

Chapter 7: Integration and Discussion

The central aim of this dissertation was to explore how complex, continuous actions can be learned effectively, given the conflict that exists between exploration and consolidation of different parts of the action. The solution to this problem is partitioning of the action into segments but while the advantages of such partitioning have been studied in theoretical models and machine learning algorithms (Doya, 2000), less is known about the implementation of this solution in animal learning models. Here we studied the learning of zebra finch syllables as a model of continuous action. We found evidence for partitioning of the syllables into segments to which exploratory variability could be applied independently. This implies that error is assessed locally, on the level of sub-syllabic structure. The second problem that arises in learning of continuous action by partition is how to determine the size of segments (granularity). Too many segments (high granularity) would present a burden to the memory, while too few segments (low granularity) would result in the original problem of the conflict between exploration and consolidation.

We will start this discussion with possible neuronal and peripheral mechanisms that could be involved in local modification of the song. So the first question is at what time scales can the known neural substrates regulate exploratory variability.

7.1 Can AFP regulate exploratory variability in short intervals?

It has been shown that anterior frontal pathway (AFP), which is a likely source of exploratory variability (Olivezky, 2005, Andalman, and Fee, 2009), can modify the song locally (Kao et al., 2005).

Micro-stimulating the LMAN (the nucleus of AFP which projects directly to RA in the song production pathway) can trigger highly time-localized and acoustic feature-specific vocal changes in the song of adult birds. A stimulation of a particular *site* in LMAN can generate changes in specific parts of the song (always at the same parts).

On the other hand, the modifications in one part of the song can be qualitatively different from those in another part. For example, micro-stimulations of the same site can increase the fundamental frequency in one syllable but decrease its magnitude in another syllable. Therefore, as this result suggests, the *site* of micro-stimulation in LMAN determines the time-positions of modifications but not necessarily their quality (the direction of modifications). On the other hand, stimulations in different sites in LMAN can have opposite effects in the same syllable. Therefore there are many sites in LMAN that can affect the same time-positions of the song but their effects on the song are qualitatively different.

This opens a question about how can LMAN induce exploration locally. If the same site always modifies the song features in a particular direction then many sites in LMAN should be activated at a particular time. This assembly of LMAN sites should only affect the same, short segment, of the song and thereby induce local exploration. In other words, different assemblies of neurons in LMAN should be assigned to different times in the song. Such organization is reminiscent of the RA, where

different assemblies of neurons are activated by the HVC at different times (Leonardo et al, 2005).

So far we have seen that AFP can modulate the song locally and that recruitment of different neuronal assemblies in LMAN could assign exploration to particular song segments. But whatever the mechanism of recruitment in LMAN is, for AFP to be able to adjust the gain of its output locally during singing, it needs to “know” the exact song time. This timing information could be provided to AFP via the HVC *Area X-projecting neurons*. Area X is the first nucleus in the AFP onto which HVC projects (see Figure 1.2 in Chapter 1). As mentioned in Chapter 1, the HVC produces a very sparse neuronal activity, which is extremely time-locked (Hahnloser et al, 2002).

Although it has been shown that lesions to Area X, which should block this time information, have no obvious overall effect on song structure or on the magnitude of noise (Goldberg and Fee, 2011), it is possible nevertheless that short time-scale modulation in vocal exploration might be gated by Area X (Kojima and Doupe, 2009), or that AFP has other means of generating a song-time dependent signal.

7.2 Can differential sensitivity of RA neurons to AFP input regulate variability at short time scales?

Local regulation of exploratory variability could also be explained by differential sensitivity of RA pre-motor neurons to AFP input, across song elements. Each pre-motor RA neuron receives inputs from several HVC and AFP neurons. As mentioned above, different assemblies of RA neurons are activated at a particular time by HVC, which results in production of time dependent song elements. As a particular song element approaches the target the weight of HVC-RA synapses could increase,

making the synapse less sensitive to the constant gain of variability coming from AFP. The AFP-RA connections are mediated by NMDA receptors, suggesting that the AFPs activity could modulate the HVC-RA synaptic weights (which are mediated by the mixture of AMPA and NMDA receptors).

Disambiguating between the two hypotheses (AFP or differential sensitivity of RA neurons) could be attempted by training birds with our AAAA->ABAB paradigm (Chapter 2) and testing the effect of micro-stimulation from AFP during singing of either syllable A or B, once the highly variable B syllable appears. Such a stimulation should cause brief vocal changes that are song-time specific as in the experiments by Kao et al. (Kao et al., 2005). The prediction is that if the sensitivity of RA neurons to AFP input is higher for the new syllable (B), such stimulation would have a stronger effect if delivered during performance of B. Alternatively, recording from LMAN should show increased activity or less inter-hemispheric synchrony (Wang et al., 2008) when singing B.

7.3 Reinforcement learning of continuous action without segmentation can be effective when the gain of exploratory variability is low

In Chapter 4 we discussed the age dependent reduction of plasticity and the decreasing gain of exploratory variability. As we saw a minimal amount of residual exploratory variability can be used in order to modify the song even at the old age, when song seems “crystallized” (Tumer and Brainard, 2007). This has been shown experimentally in the procedure where a negative reinforcement was used to induce a change the fundamental frequency of short song elements in older birds. We have

noted in Chapter 4 that no evidence was found for the ability of birds to increase their exploratory variability when exposed to negative reinforcement in those experiments. Thus with the ageing the gain of variability seems to only decrease.

Minimal variability in older birds does not cause significant deterioration of the song. Consequently the local regulation of variability may no longer be necessary even when they need to modify very short time-scale song elements in the negative reinforcement experiments.

