in which the optics of the eye are not implicated in producing the poor vision (e.g., amblyopia; Bavelier et al. 2010, Li et al. 2011).

## Cognitive Functions

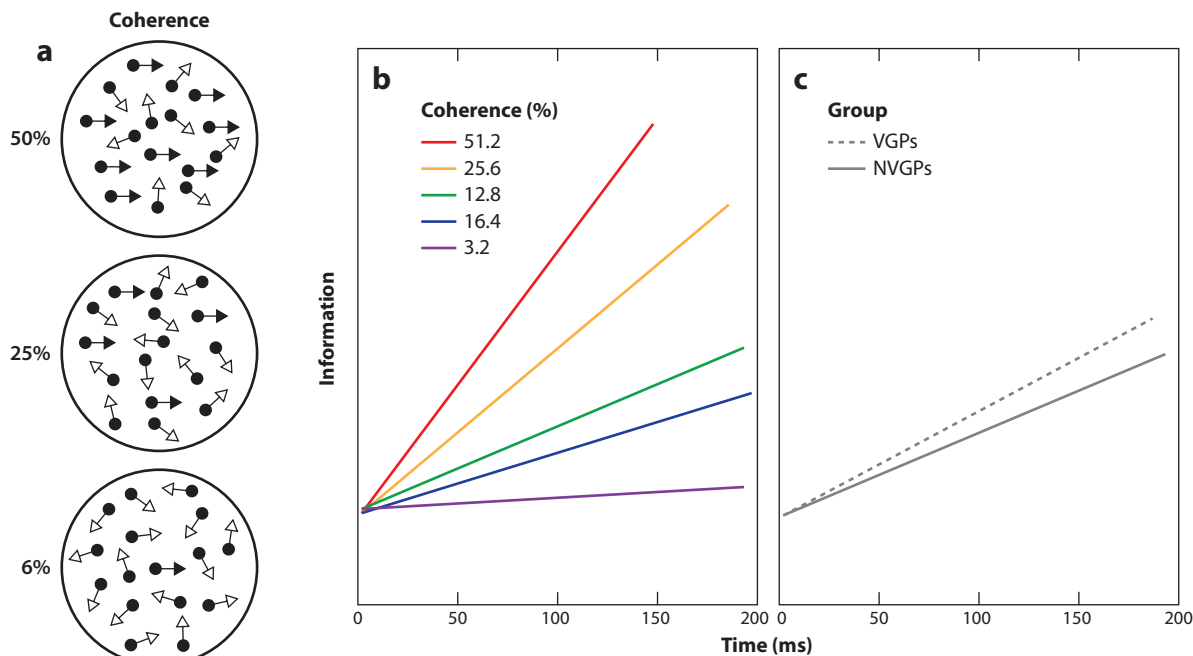
VGPs have also been documented to better their nongamer peers on several aspects of cognition such as visual short-term memory (Anderson et al. 2011, Boot et al. 2008), spatial cognition (Greenfield 2009), multitasking (Green & Bavelier 2006a), and some aspects of executive function (Anderson & Bavelier 2011, Chisholm & Kingstone 2011, Colzato et al. 2010, Karle et al. 2010; but see Bailey et al. 2010 for a different view). For example, whereas NVGPs were markedly slower and less accurate when asked to perform both a peripheral visual search task and a demanding central identification task concurrently [relative to performing the peripheral search task alone, VGPs showed no falloff in performance (Green & Bavelier 2006b)]. Several studies have also documented enhanced task-switching abilities in VGPs, meaning they pay less of a price for switching from one task to another (Andrews & Murphy 2006, Boot et al. 2008, Cain et al. 2012, Colzato et al. 2010, Green et al. 2012, Karle et al. 2010, Strobach et al. 2012). These results are all the more surprising given that such task-switching skills appear to be negatively affected by the extensive multitasking seen in many young adults who are heavy users of a variety of forms of technology (Ophir et al. 2009). This contrast highlights the need to assess

separately the effects of different technology use on brain function.

Another cognitive domain enhanced by action games is spatial cognition. The beneficial aspect of video game play on spatial cognition was noted in the early days of video game development (McClurg & Chaille 1987, Okagaki & Frensch 1994, Subrahmanyam & Greenfield 1994). More recently, action game play has been shown to enhance mental rotation abilities (Feng et al. 2007). These results have received much attention because spatial skills are typically positively correlated with mathematical achievement in school (Halpern et al. 2007, Spelke 2005). Whether action game play may indeed foster mathematical ability is currently being investigated.

## Decision Making

Benefits are also noted in decision making. In one perceptual decision-making task, for instance, VGPs and NVGPs were asked to determine whether the main flow of motion within a random dot kinematogram was to the left or to the right (**Figure 2a**). Unlike most previous tasks used to study the effect of action gaming, in this task, participants are in control of when to terminate display presentation (by making a decision and pressing the corresponding key). It thereby provides a measure of how participants accumulate information over time in the service of decision making. Indeed, these types of task are well understood in terms of one's ability to first extract and integrate information from the environment and then to stop the integration and to select an action on the basis of the accumulated information (Palmer et al. 2005, Ratcliff & McKoon 2008). By presenting trials with variable signal-to-noise levels, the task allows the full chronometric and psychometric curves to be mapped, providing a unique description of how information about motion direction accrues over time (**Figure 2b**). We found that action game play enhances the rate at which information accumulates over time by ~20% as compared with control participants (**Figure 2c**). The net result is that VGPs



**Figure 2**

(a) In this perceptual decision-making task, participants are asked to judge whether the motion is mostly leftward or rightward. The number of dots moving coherently in one direction or the other can vary from none to many, allowing the investigator perfect control over the task difficulty. (b) As the level of coherence goes from low to high, the task varies from extremely difficult to easy. Accordingly, electrophysiological recordings in monkeys show that the amount of information about motion direction accumulated in the lateral intraparietal cortex (LIP), a neuronal structure associated with such decisions, increases (adapted from Beck et al. 2008, figure 3d). (c) Another way to increase the rate at which information accumulates is to enhance the decision-making characteristics of the viewer. This was shown to be the case in action video game players (VGPs) or after training on action video games: VGPs accumulated on average 20% more information per unit of time as compared with nonaction-video game players (NVGPs) (Green et al. 2010).

can make more correct decisions per units of time. This is of practical relevance as illustrated by the recruitment by the Royal Air Force of young gamers to pilot unmanned drones or by findings indicating that young laparoscopic surgeons who are gamers outperform more seasoned surgeons, executing surgery procedure faster and as accurately if not more accurately (Daily Mail 2009, McKinley et al. 2011, Rosser et al. 2007, Schlickum et al. 2009).

### Reaction Time and Speed-Accuracy Trade-Off

More generally, a fourth domain of improvement concerns the ability to make quick and accurate decisions in response to changes in the environment, such as when one must brake

suddenly while driving. Such improvement was noted in the decision-making tasks described above. Action video game play sped up reaction times, and this was true whether the task was in the visual or the auditory modality. Such tasks entail concurrently collection reaction times and accuracy along a wide range of task difficulties, easily revealing a speed-accuracy trade-off if present. Despite faster reaction times, accuracies were left unchanged, establishing that action game play does not result in trading speed for accuracy. A meta-analysis of more than 80 experimental conditions in which gamers and nongamers have been tested confirmed that VGPs are on average 12% faster than NVGPs, yet VGPs make no more errors (Dye et al. 2009a). This relationship held from simple decision tasks leading to reaction times as short



as 250 ms, all the way to demanding, serial, visual search tasks eliciting reaction times as long as 1.5 s. The fact that the relationship was purely multiplicative, with no additive component, demonstrates that the faster reaction times seen in VGPs throughout the literature are not attributable to postdecisional factors such as faster motor execution time. Indeed, if the only difference between groups was in their ability to map a decision that had already been made into a button press on a keyboard, the difference in reaction time between groups should not depend on how long it took for the decision to be reached (i.e., would be only additive rather than multiplicative). Furthermore, the fact that there was no difference in accuracy in any of these tasks suggests that the differences also cannot be attributed to differences in criteria, or VGPs being “trigger-happy” or willing to trade reductions in accuracy for increases in speed. Whether this pattern of greater speed with matched accuracy will remain when using complex tasks with longer timescales and/or multiple task components is currently being investigated (A.F. Anderson, C.S. Green, and D. Bavelier, manuscript in preparation).

