Exercising Your Brain: A Review of Human Brain Plasticity and Training-Induced Learning

C. S. Green
University of Minnesota

D. Bavelier
University of Rochester

Human beings have an amazing capacity to learn new skills and adapt to new environments. However, several obstacles remain to be overcome in designing paradigms to broadly improve quality of life. Arguably, the most notable impediment to this goal is that learning tends to be quite specific to the trained regimen and does not transfer to even qualitatively similar tasks. This severely limits the potential benefits of learning to daily life. This review discusses training regimens that lead to the acquisition of new knowledge and strategies that can be used flexibly across a range of tasks and contexts. Possible characteristics of training regimens are proposed that may be responsible for augmented learning, including the manner in which task difficulty is progressed, the motivational state of the learner, and the type of feedback the training provides. When maximally implemented in rehabilitative paradigms, these characteristics may greatly increase the efficacy of training.

The ability to learn, or, in other words, to acquire skills and alter behavior as a result of experience, is fundamentally important to the survival of all animals. Humans are certainly no exception; our incredible capacity to learn is certainly one of the principle variables explaining the success of our species. Whereas the term *learning* is extremely broad, and interesting work exists on its every aspect from the relatively simple (e.g. nonassociative learning) to the much more complex (e.g. social learning), this review focuses mainly on skill learning. This research, which has been predominantly carried out with young adults, provides compelling evidence for common principles of learning and learning transfer. We review this work and its implications for the design of training regimens in older adults.

Skill learning is defined here as a change, typically an improvement, in perceptual, cognitive, or motor performance that comes about as a result of training and that persists for several weeks or months, thus distinguishing it from effects related to adaptation or other short-lived effects. Perhaps the most notable finding from the past century or more of research in the field is that humans have demonstrated some amount of learning in virtually every paradigm tested. Evidence for the principle that, given appropriate practice, humans improve on essentially every task, is prevalent throughout the psychology literature, ranging from the domain of perceptual learning (Fahle & Poggio, 2002) to that of motor learning (Karni et al., 1998) and cognitive training (Willis et al., 2006). An important distinction in the field concerns the time course of the learning. Many researchers have differentiated between an early, fast stage of learning that occurs on the order of minutes as the participant becomes familiar with the task and stimulus set and a much slower stage of learning triggered by practice but which requires hours and sometime days to become effective. This distinction is observed in both the perceptual (Karni & Sagi, 1993) and the motor (Karni et al., 1998) learning domains (but see Karni & Bertini, 1997, for examples of "slow" learning in purportedly "fast-learning only" paradigms and vice versa). The review herein focuses principally on the latter slow-learning effects. Furthermore, with an eye toward the potential impact of training regimens on daily life, our emphasis will be not only on durable learning effects but also on general ones. We use the term *general learning* to refer to learning effects that, at the time of retention testing, not only provide high savings on the trained task but also transfer to new tasks and new contexts (Schmidt & Bjork, 1992).

The Problem of Skill Learning

Whereas the exceptional capacity of humans to learn should certainly give heart to those seeking to design rehabilitative training paradigms (whether focused on retraining vision or language after neurological damage or slowing/reversing the normal decline in visual and cognitive skills associated with aging), several key obstacles still must be overcome. First, although it is true that the skill learning literature is filled with examples that suggest that humans can improve on virtually any perceptual or motor task (Ball & Sekuler, 1982; Brashers-Krug, Shadmehr, & Bizzi, 1996; Fahle, 2004; Fine & Jacobs, 2000; Fiorentini & Berardi, 1980; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Karni et al., 1995; Karni & Sagi, 1991; Mackrous & Proteau, 2007; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Ramachandran & Braddick, 1973; Seidler, 2004; Shiu & Pashler, 1992; Sireteanu & Rettenbach, 1995, 2000; Sowden, Rose, & Davies, 2002), most of these same instances also demonstrate a remarkable specificity of learning. In other words, improvement is observed only in the trained task, with little to no transfer of learning being observed even for very

similar untrained tasks. This is obviously a potentially severe impediment for rehabilitative programs, where the goal is to increase the quality of everyday life and which thus necessarily require a general improvement in skills. Second, the fact that training tasks are often boring and unpleasant may decrease the probability of full compliance with the regimen, which in turn will negatively affect final result. Third, improvement in performance is not always due to training-induced learning. Instead, changes in mood, level of motivation, or even desire to please the investigator can all lead to temporary improvements in performance, which without care in experimental design, can easily be mistaken for true learning effects. The key questions in the field of training-induced learning are therefore the following: First, can training regimens be identified that lead to performance improvements that generalize beyond the training context and persist over time? Second, what exact factors contribute to a more general learning outcome?

