SHORT- AND LONG-TERM CHANGES IN ATTENTION, MEMORY AND BRAIN ACTIVITY FOLLOWING EXERCISE, MOTOR LEARNING AND EXPERTISE

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ABSTRACT

How humans perceive, embody, and execute actions has been an area of intense study in cognitive neuroscience, and these investigations shed light on how we adaptively learn from and interact with an ever-changing world. All of the knowledge associated with action, including sensorimotor representations, the words we use to describe them, and the memories that store this information, are represented in distributed brain regions that comprise ‘knowledge schemas’. With repeated practice or training, one can acquire a highly specialized motor repertoire that fosters even more efficient and adaptable behaviour to achieve peak performance. Using behavioural, EEG and fMRI approaches, I will present a series of investigations that evaluate the impact of short-term exercise and long-term dance practice on the development of expert knowledge schemas. In Chapters 2 and 3, I will demonstrate that activating one domain in the schema (e.g., action processing) will prime other domains (e.g., verbal attention and working memory) to induce translational performance improvements. Subsequent chapters will reveal how familiarity with a specific genre of dance influences behavioural (Chapter 3) and neurophysiological signatures of action perception, how these motor representations are coded in sensorimotor association areas (Chapters 4), and how they change with repeated practice and performance (Chapter 5). How these findings contribute to our model of expert knowledge schemas will be discussed in Chapter 6. These findings bear efficacy for the therapeutic application of exercise and dance programs to alleviate motor, cognitive and neurophysiological impairments in several clinical populations, including people with Parkinson’s disease.

For Matthew, the O’s and the A’s

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LIST OF ABBREVIATIONS

AD – Alzheimer's Disease
AO – action observation
AON – Action Observation Network
BOLD – blood-oxygen-level-dependent
DMPFC – dorsomedial prefrontal cortex
DWP – Dancing with Parkinson's program
EBA – extrastriate body area
EEG – electroencephalogram or electroencephalography
ERD – event-related desynchronization
ERS – event-related synchronization
FEF – frontal eye field
fMRI – functional magnetic resonance imaging
iAPF – individual alpha peak frequency
IFG – inferior frontal gyrus
IPL – inferior parietal lobule
IPS – inferior parietal sulcus
KMI – kinaesthetic motor imagery
LIP – lateral intraparietal sulcus
LO – lateral occipital complex
LOTC – lateral occipitotemporal cortex
ME – motor execution
MEP – motor-evoked potential
MI – motor imagery
MT+ - visual motion complex
M1 – primary motor cortex
Nrp – non-practiced word from non-practiced category in RIF task
PD – Parkinson's Disease
PMC – premotor cortex
PMd – dorsal premotor cortex
PMv – ventral premotor cortex
RIF – Retrieval-Induced Forgetting
ROI – region of interest
Rp+ – practiced word from practiced category in RIF task
Rp- – non-practiced word from practiced category in RIF task
SMA – supplementary motor area
STS – superior temporal sulcus
VisL – Visualization of learned choreography (Chapter 5)
VisNL – Visualization of non-learned choreography (Chapter 5)
VMIQ-2 – Vividness of Movement Imagery Questionnaire 2
V1 – primary visual cortex
WM – working memory

1 CHAPTER ONE – GENERAL INTRODUCTION

Imagine a ballet dancer moving gracefully across a stage, perfectly synchronized with a movement of Tchaikovsky's *Swan Lake*. Through years of dedicated practice, rehearsal and performance, she is able to learn new sequences of choreography and execute them with extreme precision after only a couple of attempts. How her brain has adapted to this physical expertise, and whether it influences other cognitive domains like attention, memory and language, are the main focus of this thesis.

The expert dancer described above, and non-experts engaging in any type of learned voluntary movement, rely on several neurological operations to acquire and execute action. These include, but are not limited to, observing action by an exemplar (e.g., choreographer or teacher); perceiving and understanding the component movements; transforming the observed action from a third-person perspective into an embodied first-person motor representation; computing the necessary motor commands to prepare and execute the action; using sensory feedback to gauge successful execution; and adjusting or reinforcing preparatory signals accordingly to reinforce motor learning of the action. Through a series of experiments I will demonstrate how several of these operations are utilized by experts and non-experts while engaging in novel, familiar, unfamiliar, and overlearned actions. Action requires a coordinated symphony of brain networks, both cortical and subcortical, which I will present as a model or 'knowledge schema' that encompasses information in multiple cognitive domains, including attention, memory, learning, language and motor processing. With repeated exercise or training, a specialized repertoire is developed. Experts can learn novel and more difficult movements through adaptive 'trial-and-error' processes, and also combine component movements into new sequences with greater accuracy and in a shorter amount of time relative to novices. I propose this repertoire, or expert knowledge schema, facilitates improved performance and access to information across domains by activating one (e.g., sensory, motor) and priming other domains (e.g., language, attention, memory) through various neurophysiological mechanisms.

The following sections provide a general background on the research that forms the basis of the experimental chapters that follow. I begin by outlining the three central facets of action processing and the brain networks underlying them. I will then describe the neurophysiological and behavioural mechanisms by which we understand and learn action, and how motor learning, specifically of dance, induces plasticity in these brain networks and connections. By reviewing the existing literature that connects attention, motor, language, and memory structures in the brain, I will introduce a novel putative model of information processing that consolidates skill-related knowledge across these domains. Throughout the introduction I will address gaps in our current understanding of experience-dependent modulation of brain activity, cognitive performance, action processing, and motor learning that will form the bases of the specific objectives of this dissertation.

1.1 HOW THE BRAIN PROCESSES ACTION

1.1.1 The Action Observation Network

When we think of action, we typically associate it with the ability to execute a given movement. However, action also involves the capacity to think about movement(s) through visualization or planning (e.g., how should I reach for this cup?) before executing action that can be observed and appraised relative to expected outcomes. These three central components to action processing – action observation (AO), motor imagery (MI), and motor execution (ME) – help us understand and learn specific behaviours that are neurally coded as motor representations

(Grèzes & Decety, 2001). Engaging these representations through AO, MI and ME activates common underlying circuitry known as the ‘mirror neuron network’. Discovered spuriously by Giacomo Rizzolatti and colleagues when recording directly from premotor neurons in macaque monkey area F5 (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), action potentials were elicited to both observed and executed reaching movements. Together with evidence for MI-induced activation, mirror neurons have since been investigated in humans (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) to define the homologous ‘action observation network’ (AON) (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009a). The regions comprising the AON include ventral (PMv) (Binkofski & Buccino, 2006) and dorsal premotor cortices (PMd), intraparietal sulcus (IPS), superior parietal lobe (Filimon, Nelson, Hagler, & Sereno, 2007), inferior parietal lobule (IPL), inferior frontal gyrus (IFG, or Broca’s area), cingulate gyrus, cerebellum, superior temporal sulcus (STS) (Iacoboni et al., 2001), primary motor cortex (M1), and the supplementary motor area (SMA). There has been some debate regarding the activation of these and other regions primarily involved in ME, especially M1 (Roth et al., 1996) and SMA, during AO and MI when motor output signals are inhibited (for meta-analysis, see Grèzes & Decety, 2001). Nonetheless, there has been reliable activation among these nodes of the AON during all three types of action processing as revealed by several neuroimaging modalities.

The following review of AON and associated brain regions will be limited to those that are putatively part of knowledge schemas bridging sensory, motor, language, attention and memory functioning. I will begin by reviewing evidence for shared activation among these regions during action processing as revealed by functional magnetic resonance imaging (fMRI). Next, I describe the nature of oscillatory rhythms underlying action processing as measured by direct electrophysiological recordings in human and non-human primates and electroencephalography (EEG).

Non-invasive investigations on AON processing utilize fMRI to identify the distinct brain regions and distributed networks responsible for various motor functions described above. Several experimental paradigms are employed by experimenters to elicit task-related activation during AO (e.g., showing a video), MI (e.g., cued visualization or preparation of a movement), and ME under strict parameters (e.g., moving distal limbs like hands and feet to perform reaching or pointing behaviours). These include blocked designs or event-related paradigms. The former method averages brain activity over a period of seconds to infer activation by the cognitive or perceptual process during that time in contrast with another condition (e.g., AO versus rest, MI versus ME, etc.). In contrast, event-related experimental designs present a discrete stimulus (e.g., target letter) for a short duration that serves as a cue for an instructed action (e.g., button press). Averaging over many trials, researchers can identify brain areas involved in pre-cue anticipation, post-cue movement preparation, as well as pre- and post-movement phases.

The functional significance of brain activity recorded by fMRI is inferred by analyzing blood-oxygen-level-dependent (BOLD) signals that are generated by the hemodynamic response – flooding of active brain regions with oxygen-rich blood. These changes alter the magnetic susceptibility of task-relevant brain areas, resulting in clear indications of population postsynaptic activity that can be either inhibitory or excitatory (for review, see Arthurs & Boniface, 2002). By design, fMRI generates a ‘pulse’ approximately once every second and captures the resonating hemodynamic response (Huettel, Song, & McCarthy, 2008), resulting in low temporal resolution relative to direct neural recordings, EEG or magnetoencephalography

(MEG) that capture neuronal activation on the order of milliseconds. However, these methodological approaches are subject to their own limitations, including poor spatial resolution with low-density systems. What these neuroimaging modalities have in common is a sensitivity to movement while being scanned that can result in motion artifacts that translate to the head, even after preprocessing algorithms are applied, and can contaminate subsequent localization of brain activity. Capitalizing on its high spatial resolution, researchers use MRI to assess various structural brain measures including grey and white matter volume and fractional anisotropy between groups or within subjects following learning interventions. While structural analyses are not employed in this thesis, evidence from the existing literature will be discussed as they pertain to experience-dependent changes to functional brain activity.

Based on these properties of fMRI signals, researchers have developed and applied sophisticated computational algorithms to identify the direction and extent of hierarchical brain activity during action processing. According to a review by Gallivan and Culham (2015), the flow of perceived sensory information begins in primary cortices (i.e., visual, auditory, somatosensory, etc.) before converging in the parietal cortex. Depending on the motor effector (e.g., hand, arm, head, eyes) different areas of the parietal cortex (anterior and ventral IPS, superior parieto-occipital sulcus, and parietal eye field, respectively) transform information from sensory receptive field reference frames to motor reference frames that are centered around one's body position in space. These new coordinates are used to map and compute motor plans for goal-directed actions in the premotor cortex (PMC) and SMA, which are also informed by prefrontal regions that govern context and "rules". Final motor output is generated by neuronal activation in M1 to corticospinal nerves that terminate at muscle groups to perform the desired action. Although we will not focus on these brain areas in the current thesis, the cerebellum and basal ganglia are also closely tied to modulating action through sensory feedback of behavioural outcomes, especially for habitual and overlearned actions like walking and dancing in experts (Bar & DeSouza, 2016; Petrosini et al., 2003).

Each type of action processing falls within the hierarchy described above: AO involves the early stages, such that observed behaviours principally activate visual motion (MT+) processing areas and resonate with embodied knowledge representations stored in parietal and premotor regions. There are also many types of action which do not involve visual processing, including memory-guided movement (e.g., reaching for your coffee cup while reading the newspaper) or action processing in the blind. MI also shares many of the same hierarchical steps as ME except for activating corticospinal nerves, which is inhibited during visualization. The simulation of action, especially MI from a first-person kinaesthetic perspective (KMI), is a necessary precursor to ME and facilitates motor learning through AO, further demonstrating the interconnectedness of these distinct action processes. However, Gerardin et al. (2000) have shown distinct patterns of activation between imagined and executed movements. While MI activates rostral PMC and superior and inferior parietal cortex, ME predominantly activates areas around the central sulcus including primary and secondary somatosensory cortices reflecting sensory feedback that would only be elicited during ME.

In a review of AON activation during each of these processes, Jeannerod (2001) characterizes AO and MI as covert processes that are essentially tied to planning ME and evaluating its outcomes relative to pre-movement goals. While the overt process of ME does not necessarily co-occur with AO or MI, there is evidence for common activation during all processes, especially in IPL, SMA, ventral and dorsal PMC. There is also evidence for M1 activation during AO as revealed by subthreshold electromyographic activity of corresponding muscle groups (Borroni, Montagna, Cerri, & Baldissera, 2005) and using MEG (Hari et al., 1998). As mentioned previously, some researchers have found activation in contralateral M1 during MI but to a lesser extent than during ME and in only a subset of participants (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Lotze et al., 2000; Roth et al., 1996). However, these studies show activation of PMC and SMA bilaterally during MI, consistent with their involvement in the larger AON. How activation of these motor areas is modified by short-term learning and long-term expertise during action processing will be elaborated in the next sections.

1.1.2 Sensorimotor Oscillations

The dominant sensorimotor oscillatory rhythm, and the first frequency to be identified by Hans Berger (Berger, 1929), is alpha (~8-12Hz). Berger pioneered EEG by recording electrical potentials through the scalp with electrodes overlying primary visual cortex (V1) on the occipital lobes (O1 and O2 sites of the International 10-20 System) (Compston, 2010). Despite these early origins, the neural generators and functional significance of the alpha rhythm remain an area of debate (for review, see Bazanova & Vernon, 2014; Klimesch, 2012). The prevailing "idling rhythm" hypothesis stipulates that alpha is dominant in first-order thalamic nuclei and their primary sensory and motor cortical counterparts during awake, resting, and unperturbed states. This model further suggests that alpha reflects the extent to which sensory and motor cortices are disengaged from inputs of the body and environment, and is "released" rather than triggered during these states (Buzsáki, 2006). This is evidenced by Berger's early findings of increased occipital alpha amplitude when eyes are closed and no visual information is being processed relative to when eyes are open and amplitude is decreased. Upper alpha (~10-13Hz) is also referred to as the Rolandic mu rhythm when recorded around the central sulcus separating M1 and primary somatosensory cortex at Cz, C3 and C4 central electrode sites. Increased amplitude or ‘power’ of the idling mu or alpha waveform is referred to as event-related synchronization (ERS). Conversely, decreased alpha power or event-related desynchronization (ERD) is inversely related to cerebral blood flow and cortical activation by more dominant rhythms during task performance (Sadato et al., 1998).

Competing theories for alpha function and origins include the “Pacemaker” model that suggest cortical and thalamic neurons fire and entrain each other at an endogenous alpha rhythm (Buzsáki, 2006). However, these models often do not account for alpha’s role as a feedback signal in reafferent sensorimotor pathways from deep (layer 5) and superficial (layers 1 and 2) layers of primary auditory, somatosensory, and visual (V1) cortices to higher-order areas (Haegens et al., 2015; van Kerkoerle et al., 2014). This “neural efficiency hypothesis” suggests that alpha emerges from the coupling of distributed populations of neurons to ‘gate’ the transfer of information across distal regions of the cortex by top-down attentional mechanisms. This function serves to inhibit competing or non-essential information by increasing the signal-to-noise ratio in the cortex, in turn facilitating task performance by enabling efficient access to information across sensory, motor, and linguistic domains (Del Percio et al., 2011; Klimesch, Sauseng, & Hanslmayr, 2007; Luck, 2014).

ERS/ERD patterns depend on the nature of the task and cognitive process being investigated. For instance, ERS is observed during and immediately following working memory (WM) task performance (Klimesch, 1999), indicative of an alpha-encoding function, while ERD is observed during retrieval in that same region of posterior parietal cortex governing episodic and semantic memories through theta (4-7.5Hz) (Gevins, Smith, McEvoy, & Yu, 1997; Klimesch et al., 2006; Schack, Klimesch, & Sauseng, 2005). For motor tasks that rely on the mu band, ERD is elicited in corresponding areas of the homunculus while ERS suppresses activity in surrounding and more distal brain regions (Pfurtscheller & Neuper, 1994). This is similar to the center-surround inhibition model in columns of V1 (Hubel & Wiesel, 1968; H. E. Jones, Grieve, Wang, & Sillito, 2001) and lateral geniculate nucleus neurons (Wiesel & Hubel, 1966) such that 'focal ERD/surround ERS' reflects inhibition of non-essential neighbouring cortical areas (Neuper & Pfurtscheller, 2001; Suffczynski, Kalitzin, Pfurtscheller, & Lopes da Silva, 2001). The degree of ERS/ERD has additionally been shown to increase with task difficulty (i.e., greater increase in alpha power/ERS, or greater decrease in alpha power/ERD) such that greater neural resources are expended to alleviate cognitive load (Gevins et al., 1997; Klimesch, 1999; Roberts, Jones, Davis, Ly, & Anderson, 2014; Schack & Klimesch, 2002).

Within the alpha range there is a clearly identifiable peak in the power spectrum that is known as the individual peak frequency (iAPF), which differs across individuals and slows (i.e., decreases in frequency value) with age (Clark et al., 2004) and disease states like Alzheimer's (AD) (Klimesch, Schimke, Ladurner, & Pfurtscheller, 1990) and Parkinson's Disease (PD) (Moazami-Goudarzi, Sarnthein, Michels, Moukhtieva, & Jeanmonod, 2008; Soikkeli, Partanen, Soininen, Pääkkönen, & Riekkinen, 1991). As with the power or amplitude of alpha, the peak frequency within the alpha range is also influenced by various perceptual and cognitive demands (Bazanova & Vernon, 2014); when engaged by a challenging task, iAPF is faster or higher in frequency relative to rest (Angelakis, Lubar, Stathopoulou, & Kounios, 2004). This modulation of iAPF facilitates the segregation or conscious discrimination of incoming information by increasing the temporal resolution with which the visual system is updated (Samaha & Postle, 2015; Wutz & Melcher, 2013; Wutz, Weisz, Braun, & Melcher, 2014). Whether the speed of visual updating is influenced by short-term exercise or long-term expertise will be examined in Chapters 2 to 4.

The other dominant sensorimotor frequency is beta (13-30Hz), which shows ERD in somatotopic areas prior to and during movement like alpha (Pfurtscheller, Graimann, Huggins, Levine, & Schuh, 2003) but is followed by a brief 'burst' of ERS known as a 'post-movement rebound' (Crone et al., 1998; Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Pfurtscheller & Lopes da Silva, 1999). It is suggested that this rebound reflects a very short period of inhibition and possibly resetting of neural activation in M1 (Pfurtscheller, Neuper, Brunner, & da Silva, 2005; Solis-Escalante, Müller-Putz, Pfurtscheller, & Neuper, 2012). Beta is also related to cognitive aspects of sensorimotor processing such that ERS conveys task- and context-specific information during visual WM in long-range connections between the frontal eye field (FEF) and lateral intraparietal cortex (LIP) (Salazar, Dotson, Bressler, & Gray, 2012). While FEF transforms attentional visuomotor gaze signals using WM (Sajad et al., 2015; Sajad, Sadeh, Yan, Wang, & Crawford, 2016), LIP processes gaze direction of both the individual and the observed gaze of others (Shepherd, Klein, Deaner, & Platt, 2009). Although beta does not have a clear peak frequency like alpha, previous research shows modulation of preferred frequency and beta power for preferred reaching direction in M1. These frequencies were higher (~25-35Hz) during visuomotor integration and movement preparation relative to cue expectancy. When combining beta frequency and power information, the researchers predicted the preferred direction of movement with greater accuracy (Kilavik et al., 2012).

Beta also shares many functional properties with alpha, including greater ERD during more complex or difficult tasks (e.g., hand only versus hand and contralateral foot MI) (Yi et al., 2014) but shows more somatotopic focal ERD/surround ERS activation during ME versus MI (Pfurtscheller et al., 2005; Schnitzler, Salenius, Salmelin, Jousmäki, & Hari, 1997). Beta ERD is also more sustained when there are more items to hold in short-term memory resulting in greater cognitive load (Pesonen, Hämäläinen, & Krause, 2007). Together with alpha, beta exerts top-down feedback from higher order visual areas, including LIP and IPS in the posterior parietal cortex, to inform attentional selection of external stimuli through FEF and reinforces error responses to behavioural outcomes in V1 (Fries, 2015; Michalareas et al., 2016; Womelsdorf & Everling, 2015). Based on their different functions, the way alpha and beta exert top-down influences may differ; alpha as a dominant idling and/or inhibitory rhythm may suppress task-irrelevant information (van Kerkoerle et al., 2014) to allocate computational resources to task-relevant areas. Conversely, beta has been shown to counteract bottom-up information from attended stimuli through strong feedback signals from higher order visual areas (Bastos et al., 2015) and disinhibits neuronal populations involved in computing movement parameters as revealed during MI (Brinkman, Stolk, Dijkerman, de Lange, & Toni, 2014). Thus, both sensorimotor frequencies are widely distributed throughout the brain and show different patterns of activation depending on the brain regions they originate from, either sensory or motor, during perception, cognition and action. The differential contributions of alpha and beta in sensorimotor association during AO and KMI of familiar and unfamiliar stimuli will be explored in Chapter 4.

1.2 UNDERSTANDING AND LEARNING ACTION

1.2.1 Linking Action, Perception, and Language By Event Segmentation

Before one can learn to perform a new action, it must be modelled by an external actor or described by a set of verbal instructions. Both forms of learning require the transformational processing of the AON described above, as well as a capacity to understand continuous streams of action by “chunking” or “segmentation”. The former term has primarily been used in cognitive science literature to investigate linguistic processing, memory, and cognitive architectures (Gobet, Lloyd-Kelly, & Lane, 2016). I will focus on the latter process of segmentation that is rooted in Event Segmentation Theory (EST) (Zacks & Sargent, 2010), which states that continuous streams of action are chunked into component 'units'. These units or events are defined as discrete, reliable, and meaningful movements that describe relevant features of action over time (Zacks & Tversky, 2001; Zacks et al., 2001a). This unconscious perceptual process can also be overtly and deliberately enacted. When experimentally investigated, participants watch a video of an action sequence and provide a response whenever they perceive the end of one event (e.g., folding right arm of a shirt) and the beginning of another (e.g., folding left arm of shirt). These borders define and separate events which are hierarchically organized; low-level features or 'fine-grained' events like those exemplified are consolidated into higher-level concepts or 'coarse-grained' events (i.e, folding a shirt) that fall within a larger action sequence (e.g., doing the laundry).

Researchers cleverly test both the covert and overt types of event segmentation by first recording brain activity during passive viewing followed by active segmentation trials and aligning brain activity to the participant's own responses. Previous event segmentation experiments have typically investigated everyday non-specialized goal- or object-related actions, like the laundry example (Speer, Swallow, & Zacks, 2003; Zacks et al., 2001a; Zacks, Tversky, & Iyer, 2001b), with more recent interest in segmentation of social interactions (Boggia & Ristic, 2015). Segmentation borders are typically triggered by physical (change in direction, speed, etc.) or conceptual (causes, intentions, goals) changes in action and tend to have high agreement across individuals (Speer, 2004; Speer, Zacks, & Reynolds, 2007; Zacks, Swallow, Speer, & Maley, 2006a). This reliability could be due to the neural processes underlying action perception described previously, including evoked responses in MT+, STS, and FEF at event borders (Speer et al., 2003; Zacks et al., 2001a; Zacks, Kurby, Eisenberg, & Haroutunian, 2011).

Segmentation occurs at all levels of perception and across visual, somatosensory and auditory modalities. Auditory language processing (Lerner, Honey, Silbert, & Hasson, 2011) and visual segregation/integration are both mediated by temporal "windows" that receive and interpret sensory inputs over time, and form the resolution of perceptual updating. These windows are conceptually similar to event boundaries, which may also be sensitive to the phase and frequency of the alpha band (Samaha & Postle, 2015; Wutz et al., 2014; Wutz & Melcher, 2013). In subsequent chapters, we will investigate whether experience modifies segmentation of familiar and unfamiliar dance sequences (Chapter 3) and the brain activity underlying action processing and visual updating that supports segmentation (Chapters 4 and 5).

The ability to segment action sequences through the online updating of WM systems also has implications for later memory and learning of these behaviours. Event borders serve as anchors for long-term memory, with impaired recall of events and film narratives when those surrounding event borders are deleted or replaced with commercials (Boltz, 1992; Schwan & Garsoffky, 2003). Several clinical populations, including patients with schizophrenia (Zalla, Verlut, Franck, Puzenat, & Sirigu, 2004) and frontal lobe lesions (Zalla, Pradat-Diehl, & Sirigu, 2003), show deficits in segmentation ability such that the location of coarse-grained event borders vary from normative ones. Interestingly however, fine-grained segmentation of smaller component units is left intact. Individuals with mild dementia and AD show impaired fine- and coarse-grained segmentation, as well as poor recognition and order memory of segmented action (Zacks, Swallow, Vettel, & McAvoy, 2006b), demonstrating a clear link between attentional, WM, and long-term memory functioning and event segmentation.

1.2.2 Practice Makes Perfect – Short-Term Motor Learning and Long-Term Expertise

As demonstrated by the opening paragraph of this thesis, the need to organize action into steps is necessary to maintain coherence in behaviour. These sequential dependencies are themselves learned through experience and specifically through experiencing errors in behavioural outcomes. In addition to biological motion and attention regions, event borders elicit activation in the anterior cingulate cortex and other error detecting regions in the midbrain dopaminergic system including substantia nigra and ventral tegmental area. It is suggested that these regions monitor the level of prediction error for ongoing action (Blakemore, Rees, & Frith, 1998). When uncertainty reaches threshold, feedforward signals are sent to WM, attention, and orienting response areas like FEF, superior colliculus, right inferior temporal cortex, and orbitofrontal cortex to trigger an event border (Reynolds, Zacks, & Braver, 2007; Zacks et al., 2011). Prediction error signals are also generated when behavioural outcomes perceived through reafferent sensory feedback (e.g., your swing misses a pitched ball) do not match expected outcomes neurally coded with expected efference copy signals (Pynn & DeSouza, 2013). These signals are generated during motor planning stages and prime the appropriate sensory areas to anticipate reafferent feedback. When an action achieves a desired goal or outcome (e.g., swinging and hitting a pitched ball), no prediction error responses are elicited and the neural code for this successful motor plan is reinforced (Maia, 2009). With continued practice and training, these sensorimotor systems are refined and facilitate improved performance through recalibration (Cressman & Henriques, 2009; Neva & Henriques, 2013; Salomonczyk, Cressman, & Henriques, 2011).

While action is typically regarded as a hierarchical, step-wise process that concludes with ME, researchers have also investigated parallel processing of multiple behavioural outcomes, or "affordances", that compete for final selection (Cisek, 2006; 2007). Either serially or in parallel, the decision to move is met with multiple potential motor representations that can achieve the desired outcome. Based on updating of movement goals and action selection by the prefrontal cortex and basal ganglia, respectively, competition is biased towards a single motor command that is released into execution. Through the overt (sensory) and covert (efference copy) feedback processes described above and refinement of expert sensorimotor networks, the computation/preparation, evaluation, and selection of the most appropriate motor plan becomes faster and more accurate.

Repeated physical training including exercise has been shown to yield many cardiovascular benefits through the repeated movement of muscle groups to condition and strengthen them. Few studies have compared training outcomes and electrophysiological measures across AO, MI, and ME conditions, but those that have provide considerable efficacy for the former two methods. A study that compared ME and MI groups over four weeks of strength training in the fingers found surprisingly similar force gains for both groups, but greater strength in the ME group (Yue & Cole, 1992). Similar force production was also found for finger movements trained with ME and to a lesser extent with AO (Porro, Facchin, Fusi, Dri, & Fadiga, 2007). The same study included an experiment that assessed corticospinal excitability during AO, MI, and ME and found significantly greater motor evoked potentials (MEPs) for ME and MI conditions, but not AO. As demonstrated in the AON literature, MI (and especially KMI) elicits motor resonance in the absence of overt movement and is a useful tool for mental training of novel actions or sequences (Jackson, Lafleur, Malouin, Richards, & Doyon, 2001).

Nonetheless, it is clear that physical practice has the greatest efficacy for improved physical performance.

Exercise can also encompass other learning forms, including eye exercises to strengthen putative oculomotor networks and treat a variety of visual abnormalities (Rawstron et al., 2005) as well as improve performance in sports (Helveston et al., 2005) and cognitive tasks (Di Noto, Uta, & DeSouza, 2013). Exercise through athletic practice not only provides cardiovascular benefits but also a specialized motor repertoire that is developed and refined over a longer training period (i.e., years) manifesting as expertise. Through evaluations of elite chess players, expertise was initially studied by de Groot (1965) and theoretically defined by Newell and Simon (1972) as the ability to accurately and efficiently retrieve an appropriate motor command to achieve a goal while balancing dynamic and restrictive external factors on WM. This definition was later expanded to include the capability of experts to expand their WM capacity to quickly and successfully engage in highly demanding cognitive processes like planning, evaluation, and reasoning to achieve peak performance (Ericsson, 1998; Ericsson & Lehmann, 1996). To narrow the focus on the multitude of expert types that exist, I have investigated expertise in dancers.

1.2.3 Dance-Induced Neuroplasticity

For this thesis, I have used dancers, and specifically ballet dancers, as a model of expertise for several reasons: by the very nature of its genre, ballet requires strict discipline and adherence to a rigorous practice and performance schedule relative to more recreational forms of dance. This affords experimental control over participant compliance and evaluation of behavioural outcomes by external evaluators (i.e., instructors and choreographers), which would otherwise be difficult to ensure by researchers. More so than other athletic practices, dance requires skilled movements to be precisely coordinated with external auditory stimuli like music or verbal instruction. This results in expertise that is both multimodal in nature and maintains a high level of physical performance. These operational benefits to examining dancers, musicians, and other artists have formed the basis of a burgeoning field referred to as ‘neuroaesthetics’ (Chatterjee, 2011). Investigations on dance provide a more holistic understanding of action that is complex and ecologically relevant to movements performed in ‘real life’ as opposed to repetitive, finite, and manipulated movements that are specific to a laboratory task. Dance is also communicative, rhythmic, and aesthetically appraised (Bläsing et al., 2012; Brown, Martinez, & Parsons, 2006). The dance-related findings in this thesis (Di Nota, Levkov, Bar, & DeSouza, 2016); Di Nota et al., 2016a, under review; Chapters 3 to 5) contribute further to this field.

The cognitive flexibility afforded to experts is based on structural and functional plasticity of multiple brain regions, especially the AON. During initial motor learning new synaptic connections are forged, known as ‘neuroplasticity’, and this results in increased grey matter. As revealed with novice jugglers trained for five weeks, grey matter increases bilaterally in MT+, superior frontal gyrus, middle temporal gyrus and cingulate cortex after only one to two weeks of practice, and decreases two and four months post-training (Driemeyer, Boyke, Gaser, Büchel, & May, 2008). With long-term training over many years, ballet dancers had lower grey matter volume in superior frontal gyrus, left PMC, SMA, and putamen relative to non-experts, and lower white matter volumes in bilateral corticospinal tracts and corpus callosum (Hänggi, Koeneke, Bezzola, & Jäncke, 2010). These findings reflect efficiency of structural organization of the brain in regions involved in motor planning and learning. Fractional anisotropy, which measures the extent of fiber integrity (Assaf & Pasternak, 2007), is also lower in white matter tracts underlying PMC in dancers only, reflecting less diffusion across white matter tracts (Hänggi et al., 2010). The resonance of embodied motor representations has been demonstrated with fMRI while ballet dancers and practitioners of Brazilian mixed dance/martial arts capoeira view both styles of movement; dancers exhibited greater activation of PMC and IPS bilaterally, left posterior STS, and right superior parietal lobe when viewing ballet but not capoeira (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). This functional plasticity is further tuned to the specific motor repertoire assigned to each gender, which have different movement phrases that are only performed by males or females. Despite having visual familiarity with both gendered movement, only gender-specific embodied action activates PMC and parietal cortices and the cerebellum (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006).

Specificity and consolidation of motor representations is also reflected behaviourally during event segmentation of dance. Contemporary dancers identified fewer event borders while observing a familiar dance relative to non-dancers, chunking more constituent movements into a single event. This effect is further driven by embodied learning, with dancers identifying even fewer event borders after training the segmented dance sequence (Bläsing, 2015). These findings are consistent with previous evidence for increased activation in regions associated with event borders when observing dance movements that violated expectations following training with similar dance sequences (Schiffer & Schubotz, 2011). The ability to store dance movements and long sequences in long-term memory has been supported by research that shows recall cued by accompanying music up to 31 years later. Descriptions were provided verbally and demonstrated physically by some participants, and there was poorer recall of transitions, suggesting that event borders for dance may be defined differently (i.e., kinaesthetically) than non-dance object-directed movements (i.e., semantically) (Stevens, Ginsborg, & Lester, 2010).

Motor learning initially begins with input to the perceptual systems, as when a dancer observes and attempts to recreate the movements of their instructor, and involves different neural processes than the error-related learning described previously. Research by Emily Cross has revealed nodes of the AON that are specifically activated by the interaction of perceived ability and embodied experience among expert dancers learning a new piece of choreography. These include left IPS/IPL, left PMv, and left parahippocampal gyrus (Cross, Hamilton, & Grafton, 2006). Her work demonstrates common (PMC) and distinct (precentral gyrus, middle frontal gyrus) regions subserving learning through AO and ME (Cross et al., 2009a) and dissociable areas for dance training (PMv) that is performed by a human versus a robot model (STS) (Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009b). Together, these works demonstrate experience-dependent plasticity of the AON that is induced by dance training.

Dancers and other athletes commonly use MI for training, performance enhancement, affective and cognitive regulation, as well as for rehabilitation when overt movement is not possible or recommended (Bläsing et al., 2012; Jones & Stuth, 1997). While there is no evidence for the efficacy of dance learning via KMI, it has been shown to elicit greater right-hemispheric alpha ERS among dancers while creatively imagining novel sequences relative to non-dancers (Fink, Graif, & Neubauer, 2009). Comparing motor learning of complex limb-hand-foot movements via AO or MI revealed that the former condition resulted in fewer errors, greater alpha ERD during training, and greater beta ERS during ME of the learned task (Gonzalez-Rosa et al., 2015). With cognitive training on spatial and verbal tasks, improved performance is accompanied by alpha ERS in parietocentral areas, suggesting fewer cortical resources are needed after subjects become skilled (Gevins et al., 1997). Whether training to learn a specific piece of choreography results in similar modulation of oscillatory (Chapter 4) or BOLD activation in sensorimotor networks (Chapter 5), and/or whether cognitive improvements are induced by sensorimotor training (Chapter 3) are unanswered questions that will be addressed in this thesis.

The basis for the dance-related studies in this thesis come from an investigation by Bar and DeSouza (2016), which revealed functional changes to a motor representation in professional ballet dancers with learning, rehearsal and a performance programme spanning 34 weeks (see Chapter 5 for detailed methodology). Modulation of SMA, primary auditory cortex, and nodes of the basal ganglia were revealed during MI of the newly learned dance cued by music. Based on the latter findings, our lab has undertaken an ongoing research project evaluating the therapeutic efficacy of a weekly Dancing with Parkinson's program (DWP) on the neurophysiological, motor and non-motor symptoms of PD.

1.3 PUTTING IT ALL TOGETHER – KNOWLEDGE SCHEMAS

I propose that the resonance of information across domains – sensory, motor, language, memory, attention – related to actions or skills form *knowledge schemas* (Figure 1.1). The concept of knowledge frames or schemas have been described in cognitive psychology for several years. Cited over 2,000 times, Cheng, Holyoak, Nisbett and Oliver (1986) describe reasoning schemas as "clusters of rules that are highly generalized and abstracted but nonetheless defined with respect to classes of goals and … relationships" (p. 294). Cognitive schemata typically describe the content of information (from a variety of domains) that is stored in memory and learned through experience, such as the roles and contexts of social movements like waving goodbye (Schank & Abelson, 1977; Johnston, 1995). I propose that the knowledge schema related to dance, including dance-related words, contexts, and actions, is generalized in novices (Figure 1.1). With repeated training and expertise, I propose the knowledge schema becomes more refined (i.e., more efficient brain activity) and interconnected across domains, such that activating one (i.e., motor processing) primes access to another (i.e., WM, attention, language). The neural architecture underlying knowledge schemas is similar to the concept of dynamic circuit motifs (Womelsdorf & Everling, 2015; Womelsdorf, Valiante, Sahin, Miller, & Tiesinga, 2014), which use rhythmic properties of local and distributed neurons to direct visual attention. For the present model, I suggest that information is relayed across domains by the same functional brain networks and oscillations underlying action, language, and memory processing, as well as nodes interacting with visual attention networks. Actions are perceived events that unfold over time and activate motor representations in the knowledge schema of the observer. Language is needed to describe constituent movements of these events, and thus actions are putatively represented semantically as well.

The current thesis will demonstrate that: 1) priming knowledge schemas with AO, MI or ME resonates in other cognitive domains, including language, attention, and WM; and that 2) several years of long-term dance practice modifies expert knowledge schemas to be more efficient, facilitating improved performance across domains relative to non-experts with no regular or prolonged dance training.