## Attention

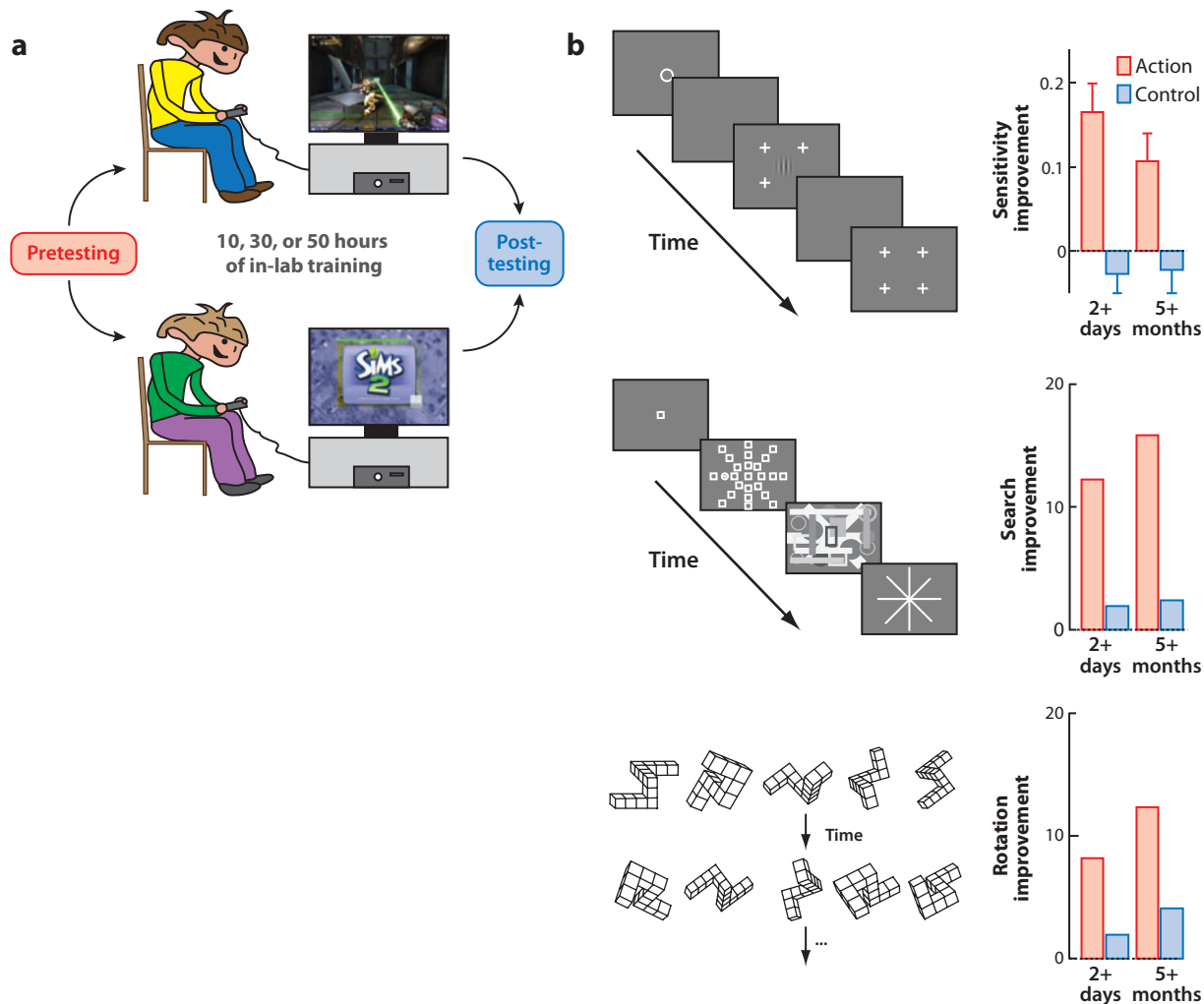
Several different facets of attention are improved following action game play. For instance, many aspects of top-down attentional control such as selective attention, divided attention, and sustained attention are enhanced in VGPs. In contrast, however, when attention is driven in a bottom-up fashion (i.e., by exogenous cueing) no differences have been found between VGPs and NVGPs, despite the fact that orienting to abrupt events is a key component of game play (Castel et al. 2005, Dye et al. 2009b, Hubert-Wallander et al. 2011). This pattern of results clearly illustrates the need for a careful investigation of those aspects of performance modified by action game play. Simply because a process is required during game play does not guarantee changes in that process. In a later section, we review in greater detail those aspects of attention and executive control that are modified by action game

experience (see Resources, Knowledge, and Learning Rules in Action Video Game Play).

## Causality

A key question concerns whether the effects of action video game play are causal or are instead reflective of population bias, wherein action gaming tends to attract individuals with inherently superior skills. Because our interest is in learning rather than in identifying individuals with extraordinary skills, causality is a crucial factor. The only way to establish firmly that the relationship is indeed causal is via well-controlled training studies (see Green & Bavelier 2012, box 1 for further discussion). In such studies, individuals who do not naturally play fast-paced, action video games are recruited and pretested on the task(s) of interest. A randomly selected sample of half of these subjects is then assigned to play an action game (e.g., Medal of Honor, Call of Duty, Unreal Tournament), whereas the other half is assigned to play an equally entertaining, but nonaction video game (e.g., Tetris, The Sims, Restaurant Empire). Note that in addition to controlling for simple test/retest effects (subjects may improve at posttest simply because they have experienced the task a second time) the presence of an active control condition guarantees that any effects observed in the action game training group are truly the result of action game play rather than simply a reflection of the power of an intervention per se. Indeed, individuals often feel special upon being included in an active intervention study and, as a result of receiving more attention, may perform better independently of the content of the intervention, an effect also known as the Hawthorne effect (Benson 2001).

Causality has been established through training studies, whereby both groups of participants come to the laboratory regularly to play 1–2 h per day over a period of 2–10 weeks, depending on the duration of the training (e.g., 10, 30, or 50 h of training were used in our work) (Figure 3). At the end of training, subjects are tested again on the same tasks of



**Figure 3**

(a) Design of training studies to evaluate causality. Participants are randomly assigned to either the experimental group or a control group before being evaluated on perceptual, attentional, or cognitive laboratory tests. Both groups are then required to play commercially developed entertainment games. All experimental games are of the action genre (Unreal Tournament, Medal of Honor, Call of Duty), whereas control games are of other genres (Tetris, The Sims, Restaurant Empire). Following the end of training (and a 24-h waiting period) subjects are retested on the original measures. If the effect of action game play is truly causal, those assigned to the experimental games should display greater improvements between pre- and posttest than those assigned to the control games. (b) Such causal effects have been established for a variety of perceptual, attention, and cognitive tasks; some studies showed that the effects are quite long-lasting because robust effects were observed not only 1–2 days after the cessation of training (red bars) but also as long as 5+ months posttraining (blue bars) (panel b adapted from Feng et al. 2007, Li et al. 2009).

interest as those during pretest. However, it is important to note that in all cases we require that participants come back in the following days for posttesting, with no less than 24 h elapsing between the cessation of training and

the beginning of posttesting. Indeed, our focus is on the durable learning effects of action game play and not on any transient effects of playing games (e.g., changes in arousal) that could contaminate posttest performance if assessed



shortly after the end of gaming. If action game play truly has a causal effect on the skill under study, we expect greater pre- to posttest improvement in the action trainees than in the control trainees. Such causal effects have been established for vision (Green & Bavelier 2007; Li et al. 2009, 2010), some cognitive functions such as multitasking (Green et al. 2012) and mental rotation (Feng et al. 2007, Spence et al. 2009), many aspects of attention (Cohen et al. 2007; Feng et al. 2007; Green & Bavelier 2003, 2006a,b; Spence et al. 2009), and decision making (Green et al. 2010).

### A COMMON MECHANISM: LEARNING TO LEARN

As illustrated above (see Benefits of Action Video Game Experience), the range of tasks seen to improve after action game play is quite atypical in the field of learning. VGPs perform better than NVGPs do on tasks neither group had previously experienced and that are, as noted earlier, quite different in nature from action game play. This finding begs the question of what exactly action video games teach that results in better performance. Rather than hypothesizing distinct mechanisms for each task improved, it seems more parsimonious to consider one common cause: learning to learn.

To understand what is meant by learning to learn, it is important first to realize that all the tasks on which VGPs have been found to improve share one fundamental computational principle: All require subjects to make a decision based on a limited amount of noisy data. Note that most everyday decisions fall into this category. Consider a radiologist reading computed tomography (CT) scans to determine the presence of bone fractures. Some scans will be clear-cut, leading to the immediate conclusion that a fracture is present. Other scans may present more subtle evidence, such that the radiologist may conclude a fracture has occurred, but his/her level of confidence will be much lower. In making these decisions, the radiologist is performing what is known as probabilistic inference. In essence, the radiologist computes

the probability that each choice (fracture or no fracture) is correct given the evidence present in the scan(s). This quantity is known as the posterior distribution over choices, which we denote  $p(c|e)$  where  $c$  are the choices, and  $e$  is the evidence (i.e.,  $c$  = "fracture" or "no fracture",  $e$  = the evidence, which in this case is the scan itself). The key computational question then concerns how to compute the most accurate posterior distribution,  $p(c|e)$ , so that the best decision can be made. The main goal of learning is indeed to improve the precision of such probabilistic inference. The very fact that trained radiologists are more competent at diagnosing subtle fractures and identifying them with more confidence exemplifies that proper training does lead to more accurate posterior distributions.

How then does this process occur in practice? During training, a young radiologist sees many scans and is explicitly told the state of the patient that generated the image (i.e., whether a fracture was present). Radiologists are trained on the statistics of the evidence  $p(e|c)$  or the probability of the evidence (how the scan looks) given a known state of the world (fracture is present/absent). Through Bayes' rule, this value,  $p(e|c)$ , is proportional to the posterior probability  $p(c|e)$  on which the decision will be based. This set of computations is termed probabilistic inference (Knill & Richards 1996). One of the major advances of systems and computational neuroscience over the past 10 years has been to show how such probabilistic computations may be implemented in networks of spiking neurons (Deneve 2008, Ma et al. 2006, Rao 2004).

Participants who first encounter a new task in the lab are not very different from young radiologists in training. Initially, there is no way for them to have perfect knowledge of the statistics of the evidence, which in turn means that the calculated posterior distribution over choices will be suboptimal. It is only through repeated exposure to the task that subjects can learn these statistics and, as a result, make decisions on the basis of a more accurate posterior distribution. By using a well-studied perceptual decision-making task (as described above in Benefits

of Action Video Game Experience), we more directly tested whether action video game experience indeed results in improvements in probabilistic inference. In this task, subjects were asked to determine whether the main flow of motion within a random dot kinematogram was to the left or to the right. Using a neural model of the task (Beck et al. 2008), we showed that the pattern of behavior after game play is captured via a single change in the model: an increase in the connectivity between the model's sensory layer, where neurons code for direction of motion, and its integration layer, where neurons accumulate the information they receive over time from the sensory layer until a criterion is reached for decision and response. This increase in connectivity can be shown to be mathematically equivalent to improved statistical inference; game experience resulted in more accurate knowledge of the statistics of the evidence for the task or more accurate knowledge of  $p(e|c)$  (Figure 2c) (Green et al. 2010). This work ruled out simpler explanations for the variety of benefits observed after action game play, including simple speed-accuracy trade-offs or faster motor execution times in VGPs.