Specificity of Learning

In the field of skill learning, transfer of learning from the trained task to even other very similar tasks is generally the exception rather than the rule. This fact is well documented in the field of perceptual learning. For instance, Fiorentini and Berardi (1980) trained participants to discriminate between two complex gratings that differed only in the relative spatial phase of the two component sinusoids. Performance on this task improved very rapidly over the course of a single training session and remained consistently high when participants were tested on two subsequent days. However, when the gratings were rotated by 90° or the spatial frequency was doubled, no evidence of transfer was observed. Karni and Sagi (1991) trained participants on the discrimination of oriented texture objects always presented in a certain region of the visual field within an array of oriented background objects. Although learning occurred for the trained stimulus, no transfer was observed if the object was moved to a new location or if the orientation of the object was changed. Learning in some types of hyperacuity tasks can also be specific for the trained retinal location, orientation, and even eye (Fahle, 2004). Ball and Sekuler (1982) trained participants to discriminate small differences in the direction of dot motion. A linear increase in performance was observed over the course of seven sessions, but following training, the authors found no effect of training on orientations more than 45° different than the trained orientation, and the effect at 45° was approximately half of that seen in the training orientation. There is also evidence that such motion training can be speed specific as well (Saffell & Matthews, 2003). Finally, in psychophysics, where visual stimuli are often backward masked, learning can be specific to even the particular structure of the given mask (Maehara & Goryo, 2003).

Similar examples of specificity can also be found in the motor domain (Bachman, 1961). For instance, Rieser, Pick, Ashmead, and Garing (1995) induced a recalibration of the motor system by altering the normal relationship between a given motor command and its result in the world. They accomplished this by towing a treadmill, on which a participant was walking, behind an automobile. By driving the car faster than the movement of the treadmill, the researchers recalibrated the system in line with the belief that less biomechanical force was required to move a given distance and vice versa when the car was driven slower than the movement of the treadmill. This recalibration was demonstrated by having participants walk to targets while blindfolded, where they observed undershoots or overshoots consistent with the training condition. Interestingly, recalibrations of walking speed did not transfer to throwing or to turning in place (although they did transfer to another form of forward locomotion: sidestepping). Comparable recalibrations of throwing likewise did not transfer to walking. Similar specificity has also been found in prism adaptation, wherein participants 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 the prism adaptation literature, there is evidence for learning that is specific to the trained limb (Martin et al., 1996), to the start and end position of the learned movement, and to the action performed (Redding, Rossetti, & Wallace, 2005; Redding & Wallace, 2006). Further examples of specificity in motor learning include manual aiming practice. Participants trained to aim at a target with the aiming hand visibly improve in their aiming movement in terms of accuracy and speed. However, these improvements do not transfer to conditions in which the hand is not visible (Proteau, 1992). A related finding is observed in young adults in stimulus–response mapping learning studies. For instance, Pashler and Baylis (1991) trained participants to associate one of three keys with certain 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 apparent (and reaction times to the previously learned symbols increased to pretraining levels).

Specificity of learning is also a feature of cognitive training. For example, a wealth of studies now exists on the impact of cognitive training in older adults. By and large, these studies demonstrate improvements on attention, memory, and reasoning tasks following training (Basak, Boot, Voss, & Kramer, 2008; Bherer et al., 2005; Plemons, Willis, & Baltes, 1978; Verhaeghen, Marcoen, & Goossens, 1992; Willis, Blieszner, & Baltes, 1981; Winocur et al., 2007). However, training differences are typically specific to the ability trained, with those individuals trained in attention experiencing gains in attention but not in memory or reasoning and vice versa (see, for example, Allaire & Marsiske, 2005; Ball et al., 2002).

Training Regimens and General Learning

Although myriad examples of highly specific learning exist, only a handful of training paradigms have been established where learning seems more general. These learning paradigms are typically more complex than laboratory manipulations and correspond to real-life experiences, such as action video game training, musical training, or athletic training.