After introducing concepts and mechanisms from a range of fields including neuroscience, cognitive psychology, and neuroaesthetics, several questions remain unanswered. It is well known that responding to visual targets using attentional networks is enhanced when there is more time between stimuli to compute the appropriate motor plan (Baldauf, 2011; Wutz et al., 2014). Does priming knowledge schemas in one domain (e.g., sensory, motor) transfer to improved performance in another (e.g., attention, WM), and is this priming sensitive to resonance of embodied motor representations coded in expert knowledge schemas? Based on the

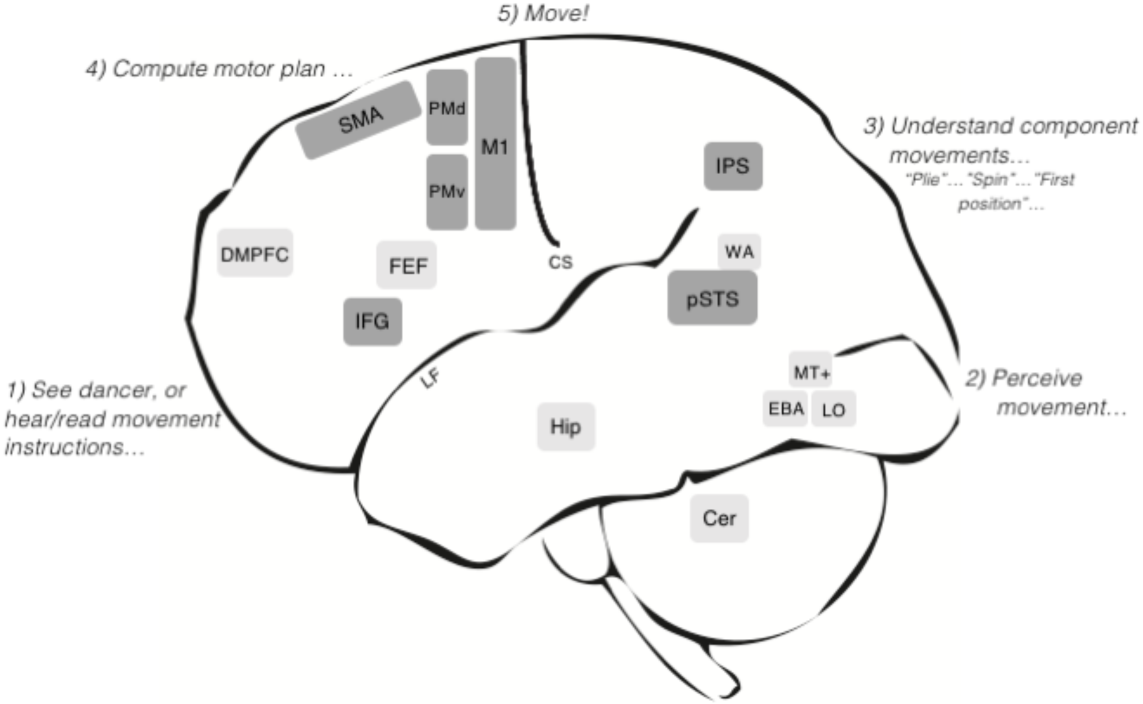

Figure 1.1. Knowledge schemas - general.
Actions or events, such as a dance sequence, are coded in knowledge schemas that include information from several cognitive domains. For observed action, various brain areas communicate reciprocally to perceive, segment, understand, encode and transform this motor representation into executed movement, and encode it into memory. Dark grey nodes are also canonical AON regions. Cer – cerebellum; CS – central sulcus; DMPFC – dorsomedial prefrontal cortex; EBA – extrastriate body area; FEF – frontal eye field; Hip – hippocampus (subcortical); IFG – inferior frontal gyrus (Broca's area, BA44/45); IPS – intraparietal sulcus; LF – lateral fissure; LO – lateral occipital complex; MT+ - human visual motion complex; M1 – primary motor cortex; PMd – dorsal premotor cortex; PMv – ventral premotor cortex; pSTS – posterior superior temporal sulcus; SMA – supplementary motor area; WA – Wernicke's Area

patterns of alpha and beta ERS/ERD that facilitate the exchange of information during action processing, are these same mechanisms responsible for cross-domain communication in (expert) knowledge schemas? I have presented evidence from other researchers on experience-dependent plasticity of action-related nodes that are part of the proposed knowledge schema model. Do these training and expertise effects also modulate activation of sensorimotor or language association areas? Are there translational benefits to refining knowledge schemas through short- or long-term physical training to other cognitive functions, including WM and language? These questions, especially as they pertain to expert dancers, remain unanswered.

1.4 OBJECTIVES

The overarching goal of this dissertation is to address gaps in our current understanding of how knowledge schemas are modified by short- and long-term exercise, and if/how resulting expertise in a sensorimotor domain (e.g., dance) transfers to improved performance in another domain (e.g., language, attention, WM). Using a variety of methodological approaches (behavioural, fMRI, and EEG), this thesis will demonstrate behavioural and neurological plasticity following short-term exercise (i.e., over the span of minutes), motor learning over an intermediate interval of weeks and months, as well as long-term plasticity following years of expertise in dance. Novel evidence will be revealed for improved performance on tasks measuring perception, attention, and WM following various movement-based interventions, which have promising implications for therapeutic applications (e.g., Rhythmic Movement Therapy, DWP). Additionally, the neural mechanisms underlying these cognitive improvements will be clarified using neuroimaging (fMRI and EEG). Finally, these projects will contribute empirical neuroscientific evidence on expert knowledge schemas underlying action, semantic, WM, and attentional processing among dancers in the growing field of neuroaesthetics. All of these insights will be revealed by a series of investigations with the following specific objectives:

Objective 1: To demonstrate short-term transference of improved attention and WM performance following motor activation of non-expert knowledge schemas. I hypothesize that activating oculomotor brain networks through a brief course of eye exercises will resonate in shared attention and language processing regions, resulting in improved response accuracy to rapidly presented visual targets when evaluated post-exercise.

Objective 2: To determine whether attention and WM are influenced by long-term physical practice manifested as expertise. I hypothesize more efficient event segmentation of familiar dance sequences, but not unfamiliar dance genres or non-dance movement sequences. Based on previous evidence for transference of WM performance (Objective 1), I predict that activation of knowledge schemas via AO of familiar dance sequences primes language areas and facilitates improved recall of experientially-relevant words. Evaluation of these experience-dependent improvements in cognitive performance will be tested in Chapter 3.

Objective 3: To reveal the neurophysiological mechanisms by which experts observe and visualize novel but familiar dance sequences relative to unfamiliar experts and non-experts. I predict faster iAPF and greater alpha and beta desynchronization (ERD) in sensorimotor regions among familiar ballet dancers during AO relative to less familiar and expert groups, indicating greater task engagement and visuotemporal updating. Further, I predict that these effects will be demonstrated during KMI of non-specialized movements, providing putative neurological evidence for transfer effects observed in Objectives 1 and 2. Chapter 4 describes the experiment that assessed this objective.

Objective 4: To propose a model for expert knowledge schemas shaped by long-term dance practice, and the neural mechanisms by which it operates. Behavioural evidence for this model will be introduced in Chapter 3, its neural underpinnings as revealed by EEG will be evaluated in Chapter 4, and modulations to sub-regions of this model will be measured with fMRI in Chapter 5. The final model will be defined and discussed in Chapter 6. I hypothesize that activation and plasticity of one domain in the expert knowledge schema (e.g., sensorimotor skills) will lead to transference of expertise effects in other domains (language, attention and WM), which together will reflect more efficient brain activity to achieve optimal performance across domains.

2 CHAPTER TWO – EYE EXERCISES ENHANCE ACCURACY AND LETTER RECOGNITION, BUT NOT REACTION TIME, IN A MODIFIED RAPID SERIAL VISUAL PRESENTATION TASK[1]

2.1 PREFACE

Eye exercises have been prescribed to resolve a multitude of eye-related problems. However, studies on the efficacy of eye exercises are lacking, mainly due to the absence of simple assessment tools in the clinic. Because similar regions of the brain are responsible for eye movements and visual attention, we used a modified rapid serial visual presentation (RSVP) to assess any measurable effect of short-term eye exercise in improvements within these domains. In the present study, twenty subjects were equally divided into control and experimental groups, each of which performed a pre-training RSVP assessment where target letters, to which subjects were asked to respond to by pressing a spacebar, were serially and rapidly presented. Response time to target letters, accuracy of correctly responding to target letters, and correct identification of target letters in each of 12 sessions was measured. The experimental group then performed active eye exercises, while the control group performed a task that minimized eye movements for 18.5 minutes. A final post-training RSVP assessment was performed by both groups and response time, accuracy, and letter identification were compared between and within subject groups both pre- and post-training. Subjects who performed eye exercises were more accurate in responding to target letters separated by one distractor and in letter identification in the post-training RSVP assessment, while latency of responses were unchanged between and within

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[1] Paula M. Di Noto, Sorin Uta & Joseph F.X. DeSouza. (2013). *PLOS ONE, 8(3)*, E59244.

groups. This suggests that eye exercises may prove useful in enhancing cognitive performance on tasks related to attention and memory over a very brief course of training, and RSVP may be a useful measure of this efficacy. Further research is needed on eye exercises to determine whether they are an effective treatment for patients with cognitive and eye-related disorders.

2.2 INTRODUCTION

Eyesight is the most evolutionarily advantageous sense for human beings. It allows for simultaneous, rapid, and efficient processing of information from the environment. This information is subsequently used to facilitate numerous cognitive functions, such as perceiving possible hazards and observation-based learning. Based on the immense reliance we have upon our vision, it is no wonder that many clinical techniques have been developed to assess and treat a multitude of eye and eye-related problems. Eye exercises are often prescribed in vision therapy to resolve issues relating to vergence, ocular motility disorders, accommodative dysfunction, amblyopia, learning disabilities, dyslexia, asthenopia, myopia, motion sickness, sports performance, stereopsis, visual field defects, and visual acuity (Rawstron, Burley & Elder, 2005). Eye exercises are also practiced to enhance sports performance and used during yoga to promote general well-being (Helveston, 2005). However, few studies exist on evaluating the outcomes and efficacy of this type of therapy (Crisp, 1950; Harvard Women's Health Watch; Karatz, 1975; Lasky & Lasky, 1990; Leary, Murray & van Selm, 1986; Rawstron et al., 2005; Rodriguez, Hopman & Hoveten, 2012; Roy, 1980). One such study found a measurable effect of eye exercise in patients with convergence problems (Gallaway & Scheiman, 1997). Additional research suggests eye exercise facilitates improvement in stereoscopic skills and visual field remnants after brain damage (Ciufredda et al., 2008); and there has been evidence to link visual attention and visual working memory (for review see Theeuwes, Belopolsky & Olivers, 2009). dAside from these areas, there exists no other research implicating eye exercise as an effective treatment for other types of visual or cognitive deficits. Despite this lack of empirical peer reviewed research, eye exercise remains a popular technique/therapy as demonstrated by a Google search of "eye exercise" conducted in April 2009 which yielded 13,400,000 results, and 244,000,000 results when searched again on April 3rd, 2012.

Perhaps the most popular type of vision therapy is the 'See Clearly' technique established by ophthalmologist William Horatio Bates (Helveston, 2005). His book, *The Cure of Imperfect Sight by Treatment without Glasses* (Bates, 1920), highlights a wide assortment of possible therapeutic eye exercises, one of which requires patients to shift their fixation between two targets repeatedly without staring. This is intended to relax the eye and correct errors in refraction leading to improved vision. Essentially, Bates' eye exercise technique employs rapid saccadic eye movements in an attempt to improve visual *acuity*, but there is no discussion in his work on how saccades affect visual *attention*. Through a review of historical literature and our present investigation, we intend to illuminate the mystery of eye movement training and its relation to visual attention.

Evidence in the field of vision research has suggested the frontal eye fields (FEF), an oculomotor region of the premotor cortex, is of paramount importance during voluntary saccade production in humans and non-human primates (Braun, Weber, Mergner & Schulte-Mönting, 1992; Pierrot-Deseilligny, Ploner, Müri, Gaymard & Rivaud-Péchoux, 2002; Taylor, Nobre & Rushworth, 2006). Pro-saccades are small, jerky eye movements towards an object or cue. Anti-saccades are, by definition, gaze shifts in the opposite direction of a presented stimulus cue (Connolly, Goodale, DeSouza, Menon & Vilis, 2000; DeSouza, Menon & Everling, 2003;

Hallett, 1978; Schlag-Rey, Amador, Sanchez & Schlag, 1997). Munoz and Everling (2004) reviewed single neuron activity in the FEF and found it to be responsible for voluntary control of anti-saccade eye movements, which are guided by instructions and attentional control. Further to this, inactivation of the FEF via chemical injection has resulted in an abolition of voluntary saccades to the contralateral visual field (Dias, Kiesau & Segraves, 1995). The FEF is also shown to be involved in visual attention tasks (Moore, 2003; Neggers et al., 2007; Taylor et al., 2006). Thus, we can reasonably suspect that repeated saccade performance will have a measurable effect on the visual attention network depending on the amplitude and frequency of saccades. Since the synapses of neurons are dynamic and adaptive (Linden, Heynen, Haslinger & Bear, 2009; Dorris, Paré & Munoz, 2000), it is theoretically possible to improve performance on a visual attention task by strengthening the connections of neurons through saccadic eye exercise over a short period of time, such as a few hours or even a few minutes.

A study by Dyckman and McDowell (2005) involved training participants on one of three eye movement tasks (anti-saccade, pro-saccade or fixation). Participants trained on the pro-saccade task made more errors on subsequent anti-saccade testing, while subjects trained on the fixation task showed no change in errors during the pro- and anti-saccade testing sessions. Subjects that underwent anti-saccade training had decreased errors while maintaining the same speed. These findings suggest that deliberate practice of eye movements can alter anti-saccade performance on later testing, and the enhancement of accuracy demonstrated in the anti-saccade training group was not a trade off for speed. Furthermore, an assertion was made that the direction of the practice effect depends on the type of training task one engages in such that the subjects' performance would improve on the task they had been trained on. While the effects of saccade practice have been shown to alter one's performance on anti-saccade tests, much remains unclear regarding its effects on visual attention performance and the putative involvement of the FEF region in relation to saccade practice effects and visual attention. What these studies do underscore, however, is the highly plastic nature of the brain and visual system, which can adjust to different requirements with sufficient training (Keck et al., 2008; Linden et al., 2009; for review see Citri & Malenka, 2007).

To the best of our knowledge, there exists no study that assesses changes in visual attention and memory following vision training with eye exercises. The majority of studies assessing the progression of vision-related problems utilize the subjective College of Optometrists in Vision Development (COVD) quality of life checklist. The 30-item questionnaire requires patients to input the frequency of personally experienced issues related to Physical-Occupational (mobility), Social Integration (personal relationships), Somatic Sensation (physical symptoms) and Psychological (overall life satisfaction) domains. Studies on patients that undergo this therapy while being evaluated with the COVD checklist show a decrease in subjective symptoms and an improved overall quality of life (Daugherty, Frantz, Allison & Gabriel, 2007). However, there is an absence of any evaluation of the quantitative behavioural or putative neural changes in the vision-related problems that subjects present with.

Because of the lack of assessed improvements in vision, attention, and working memory following therapeutic intervention, the present study was designed in an attempt to investigate whether eye exercises as visual training influence performance on a visual attention task. Dyckman and McDowell (2005) indicated their observed practice effect can be quantified in as little as 3 days. However, the present study will attempt to demonstrate improvements in visual attention after only 18.5 minutes of eye exercises as measured by rapid serial visual presentation (RSVP). Joseph, Chun and Nakayama (1997) demonstrated that RSVP is a sensitive tool capable of measuring visual attention through letter identification. This tool is especially fitting for the present investigation, which provides a limited but sufficient amount of visual training in an experimental paradigm that can be easily replicated and performed in under 20 minutes. Our paradigm will divide subjects into two groups based on their training condition: an active eye exercise group and a control group that will perform minimal eye movements. Both groups will perform RSVP twice (prior to and following their respective training conditions), which ensures that practice effects related to RSVP exposure can be eliminated and any differences in RSVP performance can then be attributed to the effects of eye exercises on visual training. Following the assumptions of Dyckman and McDowell (2005), we hypothesize that participants who undergo eye exercise will respond to RSVP with greater accuracy in a second post-training evaluation while maintaining similar response times. Similarly, we do not expect the control group to exhibit any changes in speed or accuracy during the subsequent RSVP task. If a measurable difference in visual attention is indeed detected in the post-training RSVP task, we can lend further evidence to the efficacy of eye exercises as a useful method of enhancing visual and cognitive control.

2.3 METHODS

2.3.1 Participants

Twenty participants (10 female, mean age= 26.0, SD=11.2) volunteered for the present study. All participants were free of memory problems and uncorrected vision problems. Participants were randomly assigned to one of two age- and sex-matched groups: the experimental eye exercise group (5 female, mean age=27.3, SD=11.2) or a control group (5 female, mean age=24.8, SD=11.7) that performed minimal saccadic eye movements.

The present study was approved by the York University Human Subjects Review Board and conducted in accordance with the Declaration of Helsinki. All participants provided signed consent prior to taking part in the study, and were free to withdraw at any time with no consequences.

2.3.2 Rapid Serial Visual Presentation (RSVP)

For both eye exercise and control groups, participants were assessed using RSVP before and after their respective training conditions (Figure 2.1). In RSVP, all 26 letters of the English alphabet are randomly presented in either black (RGB: 0, 0, 0) or white (RGB: 255, 255, 255) within a 30 x 30 pixel grey box (RGB: 128, 128, 128) at the center of the screen. Black letters are non-target letters while white letters represent the target to which subjects responded by button press on a computer keyboard. Each letter is presented for 33ms followed by a 50ms blank box. A trial starts with the presentation of 5 to 10 non-target letters followed by a target letter. Following presentation of the first target letter, another 0 to 4 non-target letters are shown before the next target letter. Either 2 or 3 target letters are shown per session before concluding with 14 non-target letters. This sequence is repeated a total of 10 times to constitute one trial. Our subjects were exposed to 12 trials in total. Our RSVP task replicates the one used by Joseph and colleagues (1997), except our paradigm includes second and third additional target letters that are randomly presented in the trials within each session. This was meant to ensure that each session randomly presented 2 or 3 target letters and participants were unable to predict how many times they were required to respond. The total experiment consists of 12 trials, each consisting of 10 sessions (1 session = 5-10 non target, target, [0-4 non target, target] x 1 or 2 randomized, 14 non target). Total time for the entire experiment of the modified RSVP task is approximately 10 minutes. We were interested in measuring three aspects of subjects' performance in the RSVP task: reaction time to responding to target letters, accuracy in responding to target letters, and accuracy in identifying the final target letter in every tenth session.

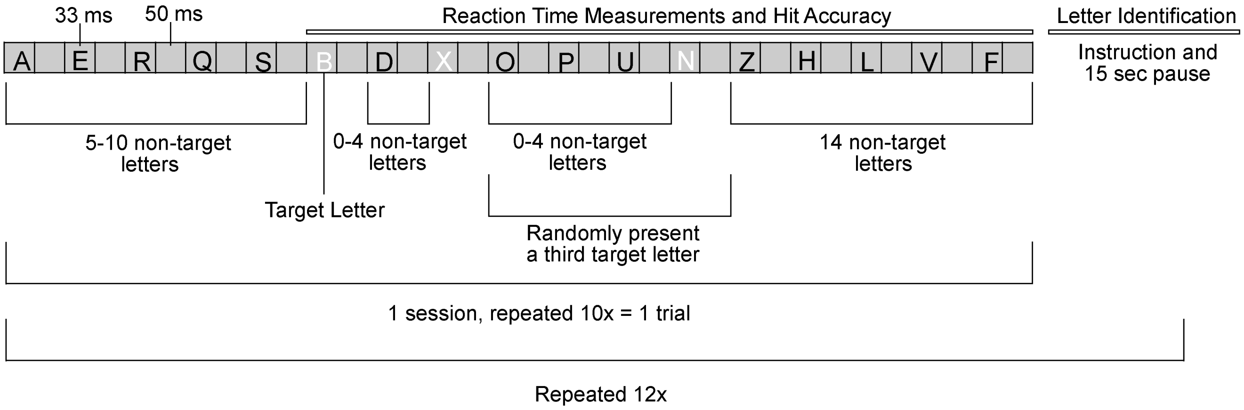

Figure 2.1. Protocol for the modified RSVP task.
All letters were presented at central fixation, with target letters appearing in white and non-target letters appearing in black font.

2.3.3 Letter Identification

Expanding upon the RSVP task presented by Joseph et al. (1997) we incorporated an instruction to identify the target letters observed during every tenth session. Participants were prompted by an instructional screen to indicate the letters presented, and were given extra time (15sec) to indicate the letters using the computer keyboard. The purpose of this evaluation was to determine whether eye exercise facilitated improvements in visual working memory as measured by letter identification, and specifically, with the number of correct responses. Overall, letter identification was required 12 times, once after the final session of every trial (Figure 2.1).

2.3.4 Eye Exercise Task

The experimental condition had ten participants perform an active eye exercise task, which involved following a white square on a black background through a series of paths described as follows (Figure 2.2). The participants were expected to make saccadic eye movements while following the square through a course of 5 horizontal figure eights, 5 large rectangles outlining the edge of the screen, 5 vertical figure eights and 5 small rectangular paths.

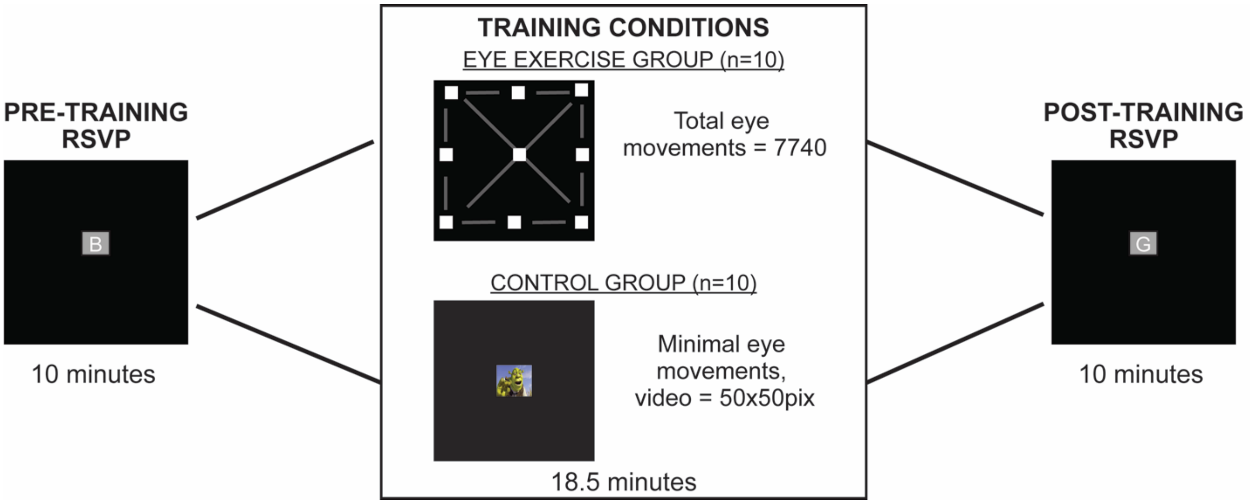

Figure 2.2. Protocol for the eye exercise and control groups.
Following a 10-minute RSVP task, subjects in the eye exercise group were instructed to follow a moving box on the screen, effectively performing 7740 saccadic eye movements. Subjects in the control group were asked to fixate on a movie clip presented in a very small (50 x 50 pixel) box on the screen. Following each training condition was a second RSVP assessment.

This cycle was repeated 4 times. The square would move to a new position every 150ms. The duration of the eye exercises was 18.5 minutes. Overall, following the square would have resulted in the performance of 7,740 saccadic eye movements, thus maximizing the amount of eye movements performed. The eyes of the subjects were observed by the experimenter during the entire task to ensure that subjects were actively participating in the task. All subjects complied with the instructions and were included in the analysis.

2.3.5 Control Task

The control group had a training condition that intended to minimize the amount of eye movements, or exercise, that the participants engaged in. As such, the control task involved participants' passive observation of an 18.5-minute clip of a movie (Shrek 3) without sound. This clip was displayed within a 50 x 50 pixel sized box surrounded by a white screen (Figure 2.2).

The dimensions were purposefully small to minimize saccadic eye movements. Any changes found in the control group were expected to be due to effects of the RSVP task and thus can be used to factor out the practice effects from the experimental group. The eyes of the subjects were observed by the experimenter to ensure that the subjects were actively participating in the task.

2.4 RESULTS

2.4.1 Reaction Time

We compared reaction time to responding to target letters in the pre-training versus post-training RSVP task with a repeated measures ANOVA and found that neither group deviated from their pre-training reaction time (training and test condition interaction: F(1, 17) = 2.334, p = 0.145) (Figure 2.3). One participant from the control group was excluded from analysis due to a malfunctioning button press and a loss of registered data. Paired sample t tests reveal that average reaction time for the eye exercise group did not differ from the control group in either the pre-training ($t(8) = 0.429$, $p > 0.1$) or post-training RSVP task ($t(8) = 0.145$, $p > 0.1$).

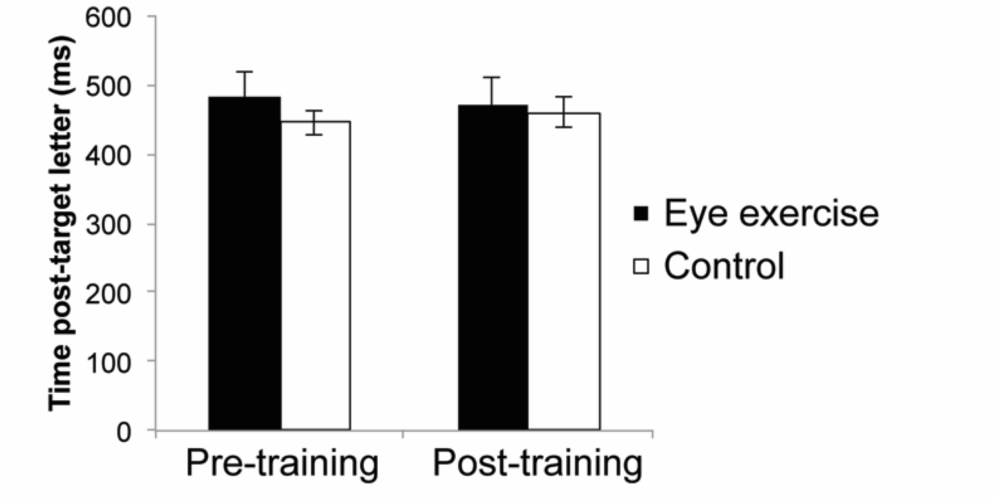

Figure 2.3. Reaction time to RSVP target letters.
No differences in reaction time to target letters were revealed between groups or between pre- or post-training assessments. Error bars show SEM.

2.4.2 Response Accuracy

Response accuracy was analyzed with a 2x2x5 repeated measures ANOVA (Table 2.1). Only the main effect of distractor was highly significant (F(4, 72) = 113.72, $p < 0.001$, $\eta_p^2 = 0.863$), with expected increases in response accuracy as the number of distractors between target letters increased from zero to four. The distractor*training interaction was approaching significance (F(4, 72) = 2.175, $p = 0.080$) but had a large effect size ($\eta_p^2 = 0.108$), suggesting an influence on response accuracy by practice effects or training effects, presumably from the eye exercise condition. This final presumption is strengthened by the significant distractor*condition interaction (F(4, 72) = 7.35, $p < 0.000$), with the eye exercise group outperforming the control group at two ($p_{Bonf} = 0.022$) and four ($p_{Bonf} = 0.030$) distractors (both p values adjusted with a Bonferroni correction). Although non-significant, the training*condition interaction had a medium effect size (F(1, 18) = 1.179, $p = 0.292$, $\eta_p^2 = 0.061$), and the three-way interaction between condition*training*group also demonstrated a small effect size (F(4, 72) = 0.363, $p = 0.834$, $\eta_p^2 = 0.020$).

Table 2.1. Response accuracy during RSVP task.

	F (df)	***p***	**Effect size (η_p^2)**
Distractor	113.724 (4,72)	.000***	.863
Training	0.663 (1,18)	.426	.036†
Distractor x Training	2.175 (4,72)	.080	.108†††
Distractor x Condition	7.350 (4,72)	.000***	.290
Training x Condition	1.179 (1,18)	.292	.061††
Distractor x Training x Condition	0.363 (4,72)	.834	.020†

*** Significant at P<.001, † Small effect size, †† Medium effect size, ††† Large effect size

Despite the lack of statistical significance of the interactions implicated in eye exercise training, graphical examination of the data (Figure 2.4) together with the overlap of significant effects and noteworthy effect sizes prompted us to examine the three-way interaction further, as it is the most informative with respect to answering our main research question: does eye exercise improve performance on cognitive tasks of visual attention and memory? Pairwise comparisons adjusted with a Bonferroni correction show a significant improvement in response accuracy for the eye exercise group only when one distractor is presented between target letters (p_{Bonf} = 0.050) and was approaching significance when target letters were presented sequentially (p_{Bonf} = 0.079, black and grey bars in Figure 2.4).

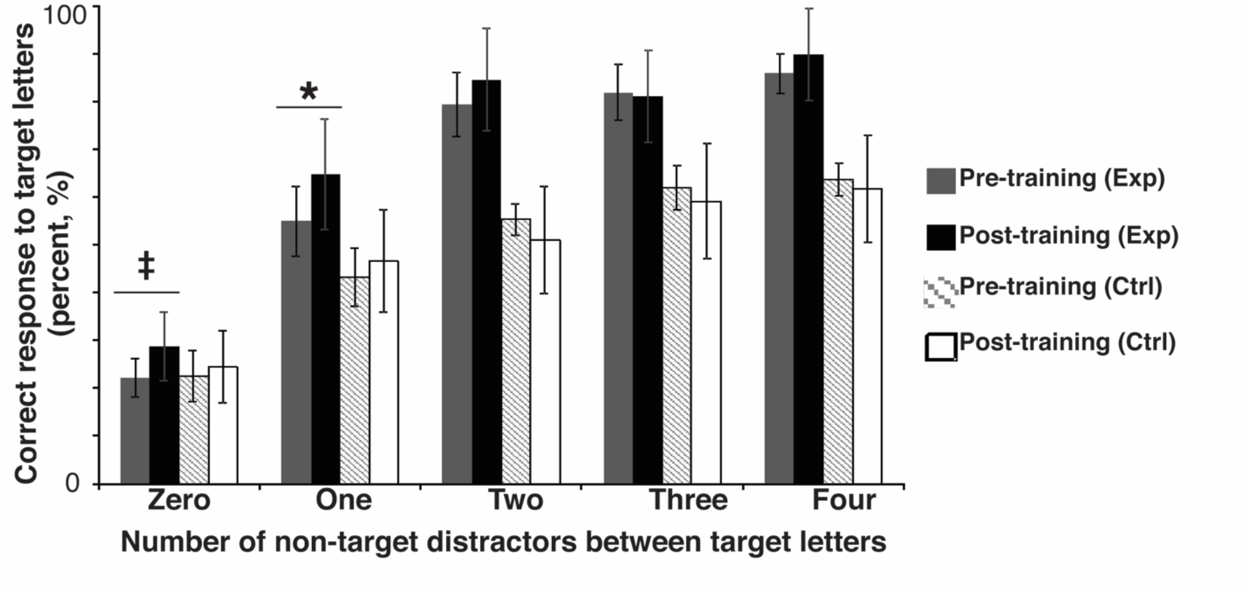

Figure 2.4. Pre- versus post-training response accuracy to RSVP target letters. Subjects who were trained with eye exercise (grey and black bars) showed significant enhancement in responding to target letters separated by one distractor ('One' condition) following eye exercise training, and were approaching significance when responding to two sequentially presented target letters ('Zero' condition). This enhancement was not shown in the control group (cross-hatched and white bars), and there were no changes in either group's accuracy of detecting targets separated by more than one distractor. Error bars show SEM. * p = 0.05, ‡ p = 0.079.

The control group failed to deviate from pre-training performance regardless of the number of distractors presented between target letters ($p > .05$). To clarify any inherent differences in response accuracy between groups pre-training, we conducted *post hoc* one-way ANOVAs for each level of distractor, which revealed subjects in the eye exercise group were better at responding to target letters separated by four distractors (F(1, 19) = 4.55, $p < 0.05$), but groups did not differ in pre-training accuracy in the remaining four distractor conditions (p >

0.1). A composite performance measure comparing correct responses to false alarms (FAs, i.e., pressing spacebar in response to non-target letters) reveal a minimal influence of FAs on response accuracy (d' = 4.12 pre-training for both groups, d' = 3.84 post-training for both groups).

2.4.3 Letter Identification

Subjects in both the eye exercise group and control group were assessed on their ability to correctly identify the final target letter presented in each of the twelve trials per RSVP session. One participant from the experimental group was excluded from analysis due to a malfunctioning button press and lack of registered data. A repeated measures ANOVA revealed a significant increase in letter identification accuracy across both groups (F(1, 17) = 5.138, p = 0.037), but with an interaction effect of training and condition only approaching significance (F(1, 17) = 3.598, p = 0.075). When exploring the nature of this interaction further, pairwise comparisons reveal that only subjects trained with active eye exercises demonstrated significant improvements in letter identification (p = 0.011), while the control group failed to deviate from their pre-training performance (p = 0.791, Figure 2.5). All subjects performed well above the chance rate for guessing the correct letter throughout the experiment (i.e., 1/26 = 3.85%) and groups did not differ in pre-training letter identification accuracy ($t(8) = -0.438$, $p > 0.1$). Sensitivity analyses reveal that only the experimental group significantly reduced the relative number of errors in their performance (d' = -0.04 pre-training, d' = 0.77 post-training, paired-samples $t(8) = -2.92$, $p < 0.01$), while the control group sensitivity measure did not change significantly (d' = 0.07 pre-training, d' = -0.09 post-training, paired-samples $t(9) = 0.738$, $p >$ 0.1). Errors were classified as incorrect letters reported (despite a correct response to target letters), no response and no reported target letters, too many letters identified both with and without responses to each target letter, no letters identified despite correct responses, no response and incorrect letters identified, and no response but correct letter identification.

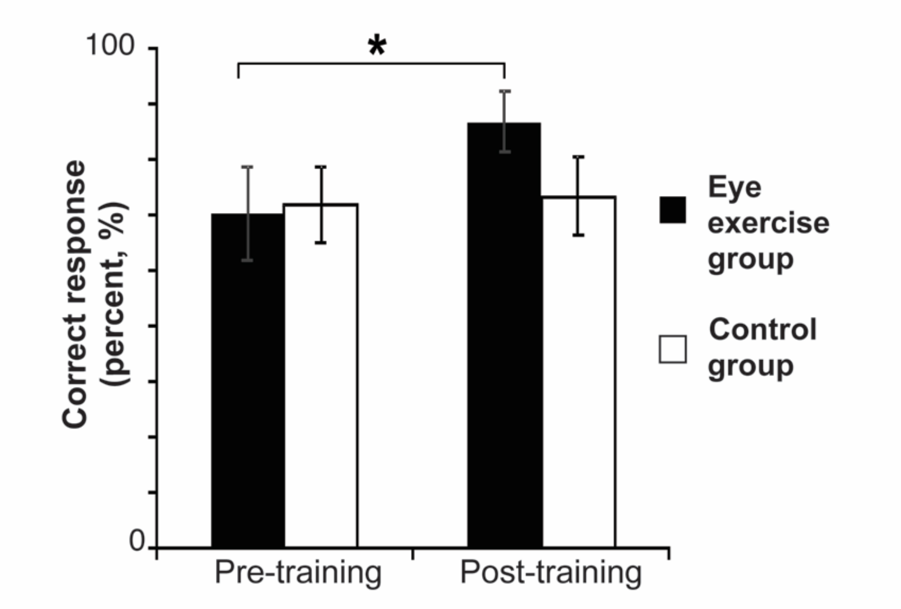

Figure 2.5. Pre- versus post-training letter identification of RSVP target letters. Subjects who were trained with eye exercises showed a significant improvement in letter identification during the post-training RSVP assessment compared to letter identification performed during the pre-training RSVP assessment. Error bars show SEM. * P<0.05.

2.5 DISCUSSION

The purpose of the present study was to determine whether eye exercises alter performance on a visual attention and memory task, which would be suggestive of vision therapy as a useful tool in treating similar and related cognitive and eye-related problems such as amblyopia, myopia, learning disabilities, motion sickness, stereopsis, visual field defects, and visual acuity. Previous studies have investigated whether vision therapy is an effective treatment for eye-related problems (Crisp, 1950; Gallaway & Scheiman, 1997; Harvard Women's Health Watch; Karatz, 1975; Lasky & Lasky, 1990; Leary, Murray & van Selm, 1986; Rawstron et al., 2005; Rodriguez, Hopman & Hoveten, 2012; Roy, 1980); however, these studies did not evaluate any enhancements of cognitive performance. To the best of our knowledge, no direct quantitative measure of improvement on accuracy of eye movements, or in the treatment of impaired cognition, exists following a session of eye exercise. To conduct such an evaluation, we chose to use a simple RSVP task modified from the one used by Joseph et al. (1997). By using a task that demands very high attentional resources at central fixation, we can conclude that the observed improvements in response accuracy (Figure 2.4) and letter identification (Figure 2.5) can be attributed to enhancement as a result of eye exercise. These enhancements may be mediated by short-term changes in neural activity through eye exercise-induced priming and/or mechanistic short-term plasticity of frontal and parietal regions and superior colliculus, which are responsible for visual attention, preparatory motor signaling of the visuomotor system, and working memory (Chan & DeSouza, 2013; Corbetta et al., 1998; DeSouza et al., 2003; Dias et al., 1995; Dorris & Munoz, 1998; Munoz & Everling, 2004; Neggers et al., 2007; Pierrot-Deseilligny et al., 2002; Taylor et al., 2006; Theeuwes et al., 2009).

Neural plasticity is defined as a change in the activity and connections among populations of neurons as a result of experience-based modification in behavior. Importantly, short-term plasticity that occurs over a very brief time span, such as minutes or hours, involves the control and regulation of dynamic activity (Dorris et al., 2000). Although plasticity requires excitatory neural activation in order to occur, the former induces changes in *patterns* of neuronal activity in addition to improved behavioral performance, both of which are maintained long-term with continued practice (Dorris et al., 2000; Dyckman & McDowell, 2005). Although we did not measure changes in cortical activity in our purported neural network, previous work has correlated enhanced oculomotor performance with short-term neuronal plasticity (Dorris et al., 2000). Based on the observed behavioral improvements in response accuracy and letter identification, we can infer that eye exercises successfully primed this network by way of excitatory neural activity which with continued practice could potentially lead to short-term plasticity of the oculomotor circuit. Thus, a brief course of eye exercises may facilitate improvements in cognitive task performance through short-term changes in cortical activity, and could prove to be an effective short-term treatment for other cognitive and eye-related disorders.

