10 Exercising Your Brain: Training-Related Brain Plasticity

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ABSTRACT Learning and brain plasticity are fundamental properties of the nervous system, and they hold considerable promise when it comes to learning a second language faster, maintaining our perceptual and cognitive skills as we age, or recovering lost functions after brain injury. Learning is critically dependent on experience and the environment that the learner has to face. A central question then concerns the types of experience that favor learning and brain plasticity. Existing research identifies three main challenges in the field. First, not all improvements in performance are durable enough to be relevant. Second, the conditions that optimize learning during the acquisition phase are not necessarily those that optimize retention. Third, learning is typically highly specific, showing little transfer from the trained task to even closely related tasks. Against these limiting factors, the emergence of complex learning environments provides promising new avenues when it comes to optimizing learning in real-world settings.

The ability to learn is fundamentally important to the survival of all animals. Brain plasticity, together with the learning it enables, therefore embodies a pivotal evolutionary force. The human species appears remarkable in this respect, as more than a century of research has demonstrated that humans possess the ability to acquire virtually any skill given appropriate training. Yet, while the exceptional capacity of humans to learn should certainly reassure those seeking to design educational or rehabilitative training programs, there are still several key obstacles that need to be overcome before these programs can reach their full potential.

The first is that brain plasticity is typically highly specific. While individuals trained on a task will improve on that very task, other tasks, even closely related ones, often show little or no improvement. Obviously, this obstacle potentially limits the benefits of learning-based interventions, be they educational or clinical. After all, it is of little use to improve a stroke patient on a visual motion task in the laboratory if this same training will not allow her to effectively see moving cars as she tries to safely cross the street.

The second obstacle is that while brain plasticity is typically adaptive and beneficial, it can also be maladaptive, dramatically so at times, as when expert string musicians suffer from dystonia or motor weaknesses in their fingers as a result of extensive practice with their instruments.

Finally, and subsumed in the first two obstacles, is the fact that we are still missing the recipe for successful brain plasticity intervention at the practical level. Our current understanding of the causal relationship between one type of training experience and the functional changes it induces through brain plasticity is still very much incomplete.

However, progress is being made in each of these areas. In particular, research in recent years has revealed the potential benefits of what are sometimes termed complex learning environments. These appear to promote behaviorally beneficial plastic changes at a more general level than previously seen. This chapter provides an overview of these recent advances.

Specificity of learning

In the field of learning, transfer of learning from the trained task to even other very similar tasks is generally the exception rather than the rule, a fact that is well documented in the field of perceptual learning. For instance, Fiorentini and Berardi (1980) trained subjects to discriminate between two complex gratings that differed only in the relative spatial phase of the two component sinusoids (figure 10.1*A*). Performance on this task improved very rapidly over the course of a single training session and remained consistently high when subjects were tested on two subsequent days. However, when the gratings were rotated by 90 degrees or the spatial frequency was doubled, no evidence of transfer was observed (figure 10.1*B*). Specificity has also been demonstrated in the discrimination of oriented texture objects, where learning is specific to the location and orientation of the trained stimuli (Karni & Sagi, 1991), in the discrimination of dot motion direction, where the learning is specific to the direction and speed of the trained stimuli (Ball & Sekuler, 1982; Saffell & Matthews, 2003), and in some types of hyperacuity tasks, where in addition to being specific for location and orientation, learning can even be specific for the trained eye (Fahle, 2004).

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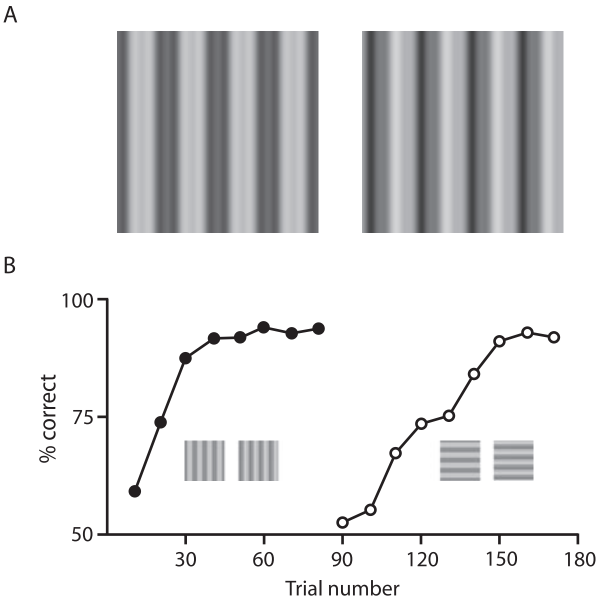

FIGURE 10.1 (*A*) Schematic illustration of the stimulus gratings to be discriminated in Fiorentini and Berardi (1980), (*B*) Subjects' performance on the vertical gratings improved steadily as training proceeded. Yet, when the gratings were abruptly rotated by 90 degrees halfway through the session, performance dropped back to pretraining levels, illustrating the high specificity of the learning.

Similar examples of specificity can also be found in the motor domain (Bachman, 1961; Rieser, Pick, Ashmead, & Garing, 1995). For example, participants trained to aim at a target with their aiming hand visible demonstrate increases in the speed and accuracy of their aiming movements. However, these improvements do not transfer to conditions in which the aiming hand is not visible (Proteau, 1992). In prism adaptation studies, subjects wear goggles that displace the visual world laterally, thus requiring a recalibration of the motor system to bring it back in alignment with the nondisplaced real world. In this literature there is evidence for learning that is specific to the trained limb (Martin, Goodkin, Bastian, & Thach, 1996), to the start and end position of the learned movement, and to the action performed (Redding, Rossetti, & Wallace, 2005; Redding & Wallace, 2006).

