



Perceptual learning: Top to bottom



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ABSTRACT

Perceptual learning has traditionally been portrayed as a bottom-up phenomenon that improves encoding or decoding of the trained stimulus. Cognitive skills such as attention and memory are thought to drive, guide and modulate learning but are, with notable exceptions, not generally considered to undergo changes themselves as a result of training with simple perceptual tasks. Moreover, shifts in threshold are interpreted as shifts in perceptual sensitivity, with no consideration for non-sensory factors (such as response bias) that may contribute to these changes. Accumulating evidence from our own research and others shows that perceptual learning is a conglomeration of effects, with training-induced changes ranging from the lowest (noise reduction in the phase locking of auditory signals) to the highest (working memory capacity) level of processing, and includes contributions from non-sensory factors that affect decision making even on a “simple” auditory task such as frequency discrimination. We discuss our emerging view of learning as a process that increases the signal-to-noise ratio associated with perceptual tasks by tackling noise sources and inefficiencies that cause performance bottlenecks, and present some implications for training populations other than young, smart, attentive and highly-motivated college students.

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1. Introduction

The brain is a noisy machine. Single-neuron, as well as neural-network dynamics are subject to both deterministic and random noise originating from processes that span the range from the molecular to the systemic (review in Faisal, Selen, & Wolpert, 2008). The concept of internal noise is fundamental to our understanding of how the brain encodes sensory stimuli, processes them and makes behaviorally relevant decisions about them. Signal detection theory (Green & Swets, 1966; Macmillan & Creelman, 2005) describes perceptual decision making in terms of the relationship between noisy decision variables (derived from noisy internal representations of the stimulus) and a subjective decision criterion. Internal noise therefore limits the accuracy of perceptual decisions and consequently of any behavioral task performance.

Dosher and Lu (2005) first suggested that perceptual learning is “learning the limiting process”: inducing changes in those processes that act as bottlenecks to performance. These changes can manifest as an increase in the signal-to-noise ratio (SNR) due to signal enhancement (Gold, Bennett, & Sekuler, 1999; Gold, Sekuler, & Bennett, 2004; Hurlbert, 2000; Wright, 1996) and/or internal noise reduction (Dosher & Lu, 1998, 2005; Jones et al., 2013; Lu & Dosher, 2008), but they can also reflect changes in non-random inefficiencies such as response bias.

In this paper we expand the idea of perceptual learning as reducing the internal noise and inefficiencies responsible for processing bottlenecks. Models based on signal detection theory do not conceive of internal noise as being of specifically sensory origin or limited to the ascending neuronal pathways or networks associated with early sensory encoding. Physiological maskers such as breathing, heartbeats and blood flow (Shaw & Piercy, 1962; Soderquist & Lindsey, 1971), as well as fluctuations in attention, motivation, memory, or other factors related to the decision process may all limit decision accuracy. Even fluctuations of unknown origin in resting state activity may modulate variations at various stages of perceptual processing (Fox et al., 2007, 2006).

The source of the performance-limiting noise depends on what is being trained and what differs between tasks. Learning can thus be a high- or a low-level phenomenon, depending on the level at which the noise originates. What is learned in a given task may depend on the specific training conditions, as performance bottlenecks may be defined by task- as well as stimulus-related

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variables, among others. Moreover, we suggest that learning transfers to untrained tasks if and when both training and transfer task are subject to the same performance-limiting noise sources (see also McGovern, Webb, & Peirce, 2012). Conversely, different limiting processes affecting the trained and transfer tasks will result in specificity (i.e. non-transfer).

This paper presents evidence from our own work in the auditory domain as well as from previous work in the visual domain in support of this hypothesis. Using simple acoustic stimuli and varying task and stimulus parameters, we show that perceptual learning involves changes in internal noise sources and inefficiencies at multiple processing levels along the decision-making pathway.

2. Perceptual learning: bottom-to-top

We use a perceptual decision model (Fig. 1) adapted from Pelli (1991) and Doshier and Lu (1998, 1999) to illustrate the levels at which internal noise may limit processing. For simplicity, we separate internal noise into processes that directly impact on sensory processing and affect the internal representations of input stimuli (hence 'sensory' internal noise, Fig. 1A), later processes that affect the formation of the decision variable (Fig. 1B) and most likely originate in higher-level, cognitive processes (e.g., comparison mechanisms relying on working memory), and other sources of inefficiency affecting the decision-making process such as