There were at least three ways in which a subject could show an improvement in visual attention on the RSVP assessment: (a) faster reaction time when responding to a target letter, (b) overall increased accuracy in responding to target letters, and (c) improved accuracy of target letter identification.

In the present study, reaction times were not significantly different in the post-training session compared to the pre-training for either group (Figure 2.3). The lack of a difference between the two groups suggests that any significance found within the subjects would have been purely due to practice effects associated with RSVP experience. This conclusion is in line with the findings of Dyckman and McDowell (2005), as subjects in their experiment did not experience changes in reaction time. Recently, it has been suggested that reaction time improves on a procedural visuo-motor task with the allowance of sleep following training (Gais et al., 2008). Thus, future studies may need to incorporate a more dispersed regime of eye exercise before any significant improvement on reaction time can be seen. Furthermore, studies have also shown that introducing physical activity to a visual response task can improve reaction time (Joyce, Graydon, McMorris & Davranche, 2009). An improvement was shown not only on tasks requiring a motor response (button press), but also on cognitive processes requiring inhibition of preplanned motor actions (suppressing response to an inhibitory cue). The effects of exercise were observed during, immediately after and at least 52 minutes after strenuous activity on an exercise bike. Thus, future studies may need to incorporate an element of physical activity to further examine its interaction with visual attention.

There were no changes to overall accuracy in response to target letters for the control group. However, following eye exercise, there was a significant increase in accuracy only when responding to two target letters separated by one non-target letter ($p = 0.050$), and was approaching significance when presented in sequence with no distractors between them ($p = 0.079$, Figure 2.4). Additionally, all main and interaction effects analyses including the training factor demonstrated at the very least small but notable effect sizes (Table 2.1). Although we hypothesized that subjects trained with eye exercises would show greater accuracy in responding to target letters than controls, we did not anticipate that the improvements would occur at only the first two levels of our five distractor conditions. We believe that the enhancement of detecting visual cues following a relatively brief (18.5 minutes) period of eye exercise during the two quickest serial presentations of target letters (presented between 50-133ms apart) perhaps reflects the strongest evidence for enhancement of visual attention following eye exercises. That subjects trained with eye exercises were able to significantly improve their performance in one of the two most rapid levels of the RSVP task suggests a high level of reactivity and adaptability of the visuomotor and attentional systems, connected by a common neural network and putatively primed by eye exercises. That the experimental and control groups did not differ at higher levels of the distractor condition could reflect ceiling effects for reaction times to target letters presented with two or more distractors between them (i.e., at least 216ms between presentation of two target letters). This finding is congruent with Dyckman and McDowell's (2005) findings, which demonstrate that response accuracy improved with eye exercise. While our exercise task involved only pro-saccadic eye movements to train for responding to a visual cue in the form of a button press, previous research has utilized fixation, anti- and pro-saccadic training to examine changes in accuracy to the desired response, which in their study was the execution of an anti-saccade. Despite the differences in training and assessment parameters, together our findings suggest an overall interaction between eye movements and improved accuracy on visual tasks. However, Dyckman and McDowell (2005) found a measurable difference in anti-saccade formation after a minimum of three days, whereas our study found significant improvements after only a short training period (18.5 minutes).

A probable neural mechanism for facilitating the observed improvement in response accuracy following eye exercises can be inferred from studies examining trans-saccadic integration, the processing of visual information along the path of an eye movement, which have demonstrated the heightened ability to recognize features of presented objects on a post-saccadic recognition test (Demeyer, De Graef, Wagemans & Verfaillie, 2009). The cognitive processes involved with recognizing the shape, color, or other features of an object may also mediate the recognition of target and non-target letters, as was required in our RSVP task. We found very similar results in a previous fMRI investigation of divided attention. Using the same RSVP task employed in this study while subjects performed pro- and anti-saccades, blood-oxygen-level-dependent (BOLD) activity was increased in oculomotor regions of the prefrontal cortex, including the FEF and dorsolateral prefrontal cortex. Additionally, longer saccade latency and more errors were produced in anti-saccade trials with short (200-250ms) instruction times (Chan & DeSouza, 2013). That the present investigation showed significant improvements in response accuracy during short and successive presentations of target letters (50 to 133ms apart) could reflect short-term plasticity and enhancement of neuronal signals in the oculomotor cortical circuit due to a brief training period of eye exercises. Further evidence in support of this putative neural mechanism in mediating increased accuracy for object recognition, such as whole words, comes from a study by Lyle and colleagues (2008) that shows enhanced recall of a word following 30 seconds of horizontal eye movements preceded by the study of a word array.

Because past research has found pursuit of a moving square through a circle path to stimulate creativity (specifically, originality and flexibility), it comes as no surprise that eye movements may similarly influence cognitive areas (Shobe, Ross & Fleck, 2009). Our study compared improvements in letter identification accuracy between groups. Following eye exercises, a significant improvement in letter identification was found ($p < .05$, d' = -0.04 pre-training, d' = 0.77 post-training). This enhancement in accuracy was not observed in our control group, who performed at a similar level to their pre-training assessment (Figure 2.5). This is in line with past research, which found horizontal eye movements also improved the recall of laboratory and everyday events (Christman, Garvey, Propper & Phaneuf, 2003). However, this was found solely for horizontal saccade formation, and not for vertical or smooth pursuit saccades. A possible mechanism for this improvement has been further suggested by Murray, Beutter, Eckstein and Stone (2003). On a visual search task, they demonstrated that during saccade formation, one could assess visual objects based on shape. From these findings, we could infer that eye movements increase one's ability to identify a change in letter shape. Indeed, it was found in our study that participants performed well above chance for observing a change in letter rather than color. If participants were unable to identify the change in letter, they would guess with an accuracy rate of 3.8% (1/26 letters in English alphabet). A study by Brunyé, Mahoney, Augustyn and Taylor (2009) supports this claim by finding that horizontal eye movements enhance the detection of changes in landmark information, specifically the shapes and locations of objects. However, their findings were only applicable to horizontal eye movements, due to a negligible effect in vertical saccades and fixation, and examined much more complex visual cues. Together these investigations from their respective varying perspectives all lend evidence to increased inter-hemispheric brain activation with the performance of repeated bilateral horizontal eye movements.

Another interesting interaction between object recognition and eye movements comes from research on the interference of neural processing as a result of eye blinks. As demonstrated by Thomas and Irwin (2006), voluntary eye blinks interfered with object identification during trans-saccadic partial reports. They named this phenomenon the *cognitive blink suppression¸* and postulated that this process hinders neural processing of visual stimuli. In relation to our study, a similar suppressive process may exert an influence on letter identification accuracy. However, our study did not involve voluntary blinking, nor did we utilize an eye tracking mechanism to track eye blinks during the experiment. Future studies could incorporate these elements to provide potential clarification on this interaction. Additionally, our future studies will examine the enlarging of pupil dilation, which has now been found to be co-activated during stimulation of a brain structure involved in attention and eye movements in non-human primates (Wang, Boehnke, White & Munoz, 2012). However, we do not feel that this phenomenon is an influential factor in explaining our results because subjects were not required to perform eye movements during the RSVP task.

More recently, vertical saccades have been shown to improve performance on item retrieval, pair association tests, and recall of contextual information, both intrinsic (color) and extrinsic (spatial location) (Parker, Relph & Dagnall, 2008). Further, smooth pursuit studies in preschool children have correlated the inability to follow an instructor's cue with lower scores on cognitive tests in phonological awareness, path copy and letter recognition (Callu et al., 2005).

This is to show that these types of eye movements deserve further study to clarify their involvement in enhancing cognition.

Together with our results, we use these lines of research to propose an underlying neural mechanism that facilitates the enhancement of visual attention and memory following eye exercises, even when performed for a very brief training period. Common functional regions of the cortex have been activated during tasks of shifting visual attention and eye movements. This wide-reaching network includes the superior temporal sulcus (STS), intraparietal sulcus (IPS), and portions of the precentral sulcus and medial frontal gyrus (Corbetta et al., 1998). It is important to note that these investigators did not examine changes in accuracy or response time over the course of task performance (i.e., with time, accounting for practice or ceiling effects). As they pertain to our investigation, however, the continued and synchronous activation of this network during the brief eye exercise task may have been sufficient to facilitate short-term plasticity (Dorris & Munoz, 1998). Similarly, eye exercise may induce neuronal potentiation, effectively “ramping up” preparatory oculomotor signals in dorsolateral prefrontal cortex and frontal eye fields (DeSouza et al., 2003), priming these pre-existing neuronal circuits to facilitate the enhancement in response accuracy seen in our results.

We further posit that a similar mechanism can be attributed to the observed improvement in letter identification for the eye exercise group, with previous research showing links between regions related to working memory, attention and eye movements. Although these investigations examine spatial memory, and not declarative memory as in the recall of a presented target letter, they implicate the lateral intraparietal area as an attentional mediator of eye movements, which are executed by the superior colliculus (Theeuwes et al., 2009). Training with eye exercise could similarly induce short-term plasticity and/or potentiation of connecting axonal signals in this cortical network, enhancing the availability of neuronal resources in the letter identification portion of the post-training RSVP task. In turn, this priming could facilitate the enhancement in letter identification observed in our results.

2.6 CONCLUSIONS

The results of this experiment found a performance enhancement for the detection of visual targets when presented in very rapid succession (i.e., separated by one or no distractors) following repetitive eye movements. Although the RSVP task did not demonstrate any differences in reaction time following the eye exercises, there was a significant increase in letter identification accuracy in the experimental group only. Theoretically, these results suggest that a common cortical network that mediates cognition, attention, and oculomotor behavior (i.e., knowledge schema) is capable of undergoing very short-term plasticity, which in turn improves subsequent performance on related tasks. However, more research needs to be done before letter identification through RSVP can be deemed an appropriate tool for measuring the progression of vision therapy, and whether vision therapy is the most effective option for cognitive and eye-related impairments. Further examinations could incorporate eye tracking, a more dispersed regime of visual training, or examine training of whole-body movements to clarify what effects visual and/or movement therapy may have on the performance of cognitive tasks.

3 CHAPTER THREE – FAMILIARITY AND EXPERTISE MODULATE EVENT SEGMENTATION OF DANCE AND RECALL OF EXPERIENTIALLY-RELEVANT WORDS[2]

3.1 PREFACE

Having demonstrated significant improvements in attention and working memory (WM) following short-term eye exercises (Di Noto et al., 2013, Chapter 2), the aim of the current study is to determine whether these cognitive processes are influenced by long-term physical practice manifested as expertise. Attention can be measured with event segmentation - a perceptual process by which observed actions are partitioned into discrete meaningful units that also facilitates their learning (Zacks et al., 2001). When segmenting dance, expertise in the observed repertoire has been shown to result in significantly fewer segments or event borders (Bläsing, 2015). Whether such expertise effects are generalized to segmenting unfamiliar genres of dance or non-dance movements has yet to be shown. The present study sought to investigate differences in segmentation of a ballet dance, a traditional Tamil Bharatanatyam dance, and a non-dance acting sequence among experts from six groups (total N=112): ballet and Bharatanatyam dancers, dancers from other genres (e.g., contemporary, jazz, tap), athletes, musicians, as well as non-experts. Between blocks of event segmentation, subjects (N=106) performed a WM Retrieval-Induced Forgetting (RIF) task. First, subjects were shown 60 category-exemplar word pairs (e.g., FRUIT – apple) from 10 categories. Dance, Instrument, and Sport categories were included to probe domain-specific WM performance and 'knowledge schema' activation among expert groups. Practice recall of a subset of exemplars was performed

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[2] Paula M. Di Nota, Michael P. Olshansky & Joseph F.X. DeSouza. Presented at Society for Neuroscience Annual Meeting and Cell Symposium: Big Questions in Neuroscience (November 2016), San Diego, CA

immediately following presentation of the word pairs. Subsequent recall of practiced words (Rp+), non-practiced words from practiced categories (Rp-), and non-practiced words from non-practiced categories (Nrp) was assessed between blocks 2 and 3 of event segmentation. Segmentation results show significantly fewer event borders among Bharatanatyam dancers when segmenting a familiar dance sequence relative to dancers from other genres during early trials (trials 1 to 5 of 10 trials, $p = 0.02$), providing novel evidence for genre-specific familiarity effects during dance segmentation. Consistent with previous studies, all participants showed significant practice effects (Rp+ > Nrp) and RIF (Nrp > Rp-) ($p_{\text{Bonf}} = 0.000$). Most importantly, we provide novel evidence for significantly enhanced recall of words from experientially-primed categories such that ballet and Bharatanatyam dancers remembered more Dance words than all other groups following observation of a familiar dance sequence. Together these findings provide novel evidence for the translational benefits of long-term expertise on perceptual and cognitive processing. By priming knowledge schemas with actions specifically tuned to the observer's motor repertoire, event segmentation becomes more efficient and WM for experientially-relevant items is improved.

3.2 INTRODUCTION

Imagine a dancer gracefully moving across a stage, performing a sequence of precisely-timed choreography. When viewing continuous streams of action, human observers unconsciously break down these series of movements into discrete chunks or *events* (Zacks et al., 2001a). Two prominent theories account for how and why we segment action in this way; according to the Theory of Event Coding, it allows an agent to perceive, understand, and perform a given set of actions that form an embodied repertoire that is both cognitive and motoric

(Hommel, 2015; Hommel, Müsseler, Aschersleben, & Prinz, 2001). The development of these knowledge schemas (see Section 1.3, Figure 1.1) also facilitate the prediction of outcomes in future interactions with similar contexts, in turn enabling adaptive learning of appropriate behaviors (Swallow & Zacks, 2008). Similarly, Event Segmentation Theory (Zacks et al., 2001,a,b; 2010) proposes that "chunking" or segmentation unfolds in real-time to meaningful, reliable and ecologically relevant features of action, as well as to conceptual changes in the goals, interactions and causal relations of observed agents (Zacks, Speer, Swallow, & Maley, 2010). This allows the observer to discern the individual component events (slicing bread, putting meat and condiments between them) of a longer meaningful sequence (making a sandwich). The 'borders' of these events define its structure, which is encoded and updated in both working and long-term memory (Swallow, Zacks, & Abrams, 2009). That segmentation also occurs when reading narratives about actions (Speer et al., 2007) demonstrates the strong link between language, action, and engrained knowledge schemas.

Event borders are structured hierarchically, with longer 'coarse' events comprised of groups of 'fine-grained' segments. When tested experimentally participants are asked to segment the largest units of 'natural and meaningful' movements to satisfy the former condition, and to segment the smallest units of activity during fine segmentation conditions (Speer et al., 2003). While experimenters are careful to not influence the nature of participants' segmentation behaviour, the ambiguity of these instructions may account for the sensitivity of event borders to individual differences (Zacks et al., 2001a) that are nonetheless reliable over time (Speer et al., 2003). This stability can be attributed to several factors, including the top-down modulation of attention by engrained knowledge schemas of constituent motor representations (Hemeren & Thill, 2011), event/object features, and sequential dependencies (i.e., that underwear are put on before pants in the sequence of 'getting dressed') acquired through experience (Schubotz, Korb, Schiffer, Stadler, & Cramon, 2012; Zacks et al., 2001b). Research on individuals with dementia has shown that aberrant segmentation behaviour predicted poorer naturalistic action performance (packing a lunchbox or schoolbag), and that medial temporal lobe volume predicted deficits in episodic memory of such tasks. These findings suggest that the ability to segment, describe, and encode action is critical for successful motor performance, and that these processes likely recruit from common underlying knowledge schemas (Bailey, Kurby, Giovannetti, & Zacks, 2013a; Bailey, Zacks, Hambrick, Zacks, Head, et al., 2013b).

The itemization of component movements that can be recombined to form a novel sequence is perhaps best exemplified by dance, which has garnered a growing body of literature in the field of cognitive neuroscience (for review see Chatterjee, 2011). While segmentation has been demonstrated during passive listening to music (Sridharan, Levitin, Chafe, Berger, & Menon, 2007), only two studies have explored the active segmentation of observed dance movements. Noble et al. (2014) had non-expert participants segment a traditional Tamil Bharatanatyam dance and identified active brain regions at the time points associated with the most frequent event borders in a separate group of non-experts. They found significant activation in inferior frontal and occipital gyri and right posterior superior temporal sulcus (pSTS). When comparing segmentation in experts with non-experts, Bläsing (2015) found that dancers familiar with the observed genre respond with fewer event borders relative to non-dancers, and with even fewer event borders after physically learning and performing the dance sequence. While these two investigations compared neurological and behavioural measures of event segmentation in non-experts and/or experts highly familiar with the genre of the experimental stimulus, it remains to be observed whether these effects are generalizable to 1) expert dancers in other genres of dance, and/or 2) experts in other physical activities, including music and athletics.

When considering dance as a (non-verbal) communicative set of temporally extended movements, it can be considered functionally similar to language. Indeed, several studies have found activation of language processing regions, including dorsomedial prefrontal cortex (DMPFC), inferior frontal gyrus (IFG), and pSTS, when processing coherence and syntax of musical (Kunert, Willems, Casasanto, Patel, & Hagoort, 2015) and dance stimuli (Bachrach, Jola, & Christophe, 2016). Verbal communication plays a central role in one's ability to segment events in time, as well as in describing them later on from memory. Such 'off-line' conceptions of events facilitate planning and understanding (Zacks et al., 2001a,b) and therefore rely on linguistic narrative structures encoded in putative knowledge schemas (Figure 1.1).

The translational cognitive benefits of physical expertise in sports, music, and dance, have been extensively explored (for review, see Debarnot, Sperduti, Di Rienzo, & Guillot, 2014). The refinement of knowledge schemas through neuroplastic changes to motor, perceptual and cognitive processing areas (Bar & DeSouza, 2016; Di Nota et al., 2016; Gaser & Schlaug, 2003; Hänggi et al., 2010; Kattenstroth, Kalisch, Holt, Tegenthoff, & Dinse, 2013; Olshansky, Bar, Fogarty, & DeSouza, 2015) is suggested to facilitate several functions to achieve peak performance. This includes WM and executive control functions like inhibition of task-irrelevant information, both of which can be assessed with the Retrieval-Induced Forgetting (RIF) task (Howard, Johnson, & Pascual-Leone, 2014; Storm & Bui, 2015). This paradigm presents subjects with category-exemplar word pairs (e.g., FRUIT – lemon, PROFESSION – accountant) from several categories before receiving retrieval practice on a subset of exemplars and categories (e.g., FRUIT – le__). This results in three types of items: practiced words from practiced categories (Rp+), non-practiced words from practiced categories (Rp-), and non-practiced words from non-practiced categories (Nrp). Upon subsequent recall of all exemplars following a brief (approximately 10 to 20 minute) retention interval, it has been shown that participants reliably recall Rp+ items best, and that Nrp items are recalled better than Rp- items. It is suggested that the retrieval practice of Rp+ items creates competition for limited working memory resources and suppresses retention of Rp- items from the practiced category at final recall (Anderson, Bjork, & Bjork, 1994; 2000; Williams & Zacks, 2001). However, whether the activation or priming of these expert knowledge schemas by one cognitive process (e.g., observing a dance sequence) influences performance in another cognitive domain (e.g., response inhibition or memory recall) remains to be seen.

The purpose of the present study was to explore whether priming knowledge schemas modifies verbal attention and WM performance as assessed by event segmentation and RIF tasks, respectively. Previously demonstrated expert effects of reduced event borders during dance segmentation (Bläsing, 2015) are limited to familiar genres of dance, and do not explore whether experts in other activities like sports or music also show modified segmentation behaviour. If so, these findings would provide novel evidence for experience-dependent familiarity effects when segmenting dance, and expertise effects more generally when segmenting non-dance movements, respectively. We will use a Ballet[3] video to test segmentation behaviour of a familiar genre for ballet dancers, who will also segment an unfamiliar Bharatanatyam video. Additionally, we will recruit Bharatanatyam dancers to test familiar and unfamiliar segmentation in another group of dancers. We will also include a non-dance Acting condition to compare event segmentation of non-dance movements among various types of

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[3] Ballet will be capitalized to denote the experimental video condition, while lowercase ballet will be used to refer to the experimental group.

experts (i.e., dancers, athletes, musicians) as well as non-experts. We predict that dancers familiar with the observed genre (i.e., ballet dancers segmenting the Ballet video) will indicate fewer event borders than dancers from unfamiliar genres (Bharatanatyam and others). We also predict that all expert groups, including dancers, athletes, and musicians, will segment all video conditions less than non-experts, demonstrating generalized expertise effects during event segmentation of dance and non-dance movements.

With respect to the RIF task, we expect well-established practice effects and RIF to be demonstrated among all participants. We also predict that experts will have improved recall of experientially-primed words via activation of embodied knowledge schemas such that all dancers (including ballet and Bharatanatyam), athletes and musicians will remember Dance, Sport and Instrument exemplars better than other categories and groups, respectively. We expect the results to be especially pronounced among dancers due to observation of dance stimuli for the event segmentation portion of the experimental paradigm.

3.3 METHODS

3.3.1 Validation Experiment

We performed a Validation Experiment with a separate group of non-expert participants for two reasons: 1) to identify one video clip from each of the three conditions that contained equal numbers of event borders in order to attribute any observed between- or within-group differences to participants' prior experience, and 2) to determine the parameters (i.e., trial, block, and experiment duration) that would optimize the number of segmentation trials per condition while including an interleaved memory task and minimizing overall experiment duration and possible fatigue.

3.3.1.1 Participants

A total of 30 participants (20 female, mean age = 23.3 years, *SD* = 4.5) were recruited from the York University community and Undergraduate Research Participant Pool (URPP), and were compensated with partial course credit. One participant's data was excluded due to non-compliance, and another two subjects were excluded following outlier analyses (i.e., for having normalized event borders exceeding 2.5 standard deviations from the mean of all participants, $z > 2.5$). Thus, a total of 27 participants (18 female, mean age = 23.4 years, *SD* = 4.5) were included in final analyses, and reported an average of 2.46 (*SD* = 3.5) years of experience in either dance, sports, or music. To reduce any possible expertise effects, we exclusively recruited non-experts for the Validation Experiment. Participants were deemed experts if they had a minimum of 5 years of experience, and had practiced their skill on a regular basis (minimum 3 times a week) within the last two years. No participants in the Validation Experiment met this criteria, and those with more than 5 years' experience discontinued regular practice more than two years prior to the study. All participants had normal or corrected vision and were free of any neurological disorders. All procedures, including the validation and main experiments, were approved by the York University Human Participants Research Review Sub-Committee (Certificate # 2013-313).

3.3.1.2 Video Stimuli and Apparatus

Three one-minute video clips were selected and saved from each of the original Ballet (4mins 53sec), Bharatanatyam (5min 5sec), and Acting (4min 46sec) MP4 video files obtained from the Perception Action and Cognition Lab website (http://paco.psy.gla.ac.uk/index.php/component/content/article/39-res/res-proj/67-watching-dance-kinesthetic-empathy). Detailed description of the movement features and musical accompaniment of the videos can be found in Jola, Abedian-Amiri, Kuppuswamy, Pollick, and

Grosbras (2012). The nine clips were generated using iMovie 2011 (Version 9.0.9 1795, Apple Inc.). It was ensured that all clips had similar sound profiles according to visual inspection of built-in waveforms provided by the movie editing software, and that no clip began or ended in the middle of a movement to reduce the potential of response errors or 'misses'. Each of the resulting nine clips were exported as M4V files with a 25fps frame rate and size of 480 x 272 pixels. To be compatible with the presentation software (MatLab, Version 7.10.0.499, The MathWorks, Inc., Natick, MA, and Psychtoolbox, Version 3, Brainard (1997)), video clips were converted to MPG format with Media Converter 2013 (Version 8, ArcSoft Inc., Fremont, California) and specified to remain at 25fps frame rate and 480 x 272 pixels. All stimuli and experimental protocols were presented using custom Matlab code on a 24-inch iMac desktop computer with adjusted 1024 x 640 resolution, resulting in 9.5 x 5.5 inch video playback (horizontal visual angle = 21.1°). Participants were provided with noise cancelling headphones (Model MDR-NC7, Sony Corp., Tokyo) to hear accompanying musical stimuli, with volume manually adjusted to each participant's comfort level before the onset of the experiment.

3.3.1.3 Procedure

Prior to briefing, participants provided informed consent and filled out a demographic questionnaire where they self-reported the type and number of years of experience in dance or any other physical craft. These responses determined which group participants would be assigned to (all non-experts for Validation Experiment). Event segmentation was defined and explained to participants, who were instructed to watch a series of nine one-minute videos (3 x ballet, 3 x Bharatanatyam, 3 x acting) and press the spacebar anytime they perceived one natural and meaningful unit of expressive movement begin, and another end (Speer et al., 2003; Zacks et al., 2001a). It was also explicitly stated that participants did not need to press the spacebar once to indicate the end of a movement and then once again immediately following to indicate the start of a subsequent movement, but that one button press was sufficient to mark the "border" between two movements. Participants were reassured that there was no right or wrong answer, and to simply do their best for each trial. They were also instructed not to worry about replicating responses on previous trials for the same video but to simply segment each video as it comes, and to focus on the movements and not the background music when identifying event borders. Although previous event segmentation studies specify fine versus coarse-grained segmentation (Zacks et al., 2001a,b), we attempted to remain as consistent with Bläsing's (2015) paradigm as possible and did not instruct participants with these terms, but rather suggested that they segment each "expressive dance move" rather than each individual component movement they see, which is more in line with coarse-grained segmentation.

Following these instructions, participants were given the opportunity to perform a practice trial during which the experimenter remained in the room to ensure participants understood the task and could perform it properly. Following a series of instruction screens that repeated the experimenter's verbal instructions, a 30-second version of one of the nine video clips was randomly selected and played twice. For the first presentation, participants were instructed not to press the spacebar but to passively watch the video in order to familiarize themselves with the scene and setting, and to be able to anticipate how to respond in the subsequent presentation. Next, participants were instructed that the same clip will play again and that they should now practice segmenting by pressing the spacebar. The experimenter observed all participants perform this practice trial, and none of them demonstrated or indicated any difficulty in performing the task. Following the practice trial, the experimenter left the testing room and continued to monitor participants for compliance through a two-way window in an adjacent room. The nine videos (3 x Ballet, 3 x Bharatanatyam, 3 x Acting) were played five times each for a total of 45 trials. Trial order was randomized to minimize practice effects and encourage stimulus-driven event segmentation of all clips. Trials were presented in four blocks of ten trials (2-second inter-trial interval) and a final shorter block of five trials (Figure 3.1a). Blocks were separated with an instruction screen that indicated how many blocks were left,

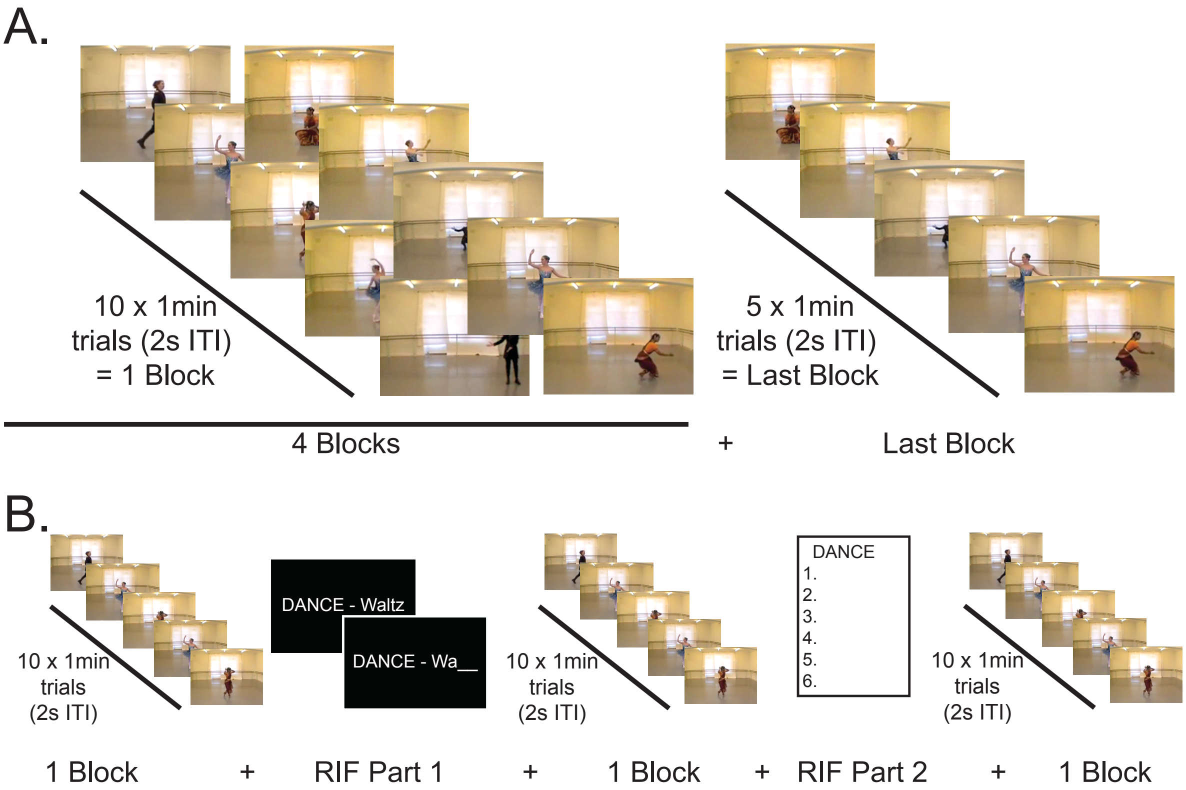

Figure 3.1. Validation and event segmentation protocols.
A. Three 1-minute clips were selected from each original video (Ballet, Bharatanatyam, Acting) for a total of nine video clips for the Validation Experiment. Subjects were presented with five trials of each clip in random order for a total of 45 trials presented in 5 blocks [(4 blocks x 10 trials) + (1 block x 5 trials)]. **B.** Based on results of the Validation Experiment, one clip from each category was chosen for the final Event Segmentation Experiment, which included a Retrieval Induced Forgetting (RIF) memory task interleaved between blocks of segmenting the videos. Each video was played 10 times in random order across 3 blocks of 10 trials each. The RIF task is comprised of two parts: Part 1 includes presentation of 60 category-exemplar word pairs (10 categories x six words each) and practice recall of 18 presented words. Following one block of event segmentation, Part 2 had participants recall as many words as possible from the original 60 category-exemplar pairs.

repeated the event segmentation instructions, and offered an optional break. Participants continued to the next block by pressing the spacebar.

3.3.1.4 Statistical Analyses

The dependent variable for the Validation and Event Segmentation Experiments were the average number of event borders for each video clip across all trials. Although it has been noted that event borders are difficult to characterize by normative criteria (Zacks et al., 2001a), previous investigations typically use analyses of variance (ANOVAs) (Zacks et al., 2001b) to compare between-group and within-subject differences in event segmentation. These methods are problematic, as the distribution of event borders typically does not satisfy the ANOVA normality assumptions. As such, the present investigation used non-parametric analyses similar to those employed by Bläsing (2015) to compare event borders between groups and within subjects over repeated trials and conditions. Specifically, the average number of event borders per condition were analyzed for normality with Shapiro-Wilk tests and subsequently compared with non-parametric related-samples Wilcoxon signed rank tests for non-normal data using SPSS (Version 22, IBM Co., Armonk, NY).

3.3.1.5 Validation Results

Statistical analyses revealed that all of the Acting video clips had significantly fewer event borders than any of the Ballet and Bharatanatyam videos (Figure 3.2). Acting Video 3 was selected for the final Event Segmentation Experiment due to having the highest number of average event borders, and will be analyzed separately from the dance videos for possible between-group effects. While Ballet Video 1 did not significantly differ from any of the Bharatanatyam video clips, it was not selected for the final experiment due to having the highest variability in responses (*SD* = 23.3). Thus, Video 2 for the Ballet and Bharatanatyam conditions were selected for the final experiment due to having the lowest significance value between them (*p* = 0.039), but will also be analyzed separately for between-group effects.

3.3.2 Event Segmentation Experiment

3.3.2.1 Participants

A total of 116 participants (89 female, mean age = 21.64 years, *SD* = 7.1) separate from those included in the Validation Experiment were recruited from the York University community and URPP, and were compensated with partial course credit. Participants were assigned to one of six groups based on self-reported previous experience: ballet, Bharatanatyam, dance (i.e., in genres other than ballet and Bharatanatyam), musician, athlete, and non-expert. Participants were required to have at least five years of experience within the last two years to be deemed experts and assigned to an expert group. Many participants had experience in multiple activities (i.e.,

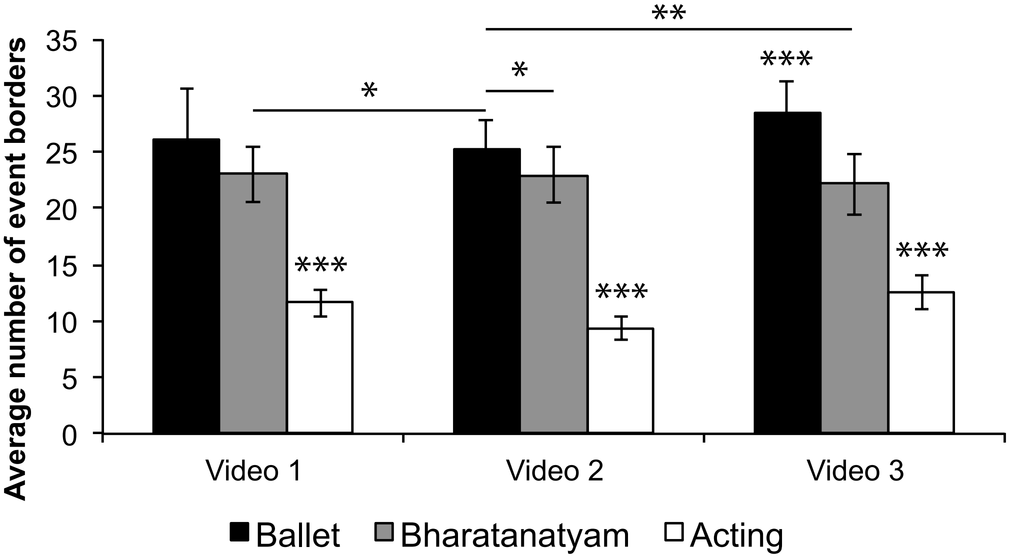

Figure 3.2. Validation experiment results.
Only ballet Video 1 did not differ from any of the other dance videos, but had the highest variation in event borders. All acting videos had significantly fewer event borders than the ballet and Bharatanatyam videos.
* P<0.05 ** P<0.01 *** P<0.001. Error bars show SEM.

ballet, music and sports), and were assigned to the group that they had the most experience in and/or self-reported as being their most practiced and mastered activity. Participants with dance experience in Bhangra and/or Bollywood were assigned to the dance group, as these genres are distinct from the South Asian/Tamil Bharatanatyam dance presented. Musician and athlete groups were included and differentiated from a general (non-dance) expert group to explore any putative and distinct contributions of musical and non-musical physical expertise, respectively. One subject from the ballet group was excluded due to medical reasons, and three participants (one dancer, one athlete and one non-expert) were excluded following group-level outlier analyses ($z > 2.5$) on the average number of event borders[4]. Thus, a total of 112 participants (88 female, mean age = 21.63 years, *SD* = 7.1, mean years of experience = 9.85, *SD* = 5.8) were included in analyses (Table 3.1).

Table 3.1. Demographic information for event segmentation and RIF tasks.
* Denote groups that have different participant data for the event segmentation and RIF portions of the experiment.

Group	**Event Segmentation**			**Retrieval-Induced Forgetting**		
	n (Female)	**Age - M (SD)**	**Years of Experience - M (SD)**	**n (Female)**	**Age - M (SD)**	**Years of Experience - M (SD)**
Ballet	19 (19)	21.8 (7.6)	12.8 (5.1)	19 (19)	21.8 (7.6)	12.8 (5.1)
Bharatanatyam	16 (16)	20.4 (5.9)	11.7 (7.4)	15 (15)	20.5 (6.1)	12.2 (7.5)
Dance*	17 (15)	24.1 (7.5)	11.4 (5.5)	17 (14)	23.8 (7.5)	11.6 (5.4)
Musician	20 (13)	21.9 (10.1)	10.9 (4.5)	20 (13)	21.9 (10.1)	10.9 (4.5)
Athlete*	20 (12)	20.1 (3.0)	9.9 (3.4)	19 (10)	20.1 (3.0)	9.6 (3.1)
Non-Expert*	20 (13)	21.7 (7.0)	3.1 (2.2)	16 (11)	21.3 (7.6)	3.1 (2.4)
Total	**112 (88)**	**21.63 (7.1)**	**9.85 (5.8)**	**106 (82)**	**21.6 (7.3)**	**10.1 (5.7)**

3.3.2.2 Procedure and Statistical Analyses

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[4] Participants were considered outliers and removed from analyses if they exceeded 2.5 standard deviations above the normalized group mean for any video condition (Ballet, Bharatanatyam, or Acting).