The modeling demonstrates that VGPs were making choices on the basis of a more accurate posterior distribution. Because these statistics could not have been directly taught by any action video games, but instead must have been learned through the course of the experiment, action video games thus taught these participants to learn the appropriate statistics for new tasks more quickly and more accurately than is possible for NVGPs.

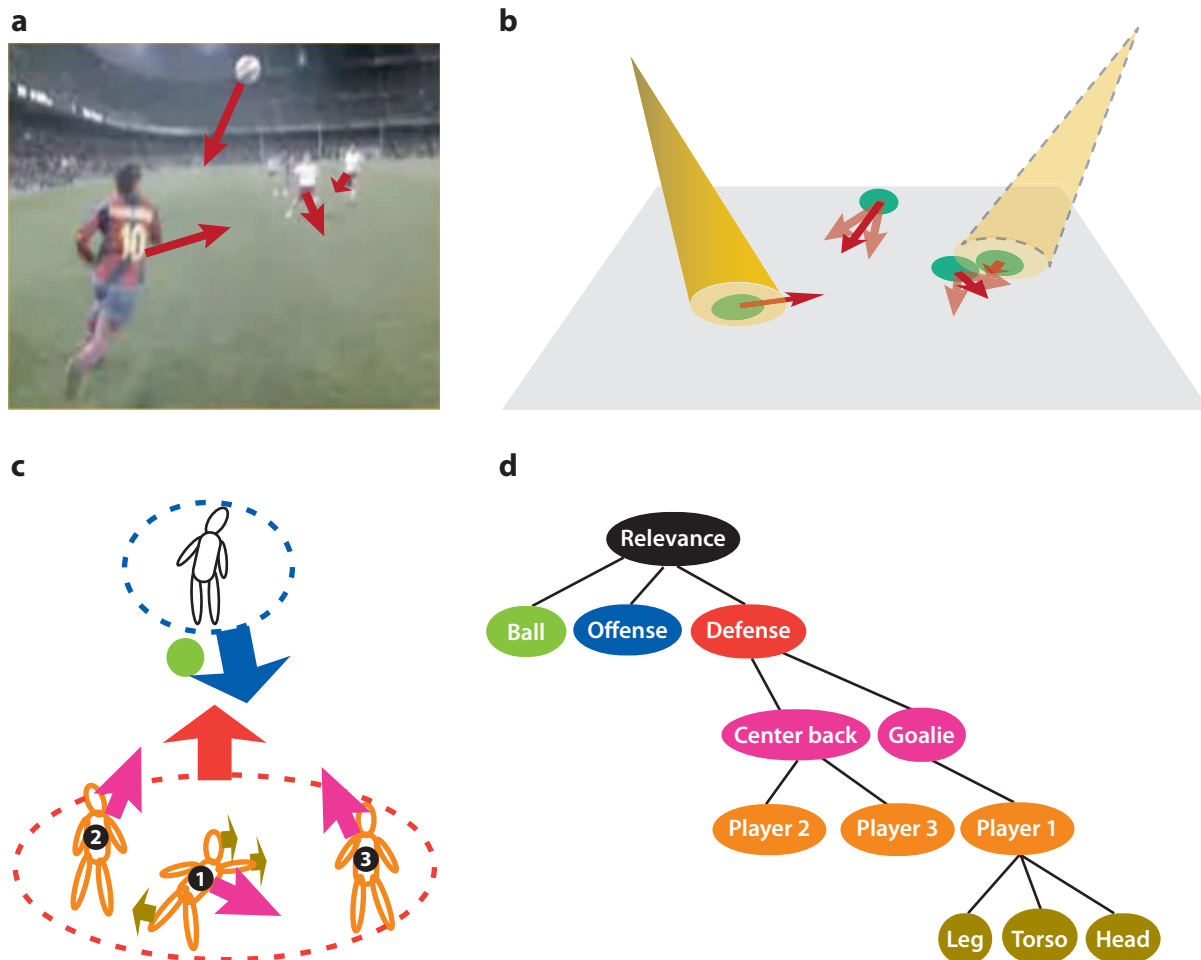
The idea that VGPs have learned to learn the statistics of the task (or what we call later the generative model of the data) can be generalized beyond the specific example of perceptual decision making. Indeed, most of the behavioral tasks on which VGPs have been shown to excel can be formalized as instances of probabilistic inference. This includes tasks that are more classically categorized as attentional, such as multiple object tracking or locating a target among distractors, both of which have recently

been modeled within the probabilistic framework, as well as more cognitive and perceptual tasks (Ma et al. 2011, Ma & Huang 2009, Vul et al. 2009).

## COMPUTATIONAL PRINCIPLES OF LEARNING TO LEARN

Learning is commonly defined as a long-term improvement in performance due to training, a process that is often modeled as the tuning of parameters within a fixed architecture. The literature has countless examples wherein learning algorithms, such as gradient descent, are implemented within neural networks to tune weights to enhance performance on the trained task (Rumelhart et al. 1987, but see Gallistel & King 2009 and Gallistel 2008 for a different view on learning). For example, in classic orientation-discrimination training tasks, subjects have to learn through experience whether the image of a Gabor patch is oriented clockwise or counterclockwise from some reference angle (e.g.,  $45^\circ$ ). Human behavior on such tasks can be easily captured with two-layer networks, in which an input layer containing oriented filters projects to an output layer that produces a clockwise or counterclockwise decision (Doshier & Lu 1998, Pouget & Thorpe 1991). Learning in such models is typically produced via changes in the synaptic weights between the two layers. The pattern of synaptic weights that optimizes performance on this task is a simple instantiation of a discriminant function and thus is completely specific to the trained reference angle. Learning at one orientation does not transfer to other orientations. These models naturally capture the high degree of specificity typically seen in perceptual learning. However, such an implementation cannot be responsible for the types of benefits associated with learning to learn.

Transfer of learning is enabled by implementations that recognize the importance of resources, knowledge, and learning rules. These core computational elements are well illustrated by real-world tasks such as playing soccer, where players must keep track of an



**Figure 4**

(a) In real-world tasks such as playing soccer, players must keep track of a complex array of moving objects, including the ball and all other players on the field. An expert player will readily recover the three-dimensional trajectories of various objects on the field, while maintaining their proper identities and roles at all times, allowing them to predict next game moves. This is possible as players gain experience with soccer play and build a rich internal model with the proper hierarchical architecture to facilitate computation.

(b) Schematic illustration of how resources can facilitate object tracking over time. Resources, shown as beams of light, are believed to be limited in number and require flexible allocation across objects as the number of objects increases. Recruiting additional resources, illustrated as the dashed beam, provides improved motion processing and tracking for more objects. (c, d) The dynamic of game play in a soccer game is best captured as the top node of a hierarchical architecture, whereby motion information is pooled across different levels of representations, from low level such as limb motion within a player to the motion of individual players to assemblies of players (offense versus defense). An appropriate abstraction allows hierarchical architectures to capture regularity across variations in task and stimuli, a key feature of learning transfer.

array of complex moving objects, including the ball and other players (**Figure 4a**). As the player moves and scans the scene, the color, shape, and motion information they receive must be converted into the three-dimensional

trajectories of objects while maintaining their identities and roles (opponent, teammate, ball, referee, spectator). This complex problem can be decomposed into a set of core skills, many of which have been psychophysically studied

in isolation, including multiple object tracking, object identification, resource allocation, and eye-movement planning. Whereas the novice player will only partially achieve the coordination of these different demands, expert players have learned through experience how best to represent game play as a function of the different identities and roles of the players and how best to allocate resources among these different demands. Accordingly, top athletes can keep track of all the players on both teams, including those out of view (Cavanagh & Alvarez 2005).

Skill acquisition in such complex domains requires more than instantiating a simple discriminant function of the type discussed above. A neural architecture that incorporates knowledge critical for the given task is needed. In the case of soccer, this knowledge encompasses tracking objects, including features important for maintaining object identity and role, developing representations that are invariant to irrelevant internal limb motions, and representing the statistical motion behavior typical of different object types (motion of the ball versus that of players). Learning the proper knowledge for the given task is critically dependent not only on the chosen neural architecture but also on the learning rules that adapt the neural architecture with experience. Finally, the ability to adapt swiftly to the different demands of such complex tasks greatly benefits from improvement in the number or allocation of core resources such as attention. Changes in any or all of these three—knowledge, learning rules, and resources—could be produced by action video game experience and could account for widespread benefits observed in VGPs. As illustrated below (see Resources, Knowledge, and Learning Rules in Action Video Game Play), there is much evidence that action video game play improves resource allocation, and there are some pointers toward knowledge and/or learning rule changes as well. Before we discuss these, we lay out a general framework for the type of probabilistic inference at the core of learning to learn and discuss how resources, knowledge, and learning rules may come to

account for the widespread benefits associated with learning to learn.

## Resources

VGPs have increased attentional resources in multiple-object-tracking tasks, allowing for more accurate representation of motion and features, which in turn enables more accurate tracking and identification (Boot et al. 2008, Dye & Bavelier 2010, Green & Bavelier 2006b, Trick et al. 2005). As illustrated in **Figure 4b**, this ability should be advantageous when playing soccer. However, such additional resources will do more than just improve performance on a single soccer action; they are also a key determinant of learning. Greater resources allow for finer-grain distinctions to be made, be they perceptual, conceptual, or in motor output. An increase in resources may therefore enable learners to achieve greater asymptotic performance (more learning capacity), or even faster learning, because critical distinctions will be more accessible to those learners with greater resources. The concept of resources we use here is closely related to that defined in the field of attention and executive control under the terms goal-directed attention or top-down control (Corbetta & Shulman 2002, Dosenbach et al. 2008, Koechlin & Summerfield 2007, Rougier et al. 2005). The cholinergic basal forebrain system may orchestrate such resource allocation. More specifically, it appears that the release of acetylcholine regulates the extent to which targets are processed and distractors are ignored (Baluch & Itti 2011, Herrero et al. 2008, Sarter et al. 2005) as well as enhances the precision of sensory representations (Goard & Dan 2009).