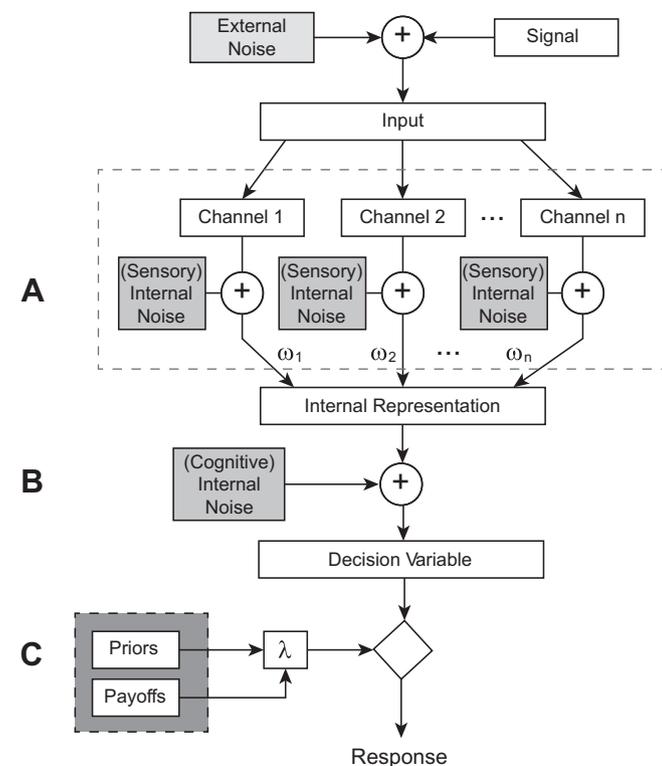


Fig. 1. A schematic perceptual decision model. The input to the system is a combination of the signal and external noise. This input is transformed into an internal representation by summing over the weighted outputs of n independent information channels, which are subject to internal noise (multiplicative, additive, or both; (A)). Note that the label 'sensory' here does not refer to the source of the noise but rather to the type of processing affected by it. In forming the decision variable the internal representation may be further affected by late internal noise (B), which is generally of cognitive origin. To make a decision the observer compares the decision variable to a criterion, λ , which may or may not be ideally placed, e.g. due to bias (C). Other sources of internal noise, such as physiological noise (e.g. heartbeat, breathing) or inattention are not explicitly included in this model.

response bias or inattention (Fig. 1C). We are only concerned with noise intrinsic to the observer (or listener); learning in the presence of external noise has been discussed extensively elsewhere (e.g., Doshier & Lu, 2005; Vaina, Sundaeswaran, & Harris, 1995), and is outside the scope of this paper.

Computational models have been used to gain insight into the underlying mechanisms of learning and transfer. Although internal noise is integral to these models (Sperling, 1989), they are rarely concerned with the source of that noise, only its effect on decision making (c.f. Lu & Doshier, 2009). In this paper we focus on how noise of various origins can place limitations on sensory and cognitive processes and how it is affected by training, rather than its computational implementation. In separating noise sources into 'sensory' and 'cognitive', we follow in the footsteps of other authors (e.g., Durlach & Braida, 1969; Oxenham & Buus, 2000; Shinn-Cunningham, 2000), though we use these labels to refer to the processes affected rather than the specific sources or origins of noise. Thus, early 'sensory' noise can result from modulation by higher-level, cognitive processes. We provide evidence here that training can affect internal noise and sources of inefficiency throughout the processing hierarchy.

2.1. Noise affecting sensory representations or their readout

We define sensory noise as variability associated with the early sensory processing leading to the formation of the internal representation of the stimulus (Fig. 1A). Sensory internal noise can be intrinsic to the physiological processes along the ascending processing pathways. In the auditory domain its sources include (but are not exclusive to) non-deterministic transduction (e.g., due to Brownian motion of cochlear hair cells; Denk, Webb, & Hudspeth, 1989), and stochastic neural encoding and transmission both in the auditory periphery (Javel & Viemeister, 2000) and more centrally (e.g., Vogels, Spileers, & Orban, 1989). Moreover, top-down processes modulate auditory sensory processes as far down the neural hierarchy as the sensory epithelium and even affect middle-ear muscle activity (e.g., Maslin et al., 2013; Munro, Walker, & Purdy, 2007), and these too may contribute noise to sensory processes (see Amitay, 2009 for a discussion of the interaction between top-down and bottom-up processing in auditory learning).

How the channels described in the model (Fig. 1A) are conceived depends on the task and the level of analysis. For example, in a yes/no detection task each channel may be a frequency-tuned filter, in which case the internal representation corresponds to activity summed across spectral regions. The internal noise associated with individual channels is of sensory origin. Alternatively, each channel may represent temporal bins, such as observation intervals in a multi-interval forced-choice task. However the channels are defined, each weight, ω , indicates the relative degree to which the corresponding channel informs the decision process. As such, $|\omega|$ may be a metric of the amount of relevant information in the individual channels (bottom up) present in each presentation interval (or spectral region) or how much attention the listener pays to that interval or aspect of the physical input. Attentional fluctuations (Faisal, Selen, & Wolpert, 2008) or variations in resting state activity (e.g., Fox et al., 2007), may differentially affect sensory processing in individual information channels.