Initial debrief, instructions and practice trial procedures were identical to the Validation Experiment. Participants were instructed to segment three one-minute videos – one Ballet, one Bharatanatyam, and one Acting (selected from the Validation Experiment). Each video was presented ten times for a total of 30 trials, which were presented in blocks of 10 (Figure 3.1b). Participants were told that they would perform a two-part memory task between blocks (see next section). The dependent variable for the event segmentation portion of the experiment is the average number of event borders per condition, which were divided into early (trials 1 to 5) and late (trials 6 to 10) trials. Within-group comparisons were performed using non-parametric Wilcoxon signed-rank tests for non-normal data.

Because the Validation Experiment failed to show similar frequency of event borders between conditions, each condition was analyzed separately. Planned comparisons include comparing each group to the familiar group for each dance condition (ballet and Bharatanatyam, respectively) using non-parametric Mann-Whitney U tests as in Bläsing (2015). For the Acting condition, between-group effects were explored with a non-parametric Kruskall-Wallis test.

3.3.3 Retrieval-Induced Forgetting (RIF) Task

3.3.3.1 Participants

Of the 113 event segmentation participants who performed the RIF task and were free of medical exclusions (87 female, mean age = 21.62 years, *SD* = 7.1), one (non-expert) was excluded for skipping the practice recall of Part 1, four subjects (three non-experts and one dancer) were excluded for completing Part 2 at the wrong time during the experiment, and two subjects (one athlete, one non-expert) did not complete Part 2. Four non-experts not included in the event segmentation portion of the experiment were tested to even out the group sizes (Table

3.1), and a total sample of 106 participants (82 female, mean age = 21.56, *SD* = 7.3) were analyzed for the RIF portion of the experiment.

3.3.3.2 Procedure

Following initial instructions on the event segmentation task, the experimenter told participants that their working memory (WM) would also be assessed between blocks of event segmentation. Participants were told that they will be presented with 60 category-word pairs (see Appendix A): the first word in each pair will be a category and shown in capital letters (e.g., CLOTHING), and the second word in each pair will be an exemplar from the category shown in lower case (e.g., pants)[5]. Participants were instructed to focus on the second word in each pair (i.e., the exemplar) as they would be required to remember them later in the experiment, similar to our Di Noto et al. (2013) study.

Category-exemplar pairs, RIF instructions and procedures were modeled according to Howard et al. (2014), programmed in custom Matlab script, and integrated with the event segmentation paradigm. Word categories included Colours, Fruits, Relatives, Tools, Weather, Vegetables, and Vehicles, as well as Instrument and Sport words that would assess recall of experientially-primed words in musicians and athletes, respectively. To test experientially-primed recall among dancers in ballet, Bharatanatyam, and dance groups, a category of Furniture words was replaced with Dance words generated by the experimenters. Exemplars were obtained by searching for synonyms of the word ‘dance’ on three vocabulary and thesaurus websites (https://myvocabulary.com, http://theseaurus.com, and www.onelook.com). The final six exemplars were chosen by cross-referencing the results of the web searches and excluding non-

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[5] The experimenter took care not to provide examples that would be presented in the experiment to avoid any priming or reinforcement of experimental stimuli.

English words related to ballet (e.g., ballet, barre, plie, pointe). The final six dance exemplars were “choreography”, “jig”, “rhythm”, “tango”, “tap”, and “waltz”.

After the first block of event segmentation (Figure 3.1b), participants performed Part 1 of the RIF task. Instructions were repeated on screen and participants were instructed to press the spacebar when they were ready to see the category-exemplar pairs. Each of the 60 pairs were presented in random order at the centre of the black screen in white font (vertical visual angle = 5.6°) for 1.5 seconds each. After the final word pair, an instruction appeared on the screen informing participants to wait for the experimenter before proceeding. Keeping track of participants’ progress through a two-way mirror, the experimenter entered the testing room and performed a practice recall of 18 words that had just been presented (for list of Rp+ words, see Appendix A). Participants were shown a category and the first two letters of an exemplar that had just been shown (e.g., “FRUIT – ap_____”) and were instructed to say the word out loud if they remembered it (“apple”). If they could not remember the word, they were instructed to say “pass”, and the next word was presented by pressing the spacebar. The experimenter recorded correct responses as a score out of 18 to assess the first dependent variable of the RIF task – percent accuracy of practice (Rp+) recall.

Following the practice recall, the experimenter explained to the participant that they would now perform another block of the event segmentation task before completing Part 2 of the memory task. Participants were provided with a sheet of paper listing each of the ten categories with a blank numbered list from one to six beneath each category (see Appendix B). Participants were instructed that Part 2 required them to write down as many words as they could recall when prompted by instructions on the screen. In accordance with RIF instructions (Anderson et al., 1994; 2000) final recall was performed approximately ten minutes after presentation of the category-exemplar pairs, which aligned perfectly with performing one block of event segmentation. As such, participants were explicitly instructed not to begin filling in the final recall sheet until instructed to do so, and not to continue with the final block of event segmentation until they had completed the recall sheet for Part 2.

Correct responses on the final recall sheet were coded as follows: practiced words from practiced categories (Rp+, e.g., FRUIT - apple), non-practiced words from practiced categories (Rp-, e.g., FRUIT – peach), and non-practiced words from non-practiced categories (Nrp, e.g., RELATIVE – cousin). For each participant, we evaluated practice effects defined as improved recall of Rp+ over Nrp, and RIF - improved recall of Nrp over Rp-. We also compared the number of Dance, Sport[6], and Instrument words recalled between groups with the expectation that experts will demonstrate improved recall for experientially-primed words during both practice and final recall relative to other groups and non-experts.

3.4 RESULTS

3.4.1 Event Segmentation

3.4.1.1 Average Event Borders

As in Bläsing (2015), early (trials 1 to 5) versus late (trials 6 to 10) trials were analyzed for each condition with Wilcoxon Signed-Rank Tests (Table 3.2). Only ballet dancers had more segments in late trials for the Ballet ($p = 0.021$) and Acting ($p = 0.001$) conditions. No other groups differed in the average number of event borders for early and late trials in any condition.

When comparing the familiar experts in each dance condition to all other groups, significant between-group effects were only observed during early trials. Specifically,

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[6] Sport words were not included in practice recall and are thus considered Nrp items. However, the number of Sport words recalled during final recall (Part 2) was compared between groups for possible expertise effects.

Bharatanatyam dancers provided significantly fewer event borders when segmenting a familiar Bharatanatyam dance compared to Dancers (U = 189.5, p = 0.022). However, there were no between-group differences in event segmentation of the Ballet condition when comparing ballet dancers to all other groups in early or late trials (p > 0.05) (Figure 3.3). For the Acting condition, there was no difference in the average number of event borders observed between groups for early [χ^2 (df=5) = 7.85, p > 0.10] or late trials [χ^2 (df=5) = 5.04, p > 0.10] (Figure 3.3).

Table 3.2. Within-group comparisons of segmenting early versus late trials.
Wilcoxon Signed-Rank Tests were used to compare the average number of event borders during early and late trials of event segmentation in the ballet, Bharatanatyam and acting conditions, respectively. * P < 0.05 ** P < 0.01

Group	**Ballet Condition**			**Bharatanatyam Condition**			**Acting Condition**		
	Mean Diff (SD)	**W**	**Sig. (P)**	**Mean Diff (SD)**	**W**	**Sig. (P)**	**Mean Diff (SD)**	**W**	**Sig. (P)**
Ballet	2.1 (7.3)	37	.021*	1.49 (.88)	31	.059	1.9 (.49)	8.5	.001**
Bharatanatyam	.65 (.88)	54.5	.501	2.5 (1.5)	26.5	.060	0.3 (0.3)	47.5	.301
Dance	1.6 (1.2)	50.5	.379	0.5 (1.1)	48	.802	-0.3 (1.5)	35.5	.814
Musician	3.2 (1.5)	33.5	.079	4.0 (2.6)	49	.339	1.2 (.53)	20	.080
Athlete	1.8 (.90)	66.5	.260	2.4 (1.4)	59	.153	1.1 (.56)	51.5	.144
Non-Expert	3.1 (1.5)	62.5	.198	3.0 (1.3)	66.5	.260	1.4 (.77)	65	.235

3.4.1.2 Movement Features of Event Borders

To identify the most common event borders, raw event segmentation data was divided into 60 1-second bins. The frequency of button presses for each bin was determined for each group and condition. A summary of the movement features for the most commonly identified event borders for each condition can be found in Table 3.3. Across all conditions, the movement features associated with the highest incidence of event borders include changing direction of movement, raising arms, and leaping to the side for the dance conditions.

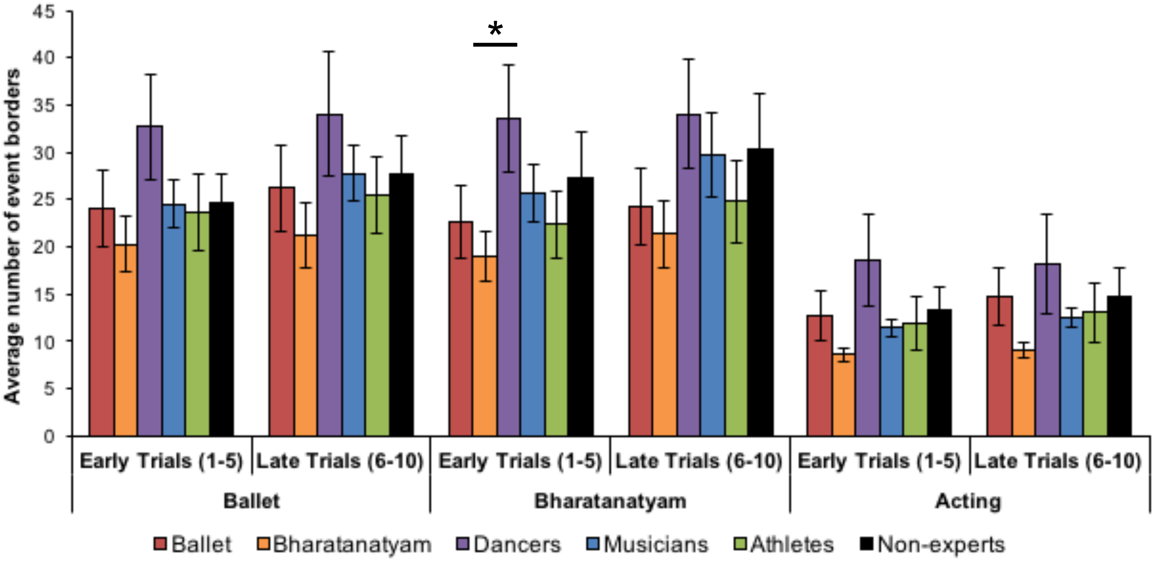

Figure 3.3. Event segmentation of dance and non-dance sequences.
Only during early trials do we observe previously shown familiarity effects in Bharatanatyam dancers segmenting a familiar dance genre compared to dancers from other genres. No other between-group differences were significant. Error bars show SEM. * $P < 0.05$

Table 3.3. Movement features of the most frequently identified event borders by condition.
Each 60-second video was divided into 1-second bins, and the frequency of button presses was determined for each bin. The movement features of the top five bins for each condition are shown here (collapsed across groups).

Condition	Bin	Movement
Ballet	30	Concluding a set of 4 spins
	8, 12	Raise arm, leg, turn head (to left and right, respectively)
	16	Change direction and pace of movement
	22, 23	Stop, change direction of movement and begin set of 4 spins
	5, 10	Large step or leap to the side
Bharatanatyam	21	Step backward, change direction, raise hand, cross leg
	54	Pause after stepping forward, raise arm, nod head and hand
	6-8	Leap to the side while moving arm above head
	25	Change direction, step, lift arms
	33, 11	Bow down with head, upper body and arm
Acting	40-43	Crouched, tap knee with hands
	45	Stops knee tapping sequence and raises arms
	5	Turn head, raise arms
	37, 55-58	Crouched, tap knee with hands
	59	Stops knee tapping sequence and raises arms

To explore putative differences in the movement features of event borders for familiar versus unfamiliar dance sequences, we compared the most frequently identified bins for the dance conditions (Ballet, Bharatanatyam) between the dance groups (ballet, Bharatanatyam, dance) (Figure 3.4). For the Ballet condition, the most commonly identified border among familiar ballet dancers was the end of a series of four spins (bin 30), which was also in the top five most salient event borders for all other groups. While Bharatanatyam dancers were as attentive to raising of limbs with concurrent turning of the head (bin 8) as ballet dancers, dancers from other genres responded more frequently to pauses and changes in the direction and pace of movement (bins 16, 23).

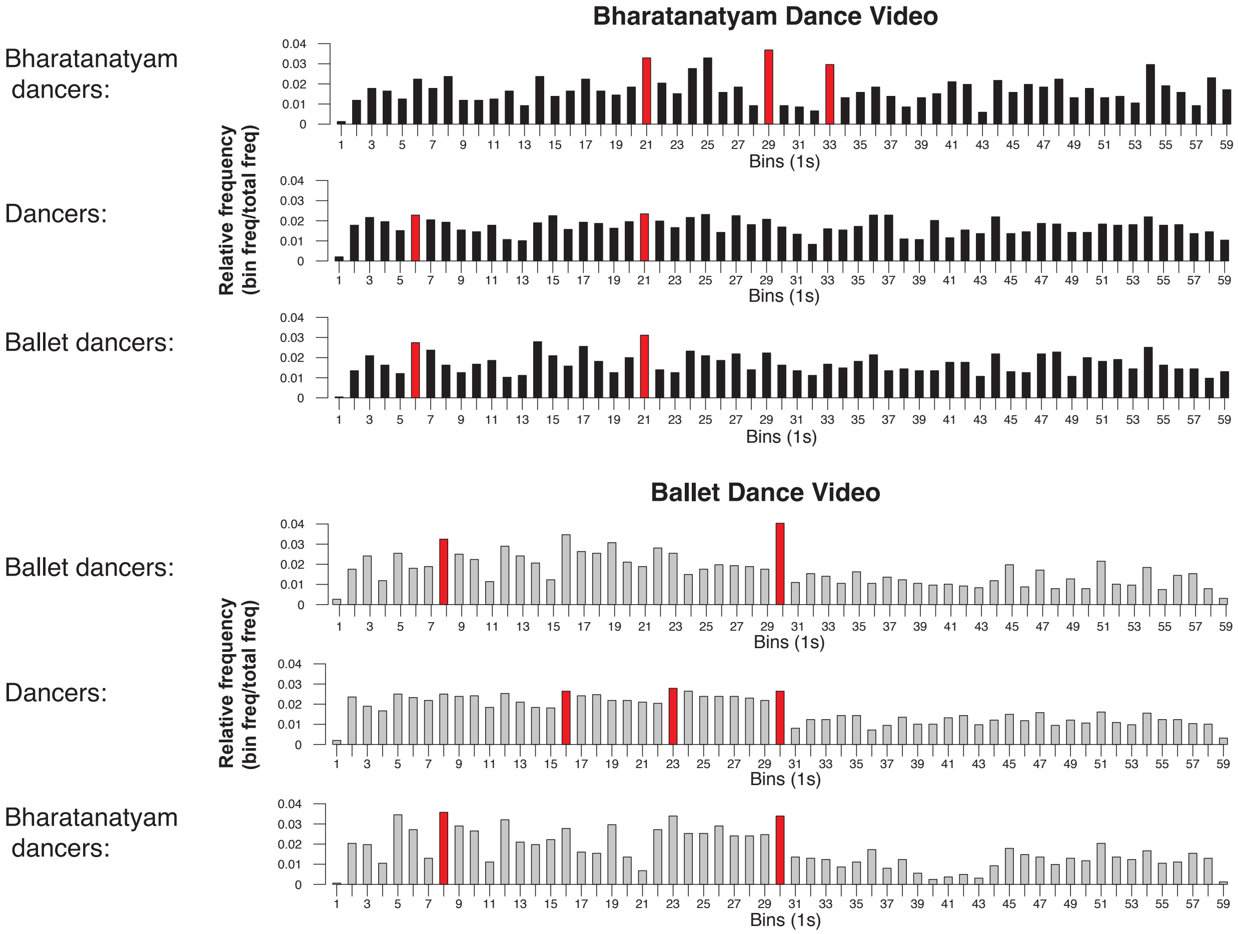

Figure 3.4. Event borders for Ballet and Bharatanatyam videos among familiar and unfamiliar dancers.

The most commonly identified event borders are marked in red. Familiar Bharatanatyam dancers identified bins 29 and 33 more frequently than other groups, while other dancers segmented bin 6. All dancers segmented the Ballet video most frequently at bin 30, and unfamiliar dancers segmented bins 16 and 23.

For the Bharatanatyam condition, all groups identified bin 21 most consistently, which showed the dancer stepping backward, changing the direction of her body, raising her arm and hand, and crossing one leg over the other. Interestingly, the second most common border among the familiar Bharatanatyam dancers was not in the top five most frequent bins for any other group, which involved a brief pause and arm and hand movement (bin 29). Bharatanatyam dancers also identified bowing down with the head, upper body and arm (bin 33) more consistently and frequently than the unfamiliar dance groups. The unfamiliar ballet and dance groups also frequently identified a leap and concurrent arm movement above the head (bin 6), which was not in the top five most frequent event borders for the Bharatanatyam dancers.

3.4.2 RIF Task

To confirm practice effects (i.e., improved recall of Rp+ items over Nrp items) during final recall and/or any between-group effects, a 2 (Items) x 6 (Groups) repeated measures ANOVA was performed. A significant practice effect was observed for all participants [F(1, 100) = 1147.043, $p = 0.000$], and a significant main effect for Group [F(5,100) = 3.049, $p = 0.013$] revealed improved recall among ballet dancers relative to musicians ($p_{Bonf} = 0.024$) (Figure 3.5). A one-way between-groups ANOVA on overall practice recall accuracy (in percent) showed no difference between groups (F(5, 100) = 1.444, $p = 0.215$). To assess practice recall of experientially-primed words, a 2 (Category – Dance, Instrument) x 6 (Groups) repeated measures ANOVA showed that Instrument words were remembered better than Dance words among all participants (Category: F(1,100) = 57.137, $p = 0.000$). A main effect of Group approached significance (F(5,100) = 2.268, *p* = 0.053) but no pairwise comparisons reached significance with Bonferroni corrections for multiple comparisons.

RIF was assessed by comparing final recall of non-practiced items from non-practiced categories (Nrp) to non-practiced items from practiced categories (Rp-) between groups with a 2 (Items) x 6 (Group) repeated measures ANOVA. All groups demonstrated RIF as revealed by a significant main effect of Item [F(1,100) = 230.910, *p* = 0.000] (Figure 3.5), with no other significant main or interaction effects (*p* > 0.05).

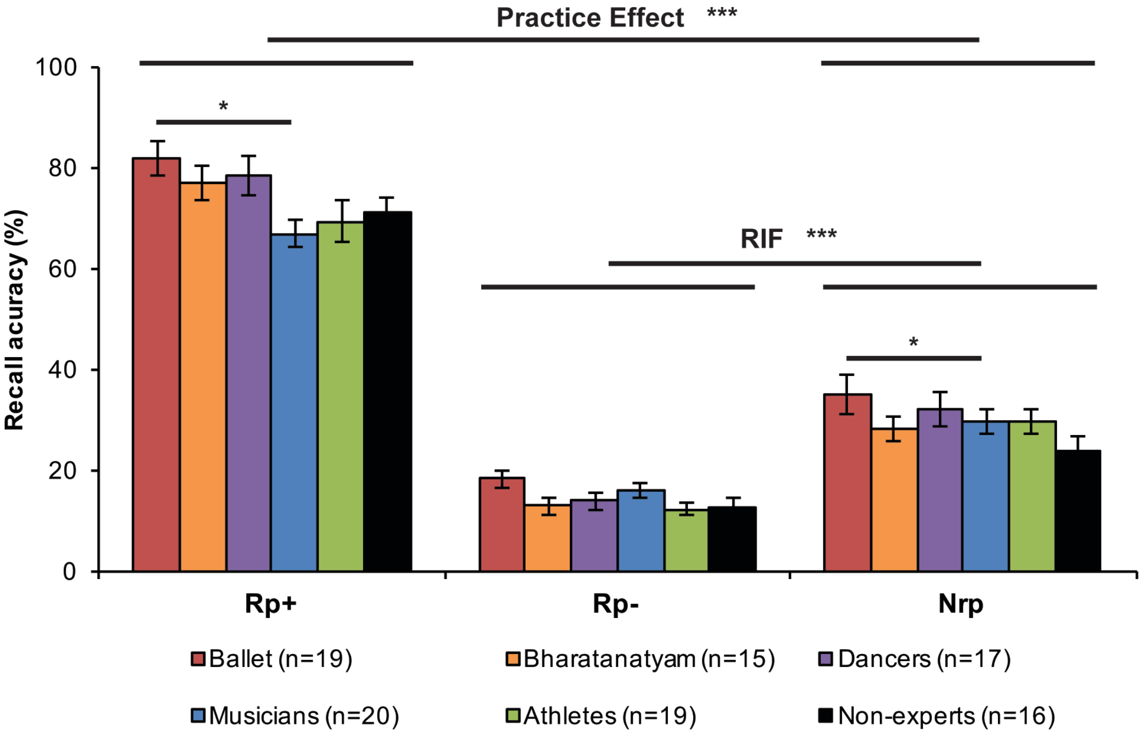

Figure 3.5. Practice effects and RIF.
All groups showed a practice effect for improved recall of practiced words (Rp+) relative to non-practiced words from non-practiced categories (Nrp). Ballet dancers also showed better recall than musicians for Rp+ and Nrp items. All groups showed retrieval-induced forgetting, or the suppression of non-practiced words from practiced categories (Rp-) relative to non-practiced words from non-practiced categories (Nrp). Error bars show SEM. * P < 0.05 *** P < 0.001

To assess transference of physical expertise to verbal WM, final recall of experientially-primed words from Dance, Sport and Instrument categories was assessed between groups with a 3 (Category) x 6 (Group) repeated measures ANOVA. A significant main effect of Category [F(2, 200) = 289.933, $p = 0.000$)] showed that Instrument words were recalled the most and Sport words were recalled the least across all groups ($p_{Bonf} = 0.000$) (Figure 3.6). A significant main effect of Group [F(5, 100) = 3.371, $p = 0.007$] also revealed improved recall among ballet dancers relative to athletes (p_{Bonf}=0.007) and non-experts ($p_{Bonf} = 0.023$), but a significant Category x Group interaction [F(10, 200) = 6.058, $p = 0.000$] revealed that ballet dancers recalled more Dance words than musicians, athletes ($p_{Bonf} = 0.000$), and non-experts (p_{Bonf} = 0.001), and Bharatanatyam dancers recalled more Dance words than athletes ($p_{Bonf} = 0.043$). These findings demonstrate improved recall of experientially-primed words for ballet and Bharatanatyam dancers, but not among musicians, athletes, or dancers with experience in other genres in dance (Figure 3.6).

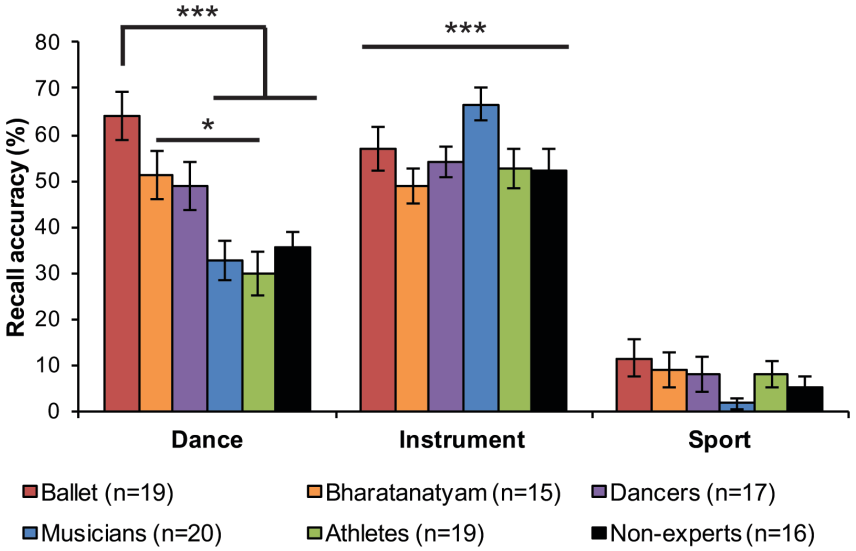

Figure 3.6. Final recall of experientially-primed words.

All groups recalled Instrument words more than Dance and Sport words. Ballet and Bharatanatyam dancers showed preferential recall of experientially-primed Dance words relative to non-dance experts as well as non-experts. Error bars show SEM. * $P < 0.05$ *** $P < 0.001$

3.5 DISCUSSION

The present investigation successfully replicated previous findings for a reduction in the number of event borders identified in a dance sequence by experts (Bläsing, 2015). It was also clarified that this pattern of event segmentation was limited to expert dancers familiar with the observed genre and did not extend to dancers with expertise in other genres of dance, or to experts in other physical activities including athletics and music. Additionally, these effects were only visible in the first five of ten trials, suggesting a decreased sensitivity of experimental measures of event segmentation over repeated trials. Unlike other movements that have been investigated in event segmentation paradigms, dance is not goal- or object-directed and is usually accompanied by music. Events or 'movements' in musical compositions can be differentiated from adjacent ones by changes in tone, tempo, rhythm, pitch, and boundary silences, and can be detected in both trained and untrained musicians (Knösche et al., 2005). Sridharan et al. (2007) investigated the brain networks underlying segmentation of movements in classical music compositions and found distinct patterns of activation during early and later parts of perceived event borders. The 'early' ventro-frontal-temporal network is suggested to subserve detection of salient events while the 'late' dorso-frontal-parietal network maintains attention and updates memory structures of the event. Increased event borders among unfamiliar experts may also be due to unpredictability and uncertainty of what steps should come next, which have resulted in prediction errors among unfamiliar groups in previous research (Reynolds et al., 2007; Zacks et al., 2011).

While the influence of familiarity has not previously been investigated during dance *segmentation*, its influence on neurophysiological responses in dance *spectators* has been explored. When observing the same dance videos as those used in the present study, two groups of spectators experienced in viewing ballet and Bharatanatyam dance showed modulation of MEPs in the arm when observing the familiar dance but not when observing the unfamiliar genre (Jola et al., 2012). Spectators attending the live performance of the recordings also showed greater arm MEPs relative to watching the recorded version of the performances, suggesting a difference in the degree of motor resonance for live and pre-recorded naturalistic dance stimuli (Jola & Grosbras, 2013). Based on previous functional imaging evidence for differences in motor resonance for familiar actions (Calvo-Merino et al., 2005; 2006), we suggest these networks are part of embodied expert knowledge schemas and directly influence segmentation behaviour as presently demonstrated.

The definitional problem of classifying an event as "discrete and meaningful" has been problematic from the earliest days of event coding and segmentation (Hommel et al., 2001; Zacks et al., 2001a), and is especially problematic when segmenting fluid, expressive and internally-guided movements like dance. The influences of attention, interest, and experience have all been acknowledged as contributors to how an observer segments a given stream of behaviour, which itself reflects cognitive flexibility. Activation of a distributed sensorimotor network has been shown at event borders, including nodes of the mirror neuron/human action observation system (Hommel et al., 2001), FEF (Zacks et al., 2001a), human MT+ complex (Schubotz et al., 2012; Speer et al., 2003) and pSTS (Zacks et al., 2006b). Beyond perception of motion dynamics, activation in the parahippocampal cortex implicated in long-term memory has also been shown to facilitate prediction of succeeding steps (Schubotz et al., 2012). Previous research shows that subsequent memory of events is impaired when there are more sub-events to recall (Faber & Gennari, 2015), which may be further impaired in unfamiliar observers that do not have embodied motor representations or knowledge schemas to rely on. Finally, observing dance and repeating (i.e., humming) musical sequences have been shown to activate nodes that are common to auditory, motor, speech and memory functioning including DMPFC (Bachrach et al., 2016) and superior parietal cortex (Hickok, Buchsbaum, Humphries, & Muftuler, 2003). These concurrent activations demonstrate the significant link between action, language and memory processing. When recruited together and consolidated into an expert knowledge schema (see Chapter 6 for discussion) over many years of experience and training, they contribute to improved perceptual and cognitive performance as demonstrated by the present results.

In the same experimental paradigm, the present investigation also demonstrates practice effects and RIF previously shown in the literature (Anderson et al., 1994; 2000; Howard et al., 2014; Storm & Bui, 2015). For the first time, we assessed differences in recall of words that are primed by one's embodied experience in dance, music, or sports relative to non-expert control subjects. We demonstrate preferential recall of experientially-primed Dance category words among ballet and Bharatanatyam dancers relative to non-dance experts and non-experts (Figure 3.6), but not among dancers from other genres despite having comparable years of experience (Table 3.1). Acquiring expertise in physical skills like dance requires combining information, both specific and abstract, related to the skill from multiple modalities through repeated and prolonged practice. What results is a specialized 'dance schema' that includes the genre-specific motor repertoire, vocabulary to define, describe, and identify these movements, and memory structures to plan and anticipate movement outcomes. We suggest that the priming of these expert knowledge schemas by observing a familiar dance resulted in the improved recall of practice words in ballet dancers (Figure 3.5) and domain-specific words in the ballet and Bharatanatyam groups (Figure 3.6).

While there is a growing body of evidence for structural and functional reorganization of sensorimotor areas with dance expertise (Bar & DeSouza, 2016; Calvo-Merino et al., 2005; 2006; Di Nota et al., 2016,a,b; Hänggi et al., 2010; Olshansky et al., 2015), the majority of research on motor expertise-memory transference comes from other skilled domains including chess, computer programming, meditation, and medical procedures and diagnoses (Besson, Chobert, & Marie, 2011; Vicente & Wang, 1998; Ericsson, Patel, & Kintsch, 2000). Evidence from athletes suggests the exposure to a wide variety of activities from an early age fosters transference of recall skills and facilitates expertise across multiple domains (Abernethy, Baker, & Côté, 2005; Del Rey et al., 1987). The closest connection between dance training and verbal memory performance comes from a study on figure skaters that shows improved motor performance and access to domain-specific vocabulary in semantic memory relative to novices. The strategies employed by experts and non-experts also differ such that the former rely on motor processes (likely reinforced by embodied knowledge schemas) and procedural memory while the latter recruit more declarative memory (Deakin & Allard, 1991; Maxwell, Masters, & Eves, 2003; Moreau, 2013). Together with the regions implicated in knowledge schemas discussed above, these studies provide a neurophysiological basis for the improved recall of domain-specific words in ballet and Bharatanatyam dancers following observation of familiar/embodied dance stimuli.

Improvements in verbal working and long-term memory have been demonstrated in individuals with music experience when tested as children (Ho, Cheung, & Chan, 2003; Moreno et al., 2011) and adults (Chan, Ho, & Cheung, 1998; Dittinger et al., 2016). Children in music, but not visual arts, programs showed improved speech segmentation abilities over two years of training. Specifically, the musically trained children could discern meaningless words from strings of nonsense syllables after one and two years of training (François, Jaillet, Takerkart, & Schön, 2014). Verbal memory improvements have also been shown when learning sung versus spoken words in patients with AD (Palisson et al., 2015), a group that is also afflicted with impaired event segmentation. Bailey and colleagues (2013b) compared AD and cognitively healthy older adults' segmentation of a various tasks and performance on a Naturalistic Action Task that involved packing a lunchbox and schoolbag. AD subjects showed increased deviance of event border locations relative to sample norms and impaired task performance, suggesting the ability to segment actions is directly related to memory and performance. There is promising evidence for improved cognitive, motor, EEG and quality of life functioning in individuals with AD and Parkinson's disease following music and dance therapy (Bearss, McDonald, Bar, & DeSouza, 2017; Dhami, Moreno, & DeSouza, 2015; Di Nota et al., 2016b). Together with the present results, these investigations lend further scientific validation to the therapeutic efficacy of these types of therapy that are multimodal, socially engaging, accessible, affordable, and fun for improving cognitive and perceptual impairments.

The most commonly identified movement features among all participants included changes in the direction of movement, raising of the arms, sideways movements during the dance conditions, and short sequences of knee tapping during the acting condition (Table 3.3, Figure 3.4). These findings are consistent with previous analyses of kinematic movement parameters that correspond to event boundaries, which include changes in pose or position, relative location, speed, and acceleration (Hemeren & Thill, 2011; Zacks, Kumar, Abrams, & Mehta, 2009a). Using narrative texts and cinematic video clips, identification of these types of movement features predicted the location of event borders for extended naturalistic scenes (Zacks et al., 2010; Zacks, Speer, & Reynolds, 2009b). The only movement to be uniquely identified by a familiar dance group was the brief pause and arm and hand movement during the Bharatanatyam dance (bin 29), which may have reflected the underlying narrative of the sung Tamil background track. To dissociate the contributions of movement and music in dance perception and segmentation, future studies should randomly and systematically present unimodal (i.e., auditory music and visual dance) and multimodal stimuli. Bläsing (2015) attempted such an investigation but presented all unimodal auditory trials after 10 audiovisual trials, confounding interpretation of any uni- and multimodal effects that may have been influenced by practice or learning effects.

The fact that we were only able to demonstrate familiarity effects in Bharatanatyam dancers and not ballet dancers for their familiar dance conditions or in athletes for recalling Sport category words could be attributed to several limitations of the experimental stimuli. Despite claiming to record three videos with a similar type, number and pace of movements (Jola et al., 2012), the results of both the validation (Figure 3.2) and main event segmentation experiment (Figure 3.3) showed that the acting video had significantly fewer event borders and movement phrases than both dance conditions, and that there was great variability in the number of segments in several one-minute portions of the ballet and Bharatanatyam dance. In fact, (Jola & Grosbras, 2013) show evidence for more perceived gestures in the Bharatanatyam video compared to the ballet and acting videos among novice viewers, and differential use of (and corticospinal excitability of) arm and finger muscles for ballet and Bharatanatyam conditions, respectively (see Supplementary File 2 in Jola et al., 2012). This greater number of gestural movements may account for the greater number of event borders observed in unfamiliar dancers (Figure 3.4). The musical accompaniment in the Bharatanatyam video features a vocal track sung in Tamil that may have also impacted participants' ability to segment movement independent of auditory, musical or lyrical cues despite receiving explicit instructions to focus on the movements and not the music (Section 3.3.1.3). This may be especially true for the familiar Bharatanatyam group who might have understood the spoken language, despite demonstrating expert segmentation behaviour.

The Sport category words used in the RIF task had the lowest recall of all experientially-primed words that we investigated (Figure 3.6) and were originally established by Battig and Montague (1969). These included *racing, sailing, climbing, fishing, skating,* and *riding*. While poor recall of these items could be attributed to the fact that they were Nrp words and not included in practice recall, RIF effects should have induced better recall of these words relative to non-practiced Dance or Instrument words. Instead, we attribute this poor performance across all groups to the nature of the items as more recreational in nature relative to more popular, commercialized or team-based sports like football, hockey, soccer or baseball that participants reported having experience with. Additionally, all of the words in the other categories were nouns while Sport words were verbs, which may have also confounded recall for these Nrp items. Future investigators utilizing this RIF word bank should consider revising and updating these items to control for this possible confound in participants' expectation of common sport exemplars.

3.6 CONCLUSIONS

The current study has extended previous findings of expertise effects during dance segmentation, revealing that reduced frequency of event borders is only evident for familiar dance sequences, and not unfamiliar ones or non-dance sequences. Based on previous evidence linking motion perception and memory structures (Bailey et al., 2013a,b), we propose that this behaviour reflects consolidation of more component movements as a result of adaptive learning strategies developed through expertise. Refinement of underlying knowledge schemas also facilitate improved recall for experientially-primed words among ballet and Bharatanatyam dancers after viewing familiar dance sequences. As shown in Chapter 2, resonance in one domain (e.g., sensorimotor) of knowledge schemas primes access to information in other domains (e.g., verbal attention and WM), and is specifically tuned to the embodied motor repertoire of the trained or untrained observer. In the following two chapters of this thesis, we will use EEG and fMRI approaches to explore the neurophysiological mechanisms underlying this ‘cross talk’ between putative nodes of expert knowledge schemas in ballet dancers while engaging with familiar stimuli during all forms of action processing - AO, MI and ME.

4 CHAPTER FOUR – EXPERIENCE-DEPENDENT MODULATION OF ALPHA AND BETA DURING ACTION OBSERVATION AND MOTOR IMAGERY OF DANCE[7]

4.1 PREFACE

EEG studies investigating the neural networks that facilitate action observation (AO) and kinaesthetic motor imagery (KMI) have shown reduced, or desynchronized, power in the alpha (8-12Hz) and beta (13-30Hz) frequency bands relative to rest, reflecting efficient activation of task-relevant areas. Functional modulation of these networks through expertise in dance has been established using fMRI, with greater activation among experts during AO. While there is evidence for experience-dependent plasticity of alpha power during AO of dance, the influence of familiarity on beta power during AO, and alpha and beta activity during KMI, remain unclear. The purpose of the present study was to measure the impact of familiarity on confidence ratings and EEG activity during (1) AO of a brief ballet sequence, (2) KMI of this same sequence, and (3) KMI of non-dance movements among ballet dancers, dancers from other genres, and non-dancers. Ballet dancers highly familiar with the genre of the experimental stimulus demonstrated higher individual alpha peak frequency (iAPF), greater alpha desynchronization, and greater task-related beta power during AO, as well as faster iAPF during KMI of non-dance movements. While no between-group differences in alpha or beta power were observed during KMI of dance or non-dance movements, all participants showed significant desynchronization relative to baseline, and further desynchronization during dance KMI relative to non-dance KMI indicative of greater cognitive load. These findings confirm and extend evidence for experience-dependent plasticity of alpha and beta activity during AO of dance and KMI. We also provide novel

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[7] Paula M. Di Nota, Julie M. Chartrand, Gabriella R. Levkov, Rodrigo Montefusco-Siegmund & Joseph F.X. DeSouza. (2017). *BMC Neuroscience*, *18(28)*, 1-14.

evidence for modulation of iAPF that is faster when tuned to the specific motor repertoire of the observer. By considering the multiple functional roles of these frequency bands during the same task (AO), we have disentangled the compounded contribution of familiarity and expertise to alpha desynchronization for mediating task engagement among familiar ballet dancers and reflecting task difficulty among unfamiliar non-dance subjects, respectively. That KMI of a complex dance sequence relative to everyday, non-dance movements recruits greater cognitive resources suggests it may be a more powerful tool in driving neural plasticity of action networks, especially among the elderly and those with movement disorders.