The role of acetylcholine in selective attention and resource allocation goes hand in hand with its recognized role in cortical map plasticity (Ji et al. 2001, Kilgard & Merzenich 1998). In a seminal study, Kilgard & Merzenich (1998) established that adult rats exposed to tones exhibited larger cortical map plasticity in the presence of episodic stimulation of the nucleus basalis. Early studies in humans also suggest a possible link between learning and

the cholinergic system. For example, intake of a choline agonist leads to improved learning when participants are asked to learn lists of words. In contrast, a choline antagonist leads to reduced learning (Sitaram et al. 1978). In this view, resource allocation acts as a key gateway to learning by refining the distinction between signal and noise and enhancing the quality and precision of the to-be-learned information. The role that the distribution of attentional resources plays in guiding learning is well exemplified by a study by Polley et al. (2006), whereby rats were trained to discriminate tones on the basis of either their frequency or their intensity. When animals performed the frequency task, changes in frequency maps were observed that correlated with behavior. In contrast, no such changes were noted in neurons coding for intensity. The opposite pattern was observed when the task focused the animals' attention on the intensity task. A similar link is also supported in humans (see Saffell & Matthews 2003). In line with this view, Li et al. (2009) have shown that prefrontal areas, known to be involved in resource allocation, code for different decision criteria as a result of learning episodes that emphasized the relevant criterion. This neural signature was present only when participants were engaged in the trained task and not just exposed to the learned stimuli. More recently, Baldassare et al. (2012) demonstrated that resting state connectivity between prefrontal areas and the visual cortex was predictive of the amount of learning in an upcoming perceptual learning task. This study is a direct illustration of how efficiency in resource allocation comes to guide learning abilities at the individual level. As we highlight below (see Resources, Knowledge, and Learning Rules in Action Video Game Play), much evidence indicates that action video game play improves top-down resource allocation, thus leading to better selective attention and enhanced precision in representations. A direct link to the acetylcholine system, however, remains to be elucidated.

More computational and memory resources can also foster learning to learn by providing

the capacity to explore alternative hypotheses and architectures to find those that best account for the knowledge being acquired. The burgeoning literature on the training of executive function testifies to this link (Klingberg 2010, Lustig et al. 2009). For example, as participants train on an N-back task and can handle more demanding updating in memory, they also show enhanced fluid intelligence as measured by the Raven's Advanced Progressive Matrices (RAPM) (Jaeggi et al. 2008). The RAPM presents visual patterns with one missing component that participants must complete. This test relies on the ability to search swiftly through many hypotheses to find the best match. Enhanced executive resources will allow such searches to be more efficient. Although executive functions appear trainable across the life span, some evidence indicates that transfer effects may be more limited in older age (Buschkuhl et al. 2008, Dahlin et al. 2008). At the neural level, working-memory training results in enhanced recruitment of the frontoparietal network associated with top-down attentional control, possibly increased myelination among related areas, as well as a decrease in cortical dopamine D1 binding potential in large parts of frontal and posterior areas (McNab et al. 2009, Olesen et al. 2004, Takeuchi et al. 2010). Whether action video game play effects are mediated by similar mechanisms remains to be assessed. Finally, having greater resources does not systematically guarantee more efficient learning; resource allocation needs to be guided by the presence of structured knowledge that helps select where useful information lies, as discussed below.

## Knowledge

Knowledge here refers to the representational structure used to guide behavior. The realization that complex behaviors cannot be appropriately captured by a chain of stimulus-response associations is far from new (Lashley 1951) and has led to a keen interest in the role of hierarchical architecture in human action

and cognition (see Botvinick 2008 for a review). Hierarchical behavior models capture the intuitive notion that tasks such as executing a play in soccer are organized into subtasks involving individual player moves, which are themselves decomposed into component actions of running, turning, kicking, and passing. In turn, knowing soccer makes learning a game such as hockey easier because the similarities between the games allow one to import skills and knowledge from one game to bootstrap learning of the other. Note that it is not just because both games share the category “goalies” that such generalization is possible. Rather, recent work in machine learning suggests that hierarchical architectures allow the decomposition of computations into multiple layers using greater and greater abstraction, a critical step for generalizable learning (Bengio 2009, Hinton 2007). In these architectures, categories such as “goalie” are distributed across multiple levels of abstraction, from sensory input to characteristic features to body plans to player types to the concept of a soccer player. In contrast, shallow architectures eschew abstraction and construct the category “goalie” by treating it as a classification problem that involves finding the right set of diagnostic features such as limb motion, jersey color or pattern, or position relative to the goal post. Although few examples of such deep coding in neuroscience exist as of yet, studies of categorization and object recognition point to the psychological grounding of deep architectures. For example, hierarchical architectures naturally account for the fact that categories appear organized around prototypes or most representative exemplars of a category, even when the prototypes do not reflect the frequency of diagnostic features (Rosch 1975). As work on the neural bases of object recognition progresses, characterizing how deep knowledge may constrain neural coding will become increasingly more relevant (DiCarlo & Cox 2007, Lee & Mumford 2003, Paupathy & Connor 2002, Yamane et al. 2008).

The shallow/deep distinction can be expressed in terms of Bayesian decision theory as the difference between learning a rich

generative model that captures hidden structure in the data versus learning a discriminative model (a discriminant function) specific to a classification problem. Learning theory has shown that discriminative models require less data to learn the observed relationships but are task specific. For example, discriminative classifiers such as support vector machines learn boundaries in feature space. The fact that these boundaries can be quite complex does not guarantee generalizable knowledge. In fact, in the case of support vector machines, the learned boundaries typically depend intimately on the characteristics of the training set. Simple changes in team uniforms or players will require relearning a new boundary to classify them. Such implementations therefore appear ill adapted when considering learning to learn. In contrast, appropriate abstraction allows hierarchical architectures to capture regularity across variations in task and stimuli. **Figure 4c,d** illustrates a hierarchy for relevant motion in a soccer game. The tree structure shows how broader categories can be constructed by pooling across categories of motion at different levels, pooling limb motions to construct player motion, pooling player motions within a player type (such as goalie), pooling player-type motions within a team type (offense or defense), and pooling all game-relevant motions, including the ball, coaches, and referees, in opposition to nonrelevant motions such as spectators and billboards.

Abstract organization admits generalization to the extent that new tasks overlap and share structure and representations. For example, despite the fact that players use skates, hockey shares many of the same motion characteristics of the teams’ offense and defense, roles of players (such as goalie), and requirements for passing and controlling the puck as does soccer. The generalization expected from a given architecture is not infinite, but will be determined instead by the level of abstraction at which knowledge is shared by the various tasks considered. Thus, for action video games to provide players with knowledge applicable to standard laboratory tasks, it must necessarily be the case that



games and the laboratory tasks share structure at some level of abstraction. And perhaps, more importantly, training paradigms must necessarily share structure at some level of abstraction for them to affect performance in real-life tasks.

The need for structured representation to support more complex task performance has led to an interest into the neural bases of hierarchical tasks that embed goals and subgoals. Although this area of research is still fairly new, the available literature points to a crucial role of prefrontal cortex structures to enable hierarchical representations and coordinate resource allocation dynamically among these as task demands vary (Badre 2008, Botvinick 2008, Koechlin 2008, Sakai 2008). Indeed, the ability to enhance neural processing selectively by allocating more resources is central to behavior optimization, but it depends fundamentally on an internal understanding of which neural pool is important to augment at each point in time. The prefrontal cortex is a crucial candidate in the representation of these more complex behaviors. Prefrontal structures are key to maintaining context and goals over time with increasingly higher levels of behavioral abstraction being coded as one moves from caudal to rostral locations along the prefrontal cortex (Christoff & Keramatain 2007, Fuster 2004). There is certainly debate about the exact nature of the abstraction, with higher planning units, greater relational complexity, more branching control, or larger contextual integration being documented as one moves rostrally within the prefrontal cortex (see figure 2 in Badre 2008 for a summary). Yet, there is common agreement about the importance of hierarchical knowledge when considering how the brain learns from its successes and failures. Neural signatures for such an architecture are emerging, e.g., in the work of Ribas-Fernandes et al. (2011) who recently demonstrated that subgoals lead to reward-prediction signals even if they are not associated with primary reinforcers. Such an outcome is predicted under the assumption that the task is represented hierarchically but not otherwise. This research should be an important avenue for future research

on learning, as the nature of the architecture fundamentally constrains the type of learning neural structures should implement.

## Learning Algorithms

A common observation is that as an architecture becomes more complex, it becomes more critical that the learning algorithm can modify the representations in ways that are aligned with the nature of the problems to be solved. Simply put, knowledge and learning rules are intimately interdependent; different architectures typically call for different learning rules. A key question then concerns how improvement in learning algorithms and their related architecture may foster learning to learn. To facilitate generalization, learning algorithms require shared structure, a fact that constrains how learning rules should modify representations. Violating these constraints destroys transferrable knowledge because changes in representation that improve performance in one task can disrupt performance in another.

Over the past 20 years, this field has witnessed dramatic improvements in the basic set of machine-learning algorithms. For instance, algorithms such as those employed in Hinton's deep-belief networks have provided evidence that there is enough shared structure in the types of learning problems encountered by humans beings to allow for the use of flexible and generalizable learning algorithms (Hinton 2007, Hinton et al. 2006, Larochelle et al. 2007, Lee et al. 2009). In this case, speech recognition and handwritten character recognition can be achieved using initially similar architectures and the same learning rule. Of note, performance after learning rivals the best algorithms specifically developed for speech recognition or character recognition respectively (Mohamed et al. 2011). This approach is appealing because the lack of structural differentiation among cortical areas suggests a broadly shared learning algorithm, at least at the cortical level.