Internal noise affects sensory processing at very early stages. We have recently demonstrated (Amitay et al., 2013) that variations in the internal representation of identical input stimuli (1-kHz tones) can drive the decision process in an odd-one-out task (Fig. 2A). We showed that electrophysiological activity variations, observed as early as 100 ms after stimulus onset and associated with sensory encoding (N1–P2 complex), can predict the perceptual decision (Fig. 2B). These variations may have reflected noise of sensory origin or random fluctuations in attention during the

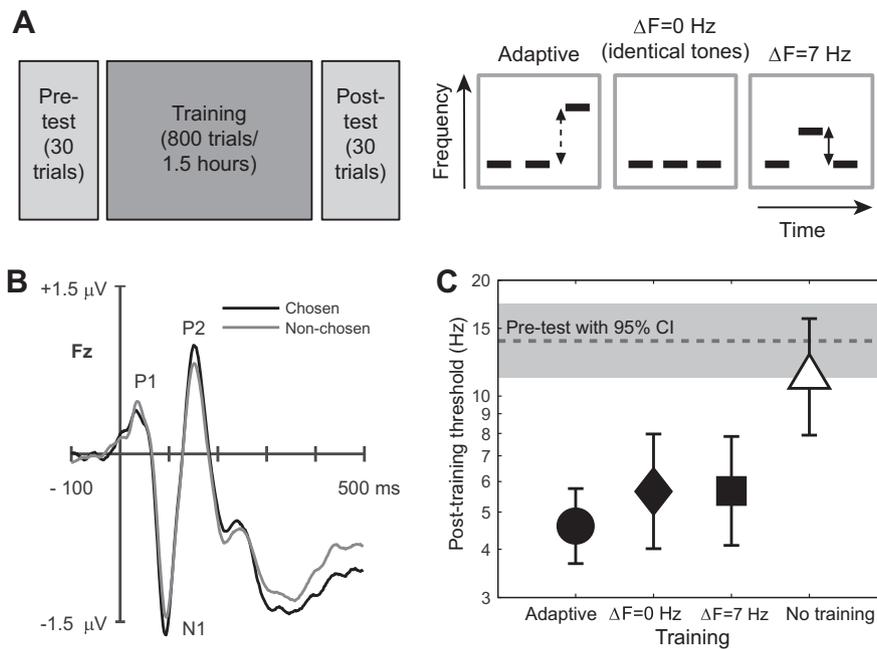


Fig. 2. Learning an impossible discrimination task. (A) Thresholds on a 3-interval, 3-alternative forced choice frequency discrimination task were assessed before and after a training phase lasting 800 trials (about an hour and a half). During training, listeners were asked to pick the odd-one-out of the 3 tones presented successively. One group trained on a task where the frequency difference between the standards and target varied adaptively (aimed at 79% correct). A second group trained on an impossible, identical-tone task in which all tones had a frequency of 1 kHz. A third group trained on a difficult task in which the target tone had a physical difference of 7 Hz from the two 1-kHz standards, and a fourth group acted as a no-training control. (B) Event-related potentials (ERPs) recorded during the performance of the impossible discrimination task showed larger amplitudes for the tones perceived to be “different” as early as the auditory N1 (~100 ms post-stimulus onset), considered to reflect early stimulus encoding. Midline frontal electrode Fz shown here (adapted from Amitay et al., 2013). (C) Training on the impossible task resulted in robust learning similar to that produced by training with actual frequency differences, either adaptively varying from easy to difficult or constant. Post-test thresholds are adjusted for variations in individual pre-test thresholds. Error bars denote 95% confidence intervals. Dashed line with grey area represent mean of sample pre-test thresholds with 95% confidence interval (adapted from Amitay, Irwin, & Moore, 2006).

multi-interval, forced-choice presentation. Moreover, such internal noise was sufficient to drive perceptual learning. Learning occurred on the same ‘odd-one-out’ frequency discrimination task in which the tones were physically identical (an impossible task; Amitay, Irwin, & Moore, 2006), and was no different in magnitude than learning produced by either adaptive training or training with a constant but very small frequency difference (Fig. 2C). Thus, discrimination learning can occur in the absence of an external signal on which to base a discrimination decision, suggesting these decisions are made based on variations produced by internal noise. Indeed, in modeling these data based on signal detection theory Michéyl, McDermott, and Oxenham (2009) showed that internal noise can in principle produce sufficiently large perceptual differences between successive presentations of the same tone to drive the decision, and hence may produce perceptual learning that is no different from “normal” learning under a very difficult condition with an actual physical difference (e.g. a 7 Hz difference, Fig. 2C).

Doshier and Lu (2005) observed that training with noisy visual displays resulted in learning that did not transfer to non-noisy (clear) displays, whereas training on clear displays resulted in transfer to the noisy displays. They reasoned that in the noisy displays it was the external noise in the stimulus that limited processing, and therefore performance improvements resulted from improved exclusion of external noise, which could not benefit displays in which no external noise was present. On the other hand, in clear displays the limitation is engendered by internal noise, and training induced reduction in this limiting factor subsequently benefitted processing in both clear and noisy displays.

There is no consensus in the visual literature on whether learning-related changes are due to internal noise reduction or improved processing efficiency, the latter constituting a systematic

rather than random limitation on performance (see Berg, 2004). The work of Gold, Bennett, and Sekuler (1999) and Gold, Sekuler, and Bennett (2004) in face and texture identification suggested that it is improvements in encoding efficiency (or ‘stimulus enhancement’) that underlie learning (see also Chung, Levi, & Li, 2006). In the ‘perceptual template’ model proposed by Doshier and Lu (1998, 1999) there is no distinction between signal enhancement and internal noise reduction (i.e., they are mathematically equivalent; see Lu & Doshier, 2009), but it is theoretically possible to separate contributions of the two mechanisms to learning.