4.2 INTRODUCTION

The three facets of movement processing – AO, MI and ME – have been shown to recruit a common 'mirror neuron' network of brain regions in both humans (Grèzes & Decety, 2001; Jeannerod, 1995) and non-human primates (Rizzolatti, Luppino, & Matelli, 1998). Each of these processes is vital in facilitating motor learning in general and especially for dance movements, which require transformation of multisensory inputs into highly specific and complex motor outputs that are reproduced with high fidelity (for review, see Bläsing et al., 2012; Laland, Wilkins, & Clayton, 2016). As a result of this experience, activation of the mirror network and associated brain regions is modulated by dance experience (Calvo-Merino et al., 2005; 2006) to facilitate subsequent motor learning (Cross et al., 2009a).

These and other evaluations of motor representations for complex movements that cannot physically be performed during neuroimaging have utilized tasks involving AO and/or KMI from an internal first-person perspective. During four fMRI scans conducted over a 34-week period, recent investigations conducted by our lab have employed both AO and KMI tasks for a novel piece of choreography that was rehearsed and performed by professional ballet dancers. Consistent with findings from Cross, Hamilton and Grafton (2006), we found plasticity in the motor representation for this specific dance sequence coded in sensorimotor brain regions over time (Bar & DeSouza, 2016), as well as decreased activation in the extrastriate body area during movement of the foot in dancers relative to novice controls (Di Nota et al., 2016).

While most of the evidence for experience-dependent plasticity has come from fMRI studies, valuable insight into the temporal dynamics of sensorimotor processing has been revealed with EEG. With respect to action processing, the rolandic 'mu' alpha rhythm (9-13Hz) recorded directly from midline primary motor and somatosensory cortices has been shown to decrease in power relative to rest, or desynchronize, when planning, imagining and executing movements (Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006), with concurrent desynchronization of the beta (13-30Hz) frequency band observed in motor cortex (Pfurtscheller & Lopes da Silva, 1999). Alpha desynchronization is also observed in other brain areas under conditions of increased attentional and cognitive effort, putatively reflecting suppression of task-irrelevant areas to enhance performance (for review, see Bazanova & Vernon, 2014 and Klimesch, 2012). Within the alpha band there is typically a maximal amplitude (iAPF) that is typically lower (i.e., slower) in the elderly (Clark et al., 2004) and higher (i.e., faster) during states of cognitive preparedness (Angelakis, Lubar, Stathopoulou, & Kounios, 2004) and under increased cognitive demand (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014).

Investigations on the influence of dance expertise on EEG activity are sparse, as most expert studies assess either proficiency in task performance, various types of athletes (for review, see Debarnot, Sperduti, Di Rienzo, & Guillot, 2014) or the influence of aerobic exercise on EEG activity among non-experts (Gutmann et al., 2015). However, a study by Ermutlu and colleagues

(2014) compared resting EEG activity across delta (0.5-4Hz), theta (4-8Hz), alpha, and beta frequency bands in fast ball sport athletes and dancers. They correctly predicted that athletes, who have to quickly anticipate observed movements and adapt their own motor responses, would show higher power in slower bands, and dancers experienced at practicing rhythmic, imaginative and repetitive movements would show higher power in the alpha and beta bands. With respect to task-related activity during movement processing, Orgs et al. (2008) recorded EEG from expert dancers and non-experts while they observed dance and non-dance movements. They found no group differences during the latter condition, and alpha desynchronization among dancers only when observing dance movements. It remains to be seen whether similar experience-dependent modulation of the alpha or beta bands occur during KMI of dance or non-dance movements, and is one of the primary goals of the present investigation.

Expanding upon the existing literature, the current study sought to compare differences in alpha and beta power during AO and KMI of a ballet dance sequence among expert dancers that were both familiar and unfamiliar with the genre, as well as non-dancers, to disentangle the effects of familiarity and expertise more generally on action processing of dance movements. Similar to Orgs et al. (Orgs et al., 2008), we also had participants perform KMI for non-dance movements in order to examine possible transference of expertise effects.

4.3 METHODS

4.3.1 Participants

Subjects were recruited through the York University Undergraduate Research Participant Pool (URPP) and compensated with course credit. The research study was approved by the Office of Research Ethics' Human Participants Review Committee (Certificate # 2013-211) and in accordance with the Declaration of Helsinki. Eligibility requirements included self-reported right-handedness and no uncorrected visual or neurological problems.

The advertised study called for participants with at least two to five years of experience in any genre of dance or related craft including gymnastics, figure skating, or sports. A total of 92 participants were tested, but 31 were excluded for the following reasons: lack of event markers in EEG data (n = 9), demographic information not provided (n = 9), reported neurological problems (n = 1), reported left-handedness (n = 4), poor EEG data quality (n = 6), and no registered alpha peak values (n = 2). A total of 61 participants (48 female) between the ages of 18 and 37 ($M = 20.7$, $SD = 4.22$) were analyzed. Participants were divided into three groups based on their self-reported experience: ballet dancers (n = 25, 22 females, mean years of experience = 10.44, $SD = 4.3$), non-ballet dancers with experience in other genres of dance (n = 21, 15 females, mean years of experience = 5.57, $SD = 3.1$), and non-dancers (n = 15, 11 females, mean years of experience = 5.8, $SD = 4.6$)[8]. Participants in both dance groups were required to have at least two years of experience. Non-ballet dance genres included belly dancing, hip hop, ballroom, Salsa, tap, modern, lyrical, acro, cultural, folk, Bollywood, jazz, break dancing, and contemporary. Non-dance subjects were not required to be experts in any particular craft, but included subjects with at least 2 years of experience in skills such as figure skating (n = 5), gymnastics (n = 4), martial arts (n = 1) and music (n = 1), as well as non-experts (n = 4).

4.3.2 Procedure

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[8] Although the ballet group has significantly more years of experience than non-ballet ($p_{\text{Bonf}}=0.000$) and non-dance groups ($p_{\text{Bonf}}=0.002$), no dependent variables were significantly correlated with years of experience except for the number of trials performed during the AO task (see Section 4.3.2.1).

After providing their informed consent to participate in the study, participants were measured and fitted with the EEG headset according to the International 10-20 System of electrode placement. Participants were instructed to remain as still as possible during the experimental tasks and were provided with ear bud headphones to hear auditory stimuli. The computer-based experiment began with a brief demographic survey and baseline recordings followed by three tasks: 1) AO and 2) KMI of a ballet dance sequence, and 3) the KMI portion of the Visual and Motor Imagery Questionnaire (VMIQ-2) (Roberts, Callow, Hardy, Markland, & Bringer, 2008). In order to minimize differences in dance imagery across participants, the AO task was performed first and allowed subjects to view the dance sequence as many times as needed in order to form a clear mental image for the subsequent KMI task.

4.3.2.1 Baseline

Four resting conditions (eyes open and eyes closed, each with and without background music) were performed in order to facilitate baseline correction of subsequent tasks. Participants were instructed to clear their minds and to follow instructions as they were given. Baseline conditions were 15-seconds each and presented in random order. A picture of a closed eye appeared on screen during the eyes closed conditions to remind subjects to keep their eyes closed in the event they opened them during the task (vertical visual angle = 13.6°), and a central fixation cross (visual angle = 0.98°) appeared during the eyes open conditions. Audio prompts cued subjects to open and close their eyes at the beginning and end of each baseline condition where appropriate. The music conditions played the first 15 seconds of Bach's *Goldberg Variations 988, Variation 1* to match the cadence and genre of the music in the AO and KMI tasks.

To evaluate possible between-group differences in baseline iAPF, log alpha peak power, and/or log beta power, three separate repeated measures analyses of variance (RM-ANOVA's) were performed with the factors of Condition (4) x Electrode (14) x Group (3)[9]. No significant between-group differences were observed ($p > 0.1$). As expected, log alpha peak power was higher during both eyes closed conditions relative to eyes open in all electrodes (Condition x Electrode: $F(20.3, 1175.9) = 32.651$, $p = 0.000$, $\eta^2 = 0.36$), as was log beta power in frontal (F3, F4), parietal (P7, P8) and occipital (O1, O2) electrodes (Condition x Electrode: F (18.6, 1079.8) = 23.510, $p = 0.000$, $\eta^2 = 0.29$).

4.3.2.2 AO Task

Following the baseline recordings, participants repeatedly viewed an 8-second video clip of a choreographed ballet dance. The clip was taken from a 6.92-minute video that was filmed during a practice at the Walter Carsen Centre for The National Ballet of Canada from Bar and DeSouza's (2016) study, and was played full screen on the computer monitor (vertical visual angle = 13.6°). The video clip featured one female dancer in the foreground and the music was from Bach's *Concerto in C Major*. Participants were asked to closely observe the choreography performed by the female dancer in order to be able to imagine themselves performing it as accurately and precisely as possible during the next experimental task. Because participants were fit for EEG recording during the experimental session, motor performance was not behaviourally assessed in the laboratory. Instead, participants were asked to rate how confident they were that they could perform the dance with complete accuracy and precision if required to on the following scale modelled after the VMIQ-2 scale (Roberts et al., 2008): 1 = *Perfectly accurate*

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[9] As with analyses of the experimental tasks, RM-ANOVA's evaluating baseline iAPF, alpha and beta power assessed and adjusted sphericity violations with Hyunh-Feldt corrected degrees of freedom and significance values as reported in the text.

and in time with the music, 2 = *Clear and reasonably accurate and in time with the music*, 3 = *Moderately accurate and in time with the music*, 4 = *Vaguely accurate and in time with the music and dim*, 5 = *No accuracy at all and unable to keep time with the music*. The clip was initially shown 10 times (Block 1) with a one-second interstimulus interval and fixation cross (visual angle = 0.98°) followed by a prompt for a confidence rating. A participant response of 1 or 2 (i.e., indicating high confidence) would induce the end of the AO task, and participants were asked if they would like to view the clip a final five times (Block 2). A response of 3 to 5 would automatically present an additional block that played the dance clip five times (Block 2). Following this shorter block, participants were once again asked to rate their confidence that they could physically perform the dance if required to. If participants respond below threshold (i.e., 3 to 5), they could watch the shorter block for a maximum of four times before automatically proceeding to the next experimental task. Participants could view the clip a maximum of 30 times across 5 blocks. The AO portion of the experiment lasted approximately 5-15 minutes.

4.3.2.3 KMI Task

Following the AO task, participants were asked to visualize themselves performing the dance sequence they had just learned with their eyes open and closed. Four blocks (2 x eyes open and 2 x eyes closed) of 25 trials each were randomly presented, resulting in a total of 100 KMI trials. During each trial, participants heard the music that had accompanied the dance clip during the AO task. Participants were asked to imagine themselves performing the dance in time with the music from an internal, first-person perspective and to feel themselves executing the movements as opposed to visualizing from a third-person perspective (i.e., 'seeing' themselves perform the dance from an external perspective). The difference in visualization perspectives was explained during initial debriefing as well as in the written instructions presented on screen to ensure the proper engagement in motor, and not visual, imagery (Sirigu & Duhamel, 2001). The dance clip was played once before each block to refresh the participant's memory and ensure that they were accurately imagining the dance. Similar to the baseline procedure, a picture of a closed eye appeared on screen during the eyes closed condition and a central fixation cross was provided during the eyes open condition. Participants were provided with audio prompts cuing them to open and close their eyes when appropriate. As with the AO task, participants were asked to rate how clearly and vividly they felt themselves performing the dance sequence at the end of each block. Ratings were once again given on a 5-point scale as follows: 1 = *Perfectly clear and as vivid (as normal vision or feel of movement)*, 2 = *Clear and reasonably vivid*, 3 = *Moderately clear and vivid*, 4 = *Vague and dim*, 5 = *No image at all, you only "know" that you are thinking of the skill*. Once an answer was recorded, participants were given the opportunity to take a break before beginning the next block. Each block lasted 3.5 to 4 minutes and the KMI task lasted approximately 15 to 20 minutes.

For the present study, only eyes closed KMI conditions will be included in the analysis so as to compare them to the next task, which was only performed with eyes closed.

4.3.2.4 VMIQ-2 Task

In order to compare each participant's EEG activity and subjective perceptual level of vividness and clarity to KMI for everyday, non-dance movements, the final experimental task required completing the third portion (KMI from a first-person perspective) of the VMIQ-2 (Roberts et al., 2008). Participants were instructed to perform KMI of 12 movements (Table 4.1) while eyes were closed in accordance with VMIQ-2 instructions. For each item, the requested action was written on the screen and the participant was instructed to first close their eyes and then press the spacebar when they were ready to begin visualizing. Participants were instructed to spend as much time as they needed to form a clear and accurate image of feeling themselves complete each action, and to press the spacebar once they had finished visualizing. Upon this second button press, participants were asked to rate how clear and vivid their KMI was for that item using the same 5-point scale from previous tasks (1 = *Perfectly clear and vivid*, 5 = *No image at all*). As this portion of the experiment was self-paced, completion time varied from one to three minutes (average duration = 4.57mins, *SD* = 4.25mins). Valid iAPF values were obtained from 59 subjects[10] who were included in the final analyses.

Table 4.1. Vividness of Movement Imagery Questionnaire Items.

Item
1. Walking
2. Running
3. Kicking a stone
4. Bending to pick up a coin
5. Running up stairs
6. Jumping sideways
7. Throwing a stone into water
8. Kicking a ball in the air
9. Running downhill
10. Riding a bike
11. Swinging on a rope
12. Jumping off a high wall

Note: The complete VMIQ-2 (Roberts et al., 2008) requires participants to imagine each of these items in turn under three conditions: internal visual imagery, external visual imagery, and kinesthetic (i.e., motor) imagery. The present study was only interested in evaluating kinesthetic motor imagery, so participants were asked to imagine themselves performing each of the items listed with their eyes closed and as though they could "feel [them]self doing the movement" as per the VMIQ-2 instructions (Roberts et al., 2008). Once they had formed a clear motor image of each item, participants were asked to rate how clearly and vividly they could feel themselves performing the movement on the following scale: 1 = *Perfectly clear and as vivid (as normal vision or feel of movement)*, 2 = *Clear and reasonably vivid*, 3 = *Moderately clear and vivid*, 4 = *Vague and dim*, 5 = *No image at all, you only "know" that you are thinking of the skill*.

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[10] Two subjects from the non-dance group did not have iAPF values for the VMIQ-2 task, but had iAPF values and were included in analyses for the AO and KMI tasks.

Following completion of the VMIQ-2, participants were asked if they felt that KMI was easier to complete with eyes closed or eyes open and their responses were recorded. Finally, the EEG headset was removed and participants were debriefed and thanked for their participation. The entire experiment from entrance to exit lasted approximately 40-55 minutes.

4.3.3 Data Acquisition, Processing and Analyses

EEG data were collected using a wireless 14-channel (AF3, AF4, F3, F4, F7, F8, FC5, FC6, T7, T8, P7, P8, O1, O2) Emotiv EPOC EEG Neuroheadset and recorded with accompanying TestBench software (Emotiv Systems, 2012, San Fransisco, CA). The headset has two reference locations (at M1 and M2), a sampling rate of 128Hz with 16-bit ADC resolution, and 0.02 to 45 Hz resolution with digital 5^{th}-order sinc notch filters at 50-60 Hz. The Emotiv neuroheadset has been validated (Badcock et al., 2013) and provides several ecological advantages to traditional research-grade EEG systems. These include affordability and portability to record EEG in environments outside of the laboratory, including a dance studio where neural activity can be evaluated on-site (Di Nota et al., 2016b). All experimental tasks were presented on a 23” flat screen monitor (Dell P2312H) and configured and presented by MediaLab (v2012.4.119, Blair Jarvis for Empirisoft Co., New York, NY). Data markers were sent from MediaLab to TestBench via a Virtual Serial Port Driver (Version 7.1, Eltima Software, 2013, Bellevue, WA). Preprocessing of the EEG data was conducted with the Fieldtrip toolbox (Version 20131117, Oostenveld, Fries, Maris, & Schoffelen, 2011) and Matlab (Version 7.10.0.499, The MathWorks, Inc., Natick, MA), and statistical analyses were performed with SPSS (Version 22, IBM Co., Armonk, NY).

For each participant, raw EEG data was first segmented according to data markers coded for events of interest (i.e., experimental tasks), and these segments were further divided into 2-

second epochs prior to being bandpass filtered (1-50Hz), demeaned, and detrended. Next, artifacts were rejected by visual inspection (*M* = 51 trials, *SD* = 18.5 out of an average 483.3 trials, *SD* = 28.5) and independent component analyses were performed to eliminate contamination of the EEG signal from eye movements and blinks (*M* = 2.15, *SD* = 0.60 components eliminated out of 14 total components). Data were fast Fourier transformed and iAPF (Hz), alpha peak power (μV^2), and average beta power across the 13-30Hz range were computed for each participant, experimental task and electrode.

To normalize the variances of power data among electrodes, alpha and beta power values were log transformed and baseline corrected with the appropriate baseline condition (i.e., eyes open or eyes closed) prior to statistical analyses. The following equations were used to compute log task-related alpha peak power (herein referred to as "alpha") and log task-related beta power (herein referred to as "beta") modeled from Gonzalez-Rosa et al. (2015):

$$\text{alpha power} = \log \text{alpha peak power (task)} - \log \text{alpha peak power (baseline)}$$

$$\text{beta power} = \log \text{beta power (task)} - \log \text{beta power (baseline)}$$

Alpha power was not subdivided into the rolandic mu (9-13Hz) frequency, as it is typically recorded from central (Cz, Fz) electrode sites that are not included in the Emotiv neuroheadset used in the current study. Instead, we isolated the iAPF within the traditional 8-12Hz bandwidth and focused statistical analyses on electrode sites overlying available and relevant sensorimotor areas including bilateral frontocentral (FC5, FC6) motor association cortex (Kuramoto, Ito, Sato, & Fujisawa, 2014), superior temporal cortex (T7, T8) involved in perceptual learning (de Souza, Yehia, Sato, & Callan, 2013) and sensory-guided KMI (Berger & Ehrsson, 2014), inferior posterior temporal gyrus (P7, P8), and primary visual occipital cortex (O1, O2) (Koessler et al., 2009).

All statistical analyses including the factor of Electrode [FC5, T7, P7, O1, O2, T8, P8, FC6] employed a RM-ANOVA design, and violations of sphericity were adjusted by reporting degrees of freedom and significance values (p) with Huynh-Feldt corrections (Field, 2005). For analyses of the AO task evaluating the factor of Time [Blocks 1 to 5], a mixed model structure was applied to the RM-ANOVA to account for the different number of blocks performed between subjects, which would not be adequately corrected for in a RM-ANOVA. Any strictly between-group analyses were performed with one-way ANOVAs. Bonferroni corrections applied to pairwise comparisons (p_{Bonf}) and effect sizes (partial eta squared, η^2) are reported where appropriate. Planned correlations were performed on demographic and behavioural data, and only on significant dependent variables, and are reported in-text. The results of each task will be presented in turn in the following order: analyses of demographic data and confidence ratings, iAPF, alpha power and beta power.

4.4 RESULTS

4.4.1 AO Task

Empirical behavioural measures of perceived confidence in performing the dance sequence included the number of blocks performed by each subject before moving on to the KMI task, and the average of subjective ratings provided after each block of the AO task. The non-dance group performed significantly more trials ($M = 24.7$, $SD = 5.8$) than both familiar ballet ($M = 18.8$, $SD = 4.9$, $p_{Bonf} = 0.008$) and unfamiliar non-ballet dancer groups ($M = 20.0$, $SD = 6.5$, $p_{Bonf} = 0.056$) [$F(2, 58) = 5.170$, $p = 0.009$], and were also less confident in their ability to actually perform the dance if required (i.e., higher confidence rating, $M = 3.0$, $SD = 0.09$)

compared to ballet (*M* = 2.4, *SD* = 0.05, *p* = 0.004) and non-ballet dance groups (*M* = 2.6, *SD* = 0.06, *p* = 0.004) [*F*(2, 58) = 4.574, *p* = 0.014] (Figure 4.1).

The number of trials performed was significantly correlated to years of dance experience (*r* = -0.252, *p* = 0.050) (Figure 4.2a), subjective ratings (*r* = 0.867, *p* = 0.000) (Figure 4.2b), and alpha power (*r* = -0.308, *p* = 0.016) (Figure 4.2c). Confidence ratings during the AO task were also significantly correlated to those obtained during the KMI task [*r* = 0.286, *p* = 0.025] (Figure 4.2d).

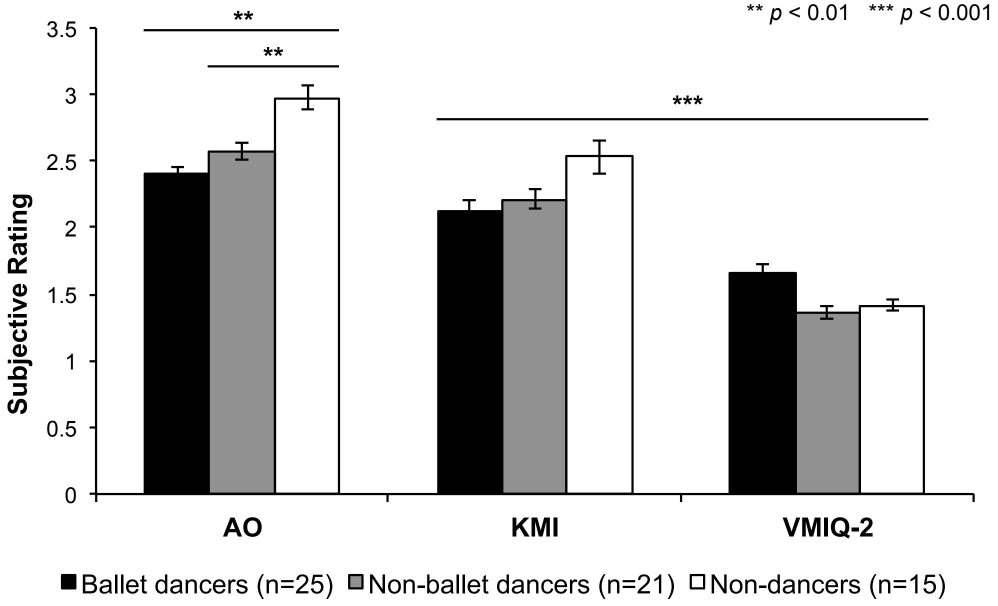

Figure 4.1. Subjective ratings of action observation and motor imagery.
Participants were asked to provide a confidence rating for how accurately they could perform the dance if they were required to for the AO task, and to rate how clearly and vividly they imagined the instructed behaviour for the KMI and VMIQ-2 tasks on a scale from 1 (*Perfectly accurate or clear*) to 5 (*Not at all, or no image at all*). Non-dancers provided significantly higher ratings (i.e., poorer perceived ability) during the AO task relative to ballet dancers (*p* = 0.004) and non-ballet dancers (*p* = 0.044). All groups provided significantly lower ratings, indicative of clearer imagery, when imagining non-expressive movements during the VMIQ-2 task relative to KMI of the newly-learned dance (ballet: *p* = 0.005, non-ballet and non-dance: *p* = 0.000). Error bars represent SEM.

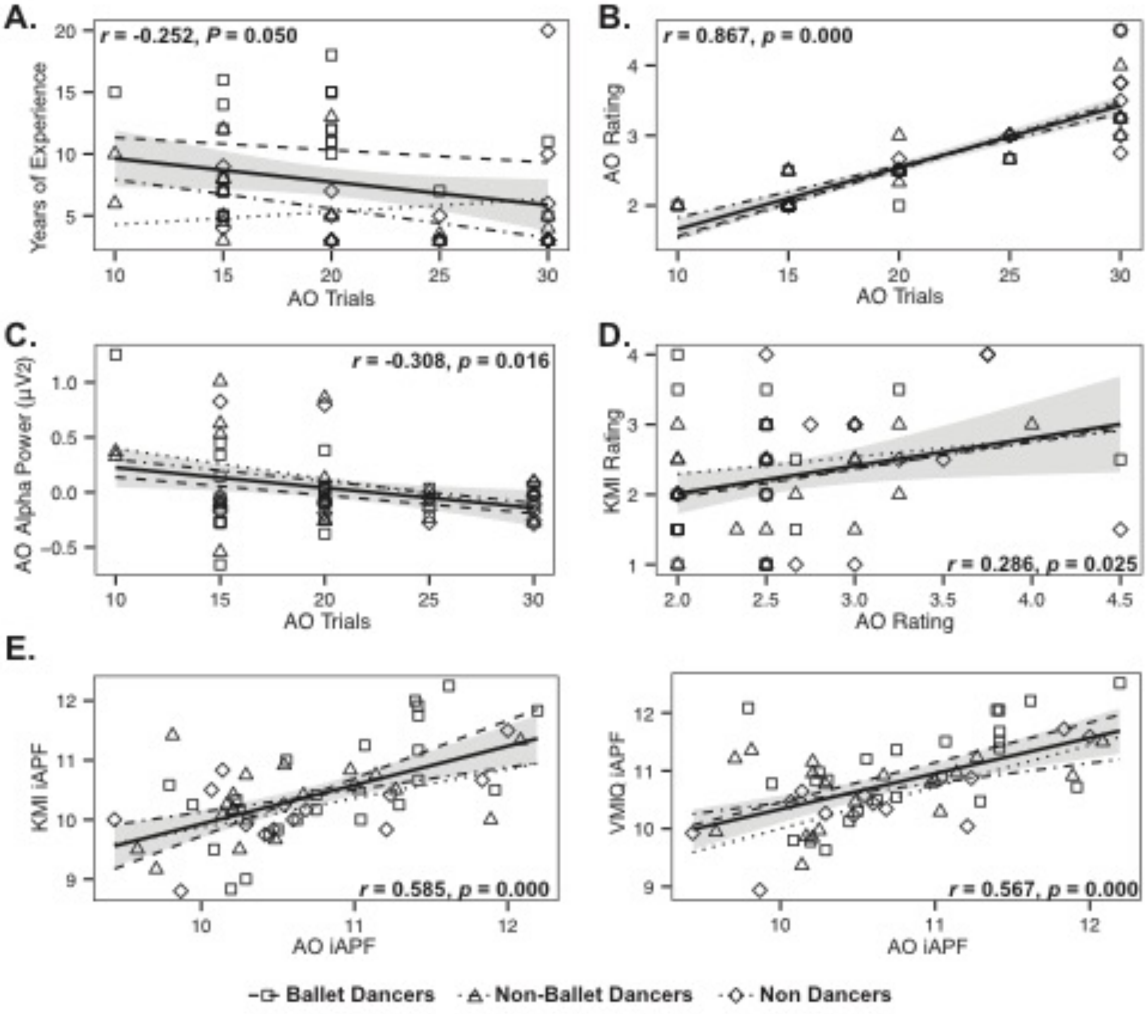

Figure 4.2. Correlations between behavioral and neural measures of action observation and motor imagery.
A. The number of trials performed during the AO task was negatively correlated to the years of experience participants had in their respective crafts (*p* = 0.050). **B.** The number of trials performed during the AO task was positively correlated to the ratings provided at the end of each AO block (*p* = 0.000). **C.** During the AO task the number of trials performed was negatively correlated to alpha power (*p* = 0.016). **D.** The ratings provided at the end of each AO block were positively correlated to clarity ratings during the KMI task (*p* = 0.025). **E.** iAPF was positively correlated between the AO and KMI tasks (*p* = 0.000), and between the AO and VMIQ-2 tasks (*p* = 0.000). Statistical analyses were performed on the average correlations across groups, shown by the solid line and shaded with a 95% confidence interval. Individual data points are represented as squares for ballet dancers, triangles for non-ballet dancers, and diamonds for non-dancers. Regression lines for ballet dancers (dash), non-ballet dancers (dot-dash), and non-dancers (dot) are shown for visualization purposes only.

Ballet dancers exhibited faster iAPF (*M* = 10.8, *SD* = 0.7) than both non-ballet dancers (*M* = 10.5, *SD* = 0.7, p_{Bonf} = 0.023) and non-dancers (*M* = 10.7, *SD* = 0.8, p_{Bonf} = 0.048) [Group: *F*(2, 25.3) = 5.467, *p* = 0.011] (Figure 4.3), and was greater among ballet dancers than non-ballet dancers during Block 2 (p_{Bonf}= 0.004) [Group x Time: *F*(8, 18.1) = 3.098, *p* = 0.022]. A significant main effect of Time [*F*(4, 18.8) = 3.655, *p* = 0.023] also showed faster iAPF during Block 1 relative to Block 4 (p_{Bonf} = 0.006), and AO iAPF was significantly correlated to iAPF during KMI [*r* = 0.585, *p* = 0.000] and VMIQ-2 [*r* = 0.567, *p* = 0.000] (Figure 4.2e).

Alpha power was greater among non-ballet dancers relative to non-dancers (p_{Bonf}= 0.000) [Group: *F*(2, 78.8) = 7.704, *p* = 0.001], but a significant Group x Time interaction [*F*(8, 37.2) =

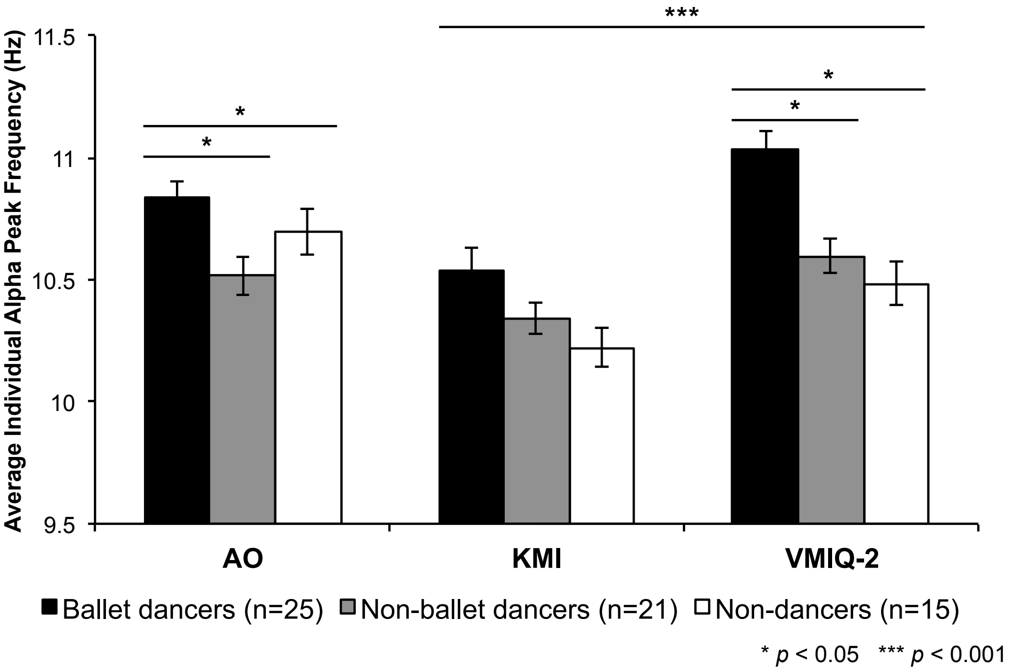

Figure 4.3. Individual alpha peak frequency (iAPF) during action observation and motor imagery.
The highly familiar ballet dance group showed faster iAPF during the AO task relative to both non-ballet dance (*p* = 0.029) and non-dance (*p* = 0.018) groups, and also demonstrated faster iAPF than non-ballet (*p* = 0.049) and non-dance groups (*p* = 0.027) during the VMIQ-2 task. No significance between group effects were observed during the KMI task, and all participants had significantly faster iAPF during the VMIQ-2 task relative to the KMI task (*p* = 0.000). Error bars represent SEM.

2.659, $p = 0.021$] revealed greater alpha power among non-ballet dancers relative to both groups during Block 1 (ballet dancers: $p_{Bonf} = 0.041$, non-dancers: $p_{Bonf} = 0.040$) and relative to ballet dancers during Block 2 ($p_{Bonf} = 0.010$), but greater alpha power among ballet dancers than non-dancers during Block 5 ($p_{Bonf} = 0.039$) (Figure 4.4a). Alpha and beta power were also significantly correlated during AO ($r = 0.504$, $p = 0.000$). Beta power was significantly greater among ballet dancers relative to both non-ballet dancers ($p_{Bonf} = 0.003$) and non-dancers ($p_{Bonf} = 0.000$) [Group: $F(2, 19.0) = 19.810$, $p = 0.000$], demonstrating modulation of beta power by familiarity with the observed stimulus (Figure 4.4b). Further, a significant main effect of Electrode [$F(7, 9.3) = 4.790$, $p = 0.016$] showed higher beta power in bilateral occipital electrodes relative to left premotor cortex (O1: $p_{Bonf} = 0.012$, O2: $p_{Bonf} = 0.024$).

4.4.2 KMI Task

Analyses of the average motor imagery ratings provided at the end of each block of the KMI task revealed no differences in clarity or vividness between groups [$F(2, 58) = 1.137$, $p = 0.328$] (Figure 4.1), and were significantly correlated to those obtained during the VMIQ-2 task ($r = 0.370$, $p = 0.003$). There were no significant group differences in task-related iAPF (Figure 4.3) or alpha power ($p > 0.05$), but comparing log alpha power during KMI to baseline revealed significant desynchronization (baseline > KMI) during motor imagery [Task: $F(1, 58) = 6.236$, $p = 0.015$, $\eta^2 = 0.098$], as well as higher alpha power in O1, O2, P7 and P8 electrodes relative to the temporal and frontal sites [Electrode: $F(4.7, 272.7) = 207.713$, $p = 0.000$, $\eta^2 = 0.782$] (Figure 4.5a). Task-related beta power was higher in left ($p_{Bonf} = 0.001$) and right ($p_{Bonf} = 0.013$) premotor cortex relative to left superior temporal cortex [Electrode: $F(4.9, 282.1) = 4.686$, $p = .000$, $\eta^2 = 0.075$]. Similar to alpha power, when comparing log beta power during KMI and

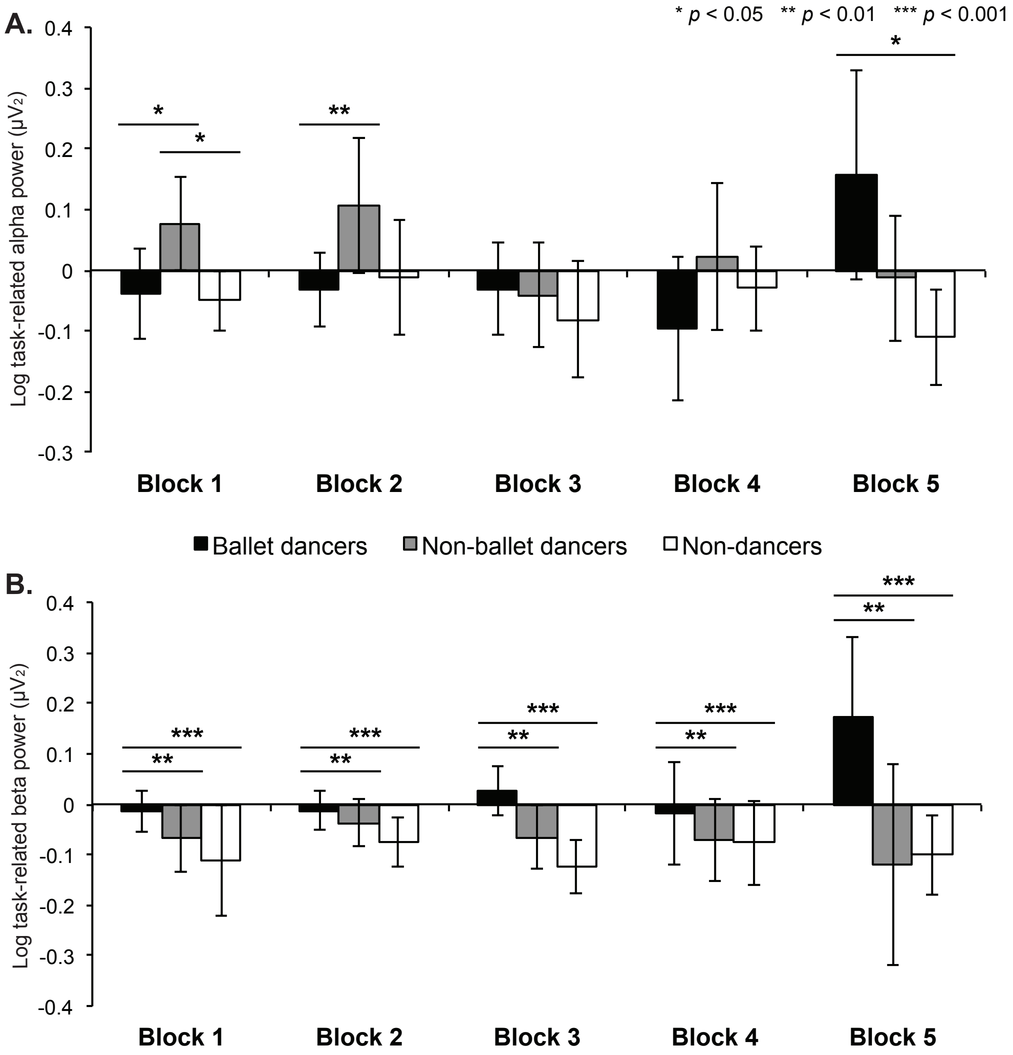

Figure 4.4. Alpha and beta power during observation of a novel ballet dance sequence. A. Log task-related (i.e., baseline corrected) alpha power was significantly higher in the non-ballet group relative to non-dancers ($p_{Bonf} = 0.000$) in all blocks, while a significant Group x Time interaction revealed higher alpha power in non-ballet dancers than the other groups at Block 1 (ballet: $p_{Bonf} = 0.041$, non-dance: $p_{Bonf} = 0.040$) and higher than ballet dancers at Block 2 ($p_{Bonf} = 0.010$), and greater alpha power in ballet dancers than non-dancers at Block 5 ($p_{Bonf} = 0.039$). **B.** Log task-related beta power was significantly higher in the ballet dancer group relative to both non-ballet dancers ($p_{Bonf} = 0.003$) and non-dancers ($p_{Bonf} = 0.000$). Error bars represent SEM.