Recent work indicates that action video game experience leads to enhanced performance on a number of tasks. For example, action game players outperform their peers on the multiple-object tracking task, wherein participants must track many independently moving objects, therefore displaying an enhanced capacity of the attentional system (Green & Bavelier, 2006b). They also perform

better on the useful field of view task, wherein participants must localize a quickly flashed target amongst a host of distracting objects (Green & Bavelier, 2006a). This skill indexes the ability to deploy attention over space (Ball, Beard, Roenker, Miller, & Griggs, 1988) and is one of the best perceptual predictors of driving accident rates in older persons, far outperforming standard measures of acuity (Myers, Ball, Kalina, Roth, & Goode, 2000). Action game players demonstrate superior capabilities on the attentional blink task, wherein participants must parse a stream of letters presented one after another at a fast pace (10 Hz), indicating faster temporal characteristics of visual attention (Green & Bavelier, 2003). Participants skilled in action game playing can also resolve visual details in the context of tightly packed distractors, as in the crowding task. In this task, flanking objects above and below a center target negatively affects the ability to identify the center target. In doing so, such participants exhibit higher spatial resolution of visual processing (Green & Bavelier, 2007). Action video game players also demonstrate enhanced mental rotation abilities (Feng, Spence, & Pratt, 2007). Action video game experience has been shown to transfer to even high-level real-world tasks, such as piloting procedures (Gopher, Weil, & Bareket, 1994).

Critically, in each of the cases above, the causative link between action video game experience and enhanced performance was demonstrated through a training study in which non–game-playing individuals were specifically trained on an action video game, and the skill in question (e.g., attentional capacity) was assessed before and after training and compared with the performance of a control group that played a non–action game for the same period of time. This point is of great importance, as properly conducted training studies are critical to advancing the level of understanding in this field. Although many individuals play video games, music, or sports as part of their everyday lives, we can only infer so much by comparing the performance of these "experts" with "nonexperts" who do not ordinarily engage in these activities. Population bias is a constant concern; it is likely that individuals with some type of inherent talent and/or skill will flock to those activities that reward their particular skill set. For instance, individuals born with superior hand–eye coordination may be quite successful at some types of video games and thus preferentially tend to play these types of games, whereas individuals born with poor hand–eye coordination may tend to avoid playing games that require this skill. It is essential to demonstrate a definitive causative link between a given form of experience and any enhancement in skills by training non-experts on the experience in question and observing the effects of this training.

Furthermore, it is not sufficient to test only an experimental group. Training studies should also include a group that controls for test–retest effects (i.e., how much improvement can be expected simply from taking the test a second time) and, just as importantly, for psychological and motivational effects. Indeed, it is well documented that individuals who experience an active interest taken in their performance tend to increase their performance more than do individuals who experience no interest taken in their performance, 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 under study but rather reflect social and motivational factors on performance. The impact of these factors on learning is important in and of itself and should

certainly be the subject of careful studies. However, the many studies that include only a no-intervention, no-contact control group cannot distinguish between the cognitive content of the training regimen and social stimulation as the source of improvement (Drew & Waters, 1986; Goldstein et al., 1997; Kawashima et al., 2005; Willis et al., 2006).

Although a training study is lacking, and thus the question of causation remains unanswered, there are also a host of other reports in the literature (for a review, see Green & Bavelier, 2006c) that those individuals who naturally play action video games outperform their non–game-playing peers on other measures of visual attention (Bialystok, 2006; Castel, Pratt, & Drummond, 2005; Greenfield, DeWinstanley, Kilpatrick, & Kaye, 1994; Griffith, Voloschin, Gibb, & Bailey, 1983; Trick, Jaspers-Fayer, & Sethi, 2005), visuomotor skills, and even job-specific skills such as laparoscopic maneuvers (Rosser et al., 2007).