Jones et al. (2013) have recently shown that internal noise can be reduced through training on a 2-interval, 2-alternative forced choice pure-tone frequency discrimination task. Each observation interval was considered a channel (Fig. 1A), affected by equal amounts of internal noise. Several different techniques were then used to extract measures of internal noise and weighting efficiency. Following the work of Gold, Bennett, and Sekuler (1999) we used model-fitting (Jesteadt, Nizami, & Schairer, 2003) and n-pass consistency (Green, 1964). In addition, a signal detection theory-based model was used to derive an encoding efficiency measure, which was also estimated using a novel classification boundary measure (for details of the methods see Jones et al., 2013). Changes in internal noise measures were significant across training for all methods (Fig. 3A), but weighting efficiency did not change significantly (Fig. 3B). Although the behavioral measures used precluded establishing the source(s) of internal noise affected, neural-network simulations based on these data suggested that noise reduction was achieved through reweighting the frequency specific channels affecting early sensory representations (Jones et al., 2013). These results are consistent with conclusions from learning of visual tasks (Lu & Doshier, 2009).

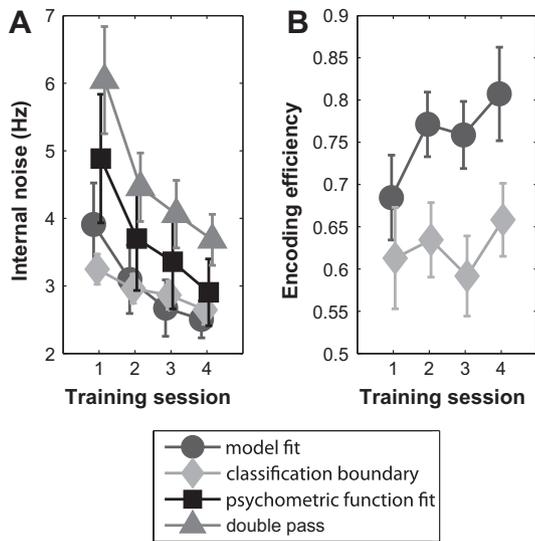


Fig. 3. Training-induced changes in internal noise in a pure-tone frequency discrimination task. (A) Internal noise was reduced across 4 sessions of 1600 trials when estimated using model fitting ($p = 0.007$), psychometric functions based on signal detection theory ($p < 0.001$), double-pass consistency ($p < 0.001$) and classification boundary ($p = 0.001$). (B) Encoding efficiency did not change significantly with training, estimated with either model fitting ($p = 0.080$) or classification boundary ($p = 0.60$). Error bars denote s.e.m. Adapted from Jones et al. (2013).

The remarkable specificity of visual learning to the trained stimulus and task parameters (e.g., Ahissar & Hochstein, 1996; Ball & Sekuler, 1987; Fahle, 1997; Fiorentini & Berardi, 1980) has led researchers to suggest learning involves modification of stimulus-specific representations (e.g., Karni & Sagi, 1991). However, the current consensus, owing in large part to the extensive modeling work of Doshier and colleagues (Liu, Lu, & Doshier, 2010; Lu, Liu, & Doshier, 2010; Petrov, Doshier, & Lu, 2005, 2006), is that learning involves task-specific reweighting of the connections between early representations and the decision variable. These models are compatible with transfer of learning when the trained and transfer tasks share the most informative neuronal representation (e.g., Webb, Roach, & McGraw, 2007), that is, the same ‘channels’ are weighted similarly to support either task. A recent updating of the model, the ‘integrated reweighting theory’ (Doshier et al., 2013), is able to account for learning transfer across retinal locations (e.g., Dill, 2002), but still unable to account for transfer due to double training – location transfer following practice of different stimuli in a new location (Xiao et al., 2008; Zhang et al., 2010). It is also unclear how these models can support asymmetric transfer (Amitay, Zhang, & Moore, 2012; Mossbridge, Scissors, & Wright, 2008), or a temporal lag of hours or days between learning and transfer (Wright, Wilson, & Sabin, 2010), as has been demonstrated in auditory learning.

Although channel reweighting models have been successful in explaining many aspects of visual learning, they generally discount the possibility that early, sensory internal noise associated with variability in neural firing is reduced through training (Law & Gold, 2009; Petrov, Doshier, & Lu, 2005). Bejjanki et al. (2011), on the other hand, suggest that training can result in direct reduction of low-level sensory internal noise, as early as the thalamo-cortical afferent connections. This view is more compatible with physiological data showing training-induced changes in low-level auditory and somatosensory cortical areas (Recanzone et al., 1992; Recanzone, Schreiner, & Merzenich, 1993).