Fine-tuning of learning algorithms may occur through improvement in error detection, error computation, reward computation, and, more generally, synaptic learning rules. This

fine tuning may involve neuromodulators, which are believed to be involved in the modulation of synaptic plasticity (Zhang et al. 2009) and in the computation of error signals (Schultz et al. 1997). Changes in the responses of the neurons synthesizing these neuromodulators could easily generalize across tasks and sensory modalities because these neurons tend to connect very wide cortical regions. Although few studies are available on this topic, action video game play likely alters patterns of neuromodulator release. For instance, an early positron emission tomography study indicated that a large release of striatal dopamine occurs when subjects play a basic shooting video game (Koeppe et al. 1998, though see the call for further replication by Egerton et al. 2009). This should be a fruitful area of research for future studies.

## RESOURCES, KNOWLEDGE, AND LEARNING RULES IN ACTION VIDEO GAME PLAY

All three factors that can contribute to learning to learn may, of course, be involved in the effects of video game training, but the experimental evidence so far has focused mainly on changes in resources and improvements in resource allocation. However, although no experiments have directly tested differences in knowledge or in learning rules, some data points do appear more consistent with these changes than does a resource-based account.

### Attentional Resources

**Enhanced resources.** The proposal that VGPs benefit from greater attentional resources is supported by the observation that, in simple flanker compatibility tasks, VGPs' reaction times show a greater sensitivity to the identity of the flanker (Dye et al. 2009b; Green & Bavelier 2003, 2006a). Thus, reaction times on the main target task showed greater speeding (respectively, slowing down) when flankers were response compatible (respectively, response incompatible) in VGPs as compared with NVGPs. According to the work

of Lavie and others (2005), in such flanker paradigms the resources utilized by the main target task determine the amount of processing the flanker receives and thus the size of the flanker compatibility effect. As the main target task exhausts more resources, the identity of the flanker affects reaction times to a lesser extent, leading to increasingly smaller compatibility effects. Green & Bavelier (2003) showed that although this pattern of results held in NVGPs, VGPs continued to show effects of flanker identity even for relatively high-load target tasks, thus suggesting the presence of greater attentional resources.

**Selective attention.** Action game play results in improved selective attention over space, over time, and to objects. VGPs exhibit more accurate spatial localization of a target whether presented in isolation as in Goldman perimetry (Buckley et al. 2010) or among distracting, irrelevant information as in the Useful Field of View task (Feng et al. 2007; Green & Bavelier 2003, 2006a; Spence et al. 2009; West et al. 2008). Action game play also enhances the ability to select relevant information over time. When viewing a stream of letters presented rapidly, one after the other, participants can typically identify the one white letter among black letters if asked. However, doing so creates a momentary blink in attention, leading the subject to be unaware of the next few items following the white letter. This effect, termed the attentional blink, is believed to measure a fundamental bottleneck in the dynamics of attention allocation (Shapiro et al. 1997). VGPs' blink is much less pronounced, with some VGPs failing to show any blink (at least at the rate of presentation tested; see Cohen et al. 2007, Green & Bavelier 2003). It is unlikely that action game play totally obliterates the attentional blink, but these data suggest a much faster rate of attentional recovery in VGPs. Such faster processing speed is in line with the reduced backward masking reviewed earlier and the report that VGPs perceive the timing of visual events more veridically than do NVGPs (Donohue et al. 2010, but see West et al. 2008 for a different view). A

third aspect of selective attention documented to change for the better after action game play is attention to objects (Boot et al. 2008; Cohen et al. 2007; Green & Bavelier 2003, 2006b; Trick et al. 2005). Using the multiple-object-tracking task (Pylyshyn & Storm 1988), VGPs have been repeatedly shown to track more objects accurately than have NVGPs (Boot et al. 2008, Green & Bavelier 2006b, Trick et al. 2005). This skill requires efficient allocation of attentional resources as objects move and cross over each other in the display. The advantage noted in VGPs in this task is consistent with either large resources or a swifter allocation of resources as a result of game play.

The ability to focus attention on a target location and ignore irrelevant distracting information is a key determinant of selective attention. Converging evidence indicates that selective attention is a strong predictor of academic achievement in young children (Stevens & Bavelier 2012), illustrating the general benefits this skill may confer. Although seldom considered in conjunction with action game play, meditative activities such as mind-body training and eastern relaxation technique also act in part by enhancing selective attention (Lutz et al. 2008, Tang & Posner 2009). Whether these two rather different treatments achieve their effects through comparable neural modulation may be a fruitful avenue of investigation in the future.

**Divided attention.** The ability to divide attention between tasks or locations was one of the first attentional benefits noted in the early days of computer games (see Greenfield 2009 for a review). For example, when asked to report the appearance of a target in a high probability, low probability, or neutral location, VGPs did not show the expected decrement (slower reaction time compared with neutral) for the low probability location, suggesting a better strategy in spreading attention due to game expertise (Greenfield et al. 1994). More recently, VGPs have shown an enhanced ability at dividing attention between a peripheral

localization task and a central identification task (Dye & Bavelier 2010, Green & Bavelier 2006a). VGPs also excelled when asked to detect a prespecified target in rapid sequences of Gabor stimuli presented in both visual fields. Concurrent event-related potential recordings indicated a larger occipital P1 component (latency 100–160 ms) in VGPs during this divided-attention task, consistent with the proposal of greater attentional modulation in early stages of processing such as the extrastriate visual cortex in VGPs (Khoe et al. 2010).

**Sustained attention and impulsivity.** Some evidence also supports the notion that sustained attention benefits from action video game play. Using the Test of Variables of Attention (T.O.V.A.), a computerized test often used to screen for attention deficit disorder, Dye et al. (2009a) found that VGPs responded faster and made no more mistakes than did NVGPs on this test. Briefly, this test requires participants to respond as fast as possible to shapes appearing at the target location, while ignoring the same shapes if they appear at another location. By manipulating the frequency of targets, the T.O.V.A. offers a measure of both impulsivity (is the observer able to withhold a response to a nontarget when most of the stimuli are targets?) and a measure of sustained attention (is the observer able to stay on task and respond quickly to a target when most of the stimuli are nontargets?). In all cases, VGPs were faster but no less accurate than were the NVGPs, indicating, if anything, enhanced performance on these aspects of attention as compared with NVGPs. It may be worth noting that VGPs were often so fast that the built-in data analysis software of the T.O.V.A. considered their reaction times to be anticipatory (200 ms or less). However, a close look at the reaction time distribution indicated that these anticipatory responses were nearly all correct responses (which would obviously be unlikely if they were driven by chance, rather than being visually evoked). In summary, VGPs are faster but not more impulsive than NVGPs and equally capable of sustaining their attention. Although some

have argued for a link between technology use and attention-deficit disorder (Rosen 2007, but see Durkin 2010), in the case of playing action games this does not appear to be the case.

**Resource allocation.** The proposal that action game play enhances top-down aspects of attention by allowing VGPs to allocate their resources more flexibly where it matters for the given task is supported by several independent sources. First, some evidence indicates that VGPs may better ignore sources of distraction, a key skill for properly allocating resources. For example, VGPs have been shown to be more capable of overcoming attentional capture. Chisholm et al. (2010, Chisholm & Kingstone 2011) compared the performance of VGPs and NVGPs on a target-search task known to engage top-down attention, while concurrently manipulating whether a singleton distractor, known to capture attention automatically, was or was not present. When top-down and bottom-up attention interact in such a way, investigators noted that although the singleton distractor captured attention in both groups, it did so to a much lesser extent in VGPs than in NVGPs. Thus VGPs may better employ executive strategies to reduce the effects of distraction. More recently, Mishra et al. (2011) made use of the steady-state visual-evoked potentials technique to examine the neural bases of the attentional enhancements noted in VGPs. They found that VGPs more efficiently suppressed unattended, potentially distracting information when presented with highly taxing displays. Participants viewed four different streams of rapidly flashing alphanumeric characters. Each stream flashed at a distinct temporal frequency, allowing retrieval of the brain signals evoked by each stream independently at all times. Thus, brain activation evoked by the attended stream could be retrieved, as could brain activation evoked by each of the unattended and potentially distracting streams. VGPs suppressed irrelevant streams to a greater extent than did NVGPs, and the extent of the suppression predicted the speed of their responses. VGPs seem to focus better on the task at hand by ignoring

other sources of potentially distracting information. This view is in line with the proposal in the literature of greater distractor suppression as one possible determinant of more efficient executive and attentional control (Clapp et al. 2011, Serences et al. 2004, Toepfer et al. 2010).

VGPs may also benefit from greater flexibility in resource allocation. The finding that VGPs switch tasks more swiftly, whether or not switches are predictable, is consistent with this view (Green et al. 2012). A recent brain-imaging study involving VGPs and NVGPs also speaks to this issue. In this study, the recruitment of the frontoparietal network of areas hypothesized to control the flexible allocation of top-down attention was compared in VGPs and NVGPs. As attentional demands increased, NVGPs showed increased activation in this network as expected. In contrast, VGPs barely engaged this network despite a matched increase in attentional demands across groups. This reduced activity in the frontoparietal network is compatible with the proposal that resource allocation may be more automatic and swift in VGPs (Bavelier et al. 2011). Furthermore, many models of the multiple-object-tracking task, on which VGPs have been seen to excel, intimate a close relationship between the number of items that can be tracked and the efficiency of resource allocation (Ma & Huang 2009, Vul et al. 2010).

In sum, much evidence demonstrates that action video game play leads to not only enhanced resources, but also a more intelligent allocation of these resources given the goals at hand. This is one of the ways action game play may result in learning to learn. We now turn to other evidence for learning to learn after action game play that suggests changes in knowledge and/or learning algorithm.