Specificity of learning is also a feature of more cognitive learning. For instance, Pashler and Baylis (1991) trained subjects to associate one of three keys with visually presented symbols (left key = P or 2, middle key = V or 8, right key = K or 7). Over the course of multiple training blocks, participant reaction time decreased significantly. However, when new symbols were added that needed to be mapped to the same keys in addition to the learned symbols (left key = P, 2, F, 9; middle key = V, 8, D, 3; right key = K, 7, J, 4), no evidence of transfer was evident. In fact, reaction times to the previously learned symbols increased to pretraining levels. Similarly, studies of object recognition point to highly specific learning. Furmanski and Engel (2000) trained subjects to name backward masked images of common objects over 5 days. Recognition thresholds decreased by up to 20%; however, little transfer was seen when a new set of objects was used. Thus learning did not proceed through general enhancement of vision or by learning the visual context in which the objects were presented but rather at an object-specific level.

Specificity of learning is not just a feature of training-induced brain plasticity. Plasticity as a result of altered experience, even early in life, also leads to surprisingly specific functional changes. For example, individuals born deaf do not exhibit a general enhancement of vision; they exhibit comparable performance to hearing individuals on a range of visual psychophysical thresholds, be it for brightness discrimination, visual flicker, different aspects of contrast sensitivity, or direction and velocity of motion (Bosworth & Dobkins, 2002; Brozinsky & Bavelier, 2004; Finney & Dobkins, 2001). Instead, enhanced performance has been reported only under specific conditions, such as processing of the visual periphery or motion processing, and mainly under conditions of attention. A review of the literature indicates that the changes documented after early deafness are best captured in terms of a change in the spatial distribution of visual spatial attention, whereby deaf individuals exhibit enhanced peripheral attention compared to hearing individuals, with little to no changes in other aspects of vision or visuospatial attention (Bavelier, Dye, & Hauser, 2006). 2

Enhanced performance through practice: Is it always learning?

Establishing the presence of experience-dependent learning effects is not always straightforward. At least two main classes of effects may masquerade as experience-dependent learning effects—transient effects and effects caused by hidden or unmeasured variables.

Many types of transient effects may indeed be causally related to the training intervention; however, they are not considered true learning effects because they last for only a few minutes following the cessation of training. An excellent example is the so-called Mozart effect, wherein listening to only 10 minutes of a Mozart sonata was reported to lead to significant performance increases on the Stanford Binet IQ spatial-reasoning task (Rauscher, Shaw, & Ky, 1993). Unfortunately, in addition to proving difficult to replicate consistently (Fudin & Lembessis, 2004; McCutcheon, 2000; Rauscher et al., 1997; Steele, Brown, & Stoecker, 1999), the validity of this enhancement as a true learning effect has been questioned, as any positive effects last only a few minutes. The source of the effect has instead been attributed to short-term arousal or mood changes, as several studies have indicated that the type of music further

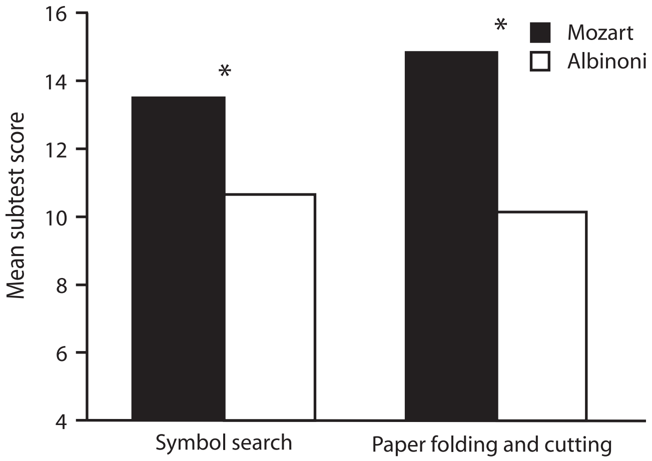

FIGURE 10.2 Participants' performance on the letter-number sequencing test (a measure of working memory skills) and the paper folding and cutting test (a measure of visuospatial constructive skills). Participants were tested shortly after listening to either an up-tempo sonata of Mozart in a major key, which conveyed a mood of happiness, or a slow-tempo adagio of Albinoni in a minor key, which conveyed a mood of sadness. Participants performed better on both tests after listening to the Mozart piece compared to the Albinoni piece. This work illustrates that the "Mozart effect" has little to do with learning per se. Rather, music listening seems to affect performance for better or for worse on a wide variety of tests by changing arousal and mood just before testing. Asterisks denote statistical significance. (Adapted from Schellenberg, Nakato, Hunter, & Tomato, 2007, figure 2; Thompson et al., 2001, figure 1.) 15

influences performance. For example, pop music such as "Country House" by Blur led to a greater spatial IQ enhancement than a piece by Mozart (Schellenberg & Hallam, 2005). Further confirming the arousal-mood hypothesis, listening to a high-tempo piece by Mozart was found to lead to better verbal IQ measures than listening to a slower piece by Albinoni (figure 10.2; Schellenberg, Nakata, Hunter, & Tomato, 2007).