This finding is further supported by the study by Charlesworth et al in which negative reinforcement is used to effectively induce changes in particular song elements of older birds, *without specifying their time-position*, thereby providing only the global error (Charlesworth et al, 2011). Consider, for example, a song bout with five song elements (A, B, C, D and E). A negative reinforcer (punishment) may be introduced at the end of the song bout if the fundamental frequency of element B is too low. The subject bird will increase the average fundamental frequency (across many renditions) in element B during the training period. In this setting birds can learn to change even multiple song elements (in any direction specified by the experimentalists) with a single negative reinforcer (single global error estimate). Importantly, Charlesworth et al did not observe any increments of variability during learning that could otherwise be expected when a bird is trying to escape the negative reinforcer. Of course, with only global reinforcement provided the variability would have to increase along the entire trajectory of the continuous action. Therefore, one reason for why increased variability was not observed in those experiments could be that such global increment of exploration would cause more deterioration of song structure than in the case when

error can be locally estimated. In any case, the result shows that segmentation of continuous action may not be necessary for learning.

Taken together the role of AFP is to provide exploratory variability signal to the motor pathway (Olivezky et al, 2005) and can maintain residual variability necessary to make short time-scale changes in older birds (Tumer and Brainard, 2007) even when the bird has no access to local error estimation (Charlesworth et al, 2011).

Exploratory variability may also be used in a more “guided” way (Andalman and Fee, 2009) such that noise injected by AFP will bias the exploration in the direction of the target and there is strong evidence that AFP can affect short segments of the song (Kao et al, 2005). What our work adds to this body of knowledge is that in younger birds the exploratory variability can also be locally regulated either directly by AFP or the changes in sensitivity in RA to the AFP input. We have suggested experiments the electro-physiologists could perform in the future to further study the mechanisms of local regulation of vocal exploration. In Chapter 4 we also suggested that experiments with negative reinforcement be performed on younger birds where one could predict more exploration in the parts that need to change.

7.4 Hierarchical learning: increasing granularity of segmentation

As noted in the beginning of this dissertation (Chapter 1) there are two problems in learning of continuous action. The first problem arises from the conflict between exploration and consolidation. This problem can be solved by partitioning the action into segments that can then be learned independently from each other. But this leads us to the second problem, namely, how to determine the sizes of segments. As noted earlier, if the granularity is too high, the burden on the memory becomes too great and

the local error assessment too demanding. If granularity is too low, then within the segments we run into the first problem again (conflict between exploration and consolidation).

The solution to this problem of granularity would be to gradually decrease the size of segments over the course of learning. This way high exploratory variability could be used across broad segments, early in the learning process, when consolidation has lower priority than exploration (because there is not much structure in place yet). Later in development, as some parts of the action are already close to the target (low error), consolidation of these parts becomes the greater priority and exploration becomes confined to only those parts of the action that still need to improve. We refer to this gradual decrement of the segment size (or increment of granularity) as *hierarchical learning*.

While we found some evidence for hierarchical learning in syllabic acoustic structure where syllables appear before the intra-syllabic events (see Chapter 4), a stronger support comes from the analysis of the respiratory pressure patterns (see Chapter 5).

We showed in Chapter 5 that during development of respiratory pressure pulses (EPs), fine temporal structure (high granularity) is added to the pre-existing coarse temporal structure (low granularity). Interestingly, this indication of hierarchical learning was only observed in tutored birds, while in birds that were never exposed to the normal song there was no indication of any increment of granularity. It is questionable if segmentation of the song ever takes place in untutored birds, even

though, as discussed in Chapter 5, over several generations of cultural learning the number of song elements increases as they become shorter.

7.5 Does the partition of song on the level of articulation precede the partition on the acoustic level?

We have seen so far that there are neural substrates that could be involved in partitioning of the continuous action of singing. At what point of song development does the partitioning occur? There is some evidence that the first segmentation of the song into syllables may occur at the level of articulation before it happens in the acoustics (Veit et al., 2011). This study shows that the establishment of precisely timed gaps between expiratory pulses (EPs) in the sub-song may precede the creation of equally well timed gaps between the syllables. However, it is important to remember that syllables are already somewhat discrete units. If we are studying the segmentation of truly continuous actions, then sub-syllabic structure would be more relevant. Sub-song itself is also not a good representative of continuous action in need of segmentation because the gaps must be created anyways for respiratory demands. Therefore even if the timing in respiratory pressure becomes more precise before the timing of acoustic structure, this does not necessarily mean that the segmentation happens first on the level of articulation. In this respect we should look into segmentation within individual EPs (uninterrupted continuous action) and compare it to the acoustic structure. However, as discussed in Chapter 5, the acoustic output is the final product of integration of respiratory, syringeal and beak activity. The imprecision of this integration may result in apparently delayed measurements of refinement on the acoustic level. This was the main motivation to compare activity in

the syrinx itself (EMG) with the respiratory pressure. But as we saw in Chapter 5, there is no apparent lack of synchronicity between developmental changes in the pressure pattern and changes in syringeal EMG activity. Nor has a delay in development of fine acoustic structure behind articulation ever been observed.

In summary, it seems that the partitioning of continuous actions into segments that could be independently evaluated and explored has to happen on multiple levels of the song production. Partitioning of continuous action can improve learning as it resolves the conflict between exploration and consolidation. We have shown that exploratory variability can be regulated locally (Chapters 2 and 4). With learning other problems, such as co-articulatory constraints and “collateral damage” of vocal changes (suggested in Chapter 6) may arise. A possible solution to those problems can be hierarchical learning (presented in Chapter 5) where segmentation of continuous action becomes progressively finer over the course of development.

We hope that our findings will contribute to generating new hypotheses about neuronal mechanisms of learning of continuous actions that could be tested by electro-physiologists in birdsong as well as in other fields.