Furthermore, and of particular relevance to the field of gerontology, several reports have demonstrated that video game play can improve perceptual, motor, and cognitive function in older persons. For instance, Drew and Waters (1986) reported significant improvements in both measures of manual dexterity (Purdue pegboard, rotary pursuit) as well as general cognitive function (Wechsler Adult Intelligence Scale—Revised Full Scale, Verbal, and Performance scores). Several groups (Clark, Lanphear, & Riddick, 1987; Dustman, Emmerson, Steinhaus, Shearer, & Dustman, 1992; Goldstein et al., 1997) have also reported significant decreases in reaction time as a result of video game experience in older persons. Although it is unfortunate that the studies listed above largely did not include intervention control groups, the results are certainly noteworthy and encouraging of further investigation. In particular, it is interesting to speculate that given the growing popularity of the Nintendo Wii, which attracts a much wider population than standard video games, including older persons, an interesting convergence may soon occur between researchers examining the effects of video games and those examining the effects of physical activity on perceptual and cognitive skills (see below).

The effects of playing video games on perceptual and cognitive skills are particularly remarkable given the typical specificity of skill learning. Indeed, in the case of action video game training, the tasks used to measure the various perceptual, attentional, and visuomotor skills are quite a departure from the "training paradigm" (i.e., action video games). There are few obvious links between chasing monsters across a star-spotted "spacescape" and determining the orientation of a single black 'T' on a uniform gray background, or between driving a car through a crowded cityscape while shooting at rival vehicles and counting the number of white squares that are quickly flashed against a black background. Although one can certainly argue that individuals are making use of similar underlying processes in action video games and in the psychophysical tasks (rapid object identification for instance), this argument flies in the face of the great many articles demonstrating that no transfer is observed if something as seemingly minor as spatial frequency or orientation is changed. Along a continuum of task similarity, it seems natural to consider orientation discrimination around 45° as closer to orientation discrimination around 135° than to avoiding laser blasts from spaceships.

However, it is not the case that action video game experience leads to enhancements in every perceptual, attentional, and/or visuomotor skill. For instance, Castel et al. (2005) showed that the

attentional orienting system appears to be similar in action video game players and in nonplayers. Furthermore, it is essential to convey the fact that not all types of video games lead to similar effects. Our work and, to some extent, the majority of the literature, has focused specifically on the effect of action video games, that is, games that are fast paced and unpredictable, require effective monitoring of the entire screen, and necessitate that decisions be made extremely rapidly. Other game types, such as puzzle games, fantasy games, or role-playing games do not have similar effects (although they may influence other types of processing).

Other types of activities in addition to video game play have also been observed to lead to reasonably generalized effects, in particular, musical and athletic training. In the music domain for instance, Schellenberg (2004) assessed the effect of music lessons on IQ. Children from a large sample were 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, Third Edition before and after training. Whereas IQ scores increased in all groups, the largest increases were observed in the two music training groups (an effect that further held in all but 2 of the 12 subtests of the full scale). Rauscher et al. (1997) monitored the spatiotemporal reasoning skills of children (3–4 years old) who were given 6 months of keyboard lessons. Significantly larger improvements in spatiotemporal reasoning were noted in the keyboard-trained children than in two control groups: a computer training group and a no-training group (see also Hetland, 2000). Researchers have also suggested that music training enhances mathematical ability and verbal memory (Gardiner, Fox, Knowles, & Jefferey, 1996; Graziano, Peterson, & Shaw, 1999; Ho, Cheung, & Chan, 2003). Perhaps the best known and most popularized effect related to music is the so-called "Mozart effect" (Rauscher, Shaw, & Ky, 1993), wherein listening to only 10 min of a Mozart sonata was found to lead to significant increases in IQ. Unfortunately, in addition to proving difficult to consistently replicate (Fudin & Lembessis, 2004; McCutcheon, 2000; Rauscher & Shaw, 1998; Steele, Brown, & Stoecker, 1999), this effect does not constitute true learning, as any positive effects last only a few minutes, potentially as a result of short-term arousal or mood changes (Thompson, Schellenberg, & Husain, 2001).

In the athletic domain, Kioumourtzoglou, Kourtessis, Michalo-poulou, and Derri (1998) compared athletes with expertise in various games (basketball, volleyball, and water polo) on a number of measures of perception and cognition. The experts demonstrated enhancements (compared with novices) in skills that are intuitively important to performance in their given games. Basketball players exhibited superior selective attention and eye–hand coordination, volleyball players outperformed novices at estimating the speed and direction of a moving object, and water polo players had faster visual reaction times and better spatial orienting abilities. Several groups have observed similar sports-related differences in the Posner cueing task (Lum, Enns, & Pratt, 2002; Nougier, Azemar, & Stein, 1992), and Kida, Oda, and Matsumura (2005) demonstrated that trained baseball players responded 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, showed no enhancements in a simple reaction time task ("press the button

when a light turns on"). In the future, training studies that establish the causal effects of athletic training would be highly beneficial.