Along the same line, studies that have examined the impact of playing violent video games on aggressive behavior may suffer from the same weakness, as the tests used to assess changes in the dependent variables of interest (behavior, cognition, affect, etc.) are typically given within minutes of the end of exposure to the violent video games. Given that violent video games are known to trigger a host of transient physiological changes associated with increased arousal and stress (i.e., "fight-or-flight" responses), it is important to demonstrate that any changes in behavior or cognition are not likewise transient in nature. It is interesting to note that while several recent papers in this field have reported changes in aggressive cognition and affect as well as desensitization to violence immediately following 30 minutes of exposure to violent video games, the same studies failed to find a significant relationship between these variables and being a regular player of violent video games, suggesting that the effects may indeed be fleeting rather than constituting true learned aggression effects (Carnagey & Anderson, 2005; Carnagey, Anderson, & Bushman, 2007).

The second class of effects that may masquerade as experience-dependent learning consists of effects caused by hidden or unmeasured variables that are unrelated to the experience of interest. While these effects may represent learning, they do not represent "experience-dependent" learning. For instance, it is well documented that individuals who have an active interest taken in their performance tend to improve more than individuals who have no such interest taken—an effect often dubbed the Hawthorne effect (Lied & Karzandjian, 1998). This effect can lead to powerful improvements in performance that have little to do with the specific cognitive training regimen being studied, but instead reflect social and motivational factors that influence performance. In the same vein, the mere presence of mental or physical stimulation may lead to performance changes in groups that are chronically understimulated (as may be the case with the institutionalized elderly), which again would not be considered experience-dependent learning as it is not dependent on the type of experience.

A related issue arises when researchers attempt to infer the presence of experience-dependent learning by examining behavioral differences in groups that perform various activities as part of their everyday lives (for instance, athletes, musicians, or video game players). The obvious concern here is population bias—in other words, inherent differences in abilities may lead to the differences in the activities experienced, rather than the other way around. For example, individuals born with superior hand-eye coordination may be quite successful at baseball and thus preferentially tend to play baseball, while individuals born with poor hand-eye coordination may tend to avoid playing baseball. A hypothetical study that examined differences in hand-eye coordination between baseball players and nonplayers may observe a difference in hand-eye coordination, but it would be erroneous to link baseball experience to superior hand-eye coordination, when a population bias was truly at the root of the effect.

Training studies aiming to establish experience-dependent learning should therefore demonstrate (1) benefits that go beyond the temporary arousal or mood changes an experience can induce, and (2) a clear causal link between the specific training experience and learning. The effect of training should be measured at least a full day after completion of training to insure that it is a robust learning effect. As illustrated by the Mozart effect, training participants for 20 minutes and immediately showing changes in measures of their performance does not mean that a long-lasting alteration of performance has taken place. Furthermore, to establish a definitive causal link between a given form of experience and any enhancement in skills, it is necessary to not only train nonexperts on the experience in question and to observe the effects of this training, but also to control for the source of this improvement. Training studies should include a group that controls for test-retest effects (i.e., how much improvement can be expected simply from repeating a test) and, just as importantly, for psychological and motivational effects. Control groups that are passive, that are only pre- and post-tested but not asked to train or only asked to train at a low level of difficulty on the same task as the experimental group, may not be ideal as such studies fail to differentiate the contribution of motivational factors such as being challenged by the training episode versus true cognitive exercising on performance changes. Finally, evaluation of the efficiency of training critically depends on the choice of outcome measures. Outcome measures closely related to the training experience are more likely to show robust improvements given the specificity of learning discussed earlier. Yet it is critical to show transfer to new tasks within the same domain if one is interested in enhancing skills in a cognitive domain rather than performance on a given specific laboratory test. For example, training on a version of a Stroop task is likely to result in reduced Stroop interference. To what extent does this improvement reflect a generalized improvement in executive skills? Various kinds of transfer and generalization tests that also measure executive skills, but do not do so in the same context or using the same stimuli as the Stroop task, would have to evaluated before concluding that the training regimen leads to an improvement in executive skills (see Schmidt & Bjork, 1992, for an excellent review of this issue).

Complex learning environments and general learning

Against a backdrop of highly specific learning, a few training regimens have recently come under close scrutiny, as they seem to induce learning that is much more general than previously thought possible. These learning paradigms are typically more complex than simple laboratory manipulations and correspond to real-life experiences such as musical training, athletic training, and action video game playing.

In the musical domain for instance, Schellenberg (2004) assessed the effect of music lessons on IQ. A large sample of children was randomly assigned to one of four groups. Two groups received music training (keyboard or vocal), one control group received drama training, and the final group received no training. The primary measures of interest were scores on the Wechsler Intelligence Scale for Children (WISC-III) before and after training. While IQ scores increased for children in all groups, the largest increases were observed in the two music training groups. This effect held in all but two of the twelve subtests of the full IQ scale, indicating a widespread beneficial effect on cognition (figure 10.3). Rauscher and colleagues (1997) monitored the spatiotemporal reasoning skills of young children (3–4 years old) who were given 6 months of musical keyboard lessons. Significantly larger improvements in spatiotemporal reasoning were noted in the keyboard-trained children than in two control groups—one a computer training and the other a no-training group (see also Hetland, 2000). Finally, it has also been suggested that music training enhances mathematical ability and verbal memory (Gardiner, Fox, Knowles, & Jefferey, 1996; Graziano, Peterson, & Shaw, 1999; Ho, Cheung, & Chan, 2003). These studies demonstrate a causal effect of music playing on a range of cognitive skills during development. Although the motor component of music lessons is likely to be a key factor, it remains unknown whether different musical activities (string playing, keyboard playing, or singing) differ in altering cognition. Similarly, it is not clear whether these differences remain into adulthood and whether they can be induced through music playing in adulthood.