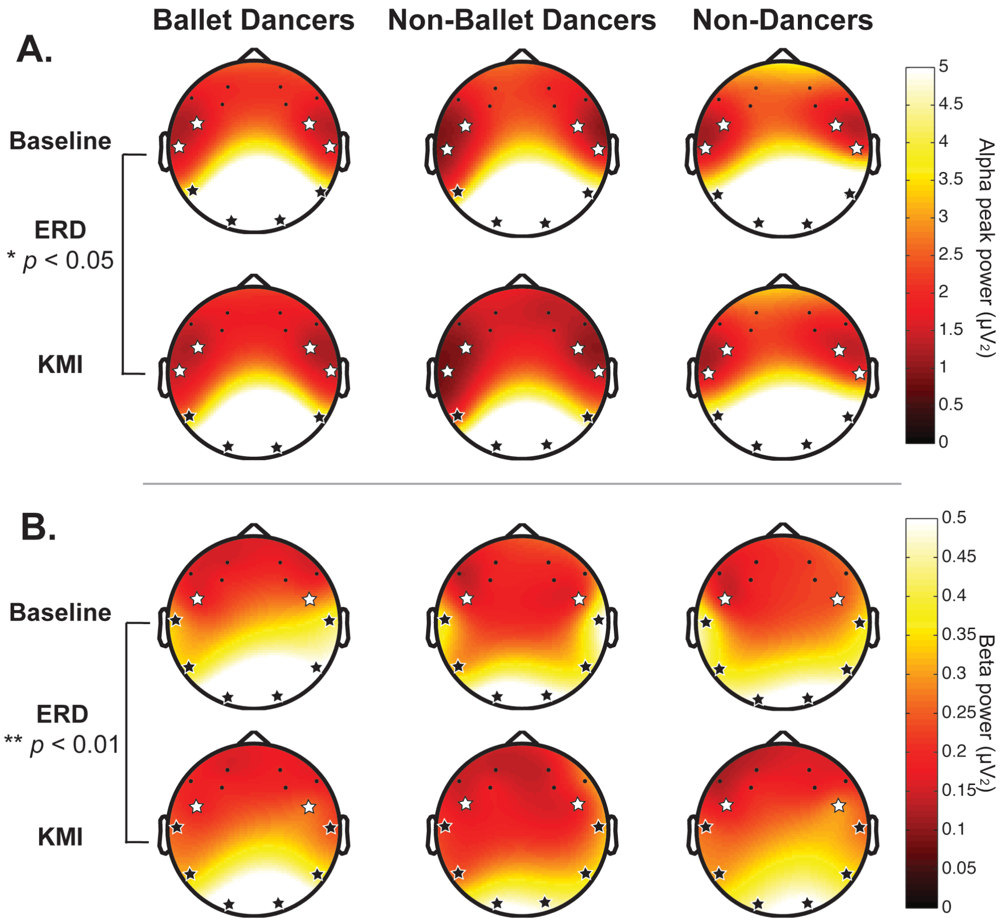

Figure 4.5. Alpha and beta power during baseline and KMI.
A. Analyses of log alpha peak power during the KMI task and matched baseline condition (eyes closed with music) revealed significant task-related desynchronization (bottom row), and a significant main effect of Electrode revealed higher alpha power in bilateral occipital and parietal sites (black stars) relative to frontocentral and temporal sites (white stars). No significant group differences were observed. **B.** Analyses of log beta power during the KMI task and matched baseline condition (eyes closed with music) revealed significant task-related desynchronization (bottom row), and a significant main effect of Electrode revealed higher alpha power in all posterior sites (black stars) relative to frontocentral sites (white stars). No significant group differences were observed.

baseline we found significant desynchronization during motor imagery [Task: F(1, 58) = 7.951, $p = 0.007$, $\eta^2 = 0.121$] especially in T7 ($p_{Bonf} = 0.000$), P7 ($p_{Bonf} = 0.008$), O1 ($p_{Bonf} = 0.026$), P8 ($p_{Bonf} = 0.006$), and T8 ($p_{Bonf} = 0.018$) [Task x Electrode: $F(4.9, 282.1) = 4.686$, $p = 0.000$, $\eta^2 = 0.075$] (Figure 4.5b). Beta power was also found to be lower in bilateral premotor cortex relative to all other electrode sites [Electrode: $F(5.1, 293.7) = 51.496$, $p = 0.000$, $\eta^2 = 0.470$].

4.4.3 VMIQ-2 Task

We confirmed that there were no inherent differences in motor imagery ability between groups with a one-way ANOVA on the average VMIQ-2 scores (i.e., across all 12 movements) [$F(2, 58) = 2.245$, $p = 0.115$] (Figure 4.1). Separate 8 (Electrode) x 3 (Group) RM-ANOVAs on iAPF, alpha and beta power, respectively, showed that iAPF was significantly faster among ballet dancers than non-ballet ($p = 0.043$) and non-dancers ($p = 0.028$) [$F(2,56) = 3.362$, $p = 0.042$, $\eta^2 = 0.107$] (Figure 4.3), and faster in occipital cortex relative to all other sites [$F(6.3, 350.3) = 5.843$, $p = 0.000$, $\eta^2 = 0.094$]. Alpha power did not differ between electrodes or groups ($p > 0.1$), and similar to the KMI task beta power was higher in bilateral premotor cortex relative to superior temporal (FC5 > T7: $p = 0.002$, T8: $p = 0.004$; FC6 > T7: $p = 0.013$, T8: $p = 0.003$), left occipital (FC5 > O1: $p = 0.014$; FC6 > O1: $p = 0.047$) and right parietal cortex (FC5 > P8: $p = 0.005$) but only at uncorrected significance levels [Electrode: $F(5.1, 286.4) = 3.489$, $p = 0.004$, $\eta^2 = 0.059$].

To compare the perceptual quality of KMI for habitual movements to KMI of a complex ballet sequence, we also performed a 2 (Task) x 3 (Group) RM-ANOVA on confidence ratings. It was confirmed that all participants reported significantly clearer and more vivid imagery during the VMIQ-2 task relative to the KMI task[5] [$F(1, 58) = 61.821$, $p = 0.000$, $\eta^2 = 0.516$, Task x Group: $F(2, 58) = 3.504$, $p = 0.037$, $\eta^2 = 0.52$, ballet dancers: $p_{Bonf} = 0.0005$, non-ballet dancers and non-dancers: $p_{Bonf} = 0.000$] (Figure 4.1). Neural features of KMI (iAPF, alpha power and beta power) were also compared between the KMI and VMIQ-2 tasks with separate 2 (Task) x 8 (Electrode) x 3 (Group) RM-ANOVAs, respectively. Significantly faster iAPF [$F(1, 56) = 31.960$, $p = 0.000$, $\eta^2 = 0.363$] (Figure 4.3) and higher alpha power [$F(1, 56) = 13.101$, $p = 0.001$, $\eta^2 = 0.19$] (Figure 5.6) were shown among all participants during the VMIQ-2 task relative to the

KMI task. A significant main effect of electrode [$F(4.8, 266.9) = 2.984, p = 0.005, \eta^2 = 0.051$] revealed faster iAPF in occipital cortex relative to left premotor cortex (O1: $p_{Bonf} = 0.004$, O2: $p_{Bonf} = 0.006$), and beta power was higher in premotor cortices than temporal (FC5 > T7: $p_{Bonf} = 0.001$, T8: $p_{Bonf} = 0.025$; FC6 > T7: $p_{Bonf} = 0.028$, T8: $p_{Bonf} = 0.014$) and right parietal cortex (FC5 > P8: $p_{Bonf} = 0.006$) [Electrode: $F(4.5, 249.9 = 5.537, p = 0.000, \eta^2 = 0.090$].

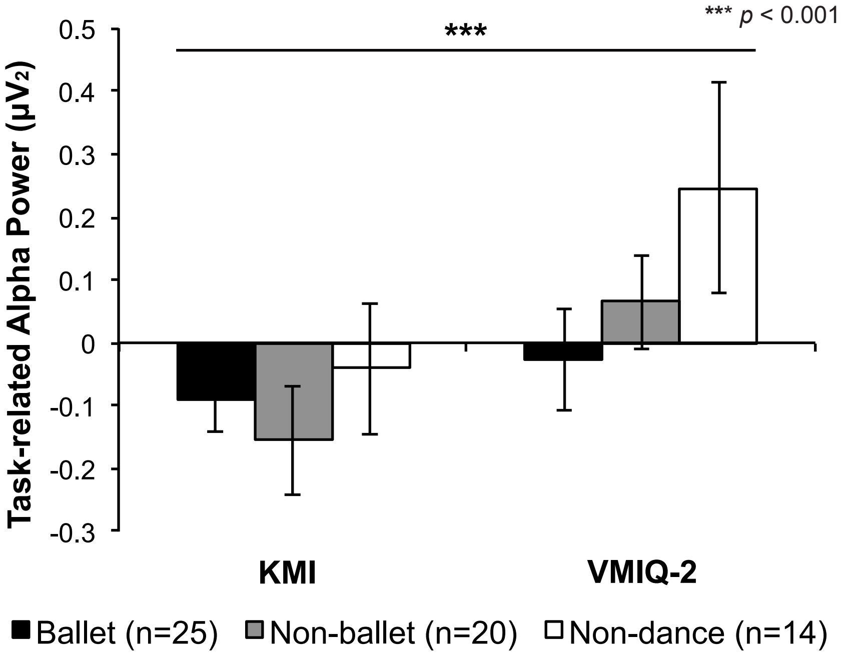

Figure 4.6. Task-related alpha power during KMI of a novel ballet dance and non-dance movements.
Log task-related (i.e., baseline-corrected) alpha power was significantly higher during the VMIQ-2 task than during KMI ($p_{Bonf} = 0.001$). Participants performed motor imagery with their eyes closed in both tasks, but showed higher alpha power when imagining non-expressive quotidian movements relative to a newly-learned complex ballet dance sequence. Error bars represent SEM.

4.5 DISCUSSION

Based on behavioral and neural indices, we demonstrate modulation of oscillatory brain activity by familiarity with an observed ballet stimulus superseding any general dance expertise effects, but no such differences were observed when subjects performed motor imagery of a ballet dance. However, ballet dancers demonstrated faster iAPF during KMI of non-dance movements. Among all participants, KMI was reportedly clearer and more vivid when imagining non-dance movements relative to a complex dance sequence, and elicited less desychnronization in both alpha and beta frequency bands. These results and how they expand upon our current understanding of experience-dependent oscillatory activity underlying movement processing will be discussed in turn.

Several behavioral indices obtained during the AO task reveal greater task engagement by familiar ballet dancers relative to the unfamiliar non-ballet dancers, who also putatively possess specialized sensorimotor networks arising from dance-related experience but in different genres, and relative to non-dancers, who served as a control group for dance-related expertise and familiarity. Ballet dancers performed significantly fewer blocks of the self-paced task, provided lower subjective ratings reflecting greater confidence in their ability to perform the dance sequence if required (Figure 4.1), and a strong positive correlation between these two variables (Figure 4.2b). The number of trials performed was also negatively correlated to alpha power (Figure 4.2c), demonstrating that subjects who were less confident in their perceived ability to perform the observed task exhibited greater alpha desynchronization than participants who performed fewer trials. Although the clarity ratings provided during the KMI task did not differ between groups, they were positively correlated to AO confidence ratings (Figure 4.2d). Examination of the oscillatory activity underlying the experimental tasks will provide greater insight into the mechanisms underlying these behavioural differences in task engagement.

4.5.1 State iAPF

Higher iAPF is reflected during states of arousal, attention and readiness to perform cognitive tasks including working memory (Angelakis et al., 2004; for review see Bazanova &

Vernon, 2014; Klimesch, 1999). However, these evaluations often compare performance outcomes to pre-task iAPF levels obtained at rest. Samaha and Postle (2015) compared performance on a two-flash fusion task to pre-task iAPF as well pre-stimulus iAPF, and found that both were correlated to lower thresholds and improved performance on this task, which serves as a measure of temporal resolution of visual perception. In order to form a clear motor image of the dance for the KMI task in the current study, ballet dancers' visual and sensorimotor systems were able to process more information during AO on a finer temporal scale. Since their iAPF did not differ from other groups in pre-task baseline conditions, we can infer that this 'state' change is driven by a combination of bottom-up perceptual features of the familiar dance genre and top-down influences from existing (embodied) knowledge of the motor repertoire (Diedrichsen & Kornysheva, 2015). Evidence for the latter is supported by the recent identification of alpha and beta as feedback signals from higher-order regions, including those where the motor representations of ballet movements and positions are coded, to primary sensory areas including the visual cortex (Michalareas et al., 2016).

It has been noted in dance-related neuroaesthetic literature that dancers, and ballet dancers in particular, use KMI as a tool for mental rehearsal in the absence of overt movement (Bläsing et al., 2012; Milton, Small, & Solodkin, 2008). Although this was not directly assessed in our participants, and no differences in imagery ability were found when comparing VMIQ-2 ratings (Figure 4.1), this long-term experience with dance KMI may also reinforce the neural pathways that optimally integrate real auditory (i.e., music) information with imagined motor signals (Berger & Ehrsson, 2014), which may account for the observed increase in iAPF among ballet dancers during VMIQ-2 relative to other groups (Figure 4.3). Taken together, results from the AO and VMIQ-2 tasks support and extend previous findings by showing that iAPF can be modulated by experience.

4.5.2 Engagement vs. Difficulty: iAPF and Alpha Power

Haegens and colleagues (2014) provide evidence for modulation of iAPF *during* task performance, with increased cognitive demand resulting in faster occipital and parietal iAPF. Accordingly, one would expect higher iAPF while visualizing a more demanding action (dance) relative to non-dance movements (VMIQ-2). However, the opposite pattern was observed (Figure 4.3). Conflicting evidence for changes in alpha *power* that accompany higher iAPF have been shown depending on the nature of the cognitive task; desynchronization has been shown to reflect the active engagement in encoding and memory retention (Pesonen, Hämäläinen, & Krause, 2007) while alpha synchronization (increased alpha power) suggests a decrease in expended cortical resources following skill learning (Gevins et al., 1997) and is related to suppression of distracting information that can interfere with encoding from parieto-occipital sources (Jensen, Bonnefond, & VanRullen, 2012; Sauseng et al., 2009) that comprise most of the source signals in the current investigation. As such, the desynchronization elicited during dance KMI may reflect processing of the dance that had just been observed and encoded in working (visual) memory while the relatively greater alpha power elicited during the VMIQ-2 task could reflect the reduced cognitive load for imagining simple movements (Table 4.1) in the face of competing stimuli or attentional demands (Figure 4.6). This pattern is consistent with the neural efficiency hypothesis (Klimesch et al., 2007), which supposes that alpha synchronization reflects inhibition of task-irrelevant areas, including posterior visual areas when performing first-person KMI (Neuper, Scherer, Reiner, & Pfurtscheller, 2005; Sirigu & Duhamel, 2001), and alpha desynchronization is highest during focused task-related activation such as what would be expected during KMI of a newly-learned task.

4.5.3 Neural Efficiency: Alpha and Beta Power

Further evidence for the neural efficiency hypothesis can be observed during the AO task, which replicates previous evidence for experience-dependent alpha desynchronization during AO (Orgs et al., 2008) but with evidence for desynchronization among non-dancers as well (Figure 4.4a). To confirm that this similar pattern of alpha power among groups on opposite ends of the familiarity continuum does not reflect the same underlying process, we can consider the observed beta power results during AO. Beta desynchronization has been shown to accompany alpha desynchronization during AO (lower beta (13-18Hz) only in Orgs et al., 2008) and KMI (McFarland, Miner, Vaughan, & Wolpaw, 2000), and is further decreased during KMI and execution of skilled movements (Nakagawa et al., 2011; G. Pfurtscheller, Woertz, Müller, Wriessnegger, & Pfurtscheller, 2002). In addition, both frequency and power of the beta band have been related to cognitive aspects of movement, including cue anticipation or expectation, visuomotor integration and preparation (Kilavik et al., 2012). Beta synchronization is typically observed during the ‘post-movement rebound’ in a wider distributed premotor and sensorimotor area (Crone et al., 1998; Ohara et al., 2000; Sochůrková, Rektor, Jurák, & Stančák, 2006) and occurs immediately following real or imagined movement as a ‘resetting’ of motor representations in these networks (Pfurtscheller & Solis-Escalante, 2009; Pfurtscheller et al., 2005; Solis-Escalante et al., 2012). If beta oscillations originate in the primary motor cortex as previously suggested (Crone et al., 1998; Pfurtscheller et al., 2002), and responsivity of the sensorimotor cortex is greater for familiar embodied actions (Calvo-Merino et al., 2005; 2006; Cross et al., 2006; 2009a,b), then perhaps the degree of beta desynchronization can also be nuanced by experience-dependent plasticity, although to a lesser degree than task-related demands. That ballet dancers exhibited less beta desynchronization than both unfamiliar groups during AO (Figure 4.4b) could possibly reflect less suppression of the distributed sensorimotor network that encodes existing genre-specific motor representations, which would only provide competition for limited neural resources among unfamiliar dancers and non-dancers. Thus, by considering activity in multiple frequency bands during the same task, the present results clarify the impact of familiarity on multiple concurrent functional roles for alpha and beta power during AO and KMI.

4.5.4 Therapeutic Applications for Dance-Induced Modulation of Sensorimotor Oscillations

A growing body of evidence is lending credit to the benefits of dance practice on general health, and especially for the elderly and those afflicted with movement disorders (for review, see Dhami et al., 2015). It is well established that iAPF is lower in the elderly (Clark et al., 2004) and especially among those with neurological disorders like Alzheimer's (Klimesch et al., 1990) and Parkinson's disease (PD) (Moazami-Goudarzi et al., 2008; Soikkeli et al., 1991). If familiarity with the observed stimulus, cultivated over years of sensorimotor practice, can elicit increased state iAPF during AO and KMI, then perhaps low-impact AO and/or KMI training programmes combined with (or in lieu of) dance practice can yield improvements in iAPF functioning. Previous work from our lab that has revealed neural efficiency of the extrastriate body area during movement among expert dancers (Di Nota et al., 2016). This has implications for PD, with recent evidence for recruitment of this brain region as an alternate motor pathway in this population (van Nuenen, Helmich, Buenen, et al., 2012a; van Nuenen, Helmich, Ferraye, et al., 2012b). Ongoing investigations on the efficacy of Dancing with Parkinson's (DWP) programs on the neural, motor and non-motor symptoms of PD led by our lab and other research teams seek to clarify the therapeutic potential of dance (Bearss et al., 2017; Di Nota et al., 2016b; Ventura et al., 2016; Westheimer et al., 2015).

4.6 CONCLUSIONS

Several important insights are revealed by the results of the current study: we provide a further understanding of experience-dependent plasticity of the neural mechanisms underlying AO and KMI of specialized and habitual movements. Specifically, we demonstrate modulation of iAPF and power in the alpha and beta frequency bands during observation of a familiar dance sequence relative to unfamiliar participants, with further expertise effects resulting in more efficient visuomotor processing during KMI of non-dance movements. While all participants demonstrated alpha and beta desynchronization during KMI, we clarify that familiarity with the imagined stimulus does not result in significant modulation of these signals, unlike AO. Together, these findings reveal the neurophysiological mechanisms underlying expert knowledge schemas that facilitate translational benefits of dance practice across sensorimotor and attentional domains. The results also lend further support for the efficacy of dance therapy for clinical populations experiencing deficiencies in these domains.

5 CHAPTER FIVE – LATERAL OCCIPITOTEMPORAL CORTEX (LOTC) ACTIVITY IS GREATEST WHILE VIEWING DANCE COMPARED TO VISUALIZATION AND MOVEMENT: LEARNING AND EXPERTISE EFFECTS[11]

5.1 PREFACE

The lateral occipitotemporal cortex (LOTC) is comprised of sub-regions selectively activated by images of human bodies (extrastriate body area, EBA), objects (lateral occipital complex, LO) and motion (MT+). However, their role in motor imagery and movement processing is unclear, as are the influences of learning and expertise on its recruitment. The purpose of our study is to examine putative changes in LOTC activation during action processing following motor learning of novel choreography in professional ballet dancers. Subjects were scanned with functional magnetic resonance imaging (fMRI) up to four times over 34 weeks and performed four tasks: viewing and visualizing a newly learned ballet dance, visualizing a dance that was not being learned, and movement of the foot. EBA, LO and MT+ were activated most while viewing dance compared to visualization and movement. Significant increases in activation were observed over time in left LO only during visualization of the unlearned dance, and all sub-regions were activated bilaterally during the viewing task after 34 weeks of performance, suggesting learning-induced plasticity. Finally, we provide novel evidence for modulation of EBA with dance experience during the motor task, with significant activation elicited in a comparison group of novice dancers only. These results provide a composite of LOTC activation during action processing of newly learned ballet choreography and movement

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[11] Paula M. Di Nota, Gabriella R. Levkov, Rachel J. Bar & Joseph F.X. DeSouza. (2016). *Experimental Brain Research, 234(7)*, 2007-2023.

of the foot. The role of these areas is confirmed as primarily subserving observation of complex sequences of whole-body movement, with new evidence for modification by experience and over the course of real world ballet learning.

5.2 INTRODUCTION

The pattern of brain activity elicited by a given movement is known as a motor representation, which can also be accessed consciously without overt physical movement through motor imagery (Jeannerod 1995; Gerardin et al. 2000; Sirigu and Duhamel 2001; Grèzes and Decety 2001; Hanakawa et al. 2008). Using functional magnetic resonance imaging (fMRI), researchers have identified common and distinct nodes of activity during action processing – the execution, observation, and visualization of movement, with common activation reported in the premotor cortex (PMC), supplementary motor area (SMA), middle frontal gyrus, cingulate gyrus, supramarginal gyrus, and inferior parietal cortex (Gerardin et al. 2000; Grèzes and Decety 2001; Hanakawa et al. 2008). These regions are suggested to be bound by the physical constraints and similar time courses for real and imagined movement (Gerardin et al. 2000) and additionally compare preparatory efference copy signals to reafferent sensory signals in order to determine if predicted and actual behavioral outcomes match during learning (Rizzolatti et al. 1998; Blakemore et al. 1998; DeSouza et al. 2000; DeSouza et al. 2002; 2003; Rizzolatti and Craighero 2004; Oosterhof et al. 2013; Pynn and DeSouza 2013). When these signals are congruent and successful movement occurs, connections between motor planning, execution, and sensory regions within the larger action observation network (AON) are strengthened, in turn facilitating future successful movement and motor learning through physical practice and during observation (Rizzolatti and Craighero 2004; Oosterhof et al. 2013).

In order to map a third-person motor representation onto the observer's AON and execute movement, observers must be able to embody the actions they perceive. The extrastriate body area (EBA) has been implicated in embodiment processing (Arzy et al. 2006; Di Dio et al. 2007; Urgesi et al. 2007; Giummarra et al. 2008) and is a functionally defined higher-order visual processing area in the lateral occipitotemporal cortex (LOTC). Preferentially activated by images, photographs and line drawings of human bodies and body parts, but not the human face, the EBA can be differentiated from other nearby category-specific areas like object-selective lateral occipital complex (LO) when contrasted with various control stimuli (Downing et al. 2001; Grill-Spector et al. 2001; Astafiev et al. 2004; Peelen and Downing 2005; Peelen et al. 2006; Orlov et al. 2010). Recent evidence demonstrates the responsiveness of EBA to goal-directed movement with and without visual feedback (Astafiev et al. 2004; Peelen and Downing 2005; Kable and Chatterjee 2006; Urgesi et al. 2006; David et al. 2007; Urgesi et al. 2007; Orlov et al. 2010), which is likely influenced by substantial overlap of this region with the human visual motion complex (MT+) also located within the LOTC (Downing et al. 2001; Kolster et al. 2010; Weiner and Grill-Spector 2011; Ferri et al. 2013). These works demonstrate an important role for the EBA and sub-regions of the LOTC in mediating sensorimotor transformations of observed action within the AON.

In addition to responding to observed movement, there is evidence for EBA activation during motor imagery of human bodies (Astafiev et al. 2004; Blanke et al. 2010). This is contrary to previous claims that motor imagery is subserved by a different network of brain regions than those involved in visual imagery (Jeannerod 1995; Sirigu and Duhamel 2001;

Tomasino and Rumiati 2004; Urgesi et al. 2007), with the latter recruiting predominantly from the left hemisphere and visual imagery mediated mostly by the right hemisphere (Gerardin et al. 2000; Grèzes and Decety 2001; Tomasino and Rumiati 2004; David et al. 2007; Urgesi et al. 2007; Hanakawa et al. 2008; Blanke et al. 2010). Also uncertain is the role of EBA during movement execution. While EBA activity is stronger in the contralateral hemisphere during visually-guided movement (Astafiev et al. 2004; Peelen and Downing 2005; David et al. 2007; Weiner and Grill-Spector 2011), limited activation has been demonstrated during movement in the absence of visual information (Astafiev et al. 2004; Peelen and Downing 2005; Orlov et al. 2010). Based on these modest activations of EBA by different motor signals (i.e. execution or imagery), higher-order visual areas in LOTC have been suggested to serve more of an interpretive function as opposed to an action-specific one (Kable and Chatterjee 2006; Herrington et al. 2012). However, recent evidence combining both anatomically and functionally driven approaches suggests that the LOTC and its sub-regions are responsible for a multitude of action representations, including preparation of goal-directed movement (Kühn et al. 2010), attributing meaning to observed and executed movement (Romaiguère et al. 2014), as well as semantic processing of action-related verbs (Bedny et al. 2008; Kemmerer et al. 2008; for comprehensive review see Lingnau and Downing 2015). We seek to clarify the extent to which the LOTC and its sub-regions are activated during different action processes (observation, imagery and execution) within the same individuals in order to understand its role within the AON.

Action processing is also an important focus of research in the emerging field of neuroaesthetics, with topics ranging from sensorimotor transformations of a dance onto the observer’s cognitive motor network, to evaluating the emotional valence of a performance, which also implicates EBA (Calvo-Merino et al. 2005, 2006; Cross et al. 2006; Di Dio et al. 2007; Cross et al. 2009a, 2009b; Calvo-Merino et al. 2010). Prolonged and intensive training has been shown to result in structural and functional changes throughout the brain (Lotze et al. 2003; Calvo-Merino et al. 2005, 2006; Limb and Braun 2008; Olsson et al. 2008). Cortical activations become more refined with practice (DeSouza & Bar, 2016), resulting in less activation compared to non-experts (Dhami, 2016), particularly in the SMA, and less activation during imagined compared to observed performance (Meister et al. 2004, 2005; Olsson et al. 2008). Although common networks are activated in both amateurs and experts while performing dance movements cued by music (Brown et al. 2006; Brown and Parsons 2008), they can become specified to the extent that they elicit different activation for stimuli that are tuned to the experience of the expert (Calvo-Merino et al. 2005, 2006; Olsson et al. 2008). Expertise also affects whether motor or visual imagery elicits a motor representation, with novices recruiting visual areas due to a lack of physical familiarity with the movement repertoire (Calvo-Merino et al. 2006; Olsson et al. 2008; Blanke et al. 2010) while experts demonstrate a broadened capacity for physical and observational learning (Cross et al. 2006, 2009a, 2009b; Foster 2013). Using functional tasks that involve observation, visualization and execution of movement that is tuned to the experience of our experts over a longer duration than previously investigated, we hope to clarify any putative differences in LOTC activation during these processes relative to novices.

With our current understanding of LOTC involvement in action processing, we still do not know to what extent this region is comparatively activated during observed, imagined, and real movements, how activity changes over the course of motor learning, and whether activation is modulated by expertise. These are the goals of the present study, which will be achieved by analyzing longitudinal EBA, MT+ and LO fMRI blood oxygen level-dependent (BOLD) activity during four tasks: viewing a novel dance sequence that is being physically learned, visualizing a novel dance sequence that is being physically learned (VisL), visualizing an improvised control dance sequence that is not physically being learned (VisNL), and a motor task that involves movement of the right foot. A portion of the VisL data has been examined for whole-brain changes in motor representations over the course of a 34-week learning and rehearsal program (Bar and DeSouza 2012; 2016; DeSouza and Bar 2012)[12] but our current research questions will employ different methods, namely anatomical and functional localizers, to focus on LOTC. Based on the existing literature, we hypothesize that LOTC activation will be greatest during viewing compared to visualization and movement tasks, and we expect differences between the movement and visualization tasks with no specific hypothesis about directionality. We also expect learning-induced changes in LOTC activity over the course of a 34-week dance program, and that activation will differ between visualization of learned (VisL) and non-learned (VisNL) dance sequences. We also predict that LOTC activation will differ between expert dancers and novices during each of the tasks, as the former group has likely developed specialized neural networks following intensive professional training compared to novices.

5.3 METHODS

5.3.1 Participants

Eighteen professional ballet dancers (6 female, mean age = 20.7 years, range = 18-50 years, mean years of dance experience = 13.1) were recruited from three cohorts of the National Ballet of Canada's Apprenticeship Program, all of which practiced and performed the dance that would comprise the experimental stimulus. Subject 14 discontinued participation due a dance

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[12] Due to time constraints in ongoing data collection, the EBA was functionally localized in only 12 subjects (see Appendix C). Justification for the validity of our anatomical ROIs is provided in Section 5.3.5.

injury that hindered learning of the choreography, Subject 15 missed Scans 2 and 3 due to an injury, and Subject 16 discontinued participation after Scan 2 (see Appendix C for summary). Due to these missing data points, we were unable to perform typical analysis of variance (ANOVA) significance tests, and have adjusted our statistical models accordingly (see Section 2.4 for further details). To evaluate putative expertise effects in LOTC activity during the experimental tasks, eight novice subjects were also scanned (5 female, age = 25.8 years, range = 18-43 years, mean years of dance experience = 4.75). Novice subjects were members of the York University community that had varied levels of dance experience (ballet, figure skating) that were significantly less than that of the expert group (F(1, 25) = 6.38, *p* = 0.019). Exclusion criteria for all participants included any history of neurological disorders, and for the novice group, any subjects that had standardized years of experience (years of experience – mean years of experience for novice group/SD) +/-1 were also excluded. Two novice participants were excluded under this criteria (Bar & DeSouza, 2016). Thus, data from twenty-six subjects and 150 imaging sessions were included. Subjects provided written consent and were compensated $25 per hour. All procedures were approved by and in accordance with the York University Human Participants Research Review Sub-Committee (Certificate number: 2013-211).

5.3.2 Procedure

Professional dancers were scanned up to four times according to a 34-week schedule that matched that of the National Ballet of Canada’s Apprenticeship Program, beginning in September and ending in late May:

- Time 1: first week of rehearsal (baseline); three dancers in the first cohort had rehearsed the portion of the dance (final minute of the sequence) included in the present scan four times, remaining dancers had not yet learned the tested portion of the dance

- Time 2: one week after baseline scan; average of seven rehearsals of the tested portion of the dance
- Time 3: five weeks (average) after Time 1; 16 performances of the entire dance for five dancers and an average of 21 rehearsals for remaining dancers
- Time 4: 33 weeks (average) after Time 1; average of 13 performances for eleven dancers and average of 26 rehearsals for twelve dancers (the second cohort discontinued the original choreography soon after Time 3)

Novice subjects did not learn the choreography of the expert dancers and were scanned at Time 1 only.

In a single scanning session, subjects performed up to 4 tasks (Appendix C). Each of the following tasks employed a block design, with five one-minute ‘On’ conditions beginning with, separated by, and ending with 30-second fixation (‘Off’) periods lasting 8.10 minutes.

Viewing task: Subjects were instructed to listen to and watch a 1-minute segment of their respective dances accompanied by music. Video stimuli were recorded by a member of the research team at the first rehearsal of the tested portion of the dance on location at the studio, which occurred between Time 1 and 2 scans. Thus, dancers only performed this task on and after Time 2, and novices (n = 6) scanned at the time of the second cohort watched the dance learned by cohort 1. Subjects were asked to fixate on a cross that was superimposed on the video at the center of the screen, which was back projected behind the scanner (visual angle = 36°) and viewed through a head coil-mounted mirror. Subjects wore MR-compatible headphones (MR Confon, Magdeburg, Germany).

Visualization task 1 (VisL): Through a pair of headphones, subjects heard the music to the choreography that they were currently learning (J.S. Bach's *Concerto in C Major* for the first dance cohort, A. Glazunov's *Opus 57* for the second dance cohort, and D. Shostakovich's *Allegro Non Troppo* for the third dance cohort) and were instructed to visualize the choreography that they had learned from a first-person internal perspective in time with the music. Novices were instructed to visualize themselves dancing to the music of the current cohort (see Appendix C) from a first-person internal perspective. A white fixation cross was presented at the center of a black screen throughout the task. Visualization training was offered to participants before each scanning session, as well as through workshops at the National Ballet of Canada offered to each cohort. To ensure the task was performed correctly according to their learning program and to the best of their ability, all dancers completed two items following each scan: a post-scanning questionnaire and a visualization test. The questionnaire asked how accurately subjects thought they visualized themselves dancing to the music, if they visualized from an internal (desired response) or external perspective, if they visualized the choreography continuously and timed exactly to the music, and whether their eyes were open or closed during visualization. One subject at one time point responded to visualizing from an external third-person perspective, and one subject at one time point reported visualizing another dance. Data from these sessions were excluded from further analyses. All but one subject reported closing their eyes during the task. For the visualization test, the video version of the stimulus was played and hidden from the dancers' view. The experimenters paused the video at five predetermined spots and asked the dancers to verbally describe or act out where in the dance the music had been paused. This procedure was repeated five times for each dancer following the final scan (Time 4) in the first cohort and following scans at Time 2, 3, and 4 in the remaining cohorts. Across all assessments, all but one dancer was accurate within 2 seconds at describing the paused moment of the dance, and the dancer who was unsure was inaccurate in three of five test trials.

Visualization task 2 (VisNL): In order to attribute changes in brain activity over time to learning a new dance sequence, a subset of subjects in cohorts 2 and 3 performed a control visualization task of a dance they were *not* learning (VisNL). Through a pair of headphones, participants heard the music to choreography that they were not currently learning (J.S. Bach's *Concerto in C Major* from Bar and DeSouza (2016)), which was selected to match the cadence and genre of the VisL stimuli. As with the VisL task, subjects were instructed to visualize themselves dancing to the music from a first-person internal perspective in an unstructured, improvised manner. Dancers also conducted a post-scanning questionnaire to ensure that they performed the task correctly (i.e., continuously from an internal first-person perspective, whether eyes were open or closed) and to the best of their ability, but no visualization test was performed. Only one subject at one time point responded to visualizing from an external third-person perspective, and this data was excluded from further analyses. All but one subject reported closing their eyes during the task.

Motor task: Subjects were instructed to maintain fixation on a cross at the center of the screen until it was replaced with the word "Wiggle", at which point they were instructed to continue fixating while moving the toes of their right foot (extending and contracting them at a rate of 1Hz), ensuring the rest of their body was completely still. This task was explained and demonstrated prior to entering the scanner to ensure the action and rate of movement was understood.

5.3.3 Image Acquisition

Functional and anatomical images of the brain were collected using a 3T Siemens TrioTim MRI scanner (Erlangen, Germany) with a 32-channel head coil, housed at the Sherman Health Science Research Centre at York University. T2*-weighted echo planar imaging using parallel imaging (GRAPPA) with an acceleration factor of 2X was used with the following parameters: 32 slices, 56x70 matrix, 210x168 mm FOV, 3x3x4 mm slice thickness, TE=30ms, flip angle of 90°, volume acquisition time of 2.0s. There were a total of 240 volumes per scan for each of the viewing, visualization, and motor tasks, and a total of 215 volumes for the EBA localizer task. Echo-planar images were co-registered with the high-resolution (1mm^3) anatomical T1-weighted images of the subject's brain taken during each scanning session (spin echo, TR = 1900ms, TE = 2.52ms, flip angle = 9°, 256 x 256 matrix). While in the scanner, subjects' heads were padded with cushions to reduce head movements. A vitamin E pill was placed beside the right hemisphere of all subjects for localization.

5.3.4 Image analysis

Preprocessing of the raw data collected from the scanner was performed with Brain Voyager QX (Version 2.4, Brain Innovation, Maastricht, The Netherlands). Functional data were coregistered with structural images, which were aligned on the anterior commissure-posterior commissure line and transformed into Talairach space. Functional data were motion corrected with a trilinear/sync interpolation and referenced to the functional volume from the previous functional run that was closest to the structural anatomical scan. Functional scans with motion artifact greater than 3mm were excluded, resulting in exclusion of only one of the 166 (or 0.6%) functional scans.