In a recent study Amitay, Zhang, and Moore (2012) modeled the specific processes that yielded reduction in sensory internal noise in a frequency discrimination training task. We found that training

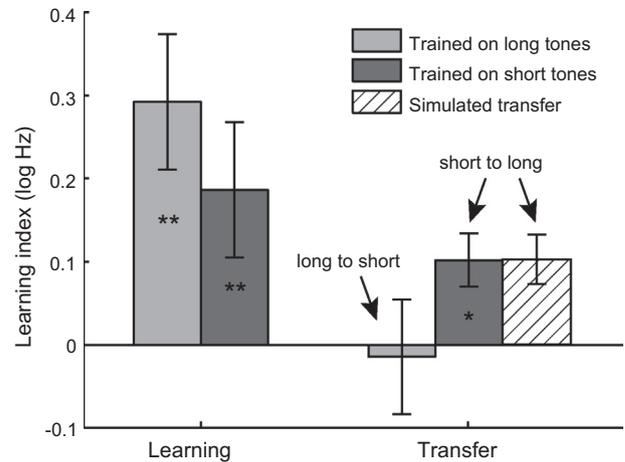


Fig. 4. Learning and transfer on a frequency discrimination task with long and short tones. Listeners had to pick the ‘odd-one-out’ of three successive tones. The frequency of the target tones varied adaptively. One group trained on long (100 ms) tones, and a second on short (15 ms) tones. The learning index is the difference between the pre- and post-training frequency discrimination limits, with the 0-line denoting no change. Significant learning is marked by * $p < 0.05$; ** $p < 0.01$, corrected for multiple comparisons (Bonferroni–Holm). Error bars denote s.e.m. Adapted from Amitay, Zhang, and Moore (2012).

in frequency discrimination of long and short tones resulted in asymmetric transfer: training with short tones transferred to long tones, but not vice versa (Fig. 4). We interpreted these results as follows: although frequency encoding is initially limited by phase-locking noise (due to stochastic neural firing in the auditory nerve) in both long and short tones, the long tones may allow for noise reduction by way of averaging the neural firing across increasingly longer temporal windows. Learning this process could not transfer to the short tones because the initial integration window already exceeded the stimulus duration. With this simple learning process inaccessible, training with short tones may have reduced phase-locking noise by reducing the jitter associated with the actual neuronal firing. Although more demanding than averaging across longer time windows, this limiting process is more general and does not depend on tone duration. Simulations of this learning mechanism accurately predicted the amount of transfer to frequency discrimination with long tones. Although the end result is the same – improved frequency representations by reduction of phase-locking noise – the learned process is different. We thus agree with Doshier and Lu (2005) in interpreting asymmetric transfer of learning as learning different limiting processes; the duration of the shorter tones presented a limitation on frequency processing that precluded increasing the integration time window, a mechanism possible with longer tones. But since the jitter in neural firing presented a limitation on both long and short tones (trained and transfer stimuli), learning to reduce it directly benefitted frequency discrimination regardless of tone duration. Since training on short tones did not enable the use of longer time windows, this particular limiting process was still in place, manifesting as ‘partial’ transfer. We also concur with Bejjanki et al. (2011) that in order to understand learning processes it isn’t sufficient to model ‘internal noise’ as a single mechanism capable of affecting only the readout of early sensory processing.

2.2. Cognitive limitations

Cognitive processes may also present limitations on processing that leads to the formation of a decision variable (Fig. 1B). Both working memory (Baddeley, 1992; Baddeley & Hitch, 1974) and attention (Moray, 1967) are limited capacity systems, and can

therefore create processing bottlenecks. Moreover, evidence suggests that both systems are malleable (Jaeggi, Berman, & Jonides, 2009; Jaeggi et al., 2008). We therefore suggest that cognitive ‘noise’ will act as a performance bottleneck in tasks that place high demands on these systems, and that perceptual learning may reflect lifting of these cognitive constraints.

Law and Gold (2008) showed that perceptual learning of visual motion direction in monkeys was correlated with changes in neuronal responses in the lateral intraparietal area (LIP) involved in attentional control (Bendixby & Platt, 2006; Sereno & Amador, 2006), rather than the middle temporal area (MT) which encodes motion direction. They speculated that these changes represent improvements in the ability to selectively attend to the relevant information in the internal ‘sensory’ representation when forming the decision variable.

Cognitive limitations may be imposed by manipulating the cognitive demands of a perceptual task. One way to increase the cognitive demands of a task is by varying the stimulus on a trial-by-trial basis. In frequency discrimination, roving the base value of the stimulus limits processing and results in higher thresholds and a more protracted learning curve compared to fixing the value of the base (or ‘standard’) stimulus throughout training (Amitay, Hawkey, & Moore, 2005). Moreover, in good listeners (those with relatively good naïve thresholds) such training resulted in an asymmetric transfer pattern, where training on roving stimuli transferred to fixed frequency stimuli but not *vice versa* (Fig. 5A). The limitation in this case is not imposed by the bottom-up processing of stimulus features (e.g., frequency), which are not sensitive to across-trial variation. We can think of at least two cognitive processes that could play a role in limiting performance in this example. Firstly, while discrimination around a fixed stimulus would benefit from selectively attending to one frequency channel, roving the frequency may require shifting the focus of attention between channels or simultaneously monitoring multiple channels. Listeners trained on a high-uncertainty condition may learn to flexibly disengage and re-engage their attention or to expand their attentional spotlight to include several channels. If this were the case, we would not expect the learning to transfer from the roving- to the fixed-frequency condition, because no such flexibility is required to perform the fixed task. Alternatively, roving the frequency may require greater involvement of working memory in updating the memory representations when the uncertainty precludes the formation of a long-term perceptual anchor (Braida et al., 1984). The latter hypothesis is supported by recent data showing that training on roving- but not fixed-frequency