In the athletic domain, Kiomourtzoglou, Kourtessis, Michalopoulou, and Derri (1998) compared athletes with expertise in various sports (basketball, volleyball, and water polo) on a number of measures of perception and cognition. Expert athletes demonstrated enhancements (compared to novices) in skills that are intuitively important to performance in their given sports. Basketball players exhibited superior selective attention and hand-eye coordination, volleyball players outperformed novices at estimating the speed and direction of a moving object, and water polo players had

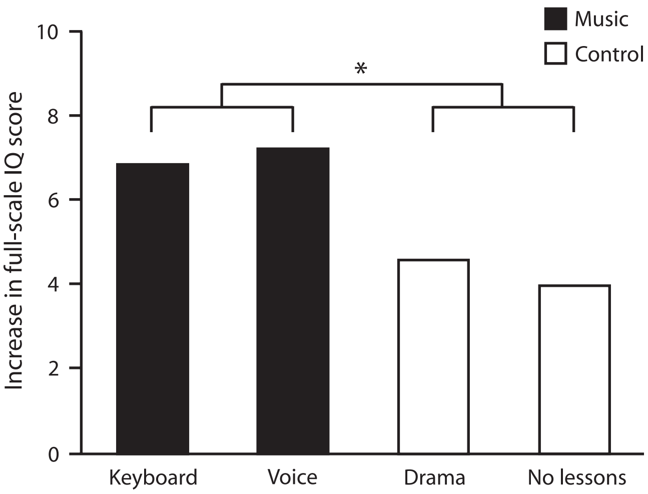

FIGURE 10.3 A large sample of children was randomly assigned to one of four groups. Two groups received music training (keyboard or vocal), a first control group received drama training, and a second control group received no training. The primary measures of interest were scores on the Wechsler Intelligence Scale for Children (WISC-III) obtained before and after training. Children in the music groups showed greater improvements between pre- and postassessment than the two control groups. This study demonstrates a causal effect of music lessons on a range of cognitive skills during development. Asterisks denote statistical significance. (Data replotted from Schellenberg, 2006.)

faster visual reaction times and better spatial orienting abilities. Lum, Enns, and Pratt (2002), McAuliffe (2004), and Nougier, Azemar, and Stein (1992) observed similar sports-related differences in a Posner cuing task, while Kida, Oda, and Matsumura (2005) demonstrated that trained baseball players respond faster than novices in a go-no-go task (press the button if you see color A, do not press the button if you see color B), but interestingly show no enhancements in 3 simple RT (press a button when a light turns on). Unfortunately, no training studies are available at this point to establish a causal link between these performance enhancements and the specific physical activity under investigation. The possibility that aerobic exercise of any sort may enhance cognitive abilities has received much attention lately with respect to aging. Consistently positive results have been reported in many cross-sectional studies comparing older adults who normally exercise with those who do not. Enhancements have been documented in tasks as varied as dual-task performance or executive attention/distractor rejection (for recent reviews see Colcombe et al., 2003; Hillman, Erickson, & Kramer, 2008; Kramer & Erickson, 2007). More training studies are needed to unambiguously establish the causal effect of aerobic exercise on perception and cognition. Yet, taken together, studies of the effect of athletic training and exercise on perception and cognition are tantalizing, and they have prompted renewed interest for demonstrating a causal link between the physical nature of the training regimen and enhancement of cognitive skills.

Perhaps the most popular training regimen over the past decade has been video games. The possibility that perceptual and cognitive abilities are enhanced in video game players has raised much attention (for a review, see Green & Bavelier, 2006b). Indeed, the variety of different skills and the degree to which they are modified in video game players appears remarkable. These include improved hand-eye coordination (Griffith, Voloschin, Gibb, & Bailey, 1983), increased processing in the periphery (Green & Bavelier, 2006c), enhanced mental rotation skills (Sims & Mayer, 2002), greater divided attention abilities (Greenfield, DeWinstanley, Kilpatrick, & Kaye, 1994), faster reaction times (Castel, Pratt, & Drummond, 2005), and even job-specific skills such as laparoscopic manipulation (Rosser, Lynch, Cuddihy, Gentile, & Merrell, 2007) and airplane piloting procedures (Gopher, Weil, & Bareket, 1994). Although intriguing, this literature has little to say about learning per se unless the causal effect of game playing is unambiguously established. So far, only a few studies have established a causal link between video game play and long-lasting changes in performance. Among these are a series of studies that provide compelling evidence that playing action video games—such as first-person perspective shooter games—promotes widespread changes ranging from early sensory functions to higher cognitive functions in adults.