## Knowledge/Learning Rule

Direct evidence for changes in knowledge or learning rules is still lacking. However, the literature contains pointers suggestive of such changes. First, the observation that action game play leads to more accurate probabilistic inference, as discussed above (see A Common

Mechanism: Learning to Learn), suggests the development of new connectivity and knowledge to enable a more efficient architecture for the given task. Although some of these benefits could be driven initially by changes in resources, the fact that they can last for five months or longer suggests more profound and long-lasting changes in representation than what is typically afforded by attentional resources. Second, a number of experiments point to improvement despite little need for resources. This is true, for example, of very basic psychophysical skills such as visual acuity or contrast sensitivity (Green & Bavelier 2007, Li et al. 2009). These paradigms displayed only one target in isolation, and no uncertainty was present on either the place and/or time of the target's arrival (fixed target location, fixed SOA). In contrast, resources such as attention are typically called on when a target needs to be selected in time or space from distractors or when the time and/or place of arrival of the stimulus is uncertain (Carrasco et al. 2002). Third, an attentional explanation is not always in line with the noted changes. For example, contrast-sensitivity improvements were not larger as spatial frequency increased (and thus stimulus size decreased) as would be predicted by attentional accounts. Rather, the beneficial effect of action game play was maximal at intermediate frequencies. These considerations point to changes in representations likely to be mediated by enhancement either in learning rule or in knowledge.

Action game playing may act by enabling more generalizable knowledge through various abstractions, including the extent to which nontask-relevant information should be suppressed (Clapp et al. 2011, Serences et al. 2004, Töpper et al. 2010), how to modify performance to maximize reward rate (Simen et al. 2009), how to combine data across feature dimensions (which depends on the presence/type of dependencies between the dimensions; Perfors & Tenenbaum 2009, Stilp et al. 2010), and how to set a proper learning rate (which depends on the belief about whether generating distributions are stationary or drifting; Behrens

et al. 2007). Although these avenues are only beginning to be explored, some support is emerging for distraction suppression and reward-rate changes after action game play. First, several studies document that action video game play alters the extent to which distracting information is suppressed. It is not always the case that VGPs show greater suppression of distractors. Rather, distractor processing appears to be greater in VGPs than in NVGPs under conditions of relatively low load. Under such conditions, task difficulty is sufficiently low for VGPs to remain efficient on the primary task and at the same time still be able to process distractors (Dye et al. 2009b, Green & Bavelier 2003). In contrast, VGPs show greater suppression of distractors under extremely high load conditions (Mishra et al. 2011). As task difficulty increases, suppression of distractors becomes necessary for VGPs to maintain their high performance on the primary task. Such differential effects may be understood if distractor processing has been encoded at a proper level of abstraction that is contingent on primary task success. Second, a key step in fostering learning is to engage the reward system (Bao et al. 2001, Koeppe et al. 1998, Roelfsema et al. 2010). A distinguishing feature of action games is the layering of events/actions at many different timescales, resulting in a complex pattern of reward in time. This feature may explain, in part, why VGPs seem to maximize reward rate in a variety of tasks (A.F. Anderson, C.S. Green, D. Bavelier, manuscript in preparation; Green et al. 2010). Further investigation of the impact of action game play on knowledge and learning rules should provide an interesting test case, as the roles of resource control, hierarchical knowledge, and learning rules are refined.

Finally, the enhanced attentional control documented earlier is not, in this view, the proximal cause of the superior performance of VGPs, i.e., an end in and of itself. Instead, it is a means to an end, with that end being the development of more generalizable knowledge as one is faced with new tasks or new environments. Such learning to learn predicts that reasonably equivalent performance



between groups should be seen early on when performing a new task, with the action gaming advantage appearing and then increasing through experience with the task. Such outcomes are being investigated in the domain of perceptual learning and decision making.

## CONCLUDING REMARKS

In sum, we propose that action game play does not teach any one particular skill but instead increases the ability to extract patterns or regularities in the environment. As exemplified by their superior attentional control skills, VGPs develop the ability to exploit task-relevant information more efficiently while better suppressing irrelevant, potentially distracting sources of information. This may stem from the ability to discover the underlying structure of the task they face more readily, perform more accurate statistical inference over the data they experience, and thus exhibit superior performance on a variety of tasks previously thought to tap unrelated capacities. In this sense, action video game play may be thought of as fostering learning to learn.

The hypothesis that action video game play may improve learning to learn is appealing because it naturally accounts for the wide range of skills enhanced in VGPs. Yet, learning to learn does not guarantee better performance on all tasks. Instead, like all forms of learning, it comes with a number of constraints that determine the nature and extent of the generalization possible. For instance, changes in knowledge produce benefits only to the extent to which new tasks share structure with action video games. No benefits are expected in tasks that share no such structure. Furthermore, and again like all forms of learning, potential drawbacks exist. For instance, an increase in resources may predict a tendency to overexplore: to test models that are more elaborate than what is required by the task at hand, which could actually result in poorer performance and slower learning. Learning to learn does not predict that VGPs will excel at all tasks, but rather provides a theoretical framework to further our understanding of key concepts underlying generalization in learning as well as better characterizing the architecture, resources, and learning algorithms that generate the remarkable power of the human brain.

## DISCLOSURE STATEMENT

D.B., C.S.G., and A.P. have patents pending concerning the use of video games for learning. D.B. is a consultant for PureTech Ventures, a company that develops approaches for various health areas, including cognition. D.B., C.S.G., and A.P. have a patent pending on action-video-game-based mathematics training; D.B. has a patent pending on action-video-game-based vision training.

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## LITERATURE CITED

Anderson AF, Bavelier D. 2011. Action game play as a tool to enhance perception, attention and cognition. In *Computer Games and Instruction*, ed. S Tobias, D Fleycher, pp. 307–29. Charlotte, NC: Information Age



- Anderson AF, Kludt R, Bavelier D. 2011. *Verbal versus visual working memory skills in action video game players*. Poster presented at the Psychonomics Soc. Meet., Seattle
- Andrews G, Murphy K. 2006. Does video-game playing improve executive function? In *Frontiers in Cognitive Psychology*, ed. MA Vanchevsky, pp. 145–61. New York: Nova Sci.
- Badre D. 2008. Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends Cogn. Sci.* 12:193–200
- Bailey K, West R, Anderson CA. 2010. A negative association between video game experience and proactive cognitive control. *Psychophysiology* 47:34–42
- Baldassare A, Lewis CM, Committeri G, Snyder AZ, Romani GL, Corbetta M. 2012. Individual variability in functional connectivity predicts performance of a perceptual task. *Proc. Natl. Acad. Sci. USA* 109:3516–21
- Baluch F, Itti L. 2011. Mechanisms of top-down attention. *Trends Neurosci.* 34:210–24
- Bao S, Chan VT, Merzenich MM. 2001. Cortical remodelling induced by activity of ventral tegmental dopamine neurons. *Nature* 412:79–83
- Bavelier D, Achtman RA, Mani M, Foecker J. 2011. Neural bases of selective attention in action video game players. *Vis. Res.* doi: 10.1016/j.visres.2011.08.007
- Bavelier D, Levi DM, Li RW, Dan Y, Hensch TK. 2010. Removing brakes on adult brain plasticity: from molecular to behavioral interventions. *J. Neurosci.* 30:14964–71
- Beck JM, Ma WJ, Kiani R, Hanks T, Churchland AK, et al. 2008. Bayesian decision making with probabilistic population codes. *Neuron* 60:1142–52
- Behrens TE, Woolrich MW, Waldon ME, Rushworth MF. 2007. Learning the value of information in an uncertain world. *Nat. Neurosci.* 10:1214–21
- Bengio Y. 2009. Learning deep architectures for AI. *Found. Trends Mach. Learn.* 2:1–127
- Benson PG. 2001. Hawthorne effect. In *The Corsini Encyclopedia of Psychology and Behavioral Science*, ed. WE Craighead, CB Nemeroff, pp. 667–68. New York: Wiley
- Binet A. 1984 (1909). *Les idées modernes sur les enfants*, transl. S Heisler. Menlo Park, CA: S. Heisler
- Boot WR, Kramer AF, Simons DJ, Fabiani M, Gratton G. 2008. The effects of video game playing on attention, memory, and executive control. *Acta Psychol.* 129:387–98
- Botvinick MM. 2008. Hierarchical models of behavior and prefrontal function. *Trends Cogn. Sci.* 12:201–8
- Buckley D, Codina C, Bhardwaj P, Pascalis O. 2010. Action video game players and deaf observers have larger Goldmann visual fields. *Vis. Res.* 50:548–56
- Buschkuhl M, Jaeggi SM, Hutchison S, Perrig-Chiello P, Däpp C, et al. 2008. Impact of working memory training on memory performance in old-old adults. *Psychol. Aging* 23:743–53
- Cain MS, Landau AN, Shimamura AP. 2012. Action video game experience reduces the cost of switching tasks. *Atten. Percept. Psychophys.* 74:641–47
- Carrasco M, Williams PE, Yeshurun Y. 2002. Covert attention increases spatial resolution with or without masks: support for signal enhancement. *J. Vis.* 2:467–79
- Castel AD, Pratt J, Drummond E. 2005. The effects of action video game experience on the time course of inhibition of return and the efficiency of visual search. *Acta Psychol.* 119:217–30
- Cavanagh P, Alvarez GA. 2005. Tracking multiple targets with multifocal attention. *Trends Cogn. Sci.* 9:349–54
- Chase WG, Simon HA. 1973. The mind's eye in chess. In *Visual Information Processing*, ed. WG Chase, pp. 215–81. New York: Academic
- Chisholm JD, Hickey C, Theeuwes J, Kingstone A. 2010. Reduced attentional capture in action video game players. *Atten. Percept. Psychophys.* 72:667–71
- Chisholm JD, J, Kingstone A. 2011. Improved top-down control reduces oculomotor capture: the case of action video game players. *Atten. Percept. Psychophys.* 74:257–62
- Christoff K, Keramatain K. 2007. Abstraction of mental representations: theoretical considerations and neuroscientific evidence. In *Perspectives on Rule-Guided Behavior*, ed. SA Bunge, JD Wallis, pp. 107–27. New York: Oxford Univ. Press
- Clapp WC, Rubens MT, Sabharwal J, Gazzaley A. 2011. Deficit in switching between functional brain networks underlies the impact of multitasking on working memory in older adults. *Proc. Natl. Acad. Sci. USA* 108:7212–17
- Cohen JE, Green CS, Bavelier D. 2007. Training visual attention with video games: Not all games are created equal. In *Computer Games and Adult Learning*, ed. H O'Neil, R Perez, pp. 205–27. Oxford, UK: Elsevier