5.3.5 Signal processing – Region of Interest Analysis

Anatomically defined regions of interest (ROIs) were created for the EBA in both hemispheres for all subjects centered on averaged Talairach coordinates and anatomical landmarks obtained from the literature (Table 5.1). According to the literature, the right EBA is averaged at (*x, y, z*) 47 (*SD* = 3.2), -66 (*SD* = 3.6), 5 (*SD* = 5.9) and the left EBA at -46 (*SD* = 2.5), -72 (*SD* = 3.1), 1 (*SD* = 4.1). Anatomical ROIs for the EBA were centered on average coordinate points drawn along each subject's lateral occipital sulcus bordering on the inferior portion of the middle occipital gyrus (Astafiev et al. 2004; Peelen and Downing 2005; Orlov et al. 2010; Weiner and Grill-Spector 2011; Ferri et al. 2013) and not exceeding the SD values of

Table 5.1. Talairach coordinates for EBA, MT+ and LO from the literature.
Note that the coordinates cited for Sinke et al., (2012) are averaged across 14 participants, but all individual subjects were included in our calculation for the average coordinates in order to determine an average that encompassed as many previously reported ROI coordinates as possible. MNI coordinates were converted to Talairach using mni2tal converter (http://noodle.med.yale.edu/~papad/mni2tal/).

Region of interest	Coordinates (X, Y, Z) Left Hemisphere			Right Hemisphere			Contrast	Citation
EBA	-48	-76	4	50	-69	1	Headless bodies > chairs	Atkinson et al. 2012
	-	-	-	47	-66	7	Bodies > faces, houses, tools	Sinke et al. 2012
	-45	-73	2	47	-68	2	Headless bodies > chairs	Taylor et al. 2010
	-	-	-	47	-63	-7	Headless bodies > chairs	Kontaris et al. 2009
	-43	-73	-7	42	-63	10	Bodies > objects	Hodzic et al. 2009
	-51	-68	3	51	-67	3	Headless bodies > chairs	Downing et al. 2007
	-45	-69	4	45	-67	5	Bodies > 19 categories	Downing et al. 2006
	-45	-74	-1	48	-70	1	Bodies > faces, tools, scenes	Peelen et al. 2006
	-45	-74	-3	48	-68	0	Headless bodies > faces, scenes, tools	Peelen and Downing 2005
	-46	-68	4	46	-62	3	Body parts > object parts	Astafiev et al. 2004
MT+	-48	-74	11	47	-76	10	Moving > static random texture	Kolster et al. 2010

LO	-44	-77	-5	48	-78	-6	Objects > scrambled	Bona et al. 2014
	-45	-75	4	43	-73	5	Objects > scrambled	Mundy et al. 2012
	-42	-87	3	41	-89	2	(Un)familiar objects > scrambled images	Kolster et al. 2010
	-	-	-	40	-74	-2	Mammals, houses, objects > textures	Grill-Spector 2003
	-41	-77	3	40	-72	2	Object > noise, blanks	Grill-Spector et al. 1999

each coordinate plane (Figure 5.1). Control ROIs for bilateral MT+ and LO were created with 5mm-radius spheres centered on average coordinates from the literature (Table 5.1), which did not overlap with EBA ROIs (Figure 5.2). Center coordinates for left LO were -43 (*SD* = 1.8), -79

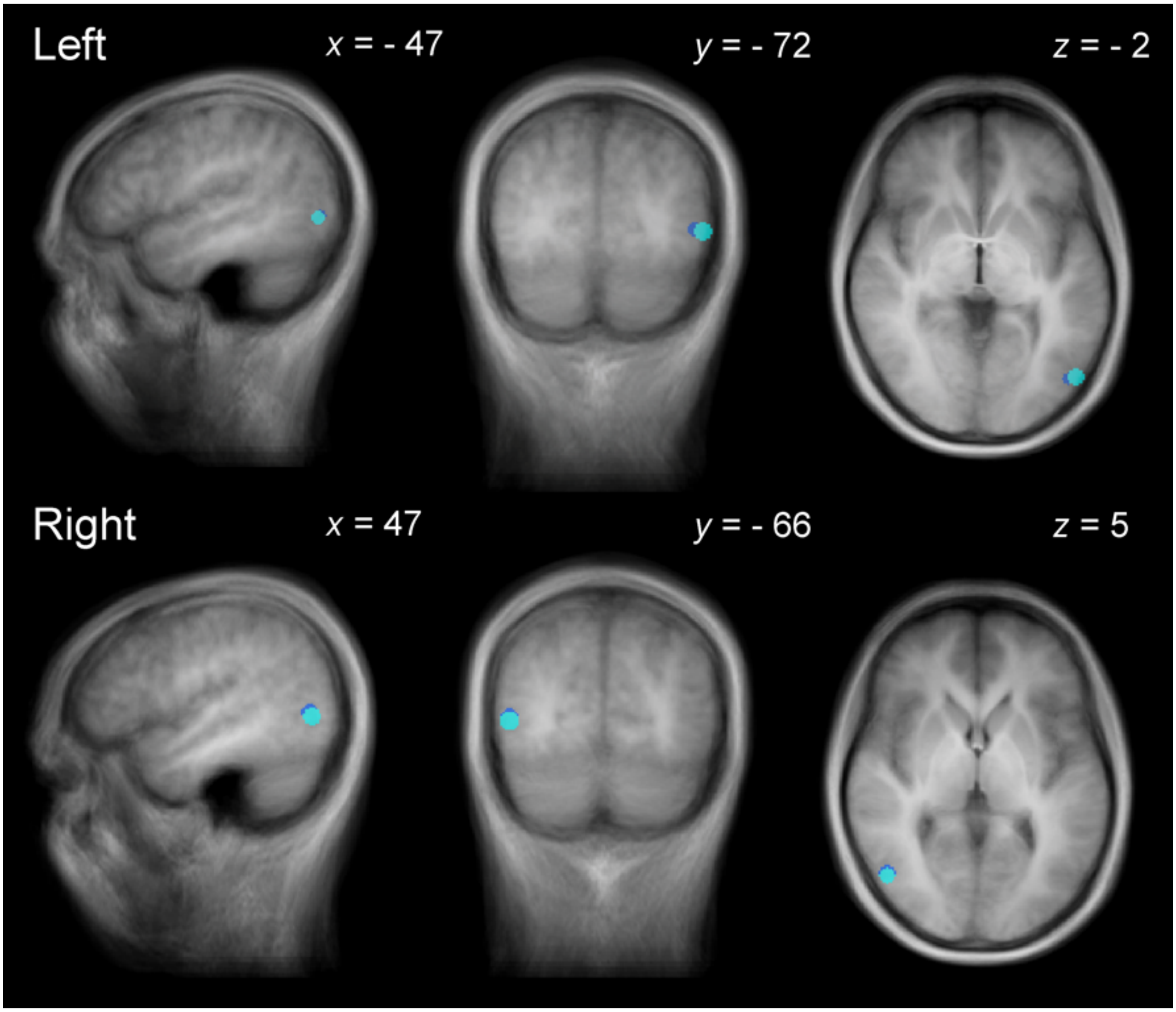

Figure 5.1. EBA regions of interest (ROIs).
To demonstrate accuracy of our anatomically-defined EBA ROIs (n=14, dark blue), we plotted their average centre coordinates with those from a functional EBA localizer on 12 subjects (light blue) on an average brain comprised of 60 Talairach-transformed structural images (all 26 subjects across multiple scans). The dark blue sphere represents the center coordinates of the anatomically-defined EBA ROIs with a radius of the averaged SD value across all coordinate planes (left: -46 (*SD* = 2.5), -72 (*SD* = 3.1), 1 (*SD* = 4.1), right: 47 (*SD* = 3.2), -66 (*SD* = 3.6), 5 (*SD* = 5.9). The light blue sphere represents the center coordinates of the functionally-defined EBA ROIs (Table 2) with a radius of the averaged SD value across all coordinate planes (left: -50 (*SD* = 3.9), -71 (*SD* = 4.0), 0 (*SD* = 5.2), right: 47 (*SD* = 3.4), -67 (*SD* = 4.7), 3 (*SD* = 5.3)

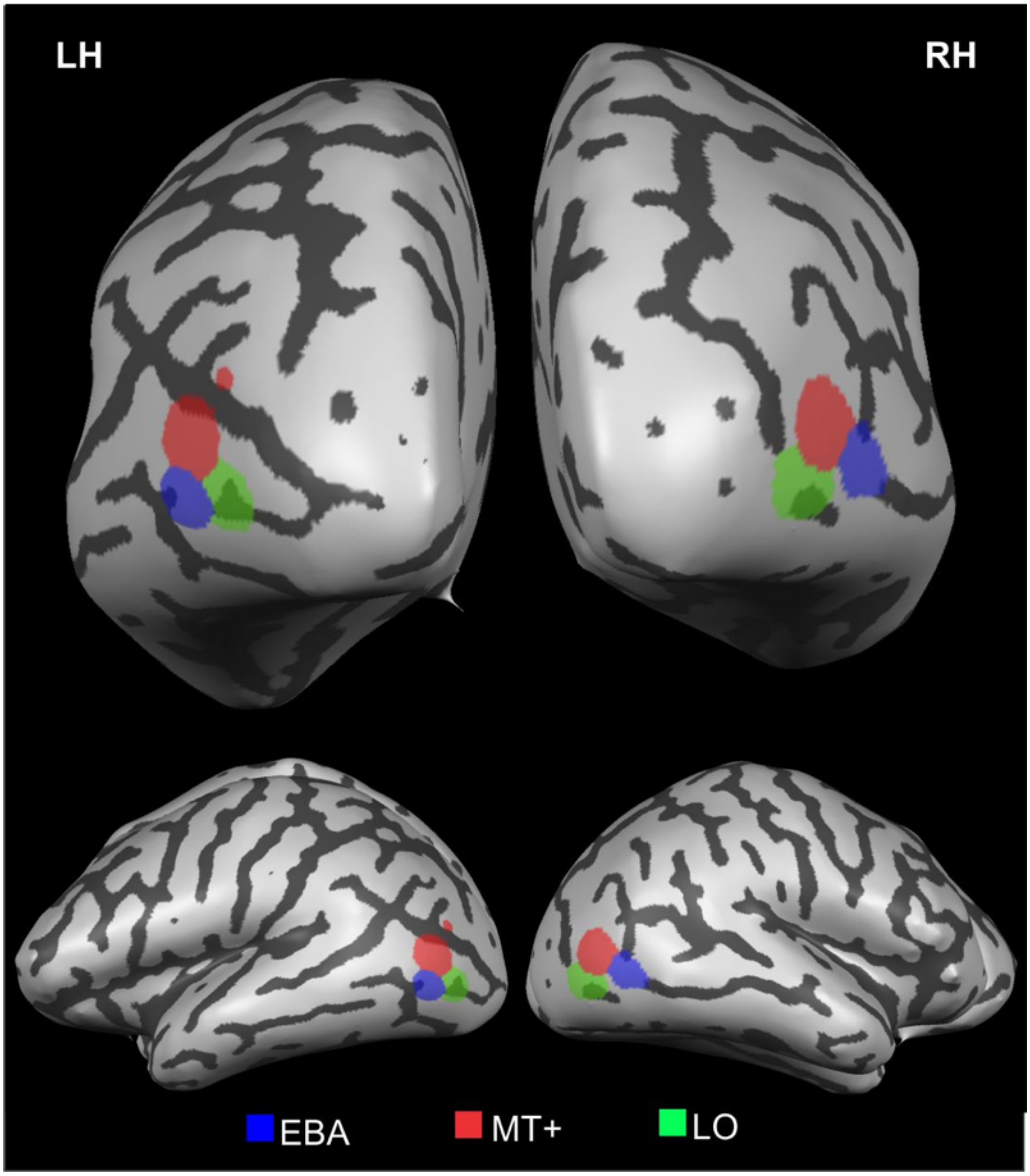

Figure 5.2. Regions of interest (ROIs) in lateral occipitotemporal cortex (LOTC). EBA (blue, averaged across anatomically- and functionally-defined ROIs), MT+ (red) and LO (green) ROIs in each of the left and right hemispheres are shown together on a surface map of a representative subject. Coordinates (*x, y, z*): left EBA: -48, -71.5, 0.5; right EBA: 47, -66.5, 4; left MT+: -48, -74, 11; right MT+: 47, -76, 10; left LO: -43, -79, 1; right LO: 42, -77, 0

(*SD* = 5.4), 1 (*SD* = 4.2) and for right LO were 42 (*SD* = 3.4), -77 (*SD* = 7.0), 0 (*SD* = 4.3) (Grill-Spector et al. 1999; Grill-Spector 2003; Kolster et al. 2010; Mundy et al. 2012; Bona et al. 2014), and center coordinates for MT+ have been reported previously (Kolster et al. 2010).

In order to validate our anatomical ROIs, we employed a functional EBA localizer approximately halfway through ongoing data collection in twelve of 26 subjects (10 dancers, 2 novices) using a standard EBA localizer task prepared in Matlab (Version 7.10.0.99 R2010a, The Mathworks, Inc., Natick, MA) and Psychophysics Toolbox (Brainard 1997). Subjects were presented with 8 'On' blocks, which were equally divided between the bodies (images of bodies and body parts, excluding faces) and objects (houses, flowers, guitars, and cars). Within each block, 20 images were randomly presented for 500ms with 500-1000ms interstimulus intervals at a visual angle of 11° (horizontally). The 'Off' blocks were 16 seconds and presented a black fixation point (visual angle = 0.2°) at the center of the screen (background colour grey, R:128, G:128, B:128). Body and object stimuli were obtained from a previously used database (Weiner and Grill-Spector 2010, 2011), and the task was an average of 8.7 minutes.

Functional ROIs were defined on a subject-by-subject basis and clusters were defined with body > object contrasts in left and right hemispheres (Table 5.2). The average coordinates for functionally-defined EBA ROIs were centered at (x, y, z) right: 47 (*SD* = 3.4), -67 (*SD* = 4.7), 3 (*SD* = 5.3) and left: -50 (*SD* = 3.9), -71 (*SD* = 4.0), 0 (*SD* = 5.2), and did not significantly differ from anatomically-defined EBA coordinates ($p>0.1$ for right: $x = t(11) = -0.425$, $y = t(11) = 0.366$, $z = t(11) = 0.000$; left: $x = t(11) = 0.447$, $y = t(11) = -0.219$, $z = t(11) = -0.165$) (Figure 5.2), demonstrating that our anatomically-defined EBA ROIs are reliably located in EBA and consistent with those that were functionally defined (Figure 5.1).

Raw timecourse data were extracted from each ROI for each subject, functional scan and time point. Those participants who performed a functional EBA localizer had data values extracted from functionally defined ROIs (n = 12) while all remaining subjects' (n = 14) EBA data were from anatomically defined ROIs. Raw data were standardized according to the

Table 5.2. Statistical thresholds for functional EBA regions of interest.
ROIs for the EBA were defined from body > object contrasts during the EBA functional localizer task in 12 subjects. A statistical threshold of $p < 0.01$ was set for all participants except for Subject 17, who only demonstrated significant EBA activity at a threshold of $p = 0.1471$. * denotes novice subjects.

	Left hemisphere				Right hemisphere			
Subject	T	df	# voxels	*x, y, z*	T	df	# voxels	*x, y, z*
6*	2.4	213	163	-48 -77 0	2.4	213	166	41 -62 2
8*	2.6	281	110	-46 -64 -2	2.6	281	27	49 -68 12
15	2.6	213	84	-52 -66 0	2.6	213	214	46 -61 1
17	1.5	211	147	-56 -72 8	1.5	211	29	50 -62 2
18	2.6	211	107	-47 -71 -4	2.6	211	307	47 -67 10
19	3.5	213	407	-47 -71 -2	3.5	213	648	51 -66 7
20	1.9	188	479	-54 -73 -6	1.9	188	225	42 -64 -3
21	4.1	223	38	-48 -71 -7	4.1	223	33	49 -67 4
22	3.4	221	898	-53 -70 -2	3.4	221	854	50 -68 -5
23	3.4	223	810	-53 -69 6	3.4	223	974	44 -63 4
24	5.6	223	943	-46 -73 -3	5.6	223	878	47 -73 6
25	2.6	221	765	-44 -78 9	2.6	221	855	43 -77 -4
Average			**412.6**	**-50 -71 0**			**434.2**	**47 -67 3**
SD			**352.9**	**+/- 3.9 4.0 5.2**			**376.4**	**+/- 3.4 4.7 5.3**

protocols for On and Off periods obtained during each scan. First, an average was obtained for all Off (Baseline) volumes, and each volume (X) was standardized according to the following equation: ((X – Baseline)/Baseline)*100. Next, On and Off standardized BOLD signals were averaged across blocks and calculated for each subject, functional scan and time point. Each average accounted for the hemodynamic response function by excluding the first two volumes in each On and Off block.

5.3.6 Statistical analyses

Separate analyses were performed for each hemisphere and ROI[13] (EBA, MT+, LO) with the exception of a final composite analysis (Section 5.4.4). We performed paired-samples *t* tests on the On versus Off standardized BOLD signals for the viewing and visualization (VisL and VisNL) tasks to determine whether any significant LOTC activation was elicited during observation and/or motor imagery of a novel dance sequence over the course of motor learning. Due to missing data points across time for each of our viewing, VisL and VisNL tasks (see Appendix C), we cannot proceed with a typical GLM or ANOVA. We have instead applied a more appropriate fixed effects mixed model, which will evaluate differences in our dependent variable (standardized BOLD signal) over a repeated measure (time) while accounting for missing cases. To examine any changes in LOTC activation over the course of motor learning and any putative expertise effects during the viewing and visualization tasks, we performed repeated measures mixed model analyses on the standardized BOLD signal for each of these tasks over the factors of Time (four levels: Time 1 to Time 4) and Group (expert ballet and novice dancers). Only for the motor task did we evaluate the standardized BOLD signal at one time point with two separate 2 x 2 repeated measures ANOVAs (one for each hemisphere) using the factors of Group (expert ballet and novice dancers) and Condition (On or Off), since we had all 26 subjects perform this task and we did not expect an improvement in participants' ability to perform this simple task with practice. All pairwise comparisons have been corrected with a Bonferroni adjustment (P_{Bonf}) to account for multiple comparisons unless otherwise specified.

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[13] Separate analyses were performed for each ROI and hemisphere to account for potential functional lateralization, and to increase the statistical power of our mixed model analyses.

5.4 RESULTS

5.4.1 Viewing Task

Paired-samples *t* tests comparing the On versus Off conditions revealed significant bilateral activation of all LOTC ROIs while viewing a complex dance sequence (Table 5.3). Pairwise tests were significant at the corrected value of p_{Bonf}= 0.00625 (p_{Bonf} = 0.05/[4 time points x 2 hemispheres] = 0.00625) at all time points in the EBA except for the right EBA at Time 2 ($t(4) = -4.104$, $p = 0.0075$) , and left EBA at Time 3 ($t(14) = -2.616$, $p = 0.0100$, denoted § in Figure 5.3), whereas MT+ and LO were only significantly activated at Time 3 (except right MT+) and Time 4. There was no difference in LOTC activation over time (left EBA: F(2, 14) = 1.174, $p > 0.10$; right EBA: F(2, 16) = 0.321, $p > 0.10$, left MT+: F(2, 16) = 1.167, $p > 0.10$; right MT+: F(2, 16) = 0.042, $p > 0.10$, left LO: F(2, 14) = 0.672, $p > 0.10$; right LO: F(2, 16) = 0.180, $p > 0.10$, Figure 5.3) or between dancer and novice groups (left EBA: F(3, 21) = 0.805, $p > 0.10$, right EBA: F(3, 21) = 0.459, $p > 0.10$, left MT+: F(3, 20) = 0.643, $p > 0.10$; right MT+: F(3, 20) = 0.346, $p > 0.10$, left LO: F(3, 21) = 0.305, $p > 0.10$; right LO: F(3, 21) = 1.393, $p > 0.10$).

Table 5.3. LOTC Activation During Viewing Task.
Paired-samples *t*-tests were conducted between On-Off average BOLD signal change for each ROI at each time point during the Viewing task. Significance was adjusted to P_{Bonf}=0.00625 to correct for multiple comparisons. Note that MT+ analyses at Time 3 and 4 contain one less participant, who was removed due to data values >3SD. *denotes significance at the corrected level (P_{Bonf}=0.00625), §denotes significance at P<0.01 (uncorrected).

Regions	L/R	df	*t*-statistic	P-value (1-tailed)
EBA				
Time 1	L	5	-3.905	.0055*
	R	5	-4.000	.0050*
Time 2	L	4	-4.621	.0050*
	R	4	-4.104	.0075§
Time 3	L	14	-2.616	.0100§
	R	14	-5.696	.0000*
Time 4	L	14	-9.623	.0000*
	R	14	-6.443	.0000*
MT+				
Time 1	L	5	-3.689	.0070§
	R	5	-3.025	.0145
Time 2	L	4	-4.060	.0075§
	R	4	-2.544	.0320
Time 3	L	13	-4.089	.0005*
	R	13	-2.022	.0320
Time 4	L	13	-5.846	.0000*
	R	13	-2.810	.0075§
LO				
Time 1	L	5	-2.202	.0395
	R	5	-3.462	.0090§
Time 2	L	4	-2.841	.0235
	R	4	-3.713	.0105
Time 3	L	14	-6.882	.0000*
	R	14	-5.283	.0000*
Time 4	L	14	-7.155	.0000*
	R	14	-5.835	.0000*

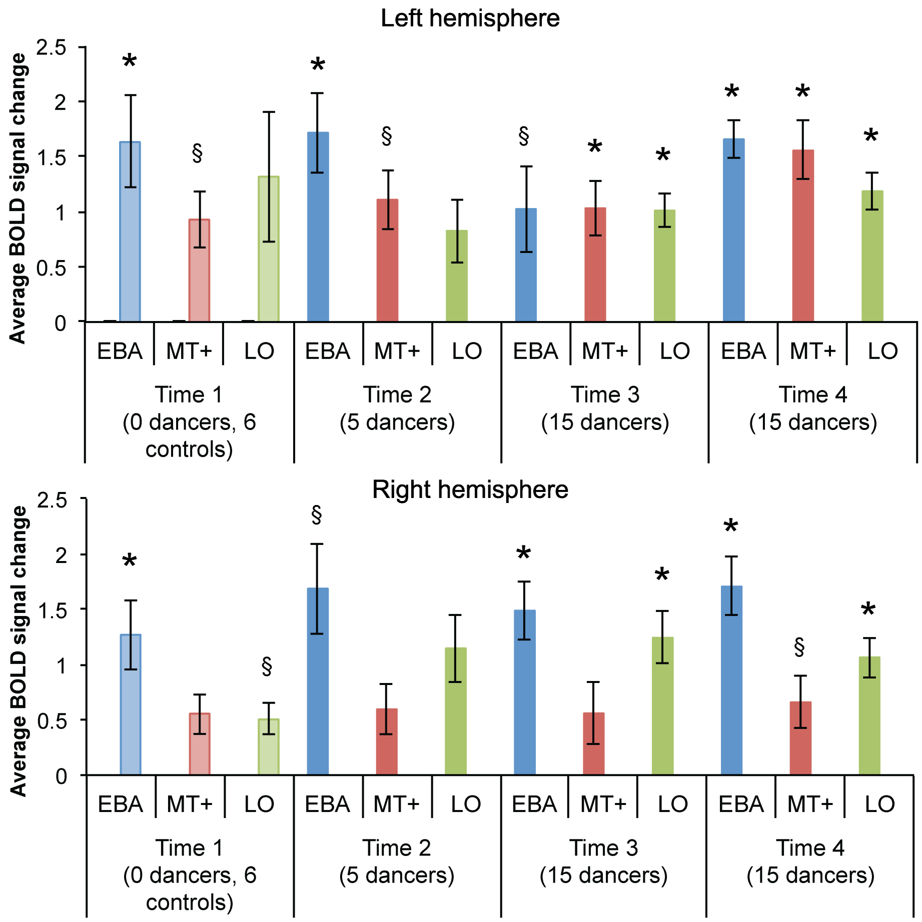

Figure 5.3. Viewing a newly learned ballet dance sequence over the course of learning. All ROIs showed significant BOLD activation in left (top graph) and right (bottom graph) hemispheres while viewing a 1-minute segment of a newly learned ballet dance compared to Off conditions. EBA was active at all time points at the adjusted level of p_{Bonf}=0.00625 (denoted *) except Time 2 (right) and Time 3 (left, denoted §), and MT+ and LO activation was only significant at Time 3 and Time 4 (except right MT+). Note that the lighter colored bars at Time 1 represent the novice group. * p_{Bonf}=0.00625, §P<0.01 (uncorrected), error bars show SEM

5.4.2 Visualization Tasks

5.4.2.1 VisL Task

Correcting for multiple comparisons (p_{Bonf}= 0.00625), none of the paired-samples *t* tests yielded significant BOLD activation during visualization of a newly learned dance (Table 5.4). Only the left EBA at Time 2, right MT+ at Time 3 and left LO at Time 2 were significant at uncorrected threshold values ($p < 0.05$), demonstrating that visualizing a dance sequence elicits very little LOTC activity, even after 34 weeks of learning and rehearsal.

Table 5.4. LOTC Activation During VisL and VisNL Tasks.
Paired-samples *t*-tests were conducted between On-Off average BOLD signal change for each ROI at each time point during the VisL and VisNL tasks. Significance was adjusted to p_{Bonf} = 0.00625 to correct for multiple comparisons. Note that MT+ analyses at Time 3 and 4 contain one less participant, who was removed due to data values >3SD. § denotes significance at $p<0.05$ (uncorrected).

		VisL Task			VisNL Task		
ROI	L/R	df	*t*-statistic	P-value (1-tailed)	df	*t*-statistic	P-value (1-tailed)
EBA							
Time 1	L	18	-0.227	.4115	12	0.308	.3815
	R	18	-0.360	.3615	12	-0.124	.4520
Time 2	L	6	1.959	.0490§	1	-0.389	.3820
	R	6	0.176	.4330	1	-0.072	.4775
Time 3	L	13	1.650	.0615	5	0.827	.2230
	R	13	1.227	.1210	5	-0.034	.4870
Time 4	L	13	-1.483	.0810	8	-0.066	.4745
	R	13	-0.401	.3475	8	1.305	.1140
MT+							
Time 1	L	17	-1.504	.0755	11	-0.779	.2260
	R	17	1.343	.0985	11	1.143	.1385
Time 2	L	6	0.702	.2545	1	26.983	.0120§
	R	6	0.782	.2320	1	1.388	.1985
Time 3	L	12	0.988	.1715	4	-0.539	.3900
	R	12	2.538	.0130§	4	1.648	.0875
Time 4	L	12	-1.758	.0520	7	-0.311	.3825
	R	12	1.341	.1025	7	2.428	.0230§
LO							
Time 1	L	18	-0.895	.1915	12	-0.244	.4055
	R	18	0.329	.3730	12	0.962	.1775
Time 2	L	6	2.198	.0350§	1	3.172	.0970
	R	6	1.073	.1625	1	-0.310	.4040
Time 3	L	13	1.637	.0630	5	-0.715	.2535
	R	13	0.819	.2135	5	-1.861	.0610
Time 4	L	13	-1.158	.1340	8	0.451	.3320
	R	13	-0.269	.3960	8	1.794	.0550

In spite of this finding, temporal changes in activation among expert dancers were revealed in EBA only. Repeated measures mixed model analyses for the left EBA found the main effect of Time to be approaching significance (F(3, 19) = 2.861, $p = 0.065$), with pairwise comparisons demonstrating significant increases in left EBA activity between Time 2 (1 week of rehearsal) and Time 4 (34 weeks) ($p < 0.05$, Figure 5.4). Time was a non-significant main effect for all other sub-regions, with no significant changes in LOTC activity while visualizing a newly learned dance over 34 weeks (right EBA: (F(3, 23) = 0.532, $p > 0.10$, left MT+: F(4, 23) = 0.945, $p > 0.1$, right MT+: F(4, 23) = 1.684, $p > 0.1$, left LO: F(3, 20) = 2.155, $p > 0.10$, right LO: F(3, 19) = 0.452, $p > 0.10$; Figure 5.4). Finally, no significant difference in LOTC activation were found between expert dancers and novice subjects (left EBA: F(4, 24) = 0.636, $p > 0.10$, right EBA: F(4, 24) = 0.456, $p > 0.10$, left MT+: F(4, 23) = 0.945, $p > 0.1$, right: F(4, 23) = 1.684, $p > 0.1$, left LO: F(4, 24) = 1.064, $p > 0.1$, right LO: F(4, 24) = 0.598, $p > 0.1$).

5.4.2.2 VisNL Task

Paired-samples *t* tests revealed that there was no significant activation of LOTC during this task relative to Off conditions, with only uncorrected significance in left MT+ at Time 2 and right MT+ at Time 4 (Table 5.4). However, significant increases in left LO activity (F(3, 8) = 4.567, $p < 0.05$) were observed from Time 1 to Time 2 ($p < 0.05$), Time 3 ($p < 0.01$), and Time 4 ($p < 0.05$), and changes in right LO activation approached significance (F(3, 8) = 3.577, $p = 0.070$) increasing between Time 1 and Time 3 ($p = 0.069$) and decreasing between Time 3 and Time 4 ($p = 0.049$) (Figure 5.4). Marginally significant decreases in right MT+ activity were also observed from Time 2 to Time 4 (F(3, 10) = 3.582, $p = 0.056$, pairwise comparison: $p = 0.058$), with no other significant longitudinal observed (left EBA: F(3, 7) = 2.032, $p > 0.1$, right EBA: F(3, 5) = 1.291, $p > 0.1$, left MT+: F(3, 9) = 0.780, $p > 0.1$). No group differences were observed in LOTC activity during the VisNL task (left EBA: F(3, 19) = 1.598, $p > 0.1$, right EBA: F(3, 19) = 1.132, $p > 0.1$, left MT+: F(3, 18) = 1.442, $p > 0.1$, right MT+: F(3, 18) = 2.319, $p > 0.1$, left LO: F(3, 19) = 2.049, $p > 0.1$, right LO: F(3, 19) = 1.347, $p > 0.1$).

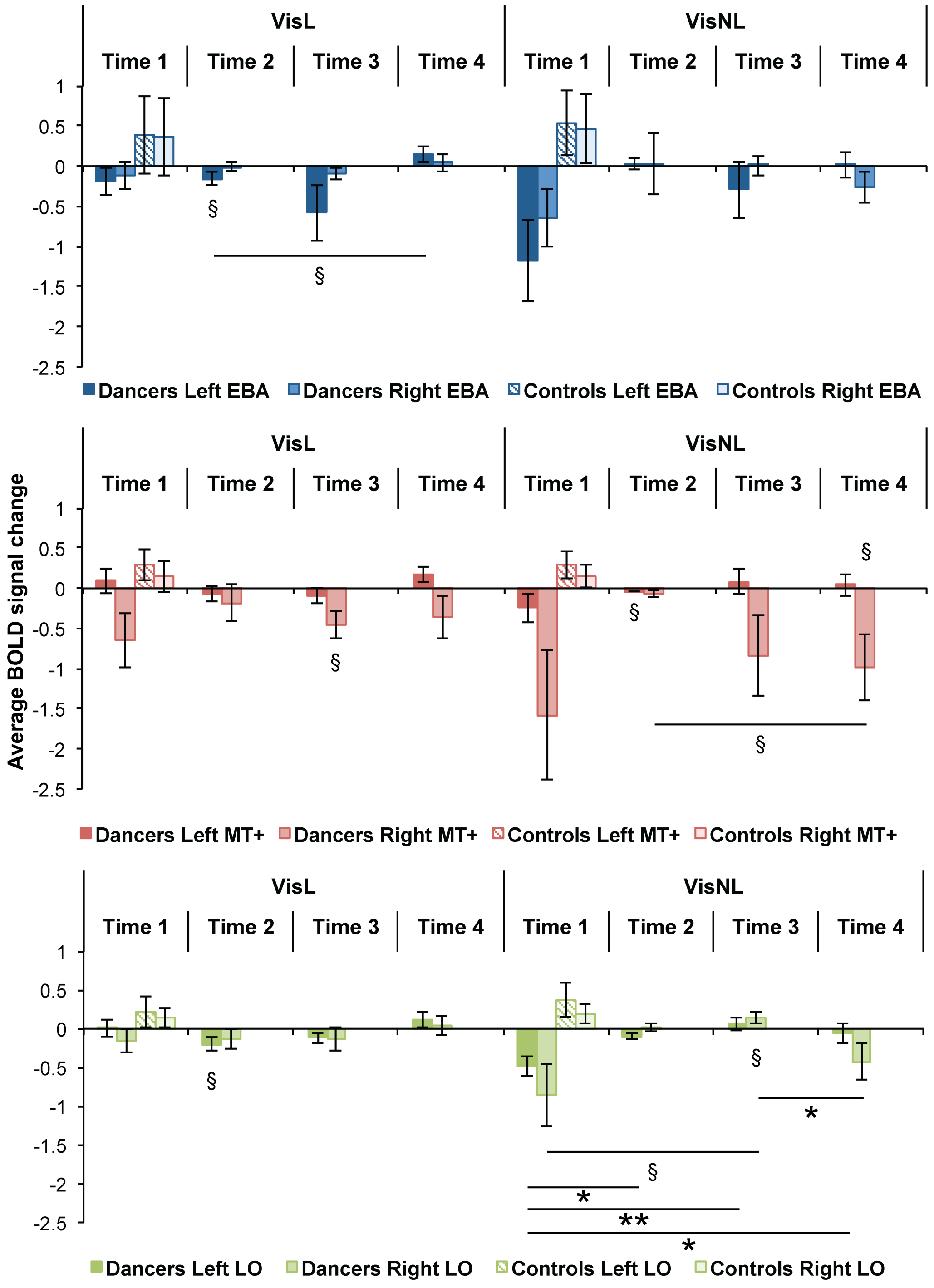

Figure 5.4. Visualizing newly learned (VisL) and non-learned (VisNL) dance over the course of motor learning in professional dancers.

Marginally significant increases in BOLD activation were observed between Time 2 and Time 4 (P<0.05) while visualizing a newly learned ballet dance in left EBA and while visualizing a non-learned dance in right MT+. Significant increases in left LO activation were observed at all time points relative to baseline (Time 1) when visualizing a dance that was not being learned. §*p* < 0.05 (uncorrected), * *p* < 0.05, ** *p* < 0.01, error bars show SEM

5.4.3 Motor Task

Movement of the right toes resulted in significant activation of left EBA with a large effect size (Condition: F(1, 23) = 4.428, $p < 0.05$, η^2=0.161). To further investigate the trend demonstrated in Figure 5.5 between groups, pairwise comparisons revealed significant left EBA activity for novice subjects only ($p < 0.05$, Figure 5.5). As expected, no significant EBA activation was demonstrated in the right hemisphere (Condition: F(1, 23) =1.348, $p > 0.1$). Movement of the right toes did not result in significant MT+ activity in either left (Condition: F(1, 23) = 0.007, $p > 0.1$) or right (F(1, 23) = 0.000, $p > 0.1$) hemisphere, or between groups (left and right: $p > 0.1$). However, significant LO activity was observed in both hemispheres (left: F(1, 23) = 6.690, $p < 0.05$; right: F(1, 23) = 4.532, $p < 0.05$).

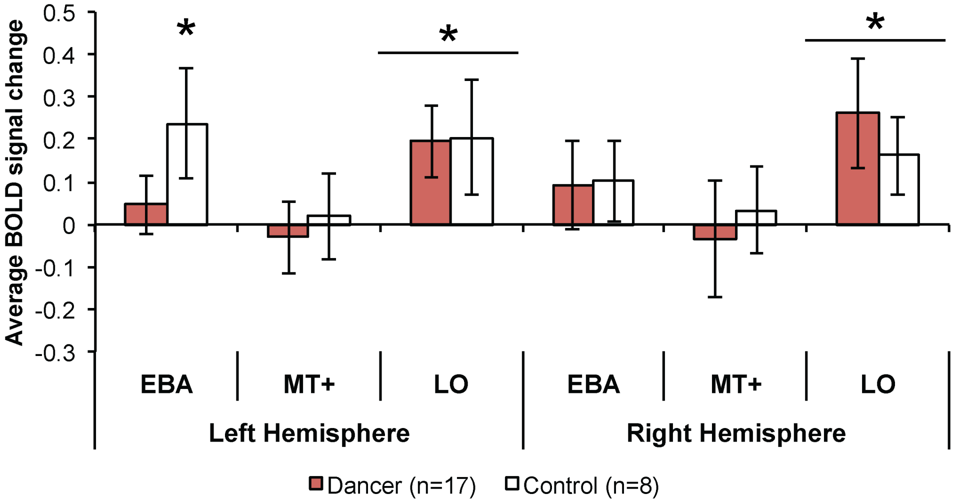

Figure 5.5. LOTC activity during motor task.
Significant contralateral activation of EBA was observed during movement of the right foot in novice subjects only (left: $p<0.05$), and significant bilateral activation was observed in LO (P<0.05). No significant activations were demonstrated in right EBA or bilateral MT+. *$p<0.05$, error bars show SEM

5.4.4 Composite Activation of Bilateral LOTC

To confirm whether BOLD activation differed among our ROIs and tasks, we performed two separate 4x3 mixed model analyses on the average BOLD signal during the On condition comparing the factors of Task (viewing, VisL, VisNL, motor) and ROI (EBA, MT+, LO) for each hemisphere, collapsing across the variables of group and time in this composite analysis to obtain a functional profile for all LOTC sub-regions during action processing (Figure 5.6).