Playing action video games improves fundamental properties of vision (Green & Bavelier, 2007; Li, Polat, Makous, 4 & Bavelier, under review). One visual ability often diminished in patients with poor vision, such as amblyopes or older adults (Bonneh, Sagi, & Polat, 2007), is the ability to read small print, with letters appearing unstable and jumbled. The tendency for the resolvability of letters to be adversely affected by near neighbors, termed crowding, is typically evaluated by asking subjects identify the orientation of a letter flanked by distractors, and by determining the smallest distance between target and distractors at which subjects can still correctly identify the target (figure 10.4*A*). Individuals with better vision can tolerate distractors being brought nearer to the target while still maintaining high-accuracy performance. To establish the causal effect of action video game playing on this visual skill, a training study was carried out whereby subjects were randomly assigned to one of two training groups: an action video games trained group (e.g., Unreal Tournament,) or a control trained group (e.g., Tetris). Each group was tested pre- and posttraining on the crowding task. Participants trained on the action game improved significantly more than those trained on the control game (figure 10.4*B*). The inclusion of a control game group allows us to measure any possible improvements due to test-retest (i.e., familiarity with the task) or to Hawthorne-like effects (Lied & Karzandjian, 1998). Finally, the control games were chosen to be pleasurable and engrossing, as the experimental training games are known to minimize differences in arousal across groups. Critically, posttraining evaluation was always performed at least a day after the completion of the training phase.

Playing action video games was also shown to enhance several different aspects of visual selective attention. Action game training improves the ability of young adults to search their visual environment for a prespecified target, to monitor moving objects in a complex visual scene, and to process a fast-paced stream of visual information (Feng, Spence, & Pratt, 2007; Green & Bavelier, 2003, 2006c, 2006d). In one such experiment, the efficiency with which attention is distributed across the visual field was measured with a visual search task called the Useful Field of View paradigm (Ball, Beard, Roenker, Miller, & Griggs, 1988). This task is akin to looking for a set of keys on a cluttered desk. Subjects are asked to localize a briefly presented peripheral target in a field of distracting objects; accuracy of performance is recorded (figure 10.5*A*). Training on an action video game for just 10 hours improved performance on that task by about 30%, an improvement which is greatly in excess of that which can be induced by training on a control game (figure 10.5*B*). In a related study, Feng (2007) showed that performance on the Useful Field of View task differs across gender, with males showing an advantage. Yet, after 10 hours of action game training, this gender difference was reduced, as

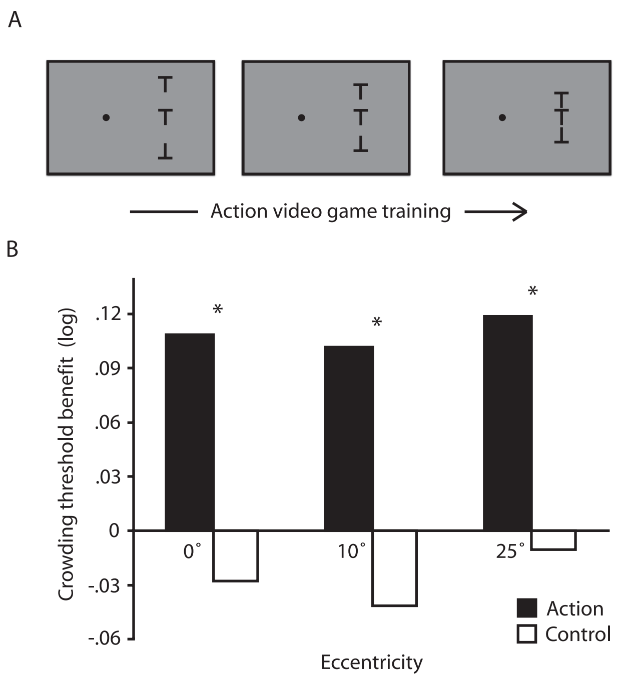

FIGURE 10.4 (*A*) Participants were presented with a display containing three vertically aligned *T*'s and asked to determine whether the central *T* was upright or inverted. Crowding thresholds were measured by determining the smallest distance between the target and the distractors at which participants could still perform this discrimination task with 79% accuracy. Enhanced performance on this task results in participants being able to process more densely packed letters, as illustrated here. Participants were either trained on an action video game hypothesized to enhance their visual resolution or on a control video game. (*B*) The crowding thresholds were measured at three different eccentricities (central vision, 10 degrees, and 25 degrees). This procedure allowed testing of central vision, often thought to have optimal performance, as well as peripheral locations, allowing one to test generalization of learning at untrained locations. The action game training group improved significantly more than the control group at all three eccentricities tested, reflecting generalization of learning at untrained locations and greater plasticity than previously thought in central vision. Asterisks denote statistical significance.

5 well as the oft-documented difference in mental rotation skills between males and females (Feng et al., 2007).

In addition to basic visual skills and selective attention, action game playing has also been linked to better performance on dual tasks (Green & Bavelier, 2006a), task switching (Green & Bavelier, 2006a), and decision-making processes (Green, Pouget, & Bavelier, 2007). A training regimen that promotes robust changes in such a wide range of skills 6 provides an existence proof that efficient learning transfer can occur given the appropriate training.