discrimination resulted in an improvement in working memory updating (as measured with a tone n-back task), and training on working memory updating differentially improved roving-frequency discrimination as compared to the fixed-frequency condition (Zhang et al., 2012). These observations point to different limiting processes being learned in roving- and fixed-frequency discrimination. When large demands are placed on working memory updating, learning the limiting process results in improved accuracy for the memory representation used for decision making. Although the demands placed on working memory are lower in the fixed-frequency condition, improved ability to update working memory representations can still benefit it. Conversely, the roving condition could not benefit from the perceptual anchoring process learned in the fixed-frequency condition, giving rise to asymmetric transfer.

That cognitive rather than sensory limitations are involved is supported by the comparison of good and poor listeners on the fixed and roving frequency discrimination (Fig. 5). In poor listeners (Fig. 5B) the difference between fixed and roving frequency discrimination is diminished, suggesting these listeners are poorer at employing a more optimal strategy for performing the fixed-frequency task. This can be either due to wider attentional filters (see Amitay, Hawkey, & Moore, 2005) or an initial inability to employ perceptual anchors (see Ahissar et al., 2006). Based on this pattern of both learning and transfer, ‘poor’ listeners may thus be subject to slightly different cognitive limitations and may be learning different limiting processes.

Training that reduces cognitive limitations is of greater potential benefit than that which affects sensory encoding or decoding. It is likely to transfer more widely to similar tasks and has the potential for far transfer – transfer to very different tasks and between modalities. This potential was demonstrated in visual studies using computer games as training tasks, which showed transfer to improved visual attention on unrelated and untrained tasks (Bavelier & Davidson, 2013; Green & Bavelier, 2003). Moreover, these changes in attention also improved perceptual processing, suggesting the training tapped into processes that limited visual perceptual performance, enabling transfer (Green & Bavelier, 2007).

2.3. Decision inefficiency

Decisions are made by comparing the decision variable to a criterion (Fig. 1C). Limitations can be introduced into the decision process at this stage rather than affecting the internal

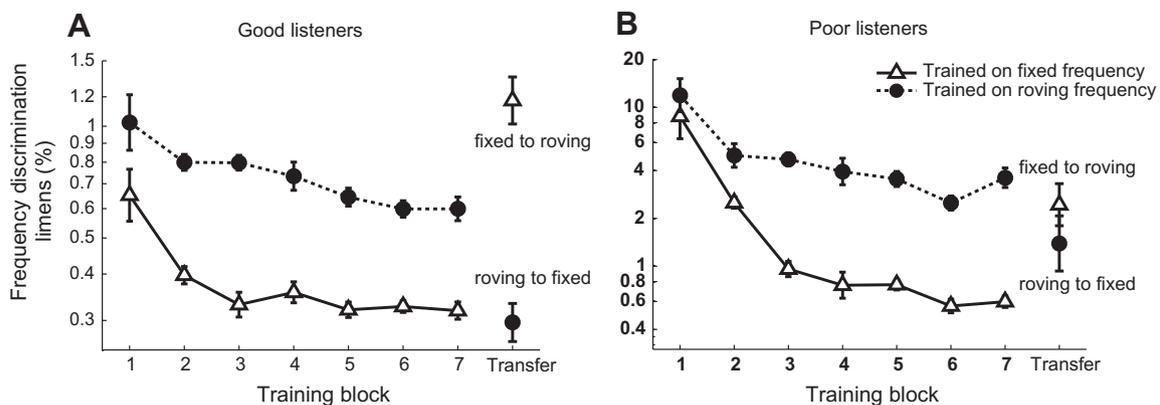


Fig. 5. Learning and transfer on a frequency discrimination task with a fixed- and roving frequency standard stimulus. Listeners were asked to pick the interval that contained the higher-frequency tone in a 2-interval, 2-alternative forced choice experiment. Each training block consisted of 500 trials. (A) In good listeners (defined by thresholds on block 1) discrimination limens (in percent of the standard frequency) were higher (poorer) and learning was slower in the roving frequency condition. However, training on roving frequency stimuli resulted in transfer to fixed frequency stimuli, but not *vice versa*. (B) In poor listeners initial discrimination limens are similar for the fixed- and roving frequency conditions both before and after training. Error bars denote s.e.m., with limens adjusted for individual initial (block 1) performance. Note the difference in y-axis scales in the two panels. Adapted from Amitay, Hawkey, and Moore (2005).

representation or decision variable. We prefer the term ‘inefficiency’ rather than ‘noise’ to describe processing limitations introduced at this stage because, as will become clear below, some of these processes are deterministic rather than random (see Berg, 2004). Bias and inattention are both sources of inefficiency during decision making. Moreover, although decisions and responses are identical in this model, this is not necessarily the case in every perceptual judgment task. For example, motor errors may result in the response deviating from that intended, or the listener may correctly identify the response but forget which key to press.