In addition to enhancements as a result of experience with specific sports, a rapidly growing body of work suggests that aerobic exercise of any sort may benefit a range of cognitive abilities, particularly in older persons, with consistently positive results having been found in many cross-sectional studies (i.e., comparing individuals who normally exercise with those who do not). Positive effects have been documented on tasks as varied as dual-task performance or executive attention/distractor rejection (for recent reviews, see Colcombe & Kramer, 2003; Hillman, Erickson, & Kramer, 2008; Kramer & Erickson, 2007). Unfortunately, as is true in the video game and music literatures, many experimental studies in this literature either have not included a control condition (Elsayed, Ismail, & Young, 1980; Stacey, Kourma, & Stones, 1985) or have included control conditions where the groups were not matched in terms of experimenter involvement (Hawkins, Kramer, & Capaldi, 1992). Furthermore, results in this literature are not always in agreement, with some groups showing positive results (Dustman et al., 1984; Hawkins et al., 1992) and others failing to show such effects (Blumenthal et al., 1991; Hill, Storandt, & Malley, 1993). Yet, several recent reviews and meta-analyses (Colcombe & Kramer, 2003; Etnier, Nowell, Landers, & Sibley, 2006; Hillman et al., 2008; Kramer & Erickson, 2007) have demonstrated that across studies, designs, and dependent measures, older adults that perform aerobic activity exhibit enhanced cognitive performance as compared with those who do not. This point finds support beyond behavioral measures, as aerobic fitness has also been linked with neuroanatomical and neurophysiological changes, including increased gray matter volume in the prefrontal and temporal areas (Colcombe & Kramer, 2003); changes in cerebral blood volume in the hippocampus (Pereira et al., 2007); and functional brain activity in a variety of areas, including superior parietal areas and the anterior cingulate cortex (Colcombe et al., 2004). Taken together with the mounting evidence that proper nutrition facilitates cognitive abilities (see Gomez-Pinilla, 2008, for a thorough review), the emerging picture confirms the old saying "mens sana in corpore sano [a healthy mind in a healthy body]."

In addition to the types of everyday experience outlined above, several groups have developed training regimens specifically designed to improve cognitive abilities, targeting, in particular, aging baby boomers and older adults. Small and large companies have been attracted to this high potential market, including Nintendo, with the BrainGames series, and smaller companies like the one developing POSIT (Mahncke, Bronstone, & Merzenich, 2006), to cite only a few. These training regimens typically use a variety of standard psychological tests, meaning that individuals are asked to perform small tests that are highly similar in content and structure with tests used on psychological assessment scales (e.g., list learning to enhance semantic memory, pattern identification to enhance visual form recognition, visual search to enhance the efficiency of visual attention, matching easily confusable consonant–vowel–consonant words to enhance appropriate use of inhibitory mechanisms, n-back tasks to increase working memory abilities). These regimens have shown clear improvements in abilities specific to those trained as well as maintenance of those gains from 3 months (Mahncke, Connor, et al., 2006) to 5 years (Willis et al., 2006). A main issue for future work remains the extent to which these gains

generalize outside of the laboratory situation to improve the everyday life of the participants. Evidence for substantial transfer effects between training and testing has been elusive thus far. The training paradigm used by Mahncke, Connor, et al. (2006) resulted in improvements in an untrained auditory memory task, and one version of the paradigm used by Willis et al. (2006) resulted in self-reported reductions in the difficulty of complex home activities such as meal preparation and shopping. Winocur et al. (2007) reported more substantial transfer to untrained tasks applicable to real-life situations; however, the use of a no-intervention control group leaves the interpretation of their effects open (particularly given the extensive and highly personal interactions that occurred between the experimental group and experimenters). As is the case in the field of brain plasticity, the greatest effects of training are observed on tasks that most closely mirror the trained task, with transfer of gains to other skills or to everyday competence rarely documented.