Determinants of learning and learning transfer

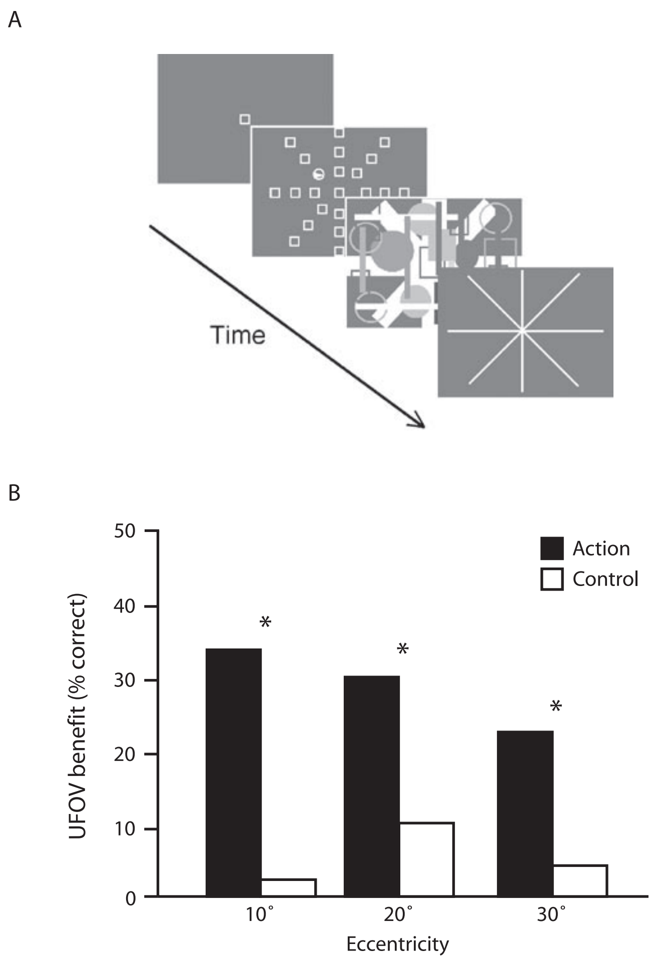

FIGURE 10.5 (*A*) Illustration of the Useful Filed of View Task as adapted by Green and Bavelier (2003). Participants viewed a briefly flashed display containing one target, a filled triangle, embedded in a circle of distractors. They were asked to report the location of the target by indicating along which of the main eight directions the target was presented. Half of the participants were trained on an action video game hypothesized to enhance their visual attention, while the other half were trained on a control game. (*B*) Percent correct target localization was measured at each of the three eccentricities tested (10, 20, and 30 degrees of visual angle) before and after training. The action game training group improved more from pre- to posttraining tests than the control game training group. This was even the case at 30 degrees of visual angle, an eccentricity seldom used in video gaming, establishing generalization of learning to untrained locations. Asterisks denote statistical significance.

A major challenge for future work is to pinpoint which factors, or combination of factors, inherent to the complex training regimens discussed earlier are responsible for the enhancement in learning and learning transfer. This point is important both theoretically, in terms of designing models of human learning and behavior, and practically, for those seeking to devise effective rehabilitation programs to ameliorate specific deficits.

The ultimate goal is to see the learner flexibly acquire new knowledge, while at the same time using prior knowledge to constrain and accelerate learning. Models of complex human learning, such as those derived from connectionism or machine learning, provide some clues about the factors that facilitate bottom-up learning based upon the statistics of the input. Recently, the framework of Bayesian inference has been proposed to provide a good first-order model of how subjects learn to optimize behavior in dynamic complex tasks, be they perceptual or cognitive in nature (Courville, Daw, & Touretzky, 2006; Ernst & Banks, 2002; Orbán, Fiser, Aslin, & Lengyel, 2008; Tenenbaum, Griffiths, & Kemp, 2006). Another key feature of recent advances has been the realization that actions and the feedback they provide about the next step to be computed can greatly reduce the computational load of a task, as well as facilitate learning and generalization (Ballard, Hayhoe, Pook, & Rao, 1997; Taagten, 2005). Finally, symbolic cognitive architectures such as SOAR and ACT-R provide insights into how knowledge representations should be structured to explain the acquisition of abstract systems of knowledge, and possibly transfer of knowledge across these systems (Anderson et al., 2004; Lehman, Laird, & Rosenbloom, 1998). Based on this variety of theoretical approaches, one can begin to identify characteristics inherent to complex training regimens that seem more likely to be at the root of general learning. These include, but are not limited to, (1) level of representation, (2) task difficulty, (3) goals, action, and feedback, and (4) motivation and arousal.

LEVELS OF REPRESENTATION Learning is more likely to be flexible and general if it occurs at the level of richly structured representations that contribute to a wide array of behaviors, rather than if it changes neural networks whose functions are highly specialized. The field of perceptual learning has identified task difficulty as one of the main factors controlling the level of representation at which learning occurs. In their reverse hierarchy theory of perceptual learning, Ahissar and Hochstein (2004) hypothesize that learning is a top-down guided process, where learning occurs at the highest level of representation that is sufficient for the given task. Easy tasks can be learned at a reasonably high level of representation that may be shared with many other tasks, allowing for sizable learning transfer. When tasks become exceedingly difficult—at least in the perceptual domain, such as in Vernier acuity tasks near the hyperacuity range—lower levels of representation with better signal-to-noise ratios are required for adequate task performance. In such cases, only tasks that make use of this low-level neural network, down to the specific retinal location and stimulus orientation, will benefit. Although the reverse hierarchy theory was developed to account for perceptual learning effects, it aligns well with the more general proposal that transfer of learned knowledge to different tasks and contexts will be more likely when learning and inference operate at higher levels of representation.