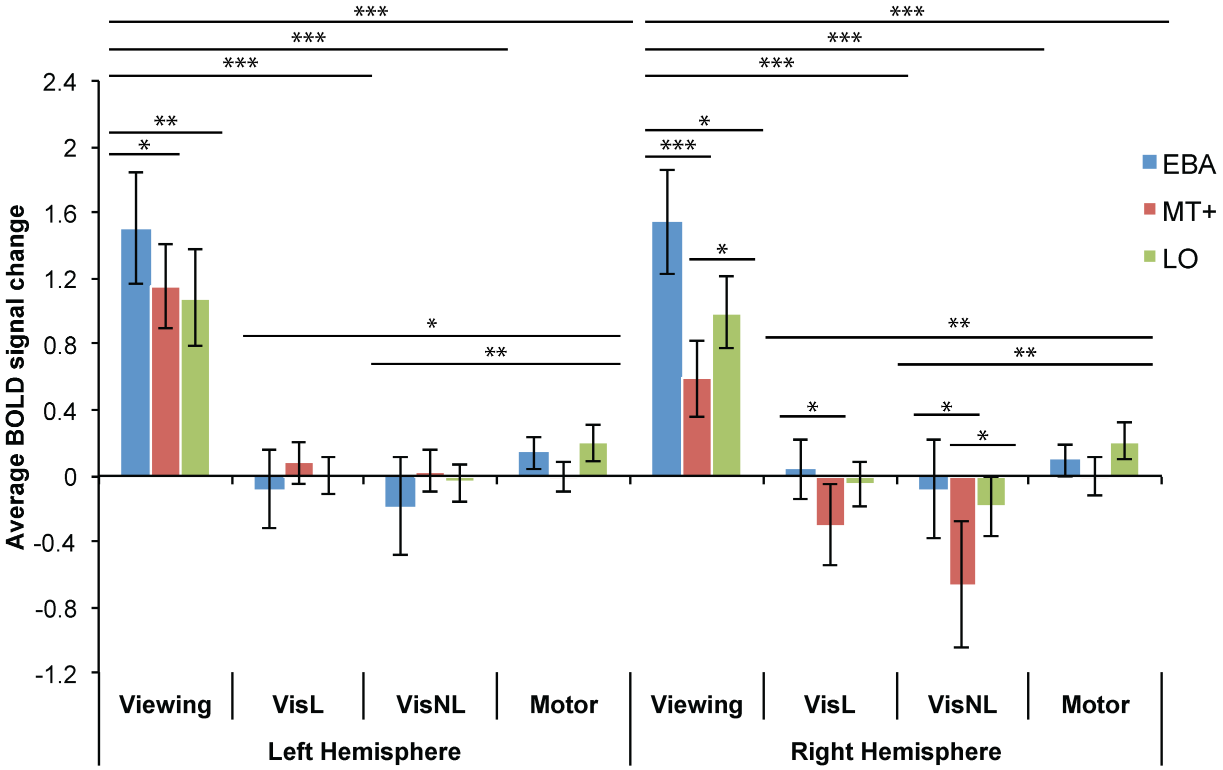

Figure 5.6. Activation in LOTC while viewing, visualizing and executing movement. Collapsing across time and groups, bilateral LOTC is activated most strongly by the viewing task compared to all other tasks in both hemispheres, and with greater activation during the motor task relative to VisL and VisNL in both hemispheres The main effect of ROI (not represented above) shows EBA > MT+, left EBA > left LO, right LO > right MT+. A significant Task x ROI interaction reveals EBA > LO and MT+ as well as LO > MT+ in the right hemisphere during the viewing task. Right EBA > MT+ during the VisL task, and right EBA and LO > MT+ during the VisNL task. *$p<0.05$, ** $p<0.01$, *** $p<0.001$, error bars show SEM

A significant main effect of task was observed in both hemispheres (left: F(3, 44) = 108.81, p <0.001, right: F(3, 52) = 74.60, p < 0.001), revealing stronger BOLD activity during the viewing task compared to both visualization tasks (p < 0.001) and the motor task (p < 0.001), no difference between the two visualization tasks (p > 0.1), and greater activation during the motor task relative to VisL (left: p < 0.05, right: p < 0.01) and VisNL (left and right: p <0.01) (Figure 5.6). A significant main effect of ROI was observed in left (F(2, 115) = 4.39, p < 0.05) and right (F(2, 88) = 17.56, p < 0.001) hemispheres, with greater EBA activation compared to LO (p < 0.05) in the left hemisphere and greater than MT+ bilaterally (left: p < 0.05, right: p < 0.001), as well as greater LO activation relative to MT+ in the right hemisphere (p < 0.001). A significant interaction between task and ROI was found in both hemispheres (left: F(6, 54) = 2.877, p < 0.05, right: F(6, 55) = 3.66, p < 0.01), with greater EBA activation bilaterally compared to LO (left: p < 0.01, right: p < 0.05) and MT+ (left: p < 0.05, right: p < 0.001) as well as greater LO activity relative to MT+ in the right hemisphere (p < 0.05) during the viewing task. Finally, right MT+ activation was significantly less than EBA during the VisL task (p < 0.05), and less than both EBA and LO during the VisNL task (p < 0.05).

5.5 DISCUSSION

5.5.1 LOTC activation is greatest during viewing compared to visualizing and executing movement

Based on a comparative analysis of LOTC sub-regions EBA, MT+ and LO during four different tasks, we found that viewing a complex dance sequence elicits significantly greater bilateral activation in all of our ROIs compared to visualization of a learned dance (p < 0.001), visualization of a non-learned dance (p < 0.001), and movement of the right foot ($p < 0.001$, Figure 5.6). Additionally, BOLD activation was greater during the motor task relative to both visualization tasks. These results clearly indicate the prioritization of LOTC activation for visual processing of complex motor sequences relative to motor execution of the foot (Lotze et al. 2003; Astafiev et al. 2004; Peelen and Downing 2005) as well as motor imagery as demonstrated within the same subjects. Most investigations of action observation use brief presentations of static postures (Downing et al. 2001; Calvo-Merino et al. 2010; Weiner and Grill-Spector 2010) or short video clips that are less than five seconds (Calvo-Merino et al. 2005; Cross et al. 2006). We were interested in evaluating LOTC activation in response to a longer (1 minute) presentation of naturalistic, whole-body movement during a dance sequence that our sample of expert ballet dancers was learning.

Our observed results expand on previous studies demonstrating greater LOTC activity during action observation of a complex ballet sequence compared to motor imagery (Astafiev et al. 2004; David et al. 2007; Blanke et al. 2010; Orlov et al. 2010) and response of the EBA to moving body stimuli (Downing et al. 2001; Kret et al. 2011; Weiner and Grill-Spector 2011; Atkinson et al. 2012). The fact that LO showed significantly less activation relative to EBA during the viewing task (left: $p < 0.01$, right: $p < 0.05$) suggests less reliance on this region during action observation. Considering the stimulus had few objects in view, this result is in line with the established role of LO in mediating category-specific object processing (Grill-Spector et al. 2001; Grill-Spector 2003).

5.5.2 LOTC modulation by experience

While dancing is inherently multisensory and involves many interacting brain networks (Cross et al. 2006; Brown et al. 2006; Brown and Parsons 2008; Cross et al. 2009a, 2009b; Foster 2013;

Bar & DeSouza, 2016), our focus was on the influence of visual inputs to the LOTC of professional ballet dancers over the course of learning a novel piece of choreography. We found significant activation of EBA during all time points of the viewing task (Figure 5.3) and significant LO and MT+ activation in both hemispheres after only 5 (except in right MT+) and 34-weeks of rehearsal and performance in expert dancers (Table 5.3). Since we did not observe significant changes in activation during the VisL task, we are cautious to conclude that the observed changes are a result of learning a novel complex dance sequence. However, they do provide indications of LOTC plasticity over a 8-month period. This is further supported by our findings of significant increases in bilateral LO and right MT+ activity at both corrected and uncorrected levels of significance during the VisNL task (Figure 5.4). Together with the significant activation of contralateral EBA in novices only ($p < 0.05$, Figure 5.5) during the motor task, the present results are suggestive of LOTC modulation by experience, with a decreased reliance on these higher-order visual areas in expert dancers relative to novice controls.

LOTC BOLD signals were generally low in experts while visualizing their newly-learned dance (VisL) as well as in both groups while visualizing an non-learned ballet dance to similar musical stimuli (VisNL, Table 5.4). However, modulation of BOLD signals in left LO over time among dancers was robust and showed a significant main effect (Figure 5.4). These results potentially reflect a greater reliance on LO during motor imagery of familiar and meaningful stimuli relative to visualizing a specific learned sequence. This more general process of visualizing an improvised dance (VisNL) may also recruit MT+ during imagery of the movement repertoire using kinesthetic information obtained during habit-forming of over-learned movements (Bar and DeSouza 2012; 2016; DeSouza and Bar 2012) as demonstrated by near-significant activation at later time points (Table 5.4, Figure 5.4). Previous research on sequential hand movements similarly show increases in brain activity as both execution and imagery shift from novel to skilled (Lacourse et al. 2005). Additionally, performance of spontaneous improvised musical performance relative to over-learned sequences has shown widespread deactivation of prefrontal cortex and limbic structures with concurrently increased activation of AON regions including ventral and dorsal PMC, SMA, anterior portions of middle temporal gyrus, and lateral occipital gyri (Limb & Braun 2008). Further inspection of the current dataset of these regions could reveal similar evidence of disengagement from goal-directed, sequenced behavior during the visualization of improvised and highly creative dance movements.

That significant longitudinal changes were lateralized to the left hemisphere is in line with previous evidence of LOTC activation during action observation and execution (Romaiguère et al., 2014). Additionally, it has been suggested that motor imagery, as opposed to non-kinesthetic visual imagery, is functionally lateralized to the left hemisphere (Sirigu and Duhamel 2001; Tomasino and Rumiati 2004; Blanke et al. 2010) despite evidence for bilateral activation (Urgesi et al. 2006; Calvo-Merino et al. 2010; Olshansky et al. 2014; Bar & DeSouza, 2016). Based on our results (Figure 5.4) and the visualization training and post-scan evaluations undertaken by subjects following each scan, we can be confident that our dancers were properly engaged in first-person motor imagery. The observed increases in LO activity during visualization in the present study are congruent with the trend of activation demonstrated in preliminary findings on a portion of this sample showing increased activation in SMA and auditory cortex following motor learning using a different (GLM) methodological approach (Bar and DeSouza 2012; 2016; DeSouza and Bar 2012). We suggest that the minimal activation observed in LOTC during visualization might reflect the early consolidation of newly learned, complex, whole body movements in an intricately timed dance sequence. Low statistical power resulting from different numbers of dancers performing the tasks at each time point is the likely cause of non- and near-significant main effects in the present analyses.

The expert dancers in the present study are professionals from the National Ballet of Canada and have a rigorous, full-time rehearsal and performance schedule. As such, we expected some attrition, which is not uncommon in longitudinal studies, as a result of scheduling conflicts, injury, and changes to the dance program. In anticipation of possible attrition, we tested as many dancers at as many time points as we could, resulting in an unbalanced expert sample relative to the control novice group (see Appendix C). We accounted for this inequality in our statistical analyses by employing mixed models wherever applicable (Section 5.3.6), and despite the smaller sample size, significant EBA activation with a large effect size was observed in novices only during the motor task (Section 5.4.3). We will continue to investigate these longitudinal changes in our dancers as we add to this dataset over the years, and will explore whole-brain changes in network activity induced by motor learning. Based on the intensive training and performance schedule of our expert ballet dancers, we are confident that any task-specific MRI-induced practice effects would be overshadowed by behavioral and learning-related effects.

5.5.3 LOTC and movement: expertise effects and involvement of LO

Consistent with previous evidence presented by Astafiev et al. (2004) and Peelen and Downing (2005), the left EBA was significantly activated during movement of the right foot, suggesting a role for EBA in the execution of movement. Our finding that only left EBA showed activation is congruent with the functional lateralization of sensorimotor processing to contralateral hemispheres in the brain (Afifi and Bergman 2005). However, significant activation was only demonstrated in the novice group ($p < 0.05$), and not among expert dancers. These patterns reflect less reliance on higher-order visual areas for action processing in expert ballet dancers who, despite being very mindful of the positioning of their feet both when moving and posing, rely on a more specialized motor network during movement. In contrast, the lack of experience with deliberate and timed motor control among novices may result in recruitment of LOTC as a compensatory mechanism for mediating unfamiliar movement relative to expert dancers (Olsson et al. 2008). Although the stimuli during viewing and visualization tasks were context specific to expert ballet dancers, there was no significant modulatory effect of experience on LOTC activation, contrary to what has been shown in the AON literature for familiar stimuli (Calvo-Merino et al. 2005, 2006; Cross et al. 2006, 2009a, 2009b) and in EBA for aesthetically pleasing imagery (Calvo-Merino et al. 2010). The lack of between-group differences may be due to visual signals elicited from body images overriding any context-specific effects of stimulus type, or the dance experience of some of the novice subjects (see Appendix C). Nonetheless, patterns of LOTC activity have been suggested to encode motor representations and our ability to prepare for voluntary movements (Kühn et al. 2010) and relate observed action to meaning and stored knowledge (Lingnau & Downing 2015). The significant activation of bilateral LO at the third and fourth time points of the viewing task (Figure 5.3) may reflect anticipation of steps in the choreography, or an enhanced connection to its emotional and/or narrative meaning with repeated rehearsal and performance over time (Romaiguère et al. 2014).

Previous research has demonstrated greater and more diffuse activity in motor regions among novices compared to expert musicians, whose repeated exposure to transforming visual information into motor commands cued by auditory stimuli have consolidated activity within these circuits (Lotze et al. 2003; Meister et al. 2004, 2005; Grahn and Rowe 2009). The significant activation observed during the motor task in bilateral LO ($p < 0.05$, Figure 5.5) is consistent with this notion. That activity is significant in both groups may also reflect visual processing of the semantic instruction to “wiggle” the toes of the right foot (see Section 5.3.2), as LOTC activation has been demonstrated in response to action-related verbs (Bedny et al. 2008; Kemmerer et al. 2008). However, we cannot dissociate semantic processing from putative involvement in movement execution as both were performed during this task.

Due to the different number of participants at each time point (see Appendix C), we took an ROI-based approach to analyzing our data offline with mixed models to preserve statistical power in the presence of missing data points. We extracted and standardized the average BOLD signal change in three anatomically localized regions of LOTC (EBA, MT+, LO) in our longitudinal study of ballet dancers in order to test changes in activity over the course of up to four fMRI scanning sessions that spanned a single season of dancing. To demonstrate that our anatomically-defined EBA ROIs were indeed capturing visual processing of body information, we performed a standard functional localizer in twelve subjects (Figure 5.2). Plotting our functional and anatomical EBA ROIs together with adjacent MT+ and LO ROIs defined by coordinates obtained from the literature (Table 5.1) demonstrate that our ROIs are robust and accurately represent each respective sub-region of the LOTC. Results from our viewing task (Table 5.3, Figure 5.3) also confirm that our anatomical ROIs were accurate in sufficiently capturing EBA activation, with significant EBA activation at all time points elicited by observation of dynamic images of human bodies and body parts. Additionally, our finding that contralateral (left) EBA was significantly activated during the motor task is congruent with the functional lateralization of sensorimotor processing to contralateral hemispheres in the brain (Afifi and Bergman 2005). Our continued longitudinal studies on subsequent cohorts of dancers from the National Ballet of Canada and other dance programs will employ functional localizers for each individual subject to ensure individual variability in ROIs are accounted and controlled for. Future investigations on changes in the mental representation of a dance sequence over the course of learning could focus on the connectivity of LOTC sub-regions to the larger action observation network, as indications for the involvement of EBA as a compensatory motor processing region have been demonstrated in clinical populations (van Nuenen et al. 2012a, 2012b).

5.6 CONCLUSIONS

The current findings reveal that experience-dependent plasticity induced by dance training is not only limited to nodes within the canonical AON, but also extend to higher-order visual areas in the LOTC. Additionally, we demonstrate learning-induced plasticity within these expert networks over the course of a 34-week rehearsal and performance schedule in professional ballet dancers. We also clarify that higher-order visual areas in the LOTC are not centrally involved in KMI of dance sequences that are novel or familiar, but may respond to semantic representations of action in expert and non-experts. The neural and cognitive efficiency with which dancers access embodied motor representations provide further insight into the modifications to knowledge schemas by expertise.

6 CHAPTER SIX – GENERAL DISCUSSION

6.1 SUMMARY AND CONCLUSIONS

6.1.1 Expert Knowledge Schemas

The current body of work presents evidence for the refinement of expert knowledge schemas (Figure 6.1) coding skill-related sensory, motor, linguistic, attentional, and memory functions as a result of short-term exercise (Chapter 2) and long-term dance training (Chapters 3 to 5). Such modulation of these knowledge schemas facilitates optimal performance across domains when one domain is primed (Chapter 2 and 3). With evidence from EEG (Chapter 4) and fMRI (Chapter 5), the neurophysiological mechanisms underlying these transference effects are clarified. Finally, these works extend current understanding of the perceptual and cognitive processes underlying dance perception among familiar experts and unfamiliar novices, answering important questions in the fields of cognitive psychology and neuroaesthetics.

In Chapter 2 we discovered that eye exercises produce significant improvements in attention and visual WM following a much shorter course of training (18.5 minutes) than has been shown in the past (Dyckman & McDowell, 2005). I posit that these translational cognitive benefits were primed by activating the oculomotor system, namely the FEF, which is implicated in voluntary saccade generation (Munoz & Everling, 2004; Dias et al., 1995), visual attention (Neggers et al., 2007; Moore et al., 2003; Sajad et al., 2015; 2016; Taylor et al., 2006), and processing event borders (Zacks et al., 2001a). FEF feeds-forward to other frontal brain regions like DMPFC and IFG that are at the junction of speech (motor), language, and memory processing (Bachrach et al., 2015; Kunert et al., 2015). I suggest that priming these network areas with eye exercises, or attending to visual stimuli like a familiar dance, may account for the improved cognitive performance observed among experts (Figure 3.7) and novices (Figure 2.4, Figure 2.5) alike.

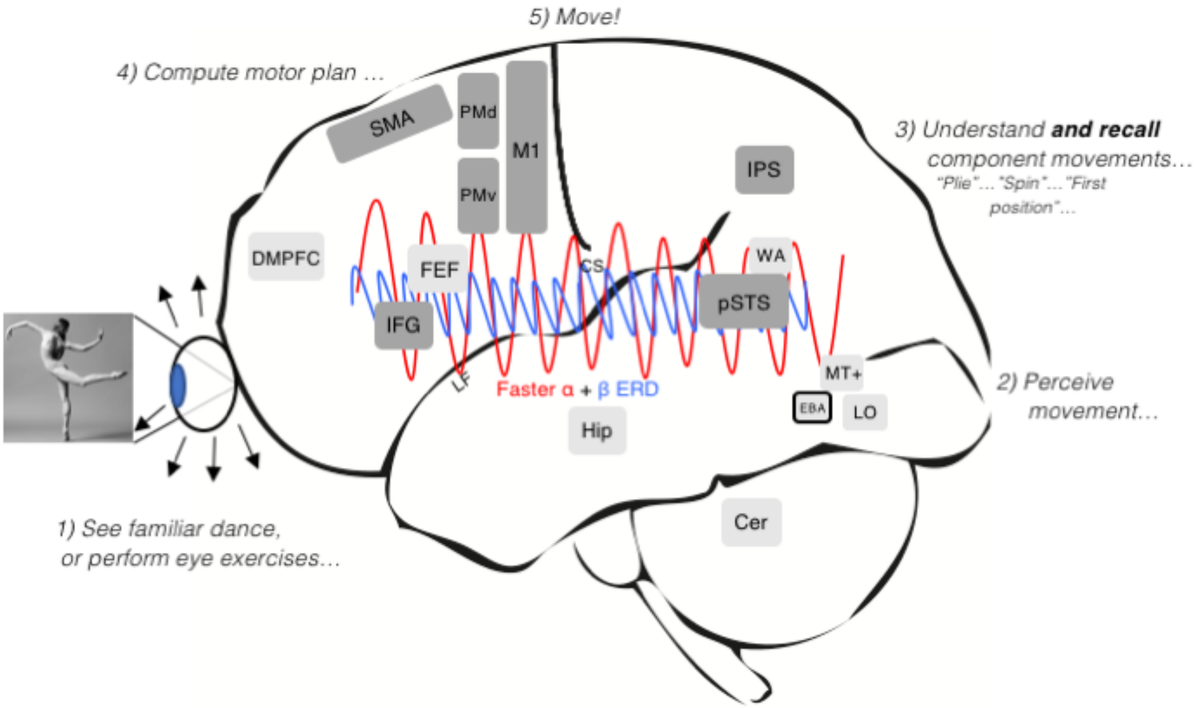

Figure 6.1. Expert knowledge schema for dance.
With continued practice, the information related to a given skill (e.g., dance) becomes consolidated into an expert knowledge schema. The projects in this thesis demonstrate activation of these schemas by eye exercises or viewing familiar dance genres that induce resonance of embodied motor representations. Via faster iAPF and beta ERS relative to controls, experts are afforded faster access to information in other domains (e.g., language, memory) to facilitate improved performance on attention and WM tasks. Brain activity also becomes more efficient, with less reliance on higher-order visual areas like EBA during movement (Chapter 5). Brain regions are approximately localized. Dark grey nodes are also canonical AON regions. Cer – cerebellum; CS – central sulcus; DMPFC – dorsomedial prefrontal cortex; EBA – extrastriate body area; FEF – frontal eye field; Hip – hippocampus (subcortical); IFG – inferior frontal gyrus (Broca's area, BA44/45); IPS – intraparietal sulcus; LF – lateral fissure; LO – lateral occipital complex; MT+ - human visual motion complex; M1 – primary motor cortex; PMd – dorsal premotor cortex; PMv – ventral premotor cortex; pSTS – posterior superior temporal sulcus; SMA – supplementary motor area; WA – Wernicke's Area

As part of the proposed knowledge schema that is subject to experience-dependent plasticity, one may question whether FEF is also sensitive to these changes. Employing an experimental design that tracked eye movements and fixations, Afonso and colleagues (2012) had highly-skilled (starting players at national level) and skilled (practice at national level, fewer years of experience) volleyball players simulate game play. Participants were also prompted to use their linguistic faculties to describe their perceptions and strategies after the game task. The highly-skilled group showed more exploratory visual search patterns, including a greater number of fixations for longer durations to functionally relevant areas (e.g., space between other players), while skilled participants fixated on the ball trajectory and specific players more frequently. Finally, the highly-skilled players also used a greater number verbal concepts that were more sophisticated and descriptive. These behavioural results complement the findings in Chapter 3, linking improved control of eye movement, language, and memory functions among highly-skilled experts, and provide further evidence for cross-domain enhancements when priming expert knowledge schemas with AO of familiar actions.

6.1.2 Oscillatory Mechanism

The mechanism by which distal nodes of expert knowledge schemas transfer information involves synchronization among neuronal populations, specifically in the alpha and beta sensorimotor frequency bands. This is the same mechanism purportedly underlying the online process of event segmentation (Hommel et al., 2001; Hommel, 2015) and which serves to integrate (or segregate) separate visual features into a single event or percept (Samaha & Postle, 2015; Wutz et al., 2014). Experience-dependent modulation of activity in motor (Orgs et al., 2008) and visual areas including occipital cortex (Di Nota et al., under review, Chapter 4; Di Nota, Levkov, Bar & DeSouza, 2016, Chapter 5) has been revealed during dance observation, with faster iAPF, alpha ERD, and beta ERS, reflecting greater task engagement among experts. Concurrent activation of frontocentral regions (including FEF) and V1 have shown similar modulation of alpha and beta when producing simple prosaccades (ERS) relative to more difficult antisaccades (ERD) (Cordones, Gómez, & Escudero, 2013), in line with previously identified patterns of ERS/ERD associated with cognitive load in other paradigms (Gevins et al., 1997; Klimesch et al., 1999; Roberts et al., 2014; Schack & Klimesch, 2002).

I propose that resonance of motor representations coded in expert knowledge schemas during AO of embodied/familiar dance (Figure 6.1) primes language, memory, and attentional nodes via faster iAPF (Figure 4.3) and more efficient suppression of task-irrelevant areas to enhance task-relevant signal processing via alpha ERD and beta ERS, respectively (Figure 4.4). As demonstrated previously in the AON (Calvo-Merino et al., 2005; 2006), these oscillatory modulations in expert knowledge schemas are highly tuned to the specificity of embodied motor representations as evidenced by improved WM (Figure 3.7) and attentional performance (Figure 3.4) among ballet and Bharatanatyam dancers, whose genre of dance were presented as experimental stimuli.

Faster and more efficient communication across domains in the expert knowledge schema serves to provide quicker access to information that will help achieve peak performance, which is typically the goal in athletic practice as well as in experimental cognitive tasks. This efficiency is conditioned over many hours of training and repeated exposure to comparing expected (i.e., efference copy) to actual (i.e., reafferent inputs) behavioural outcomes during imitative learning. This efficiency may also account for the generalization of faster iAPF during KMI of non-dance movements among expert ballet dancers (Figure 4.3). This is supported by a distinction in the movement literature regarding action that is already part of the actor’s motor repertoire and does not involve learning (such as the VMIQ-2 items), and imitating movement that requires effortful perception and planning of a novel movement or sequence. While constituent movements may form part of an existing repertoire, dancers engage imitative learning processes whenever they learn a novel piece of choreography and have to recombine new sets of constituent movements. To accomplish this, the observer engages the AON to transform modelled behaviour and enact it via novel motor representations (Rizzolatti et al., 1998). STS is recruited to segment the observed action (Speer et al., 2003; Zacks et al., 2001a) and also to compare reafferent and efference copy signals (Iacoboni et al., 2001; Zacks et al., 2011).

6.1.3 Linking Memory to Language

To develop expert knowledge schemas, dancers are subject to adaptive learning strategies that consolidate 'multi-domain' events from WM to long-term memory. Each movement that a dancer learns has a semantic label (e.g., 'plie'), a specific motor plan, preparatory activation within the proposed network, efference copy commands after execution, and needs to be recalled when trained with new choreography. Access between STM and LTM is facilitated by phase synchronization of theta and upper alpha (Schack et al., 2005), which may facilitate quick access to remembered movement sequences after long periods of time (Stevens et al., 2010). The increased iAPF exhibited during AO and KMI of non-dance movements (Figure 4.3) may also be driven by this alpha link between memory and action nodes in expert knowledge schemas, in turn priming recall of experientially-relevant words (Figure 3.7). Evidence for this priming effect and efficient consolidation of embodied action have been demonstrated in this thesis both behaviourally through segmentation behaviour (Figure 3.3, Bläsing, 2015) and neurologically via a decreased reliance on higher-order visual areas during movement (Figure 5.5).

Just as single events activate multiple domains within the expert knowledge schema, we have seen that several brain regions are activated by multiple domains. Language areas including superior temporal cortex (STG and STS) and Broca's area (IFG) respond reliably to both spoken and written narratives, demonstrating modality invariance in these regions (Regev, Honey, Simony, & Hasson, 2013). Connectivity among these regions is evidenced by altered learning and action chunking when Broca's area is disrupted (Alamia et al., 2016). There is also evidence for longer fixation on target items when they are linguistically and visually salient (Cavicchio, Melcher, & Poesio, 2014). If the video that a participant watched activated an embodied motor representation (e.g., Bharatanatyam dance and music), and one of the words presented during Part 1 of the RIF task was also salient through experience (e.g., *choreography*), then perhaps this exchange of information also translated to attentional (Figure 3.3, Figure 3.4, Table 3.3) and WM domains (Figure 3.7). The evidence provided in this thesis supports this dynamic exchange in expert knowledge schemas.

6.2 LIMITATIONS

Several general methodological shortfalls in fMRI and EEG techniques have been described already (see Section 1.1.1), as well as in the EEG apparatus employed in Chapter 4 (see Section 4.3.3). When conducting neuroimaging experiments that are typically very costly and time-sensitive during training-based paradigms, it is crucial that all parameters are programmed correctly to avoid loss of data. In Chapter 4, there was significant attrition in the number of tested participants (n = 92) relative to the number that was included in final analyses (n = 61) due to factors that can be attributed to learning a novel technical skill. I have since generated an analysis pipeline for my lab and instructional Wiki (https://bitbucket.org/joelab/eeg-tutorial/wiki) based on these hard-learned lessons. There are also challenges that accompany previously collected or 'inherited' data; Chapter 5 also had significant attrition in the number of professional ballet dancers scanned over four time points (see Appendix C) during a programme that varied between 34 to 38 weeks (see Section 5.3).

While experimental stimuli that have previously been used in peer-reviewed publications (Grill-Spector, 2003; et al., 1999; 2001) may seem like a safe choice when conducting one's own experiment (e.g., EBA localizer stimuli in Chapter 5), we have demonstrated that they are not always as controlled in practice by the developers. The dance stimuli used in Chapter 3 were supposedly equal in the number and pace of movements across ballet, Bharatanatyam, and acting conditions (Jola et al., 2012). However, choosing three one-minute clips from each video and testing them in both Validation (Figure 3.2) and main event segmentation experiments (Figure 3.3) revealed significantly fewer event borders in the acting video. Additionally, the Bharatanatyam condition featured sung lyrics in the background music, which inevitably triggered linguistic responses in the familiar participants. Controlling the auditory and visual components of dance are thus challenging, but provide the opportunity to evaluate responses to each modality either separately or together in order to dissociate musical and expressive movement processing.

6.3 FUTURE DIRECTIONS

In an ideal world with unlimited time and funding, and compliant participants that show up (on time) for multiple scans, I would use all methodological approaches in this thesis for each Chapter. This holistic approach would provide definitive evidence for the proposed expert knowledge schema and its underlying neural mechanisms. To optimize and direct future investigations, employing eye tracking and event-related MEG/EEG during the event segmentation paradigm (Chapter 3) would provide much neurophysiological evidence for the proposed priming effect. Similarly, these brain data could reveal structural and functional connectivity among language and motor areas that encode and facilitate retrieval of domain-specific words. Our lab intends to collect MRI data on time- (i.e., four scans over 34 weeks), age-, and sex-matched controls for the professional ballet dancers used in Chapter 5 to investigate these hypotheses, as well as to clarify learning-induced plasticity across the whole brain. Tracking the fixation locations and gaze shifts among familiar versus unfamiliar dancers during AO (Chapters 3, 4, and 5) would also allow us to investigate the specific movement features attributed to event borders or changes in underlying activation of knowledge schemas.

Cognitive and performance enhancement through various types of training are gaining steam in ‘popular science’. ‘Mental’ training using wearable technology has commercial appeal and is based in meditation practices that have been studied for decades (if not centuries among non-Western practitioners) with respect to cognitive or attentional control and emotional regulation (Debarnot et al., 2014; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Slagter et al., 2007; Teper & Inzlicht, 2013). Changes in sensorimotor alpha and beta power are also utilized (and visualized) in neurofeedback experiments, which is itself a skill that can be trained and enhance motor performance (Mottaz et al., 2015). Additonally, these signals can be used to control brain-computer interfaces (BCIs), and possibly with greater control among individuals with experience-related plasticity to the oscillatory networks mentioned above.

The insights provided by the results in this thesis have several promising therapeutic applications:

- demonstrating the efficacy of a very short course of eye exercises on improved attention and WM (Chapter 2);
- providing evidence for transference of physical expertise to attention, language, and memory functioning (Chapter 3) that can help people with deficits in any of these domains, including people with PD; and

- clarifying the modulation of sensorimotor oscillatory bands by experience (Chapter 4) to help develop more effective BCIs that can assist those with mobility or communication restrictions.

As I have learned through my experience with my lab's ongoing DWP project, finding therapeutic solutions for people with PD, AD, and other movement-related disorders is one of the most urgent public health concerns affecting Canadians (Ng et al., 2015). Participation in this project has allowed me to witness firsthand the transformative power of dance that provides social, emotional, motoric, and neurophysiological benefits and improved quality of life to individuals with PD as well as healthy able-bodied individuals. The insights generated by my work underscore the efficacy of dance as a form of exercise or therapy that is accessible, engaging, cost-effective, and fun.

6.4 FINAL THOUGHT

"Rhythm is a dancer, it's a soul's companion, you can feel it everywhere;
lift your hands and voices; free your mind and join us; you can feel it in the air."

Benites, Garett III & Austin, 1992
A.K.A. SNAP!

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APPENDIX A

Category-exemplar word pairs presented during RIF task. A '1' indicates the designation of each pair as a practiced word from a practiced category (Rp+), non-practiced word from a practiced category (Rp-), or a non-practiced word from a non-practiced category (Nrp).

Word	**Practiced word, practiced category: Rp+**	**Non-practiced word, practiced category: Rp-**	**Non-Practiced word, non-practiced category: Nrp**
COLOUR - black		1	
COLOUR - blue		1	
COLOUR - brown	1		
COLOUR - green		1	
COLOUR - purple	1		
COLOUR - yellow	1		
FRUIT - apple	1		
FRUIT - banana		1	
FRUIT - cherry	1		
FRUIT - grape	1		
FRUIT - peach		1	
FRUIT - pear		1	
DANCE - choreography	1		
DANCE - jig	1		
DANCE - rhythm	1	1	
DANCE - tango		1	
DANCE - tap			
DANCE - waltz		1	
INSTRUMENT - drum	1		
INSTRUMENT - flute		1	
INSTRUMENT - guitar		1	
INSTRUMENT - piano	1		
INSTRUMENT - trumpet		1	
INSTRUMENT - violin	1		
RELATIVE - cousin			1
RELATIVE - daughter			1
RELATIVE - father			1
RELATIVE - husband			1
RELATIVE - sister			1
RELATIVE - uncle			1
SPORTS - climbing			1
SPORTS - fishing			1
SPORTS - racing			1
SPORTS - riding			1
SPORTS - sailing			1
SPORTS - skating			1

TOOL - drill		1	
TOOL - hammer		1	
TOOL - ladder	1		
TOOL - nail	1		
TOOL - ruler		1	
TOOL - screw	1		
VEGETABLE - beans			1
VEGETABLE - carrot			1
VEGETABLE - corn			1
VEGETABLE - lettuce			1
VEGETABLE - peas			1
VEGETABLE - potato			1
VEHICLE - bicycle	1		
VEHICLE - boat		1	
VEHICLE - bus	1		
VEHICLE - plane	1		
VEHICLE - train		1	
VEHICLE - truck		1	
WEATHER - clouds			1
WEATHER - rain			1
WEATHER - snow			1
WEATHER - storm			1
WEATHER - thunder			1
WEATHER - wind			1

APPENDIX B

URPP #: _____________ Date: _____________ Group: B / I / D / M / A / N Condition: Exp / Pass

COLOUR
1)
2)
3)
4)
5)
6)

FRUIT
1)
2)
3)
4)
5)
6)

DANCE
1)
2)
3)
4)
5)
6)

INSTRUMENT
1)
2)
3)
4)
5)
6)

RELATIVE
1)
2)
3)
4)
5)
6)

SPORTS
1)
2)
3)
4)
5)
6)

TOOL
1)
2)
3)
4)
5)
6)

VEGETABLE
1)
2)
3)
4)
5)
6)

VEHICLE
1)
2)
3)
4)
5)
6)

WEATHER
1)
2)
3)
4)
5)
6)

APPENDIX C

Subject	Group (1= control, 2=dancer)	Sex	Age	Years of Dance Experience	EBA Localizer	Motor Localizer	View	Vis Own	Vis Ctrl	View	Vis Own	Vis Ctrl	View	Vis Own	Vis Ctrl	View	Vis Own	Vis Ctrl
1	1	F	21	17		x		x										
2	1	F	27	20		x		x										
3	1	F	37	15		x		x										
4	1	M	19	0		x		x										
5	1	M	18	0		x	x	x										
6	1	F	18	10		x	x	x										
7	1	F	21	12		x	x	x										
8	1	F	24	0	x	x	x	x										
9	1	F	26	0		x	x	x										
10	1	M	43	1	x	x	x	x										
11	2	M	22	12		x		x		x	x		x	x		x	x	
12	2	M	50	44		x		x		x	x		x	x		x	x	
13	2	M	19	7.5		x		x		x	x		x	x		x	x	
14	2	M	21	7		x				x	x		x	x		x	x	
15	2	M	19	15		x				x	x		x	x		x	x	
16	2	F	18	15		x												
17	2	M	18	14	x	x		x								x	x	x
18	2	F	18	14		x					x	x						
19	2	M	20	10	x	x		x			x	x	x	x		x		x
20	2	M	20	7	x	x		x					x	x		x	x	x
21	2	M	18	8	x	x						x	x	x		x	x	x
22	2	M	18	12	x	x		x	x				x	x	x	x	x	x
23	2	F	19	12	x	x		x	x				x	x	x	x	x	x
24	2	M	19	13	x	x		x	x				x	x	x	x	x	x
25	2	F	19	14	x	x		x	x				x	x	x	x	x	x
26	2	F	18	10	x	x		x	x				x	x	x	x	x	x
27	2	M	18	6	x	x							x	x	x	x	x	x
28	2	F	19	16									x	x	x			
	CONTROL AVG	**7F, 3M**	**25.4**	**7.5**	**2**	**10**	**6**	**10**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
	CONTROL SD		8.42	8.14														
	DANCER AVG	**6F, 12M**	**20.7**	**13.14**	**10**	**17**	**0**	**11**	**5**	**5**	**7**	**3**	**15**	**15**	**7**	**15**	**14**	**10**
	DANCER SD		7.39	8.32														