It is interesting to note one key difference between the "natural" training regimens discussed above (sports, music, video games) and those that have been designed for the specific purpose of brain training. The natural training regimens are exceedingly complex and tap many systems in parallel. In video games developed for entertainment, for instance, one may be simultaneously engaged in memory tasks (e.g., spatial memory for the route to the enemy fortress, semantic memory for weapons at one's disposal or enemies still active), executive tasks (e.g., resource and weapon allocation, dual tasking), visual attention tasks (multiple object tracking, distractor rejection), visuomotor tasks (e.g., steering, piloting), and rapid object recognition, to cite just a few. The same need for highly parallel processing across domains is prevalent in athletics and, to varying degrees, in learning to play a musical instrument. Conversely, when researchers have designed training regimens for the purpose of brain/cognitive training, they have purposefully separated these tasks or domains. The training is typically broken down into subdomains, with semantic memory being trained entirely separately from inhibition control, which, in turn, is trained separately from speed of processing. The existing research suggests that such blocked learning leads to faster learning during the acquisition phase, yet it can be detrimental during the retention phase, leading to less robust retention and to lesser transfer across tasks (Ahissar & Hochstein, 2004; Schmidt & Bjork, 1992). For example, Clopper and Pisoni (2004) asked two groups of participants to classify sentences according to the dialect region of the speakers' native region. A first group of participants was trained with each dialect being represented by a single speaker. A second group of participants was trained with three different speakers for each dialect. The group that received the more variable training learned more slowly initially but was more accurate in a retention test involving new speakers with new sentences.

Mechanisms of Learning

Learning mechanisms surely vary in their specific implementation across different perceptual and cognitive domains. Learning to recognize faces or to speak seems effortless and occurs naturally during the course of development; in contrast, learning to read has to be taught in an explicit fashion. However, it remains that some mechanisms of learning appear to be shared across domains. Their

further characterization will be critical to our general understanding of learning principles.

The reverse hierarchy theory, which was initially proposed by Ahissar and Hochstein (2004) to account for learning in the perceptual domain, has such general appeal. The authors hypothesized that information flows in a feed-forward manner through hierarchically organized structures, with information at the lower levels of processing decaying as information flows upward. Yet, if information at the higher level is insufficient to sustain task performance, feedback searches can be initiated downward in the hierarchical structure to locate the most informative levels of representation. In short, this view holds that learning is a top-down guided process, wherein learning occurs at the highest level that suffices for the given task. Specificity of learning and the degree of generalization are naturally accounted for in this framework. Tasks handled at high levels of the hierarchical organization will demonstrate transfer of learning. Tasks that require backward searches and lower levels of representation will lead to highly specific learning. Although originally designed to account for results in the perceptual learning literature, the reverse hierarchy model captures many features of learning beyond those in the field of psychophysics. Recently, the model has been successfully applied to the field of word recognition and sentence processing (Ahissar & Hochstein, 2004). It also naturally predicts the fact that variability in learning experience will result in less extensive learning during the acquisition phase but larger transfer to new tasks during retention tests. Furthermore, the model predicts that tasks that require very low-level representations will show less generalization of learning than those that rely on higher levels of representation. A potential weakness of reverse hierarchy theory is that it has not always been easy to predict, from the study design, which level of processing will be the highest one sufficient to carry out the task (and without such clear a priori predictions, the argument can quickly become circular). As the hierarchical level at which learning occurs and the amount of generalization are difficult to manipulate independently, validation of the theory is still pending.

Other models of complex human learning, such as those derived from connectionism or machine learning, also provide clues about the general mechanisms of bottom-up learning. Much is based on inferring the statistical structure of the world with which the learner is faced. Recently, the framework of Bayesian inference has been proposed to provide a good first-order model of how participants learn to optimize behavior in dynamic complex tasks, whether 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). More generally, the field of reinforcement learning has been instrumental in promoting the development of general principles for learning rules and providing clues as to the factors that promote learning transfer. The determinants of learning discussed below are largely inspired from this work.

Determinants of Learning and Learning Transfer

As a whole, the literature on the effects of video game, music, and sports experience demonstrate that general learning is possible. However, each of these training regimens is exceedingly complex and differs from traditional training regimens in many ways. A major challenge for future work is to pinpoint what aspects or combination of aspects inherent to these activities is responsible for enhancement in learning and learning transfer. This point is exceedingly important, both theoretically, in terms of designing models of human learning and behavior, and practically, for those seeking to devise rehabilitation paradigms to ameliorate daily life (Schmidt & Bjork, 1992). Fortunately, on the basis of the literatures from a variety of somewhat disparate fields, there are characteristics inherent to these complex training regimens that seem more likely to be at the root of the observed enhancements than others. We discuss these characteristics from the vantage point of video games, but musical and sports training also embody these characteristics to some extent.