Bias is the predilection to choose a certain response option over others regardless of the sensory evidence. In terms of the model in Fig. 1, bias is a systematic deviation from the ideal criterion (λ) placement. Since criteria should be placed so as to maximize overall accuracy on the task, bias invariably reduces performance. Bias may occur if, for example, the listener perceives the relative utility (or payoff) of each response outcome to be asymmetric (Maddox & Bohil, 2001), or if they perceive the relative probability of each trial-type occurring to be asymmetric (priors; e.g., Tanner, Haller, & Atkinson, 1967).

Recent computational models in vision have explicitly included both bias control and external feedback (information about the correctness of previous decisions) in modifying the decision unit (e.g., Doshier et al., 2013; Liu, Lu, & Doshier, 2010). The role of the bias control module is to reduce the dependence of decisions on factors induced by the learning context (i.e. extraneous to the perceptual aspects of the task). External feedback can bias the decision criterion directly. Although a wider discussion of the role of feedback in learning is outside the scope of this paper, its role in affecting bias (and subsequently the decision criterion) is reviewed here.

A series of experiments by Herzog and colleagues (Herzog et al., 2006; Herzog & Fahle, 1999) showed criterion shifts can be affected through false or misleading feedback without a concomitant change in perceptual sensitivity. Performance on a vernier acuity task deteriorated rapidly when the decision criterion was biased by trial-by-trial feedback that suggested the offset was opposite of the presented offset (‘reverse feedback’; Herzog & Fahle, 1999). Moreover, the criterion can be simultaneously and independently controlled for several different vernier stimuli at different locations (Herzog et al., 2006), supporting the conclusion that no change in sensitivity has occurred. In effect, the feedback manipulated the ‘payoffs’ (Fig. 1C): listeners “learned” to respond in a way that minimized “errors” regardless of whether they were real errors or not, likely by learning the statistical characteristics of the task (the biased feedback meant that the ratio of left to right “correct” feedback was no longer 1; Aberg & Herzog, 2012). The time-course of these performance ‘improvements’ was also unlike the usually observed changes in perceptual sensitivity: when the feedback was corrected, performance accuracy was quickly regained as the criterion shifted back, suggesting no long-lasting (mis)learning effects (Herzog & Fahle, 1999), and criterion shifts were not retained over a consolidation period (overnight), nor induced by blocked feedback (Aberg & Herzog, 2012).

It is important to note that not all types of false feedback prevent perceptual learning. When positive feedback at chance level is provided randomly in an identical-tone discrimination task, near-normal learning occurs (Amitay, Irwin, & Moore, 2006) despite the feedback being completely uninformative. Learning also occurs when the feedback is well below chance (at 10% in a 3-interval, 3-alternative forced choice task; Amitay et al., 2010). It should be noted that according to the Hebbian reweighting model proposed by Liu, Lu, and Doshier (2010) such learning should not be possible as feedback is crucial for learning when performance is near chance. Current learning models therefore fail to account for learning on this ‘impossible’ training task.

Biases do not have to be artificially introduced into training to affect learning. We have observed a preference for one response over another in a yes-no amplitude-modulation detection task (Ratcliffe et al., 2012). In a 1-interval forced choice task listeners were asked whether the tone they heard was modulated or not. In general, listeners were initially liberal, responding ‘yes’ (signal present) more often than ‘no’ (signal absent). They become progressively less biased with training. This change in bias accounts for approximately one third of the improvement observed on the task, suggesting initial thresholds are underestimated. Training-induced changes in bias were demonstrated even in multiple-interval forced-choice paradigms, generally considered to yield bias-free threshold estimates. We have previously shown that response bias in a 3-interval, forced-choice intensity discrimination task can be reduced during training, even in the absence of threshold shifts (Halliday et al., 2011).

Bias can also depend on stimuli and responses in preceding trials. This ‘dynamic’ form of bias also plays a role in learning. In a two-interval forced-choice frequency discrimination task, listeners were more likely to repeat a previously correct response and alternate following an incorrect response (Jones, Moore, & Amitay, 2012). This propensity was reduced (though not completely eliminated) through training.

A further limitation on performance is inattentiveness – lapses in concentration resulting in the listener not perceiving or misperceiving the stimulus, or otherwise rendering the listener incapable of making an informed judgment. It represents a complete departure from the decision process described above. This inefficiency is largely negligible when testing ‘normal’ young adults with the types of task generally used in learning experiments (i.e., where the sets of responses are small and clearly labeled, and where emphasis is placed on the accuracy of responses, rather than speed). For example, Jones et al. (2013) showed that for young adults inattentiveness is negligible and unaffected by training. However, it may be more substantive amongst children (see for example Moore, 2012; Moore et al., 2010) or non-typical populations, and may, under these circumstances, prove to be a limiting process.