A key factor in ensuring flexible learning is high variability. Variability is important both at the level of the exemplars to be learned and the context in which they appear (Schmidt & Bjork, 1992). For example, subjects learn to recognize objects in a more flexible way if the objects are presented in a highly variable context (Brady & Kersten, 2003). High contextual variability ensures that subjects learn to ignore the specifics of the objects, such as are brought about by changes in view, lighting, camouflage, or shape, and rather learn to extract more general principles about object category. Statistical approaches such as mutual information show that subjects implicitly develop knowledge of the fragments or chunks that carry information about the categories to be learned (Hegdé, Bart, & Kersten, 2008; Orbán et al., 2008). A key issue then arises as to when these informative fragments allow for learning that generalizes as compared to learning that is item specific. Work on object classification and artificial grammar learning shows that low input variability induces learning at levels of representation that are specific to the items being learned, and thus too rigid to generalize to new stimuli. High variability is crucial in ensuring that the newly learned informative fragments be at levels of representation that can flexibly recombine (Gomez, 2002; Onnis, Monaghan, Christiansen, & Chater, 2004; Reeler, Newport, & Aslin, 2008). Research on the video game Tetris and its effect on mental rotation illustrates this point well. Even though mental rotation is at a premium in Tetris, expert Tetris players have been found to exhibit mental rotation capacities similar to those of naive subjects, except when tested on Tetris or Tetris-like shapes (Sims & Mayer, 2002). The use of a limited number of shapes in Tetris allows the learner to memorize spatial configurations and moves (Destefano & Gray, 2007). This approach allows for the development of excellent expertise at the game itself, but what is learned in this low-variability game is less likely to generalize to other environments. By this view, an efficient scheme to enforce mental rotation learning would be to use a highly variable set of objects preventing learning of specific configurations.

TASK DIFFICULTY The proposal that task difficulty controls the type and rate of learning is implicit in all theories of learning. The perceptual learning literature nicely illustrates the impact of manipulating task difficulty appropriately (Sireteanu & Rettenbach, 1995, 2000). In particular, when it comes to promoting learning transfer, harder tasks are at a disadvantage. For example, in a task where participants had to view arrays of oriented lines and determine which contained a single oddly oriented line, task difficulty was manipulated by limiting exposure time (Ahissar & Hochstein, 1997). With practice, the minimal exposure time that could be tolerated by the participants decreased substantially. Interestingly, when the task was started at a difficult level (short exposure times), learning was slow and specific for the trained orientation and location. When the task was made easier by starting with long exposure times, learning progressed quickly and transferred to novel orientations. Other conditions that made the task more difficult, such as using small differences in orientation between target and nontarget lines or greater visual eccentricity, also led to the same effect. In the same vein, Liu and Weinshall (2000) demonstrated that learning an easy motion-direction discrimination (9 degrees of motion direction) transferred substantially to novel orientations, whereas Ball and Sekuler (1982) had previously reported no such transfer using the same task but with a greater degree of difficulty (3 degrees of motion direction). Similarly, albeit with barn owls rather than human subjects, Linkenhoker and Knudsen (2002) demonstrated that adult barn owls could adjust to sizable shifts in visual experience (brought about by prism goggles) when the shifts were made in small enough increments. In contrast, large shifts led to no learning in these adult barn owls.

This is not to say that efficient learning will occur through exposure of the learner to situations that are easy to master. In fact, easy tasks that typically require the reenactment of already mastered skills lead to little to no learning (Olesen, Westerberg, & Klingberg, 2004). Intuitively the task difficulty should be set such that the learner can gain some satisfaction from his or her performance. In other words, it should be challenging enough to avoid boredom and lack of interest, but not too hard to allow for sizable positive feedback. This balance may be understood more formally as choosing the task difficulty that allows the learner to optimize over time the amount of reward gained from doing the task. Strikingly, the video game industry may have focused in on the conditions for generalized learning by using variable entry level, and therefore allowing each learner to enter the learning task at the proper level of challenge, and by implementing incremental increases in task difficulty as the game progresses. In our own work on video game training we have acknowledged these principles explicitly by progressing players to the next level of difficulty during training only when they have demonstrated sufficient mastery of their current level. This is not to say that the type of game is unimportant, rather that an appropriate training regimen must also be administered in an appropriate manner.

GOALS, ACTION, AND FEEDBACK A productive view of learning holds that it derives from the need to minimize "surprise," or the difference between the anticipated outcome of an event or action and its actual outcome (Courville et al., 2006; Schultz, Dayan, & Montague, 1997). In that framework, actions provide a means of choice for
8 learners to evaluate their internal representations and fine-tune them if a discrepancy is noted between the actual and predicted outcome of the action (Sutton & Barto, 1998). Learning is thus critically under the control of the expected value, or reward, that the learner ascribes to a future event or action and the actual value received as the event or action unfolds.

Although clearly critical for learning, the exact role that feedback plays in learning is a subject of much debate. There are numerous examples demonstrating that feedback is necessary for learning (Herzog & Fahle, 1997; Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006). Yet many counterexamples also exist (Amitay, Irwin, & Moore, 2006; Ball & Sekuler, 1987; Fahle, Edelman, & Poggio, 1995; Karni & Sagi, 1991). The extent to which these are counterexamples is complicated by the fact that, even when experimenter-generated explicit feedback is not provided, if above-threshold stimuli are employed subjects will nevertheless have varying degrees of confidence that their response was correct. Such internally generated confidence judgments could themselves act as feedback signals (Mollon & Danilova, 1996). An added complication stems from the finding that the type of feedback that optimizes learning during performance acquisition is not necessarily that which optimizes learning in the long run (Schmidt & Bjork, 1992). For example, during the learning of a complex arm movement, subjects provided with feedback about their movement-time error after every trial learned faster than those provided with the same feedback but in a summary form every 15 trials. Yet upon retesting two days later, those provided with feedback every 15 trials showed greater accuracy and thus better performance on the task than those provided with feedback
every trial (Schmidt, Young, Swinnen, and Shapiro, 1989). 9
Whether feedback frequency systematically affects skill acquisition differently than skill retention remains to be firmly established; yet such findings certainly call for caution in considering the roles of feedback in learning.