- Colzato LS, van Leeuwen PJA, van den Wildenberg WPM, Hommel B. 2010. DOOM'd to switch: superior cognitive flexibility in players of first person shooter games. *Front. Psychol.* 1:1–5
- Corbetta M, Shulman G. 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3:201–15
- Dahlin E, Nyberg L, Bäckman L, Neely AS. 2008. Plasticity of executive functioning in young and older adults: immediate training gains, transfer, and long-term maintenance. *Psychol. Aging* 23:720–30
- Daily Mail. 2009. RAF jettisons its top guns: drones to fly sensitive missions over Afghanistan. *Daily Mail Online* Feb. 28: <http://www.dailymail.co.uk/news/worldnews/article-1158084/RAF-jettisons-Top-Guns-Drones-fly-sensitive-missions-Afghanistan.html>
- Deneve S. 2008. Bayesian spiking neurons I: inference. *Neural Comput.* 20:91–117
- DiCarlo JJ, Cox DD. 2007. Untangling invariant object recognition. *Trends Cogn. Sci.* 11:333–41
- Donohue SE, Woldorff MG, Mitroff SR. 2010. Video game players show more precise multisensory temporal processing abilities. *Atten. Percept. Psychophys.* 72:1120–29
- Dosenbach NUF, Fair DA, Cohen AL, Schlaggar BL, Petersen SE. 2008. A dual-networks architecture of top-down control. *Trends Cogn. Sci.* 12:99–105
- Doshier BA, Lu Z-L. 1998. Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc. Natl. Acad. Sci. USA* 95:13988–93
- Durkin K. 2010. Videogames and young people with developmental disorders. *Rev. Gen. Psychol.* 14:122–40
- Dye MW, Green CS, Bavelier D. 2009a. Increasing speed of processing with action video games. *Curr. Dir. Psychol. Sci.* 18:321–26
- Dye MWG, Bavelier D. 2010. Differential development of visual attention skills in school-age children. *Vis. Res.* 50:452–59
- Dye MWG, Green CS, Bavelier D. 2009b. The development of attention skills in action video game players. *Neuropsychologia* 47:1780–89
- Egerton A, Mehta MA, Montgomery AJ, Lappin JM, Howes OD, et al. 2009. The dopaminergic basis of human behaviors: a review of molecular imaging studies. *Neurosci. Biobehav. Rev.* 33:1109–32
- Erickson KI, Kramer AF. 2009. Aerobic exercise effects on cognitive and neural plasticity in older adults. *Br. J. Sports Med.* 43:22–24
- Feng J, Spence I, Pratt J. 2007. Playing an action videogame reduces gender differences in spatial cognition. *Psychol. Sci.* 18:850–55
- Frey SH, Fogassi L, Grafton S, Picard N, Rothwell JC, et al. 2011. Neurological principles and rehabilitation of action disorders: computation, anatomy, and physiology (CAP) model. *Neurorehabil. Neural Repair* 25(5):6S–20
- Fuster JM. 2004. Upper processing stages of the perception-action cycle. *Trends Cogn. Sci.* 8:143–45
- Gallistel CR. 2008. Learning and representation. In *Learning Theory and Behavior*. Vol. 1: *Learning and Memory: A Comprehensive Reference*, ed. R Menzel, pp. 529–48. Oxford: Elsevier
- Gallistel CR, King AP. 2009. *Memory and the Computational Brain: Why Cognitive Science Will Transform Neuroscience*. New York: Wiley/Blackwell
- Goard M, Dan Y. 2009. Basal forebrain activation enhances cortical coding of natural scenes. *Nat. Neurosci.* 12:1444–49
- Godden D, Baddeley A. 1975. Context dependent memory in two natural environments. *Br. J. Psychol.* 66:325–31
- Green CS, Bavelier D. 2003. Action video games modify visual selective attention. *Nature* 423:534–37
- Green CS, Bavelier D. 2006a. Effects of action video game playing on the spatial distribution of visual selective attention. *J. Exp. Psychol.: Hum. Percept. Perform.* 32:1465–78
- Green CS, Bavelier D. 2006b. Enumeration versus multiple object tracking: the case of action video game players. *Cognition* 101:217–45
- Green CS, Bavelier D. 2007. Action video game experience alters the spatial resolution of vision. *Psychol. Sci.* 18:88–94
- Green CS, Bavelier D. 2012. Learning, attentional control and action video games. *Curr. Biol.* 22:R167–206
- Green CS, Pouget A, Bavelier D. 2010. Improved probabilistic inference as a general learning mechanism with action video games. *Curr. Biol.* 20:1573–79

- Green CS, Sugarman MA, Medford K, Klobusicky E, Bavelier D. 2012. The effect of action video games on task switching. *Comput. Hum. Behav.* 12:984–94
- Greenfield PM. 2009. Technology and informal education: What is taught, what is learned. *Science* 323:69–71
- Greenfield PM, DeWinstanley P, Kilpatrick H, Kaye D. 1994. Action video games and informal education: effects on strategies for dividing visual attention. *J. Appl. Dev. Psychol.* 15:105–23
- Halpern DF, Benbow CP, Geary DC, Gur RC, Hyde JS, Gernsbacher MA. 2007. The science of sex differences in science and mathematics. *Psychol. Sci. Public Interest* 8:1–51
- Harlow HF. 1949. The formation of learning sets. *Psychol. Rev.* 56:51–65
- Herrero JL, Roberts MJ, Delicato LS, Giesemann MA, Dayan P, Thiele A. 2008. Acetylcholine contributes through muscarinic receptors to attentional modulation in V1. *Nature* 454:1110–14
- Hillman CH, Erickson KI, Kramer AF. 2008. Be smart, exercise your heart: exercise effects on brain and cognition. *Nat. Rev. Neurosci.* 9:58–65
- Hinton GE. 2007. Learning multiple layers of representation. *Trends Cogn. Sci.* 11:428–34
- Hinton GE, Osindero S, Tej YH. 2006. A fast learning algorithm for deep belief nets. *Neural Comput.* 18:1527–54
- Hubert-Wallander BP, Green CS, Sugarman M, Bavelier D. 2011. Altering the rate of visual search through experience: the case of action video game players. *Atten. Percept. Psychophys.* 73:2399–412
- Jaeggi SM, Buschkuhl M, Jonides J, Perrig WJ. 2008. Improving fluid intelligence with training on working memory. *Proc. Natl. Acad. Sci. USA* 105:6829–33
- Ji W, Gao E, Suga N. 2001. Effects of acetylcholine and atropine on plasticity of central auditory neurons caused by conditioning in bats. *J. Neurophysiol.* 86:211–25
- Karle JW, Watter S, Shedden JM. 2010. Task switching in video game players: benefits of selective attention but not resistance to proactive interference. *Acta Psychol.* 134:70–78
- Kemp C, Goodman ND, Tenenbaum JB. 2010. Learning to learn causal models. *Cogn. Sci.* 23:1–59
- Khoe WW, Bavelier D, Hillyard SA. 2010. Enhanced attentional modulation of early visual processing in video game players. *Soc. Neurosci. Meet. Plann. Abstr.* 399.1
- Kilgard MP, Merzenich MM. 1998. Cortical map reorganization enabled by nucleus basalis activity. *Science* 279:1714–18
- Klingberg T. 2010. Training and plasticity of working memory. *Trends Cogn. Sci.* 14:317–24
- Knill DC, Richards W. 1996. *Perception as Bayesian Inference*. Cambridge, UK: Cambridge Univ. Press
- Koechlin E. 2008. The cognitive architecture of the human lateral prefrontal cortex. In *Attention and Performance*, ed. P Haggard, Y Rosetti, M Kawato, pp. 483–509. New York: Oxford Univ. Press
- Koechlin E, Summerfield C. 2007. An information theoretical approach to prefrontal executive function. *Trends Cogn. Sci.* 11:229–35
- Koepp MJ, Gunn RN, Lawrence AD, Cunningham VJ, Dagher A, et al. 1998. Evidence for striatal dopamine release during a video game. *Nature* 393:266–68
- Larochelle H, Erhan D, Courville A, Bergstra J, Bengio Y. 2007. *An empirical evaluation of deep architectures on problems with many factors of variation*. Presented at Proc. Int. Conf. Mach. Learn., 24th, Corvallis, Or.
- Lashley KS. 1951. The problem of serial order in behavior. In *Cerebral Mechanisms in Behavior*, ed. LA Jeffress, pp. 112–36. New York: Wiley
- Lavie N. 2005. Distracted and confused? Selective attention under load. *Trends Cogn. Sci.* 9:75–82
- Lee H, Grosse R, Ranganath R, Ng AY. 2009. *Convolutional deep belief networks for scalable unsupervised learning of hierarchical representations*. Presented at Proc. Int. Conf. Mach. Learn., 26th, Montreal
- Lee TS, Mumford D. 2003. Hierarchical Bayesian inference in the visual cortex. *J. Opt. Soc. Am.* 20:1434–48
- Legge GE, Rubin GS, Pelli DG, Schleske MM. 1985. Psychophysics of reading—II. Low vision. *Vis. Res.* 25:253–65
- Li R, Ngo C, Nguyen J, Levi DM. 2011. Video game play induces plasticity in the visual system of adults with amblyopia. *Public Libr. Sci.* 9(8):e1001135
- Li R, Polat U, Makous W, Bavelier D. 2009. Enhancing the contrast sensitivity function through action video game training. *Nat. Neurosci.* 12:549–51
- Li RW, Polat U, Scalzo F, Bavelier D. 2010. Reducing backward masking through action game training. *J. Vis.* 10:1–13