Task Difficulty

The principle of utilizing small incremental increases in task difficulty is implicit in nearly every video game. As players progress through levels, they learn new skills and techniques that allow the player to master game circumstances that would have been impossible at the game outset. In our own work on video game training, we have acknowledged this principle explicitly, by advancing players to the next level of difficulty during training only when they have demonstrated sufficient mastery of their current level (Green & Bavelier, 2006a, 2006b, 2007). Similarly, albeit with barn owls rather than human participants, Linkenhoker and Knudsen (2002) demonstrated that adult barn owls could adjust to sizable shifts in visual experience (using prism goggles) when the shifts were made in small enough increments. In contrast, large shifts led to no learning in these adult barn owls. The idea of manipulating task difficulty appropriately has also been noted by Sireteanu and Rettenbach (1995, 2000) and Ahissar Hochstein (2000). Ahissar and Hochstein (2004), in particular, have remarked upon the conditions of difficulty in which learning seems to transfer most. Their basic task involved asking participants to view arrays of oriented lines and to determine which contained a single oddly oriented line. This task can be made arbitrarily difficult by limiting exposure time as well as the time between exposure and a subsequent mask. With practice, the time between target and mask onsets that could be tolerated by the participants decreased substantially. Interestingly, when the task was started at a difficult level (short times between target and mask, small difference in orientation between oddball and background, and/or greater eccentricity), learning was slow and specific for the trained orientation and location. When the task was made easier (in particular by starting with long intervals between stimulus and mask), learning progressed quickly and transferred to novel orientations. In the same vein, Liu and Weinshall (2000), using much the same motion direction discrimination paradigm as Ball and Sekuler (1982), where no transfer was observed, demonstrated that learning an "easy" discrimination (discrimination of 9° of motion direction rather than 3°) transferred substantially to novel orientations.

Motivation and Arousal

The concept of setting a proper task difficulty leads to the consideration of additional factors that could potentially influence the outcome of training: motivation and arousal. Whereas motivation and arousal have been largely (if not completely) ignored in the field of skill learning (but see Ackerman & Cianciolo, 2000; Ackerman, Kanfer, & Goff, 1995), these factors have been and continue to be actively considered in social psychology, education, and many other fields concerned with learning. For instance, motivation is a critical component of most major theories of learning in these fields, with motivation level being posited to depend highly on the individual's internal belief about his or her ability to meet the current challenge. Vygotsky's (1978) "zone of proximal development" corresponds well with the skill learning literature discussed above. 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 no learning will ever occur if the task is too difficult or too easy (Amitay, Irwin, & Moore, 2006; Seitz & Watanabe, 2003; Watanabe, Nanez, & Sasaki, 2001), but learning rate should be at a maximum when the task is challenging, yet still doable.

Like motivation, arousal is at the heart of many learning theories in the social sciences, but for the most part has also been overlooked in the field of skill learning. Although it is difficult to find a consistent operational definition for the term (Anderson, 1990; Neiss, 1988), *arousal* is often thought of as an abstract construct encompassing a variety of processes, including those that mediate alertness and wakefulness, and has been defined in terms of autonomic responses (e.g., changes in heart and breathing rate, pupil dilation, changes in skin conductivity), neurophysiological responses (e.g., activity in the reticular formation, as well as in cholinergic ponto-mesencephalic, noradrenergic locus coeruleus and dopaminergic ventral mesencephalic neurons), and/or behavioral responses (e.g. increased attentiveness). The term *arousal* is also often treated as being synonymous with the stress response (i.e., fight or flight), although some authors have proposed distinctions between the two (e.g., that stress only occurs when task demands exceed an individual's ability; see Westman & Eden, 1996). Video games are known to strongly elicit both the autonomic responses (Hebert, Beland, Dionne-Fournelle, Crete, & Lupien, 2005; Segal & Dietz, 1991; Shosnik, Chatterton, Swisher, & Park, 2000) and the neurophysiological responses (Koepp et al., 1998) characteristic of arousal, with these responses constituting a subjectively salient difference between traditional learning paradigms and video games. The Yerkes–Dodson law (Yerkes & Dodson, 1908) predicts that learning is a U-shaped function of arousal level. 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 is some level of arousal that leads to a maximum amount of learning, which no doubt differs greatly among individuals. In light of this theory, it is interesting to note that the level of arousal in standard skill learning paradigms is almost certainly toward the very lowest end of the spectrum, which again predicts very low amounts of