While most major theories of learning require that some type of learning signal be present (often in the form of an error signal), they do not necessarily require that the feedback be explicit, nor do they require that feedback be given on a trial-to-trial basis. There are many algorithms that can learn quite efficiently when feedback is only given after a series of actions have been completed (Walsh, Nouri, & Littman, 2007). This is analogous to the situation that commonly occurs in action video games, where feedback (typically in the form of killing an opponent or dying) only becomes available at the conclusion of a very complicated pattern of actions. How best to solve this credit assignment problem, as well as how this affects the generality of what is learned, is a topic of ongoing research (Fu & Anderson, 2008; Ponzi, 2008). Interestingly, complex learning environments with the variety of actions they encompass allow for error signals that are varied both in nature and in time scale, a feature that may facilitate flexible learning.

The importance of reward in learning is already supported by neurophysiology studies which show that the brain systems thought to convey the utility of reward, such as the ventral tegmental area and the nucleus basilis, play a large role in producing plastic changes in sensory areas. In particular, when specific auditory tones are paired with stimulation of either of these structures, the area of primary auditory cortex that represents the given tone increases dramatically (Bao, Chan, & Merzenich, 2001; Kilgard & Merzenich, 1998). Interestingly, at least some of the brain areas known to be sensitive to reward have been shown to be extremely active when individuals play action video games. For instance, Koepp and colleagues (1998) demonstrated that roughly the same amount of dopamine is released in the basal ganglia when playing an action video game as when methamphetamines are injected intravenously. Determining the exact role of reward-processing areas in the promotion of learning and neural plasticity will continue to be an area of active research.

MOTIVATION AND AROUSAL Motivation is a critical component of most major theories of learning, with motivation level being posited to depend highly on an individual's internal belief about her ability to meet the current challenge. Vygotsky's (1978) concept of a zone of proximal development matches well with the skill-learning literature discussed previously. According to this theory, motivation is highest and learning is most efficient when tasks are made just slightly more difficult than can be matched by the individual's current ability. Tasks that are much too difficult or much too easy will lead to lower levels of motivation and thus substantially reduced learning. This is not to say that learning will never occur if the task is too difficult or too easy (Amitay et al., 2006; Seitz & Watanabe, 2003; Watanabe, Nanez, & Sasake, 2001), but learning rate should be at a maximum when the task is challenging, yet still achievable.

Like motivation, arousal is a key component of many learning theories. The Yerkes-Dodson law predicts that learning is a U-shaped function of arousal level (Yerkes & Dodson, 1908). Training paradigms that lead to low levels of arousal will tend to lead to low amounts of learning, as will training paradigms that lead to excessively high levels of arousal (Frankenhaeuser & Gardell, 1976). Between these extremes there is an arousal level that leads to a maximum amount of learning, which no doubt differs greatly between individuals. Interestingly, video games are known to elicit both the autonomic responses (Hebert, Beland, Dionne-Fournelle, Crete, & Lupien, 2005; Segal & Dietz, 1991; Shosnik, Chatterton, Swisher, & Park, 2000) and neurophysiological responses (Koepp et al., 1998) that are characteristic of arousal. These responses represent a salient difference between traditional learning paradigms and video game play. In the same vein, although again with barn owls, Bergan, Ro, Ro, & Knudsen (2005) observed that adult owls who were forced to hunt (an activity that involves motivation and arousal) while wearing displacing prisms demonstrated significant learning compared to adult owls who wore the prisms for the same period of time, but who were fed dead prey. The latter failed to adapt to the displacing prism.

Conclusions

The field of experience-dependent plasticity is rapidly expanding, thanks in part to new technologies. Cognitive training on handheld devices and job-related training in immersive environments are now within the reach of most institutions, if not individuals. This trend is exciting because the most successful interventions, when it comes to ameliorating deficits in patients or enhancing skills in an educational context, rely on complex training regimens. These regimens require the simultaneous use of perceptual, attentional, memory, and motor skills to trigger learning that goes beyond the specifics of the training regimen itself. New technologies are perfectly positioned to enhance the development of such complex learning environments. For all the excitement, challenges lie ahead. First among these is developing an understanding of which ingredients should be included in training regimens in order to promote widespread learning. Studies of the neural bases of arousal, motivation, and reward processing hold promise in that respect. Second, although the type of improvement desired is usually clear, as when educators or rehabilitation therapists state their goals for a student or a patient, identifying the cognitive component of a training regimen aimed at realizing those goals is not always so straightforward. At first glance, playing action video game does not appear to be a mind-enhancing activity. Yet it seems to generate beneficial effects for perception, attention, and decision making beyond what one may have expected. In contrast, the game Tetris clearly requires mental rotation, and yet it does not lead to a general benefit in mental rotation skill. Cognitive analysis is needed to determine the level of representation at which the learning is most likely to occur given the nature of the training regimen. We are understanding more about the conditions necessary to develop interventions that will lead to generalizable learning effects, and these hold promise for benefiting individuals and the societies within which they live.

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12.	AUTHOR: Green & Bavelier ’06b: Pls give place of publication.	
13.	AUTHOR: Li, Polat . . . : Can this be updated?	
14.	AUTHOR: Onnis: Pls give place.	
15.	AUTHOR: We don’t have Thompson et al. ’01.	
16.	AUTHOR: Confirm affiliations.	