- Li S, Mayhew SD, Kourtzi Z. 2009. Learning shapes the representation of behavioral choice in the human brain. *Neuron* 62:441–52
- Lustig C, Shah P, Seidler R, Reuter PA. 2009. Aging, training, and the brain: a review and future directions. *Neuropsychol. Rev.* 19:504–22
- Lutz A, Slagter HA, Dunne JD, Davidson RJ. 2008. Attention regulation and monitoring in meditation. *Trends Cogn. Sci.* 12:163–69
- Ma WJ, Beck JM, Latham PE, Pouget A. 2006. Bayesian inference with probabilistic population codes. *Nat. Neurosci.* 9:1432–38
- Ma WJ, Huang W. 2009. No capacity limit in attentional tracking: evidence for probabilistic inference under a resource constraint. *J. Vis.* 9:1–30
- McClurg PA, Chaille C. 1987. Computer games: environments for developing spatial cognition. *J. Educ. Comput. Res.* 3:95–111
- McKinley RA, McIntire LK, Funke MA. 2011. Operator selection for unmanned aerial systems: comparing video game players and pilots. *Aviat. Space Environ. Med.* 82:635–42
- McNab F, Varrone A, Farde L, Jucaite A, Bystritsky P, et al. 2009. Changes in cortical dopamine D1 receptor binding associated with cognitive training. *Science* 323:800–2
- Mishra J, Zinni M, Bavelier D, Hillyard SA. 2011. Neural basis of superior performance of video-game players in an attention-demanding task. *J. Neurosci.* 31:992–98
- Mohamed A, Dahl GE, Hinton G. 2011. Acoustic modeling using deep belief networks. *IEEE Trans. Audio, Speech, Lang. Proc.*
- Okagaki L, Frensch PA. 1994. Effects of video game playing on measures of spatial performance: gender effects in late adolescence. *J. Appl. Dev. Psychol.* 15:33–58
- Olesen P, Westerberg H, Klingberg T. 2004. Increased prefrontal and parietal activity after training of working memory. *Nat. Neurosci.* 7:75–79
- Ophir E, Nass C, Wagner AD. 2009. Cognitive control in media multitaskers. *Proc. Natl. Acad. Sci. USA* 106:15583–87
- Palmer J, Huk AC, Shadlen MN. 2005. The effect of stimulus strength on the speed and accuracy of a perceptual decision. *J. Vis.* 5:376–404
- Paupathy A, Connor CE. 2002. Population coding of shape in area V4. *Nat. Neurosci.* 5:1332–38
- Perfors AF, Tenenbaum JB. 2009. *Learning to learn categories*. Presented at Annu. Conf. Cogn. Sci. Soc., 31st, Amsterdam
- Polley DB, Steinberg EE, Merzenich MM. 2006. Perceptual learning directs auditory cortical map reorganization through top-down influences. *J. Neurosci.* 26:4970–82
- Pouget A, Thorpe SJ. 1991. Connectionist model of orientation identification. *Connect. Sci.* 3:127–42
- Pylshyn ZW, Storm RW. 1988. Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spat. Vis.* 3:179–97
- Rao RP. 2004. Bayesian computation in recurrent neural circuits. *Neural Comput.* 16:1–38
- Ratcliff R, McKoon G. 2008. The diffusion decision model: theory and data on two-choice decision tasks. *Neural Comput.* 20:873–922
- Renner MJ, Rosenzweig MR. 1987. *Enriched and Impoverished Environments Effects on Brain and Behavior Recent Research in Psychology*. New York: Springer-Verlag
- Ribas-Fernandes JJF, Solway A, Diuk C, McGuire JT, Barto AG, et al. 2011. A neural signature of hierarchical reinforcement learning. *Neuron* 71:370–79
- Roelfsema PR, van Ooyen A, Watanabe T. 2010. Perceptual learning rules based on reinforcers and attention. *Trends Cogn. Sci.* 14:64–71
- Rosch E. 1975. Cognitive representations of semantic categories. *J. Exp. Psychol. Gen.* 104:192–233
- Rosen LD. 2007. *Me, MySpace, and I*. New York: Macmillan
- Rosser JCJ, Lynch PJ, Cuddihy L, Gentile DA, Klonsky J, Merrell R. 2007. The impact of video games on training surgeons in the 21st century. *Arch. Surg.* 142:181–86
- Rougier NP, Noelle DC, Braver TS, Cohen JD, O'Reilly RC. 2005. Prefrontal cortex and flexible cognitive control: rules without symbols. *Proc. Natl. Acad. Sci. USA* 102:7338–43
- Rumelhart DE, McClelland JL, PDP Res. Group. 1987. *Parallel Distributed Processing—Vol. 1*. Boston, MA: MIT Press

- Saffell T, Matthews N. 2003. Task-specific perceptual learning on speed and direction discrimination. *Vis. Res.* 43(12):1365–74
- Sakai K. 2008. Task set and prefrontal cortex. *Annu. Rev. Neurosci.* 31:219–45
- Sarter M, Hasselmo ME, Bruno JP, Givens B. 2005. Unraveling the attentional functions of cortical cholinergic inputs: interactions between signal-driven and cognitive modulation of signal detection. *Brain Res. Rev.* 48:98–111
- Schellenberg EG. 2004. Music lessons enhance IQ. *Psychol. Sci.* 15:511–14
- Schlickum MK, Hedman L, Enochsson L, Kjellin A, Fellander-Tsai L. 2009. Systematic video game training in surgical novices improves performance in virtual reality endoscopic surgical simulators: a prospective randomized study. *World J. Surg.* 33:2360–67
- Schultz W, Dayan P, Montague PR. 1997. A neural substrate of prediction and reward. *Science* 275:1593–99
- Serences JT, Yantis S, Culbertson A, Awh E. 2004. Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J. Neurophysiol.* 92:3538–45
- Shapiro DC, Schmidt RA. 1982. The schema theory: recent evidence and developmental implications. In *The Development of Movement Control and Co-ordination*, ed. JAS Kelso, JE Clark, pp. 113–50. New York: Wiley
- Shapiro KL, Arnell KM, Raymond JE. 1997. The attentional blink. *Trends Cogn. Sci.* 1:291–96
- Simen P, Contreras D, Buck C, Hu P, Holmes P, Cohen D. 2009. Reward rate optimization in two-alternative decision making: empirical tests of theoretical predictions. *J. Exp. Psychol.: Hum. Percept. Perform.* 35:1865–97
- Sitaram N, Weingartner H, Gillin JC. 1978. Human serial learning: enhancement with arecholine and choline impairment with scopolamine. *Science* 201:274–76
- Spelke ES. 2005. Sex differences in intrinsic aptitude for mathematics and science?: A critical review. *Am. Psychol.* 60:950–58
- Spence I, Feng J. 2010. Video games and spatial cognition. *Rev. Gen. Psychol.* 14:92–104
- Spence I, Yu JJ, Feng J, Marshman J. 2009. Women match men when learning a spatial skill. *J. Exp. Psychol.: Learn. Mem. Cogn.* 35:1097–103
- Stevens C, Bavelier D. 2012. The role of selective attention on academic foundations: a cognitive neuroscience perspective. *Dev. Cogn. Neurosci.* 2:S30–48
- Stilp CE, Rogers TT, Kluender KR. 2010. Rapid efficient coding of correlated complex acoustic properties. *Proc. Natl. Acad. Sci. USA* 107:21914–19
- Strobach T, Frensch PA, Schubert T. 2012. Video game practice optimizes executive control skills in dual tasks and task switching situations. *Acta Psychol.* 140:13–24
- Subrahmanyam K, Greenfield PM. 1994. Effect of video game practice on spatial skills in girls and boys. *J. Appl. Dev. Psychol.* 15:13–32
- Takeuchi H, Sekiguchi A, Taki Y, Yokoyama S, Yomogida Y, et al. 2010. Training of working memory impacts structural connectivity. *J. Neurosci.* 30:3297–303
- Tang YY, Posner MI. 2009. Attention training and attention state training. *Trends Cogn. Sci.* 13:222–27
- Thorndike EL, Woodworth RS. 1901. The influence of improvement in one mental function upon the efficiency of other functions. (I). *Psychol. Rev.* 8:247–61
- Toepper M, Gebhardt H, Beblo T, Thomas C, Driessen M, et al. 2010. Functional correlates of distractor suppression during spatial working memory encoding. *Neuroscience* 165:1244–53
- Trick LM, Jaspers-Fayer F, Sethi N. 2005. Multiple-object tracking in children: the “Catch the Spies” task. *Cogn. Dev.* 20:373–87
- Vul E, Frank MC, Alvarez GA, Tenenbaum JB. 2010. Explaining human multiple object tracking as resource-constrained approximate inference in a dynamic probabilistic model. *Adv. Neural Inf. Proc. Syst.* 32:1955–63
- Vul E, Hanus D, Kanwisher N. 2009. Attention as inference: Selection is probabilistic; responses are all-or-none samples. *J. Exp. Psychol. Gen.* 138(4):546–60
- West GL, Stevens SA, Pun C, Pratt J. 2008. Visuospatial experience modulates attentional capture: evidence from action video game players. *J. Vis.* 8:1–9
- Yamane Y, Carlson ET, Bowman KC, Wang Z, Connor CE. 2008. A neural code for three-dimensional object shape in macaque inferotemporal cortex. *Nat. Neurosci.* 11:1352–60

Zhang J-C, Lau P-M, Bi G-Q. 2009. Gain in sensitivity and loss in temporal contrast of STDP by dopaminergic modulation at hippocampal synapses. *Proc. Natl. Acad. Sci. USA* 106:13028–33

---

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Green CS, Pouget A, Bavelier D. 2010. Improved probabilistic inference, as a general learning mechanism with action video games. *Curr. Biol.* 20:1573–79

Hinton GE. 2007. Learning multiple layers of representation. *Trends Cogn. Sci.* 11:428–34

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