learning, whereas action video games, for example, likely lead to a much more optimal level of arousal and thus greater amounts of learning. In this vein, although again investigated with owls, Bergan, Ro, Ro, and Knudsen (2005) observed that owls who were forced to hunt (an activity that involves motivation and arousal, as well as reward, which is discussed subsequently) while wearing displacing prisms demonstrated significant increases in accuracy compared with owls who wore the prisms for the same period of time but were fed dead prey.

Feedback

Another possible factor in learning is feedback and the utility of rewards (of which motivation and arousal are likely to serve at least partially as functions). The exact role that feedback plays in learning is a subject of much debate within the field. Numerous examples have demonstrated that feedback is necessary for learning (Herzog & Fahle, 1997; Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006), whereas many counterexamples have demonstrated that feedback is not necessary for learning (Amitay et al., 2006; Ball & Sekuler, 1987; Fahle, Edelman, & Poggio, 1995; Karni & Sagi, 1991). Complicating matters is that even when experimenter-generated explicit feedback is not provided, if above-threshold stimuli are used, participants will nevertheless have varying degrees of confidence that their response was correct, which could act as a de facto feedback signal (Mollon & Danilova, 1996). Whereas 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 signal 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 even if feedback is given only after a series of actions has been completed. The latter case is most analogous to action video games where feedback (typically in the form of killing an opponent or dying oneself) becomes available only at the conclusion of a very complicated pattern of actions. How best to solve this credit assignment problem and how this affects the generality of what is learned is a topic of ongoing research in the field (Fu & Anderson, 2008).

Whereas the role of feedback has been studied extensively (if not to any conclusive end), the effect of the utility of the feedback has been largely overlooked (but see Seitz & Dinse, 2007). *Utility,* a term most commonly used in economics, describes the relative desirability of a reward, thereby explicitly recognizing the idea that the same physical reward is not necessarily worth the same amount to every person. In fact, there is a large amount of variability in the utility of given rewards, both between participants and even within participants (for instance, the utility of an energy bar depends on both the individual's like or dislike of energy bars as well as their current level of hunger). There is a wealth of evidence in the neurophysiology literature demonstrating that the brain systems thought to convey the utility of reward, such as the ventral tegmental area (VTA) and the nucleus basilis (NB), play a large role in producing plastic changes in sensory areas. In particular, when specific auditory tones are paired with stimulation of either the VTA (dopaminergic) or the NB (cholinergic), 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 these same areas have been shown to be extremely active when individuals play action video

games. For instance, Koepp et al. (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. How areas involved in the processing of reward play into learning and neural plasticity will continue to be an area of active research.

Variability

The final key factor in ensuring flexible learning that we discuss is variability in task and input. Variability is important at both the level of the exemplars to be learned and the context in which they appear (Schmidt & Bjork, 1992). For example, participants learn to recognize objects in a more flexible way if the objects are presented in a highly variable context (Brady & Kersten, 2003), which forces participants to extract more general principles about object category (rather than focusing on specific features that may be dependent on viewpoint, lighting conditions, etc.). 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, which are 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; Newport, & Aslin, 2008).

Conclusion

The capacity of the human brain to learn and adapt is unequalled. This review touched on only a few of the hundreds of skills in which significant learning has been well established. Yet, learning is typically so specific to the learned skill that it shows little generalization to related tasks or new environments, limiting the practical impact of the learning so potently demonstrated in the laboratory. This specificity of learning is a major obstacle to the design of efficient rehabilitation paradigms, whether they are targeted to overcoming deficits related to injury or to slowing/reversing the normal declines associated with aging.

Recently, several types of experience, including action video game experience, musical training, and athletic training, have been shown to lead to quite widespread effects on perception, motor skills, and cognition. Although these experiences are exceedingly complex, they offer new insights as to what differences between these and traditional methods of training/testing are most critical for the differences in learning outcome and, in particular, generalization of learning.

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