3. Development and learning

The proposed view of the learning process has implications for perceptual learning throughout development. Evidence suggests that children suffer from greater levels of internal noise than young adults (Buss, Hall, & Grose, 2006). Sensory- and cognitive processes have different developmental trajectories. The ascending, sensory system is largely mature by the age of 2 years (Moore, 2002) while cognitive functions continue to develop well into adulthood (Moore, 2012). It is therefore likely that most of the differences between child and adult learning lie in cognitive rather than sensory constraints. It seems likely that decision inefficiencies will affect children, though we are not aware of any direct evidence to support that supposition.

Halliday et al. (2008) observed that 6–11 year old children who showed progressive improvement on a frequency-discrimination training task, and achieved adult-like discrimination thresholds, tended to be older and, importantly, more attentive (i.e., having fewer attentional lapses). Banai (2008) has also observed that children showed adult-like frequency discrimination performance by age 8 when tested using an oddball procedure, but children as old as 14 did not show adult-like performance on the same discrimination task when presented in a 2-interval, ‘high-low’ identification procedure. However, since there was no association between elevated thresholds and greater variability in performance (taken as an index of attention), Banai and colleagues concluded that attention is unlikely to be the sole source of

processing limitation. Verbal working memory is one candidate limiting process, shown to be associated with poor auditory perceptual performance in reading-disabled individuals (Banai & Ahissar, 2004). However, Halliday et al. (2008) did not find differences in a working memory measure (digit span) between learners and non-learners.

Thus, children may be learning different limiting processes to young adults. Such learning is also likely to result in different transfer patterns depending on task parameters. We would expect children to benefit more from training targeting cognitive skills, such as increasing sustained and selective attention and working memory. Indeed, Bavelier, Green, and Dye (2010) have argued that computer games may prove to have beneficial side-effects in training a wide skill set. If, as we have argued, these skills also present a greater limitation on perceptual performance in children, they should benefit more from cognitive training than training on perceptual tasks that produce more specific improvements in adults. We should therefore be cautious when applying learning rules derived from training young adults to developmental populations.

A similar argument may be made for learning in older adults, many of whom undergo cognitive and sensory decline, and other populations whose difficulties are associated with sensory and/or cognitive impairments, such as developmental disorders of language (dyslexia, specific language impairment) and attention (attention deficit hyperactivity disorder). For example, it has been suggested that adults with dyslexia are unable to use stable perceptual anchors for frequency discrimination, resulting in differentially worse performance on fixed-frequency than roving-frequency discrimination when compared to normal readers (Ahissar, 2007). Teenagers with reading disability also showed transfer from frequency-discrimination training to improved working memory, suggesting the removal of cognitive-based constraints on perceptual processing (Banai & Ahissar, 2009).

4. Conclusions and implications

The studies described above provide both direct and indirect evidence that perceptual learning involves an overall increase in signal-to-noise ratio which can in large part be attributed to decreasing sensory and cognitive internal noise, as well as improving decision inefficiency. Moreover, they show that, depending on task and stimulus parameters, different noise sources may limit processing even for the same perceptual judgement. Sensory and cognitive noise can independently affect what is learned; what determines the level at which learning occurs depends on the level of the performance bottleneck – the noisy processes that limit performance on the training task. As a direct consequence of this framework, transfer depends on there being the same noise source (or inefficiency) constraining performance in both the trained and transfer tasks.

Finally, we would like to highlight two implications of this hypothesis. From a theoretical perspective, perceptual learning may not be the single process of continuous improvement it is generally considered to be. Learning curves may reflect changes in multiple mechanisms, probably consecutive but possibly concurrent, as they reflect changes in different underlying noise sources. As the initial performance-limiting process is dealt with, other sources may become more influential in limiting performance. This implication suggests that different points along the learning curve may also be associated with different transfer patterns, as these noise sources may be shared with different aspects of other tasks. Thus, transfer and specificity of learning do not depend on the length of practice, *per se* (Jeter et al., 2010), but on the cascade of limitations lifted by training. There is some evidence to support this suggestion. For example, Wright, Wilson, and Sabin (2010) showed that transfer of learning to an untrained task lags behind

learning on the trained task. A possible interpretation of this phenomenon is that learning did not commence with the performance-limiting noise that was shared between the two tasks. Rather, other limitations were lifted prior to the one that could transfer to the untrained task.

From an applied perspective, learning the limiting process has implications for the various commercially available training programs using perceptual tasks to improve cognitive (e.g., Cogmed™; Klingberg et al., 2005) or language outcomes (LACE™; Sabes & Sweetow, 2007; Sweetow & Sabes, 2006) in elderly adults or in children with language impairment (e.g., Fast Forward™; Tallal et al., 1996). The reason the evidence for their efficacy is so inconsistent may lie in the choice of outcome measures, and whether or not they share performance limitations with the training tasks incorporated in the training schedule. What these programs are actually training may be very different from the claims made by their authors. For example, it is possible that Fast ForWord™ does not improve language by lifting the sensory-perceptual constraints on brief and rapidly presented stimuli *per se*, but rather by training the ability to attend to the auditory stimuli or the ability of working memory to update the rapidly changing stimuli. A better understanding of the limiting processes and how training lifts these limitations will help develop and optimize training programs aimed directly at specific difficulties experienced by these populations.

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