



Review article

The Neuroscience of Dance: A Conceptual Framework and Systematic Review

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ABSTRACT

Ancient and culturally universal, dance pervades many areas of life and has multiple benefits. In this article, we provide a conceptual framework and systematic review, as a guide for researching the neuroscience of dance. We identified relevant articles following PRISMA guidelines, and summarised and evaluated all original results. We identified avenues for future research in: the interactive and collective aspects of dance; groove; dance performance; dance observation; and dance therapy. Furthermore, the interactive and collective aspects of dance constitute a vital part of the field but have received almost no attention from a neuroscientific perspective so far. Dance and music engage overlapping brain networks, including common regions involved in perception, action, and emotion. In music and dance, rhythm, melody, and harmony are processed in an active, sustained pleasure cycle giving rise to action, emotion, and learning, led by activity in specific hedonic brain networks. The neuroscience of dance is an exciting field, which may yield information concerning links between psychological processes and behaviour, human flourishing, and the concept of *eudaimonia*.

1. Introduction

1.1. What is dance?

Dance can be easy to recognise, but devising an accurate description of it is more difficult. According to one authority in the field, dance is “composed, from the dancer’s perspective, of purposeful, intentionally rhythmical, and culturally patterned sequences of non-verbal body movements which are not ordinary motor activities, the motion having inherent and aesthetic value” (Hanna, 1987). Dance is also highly

multi-faceted, with spatial and temporal aspects, and combines visual and auditory art. It can be either participatory, or merely observed, and is unusual as an art form in that it can also be considered a sport.

1.2. The history and utility of dance

Dance is culturally universal (Adler, 2009; Brown, 1991; Conard et al., 2009; Grafton and Cross, 2008; Levitin et al., 2018; Lomax, 1978; Spencer, 1985) and has probably always been part of the human condition (Hanna, 1987; Karpati et al., 2015; Mithen, 2011). It leaves so few

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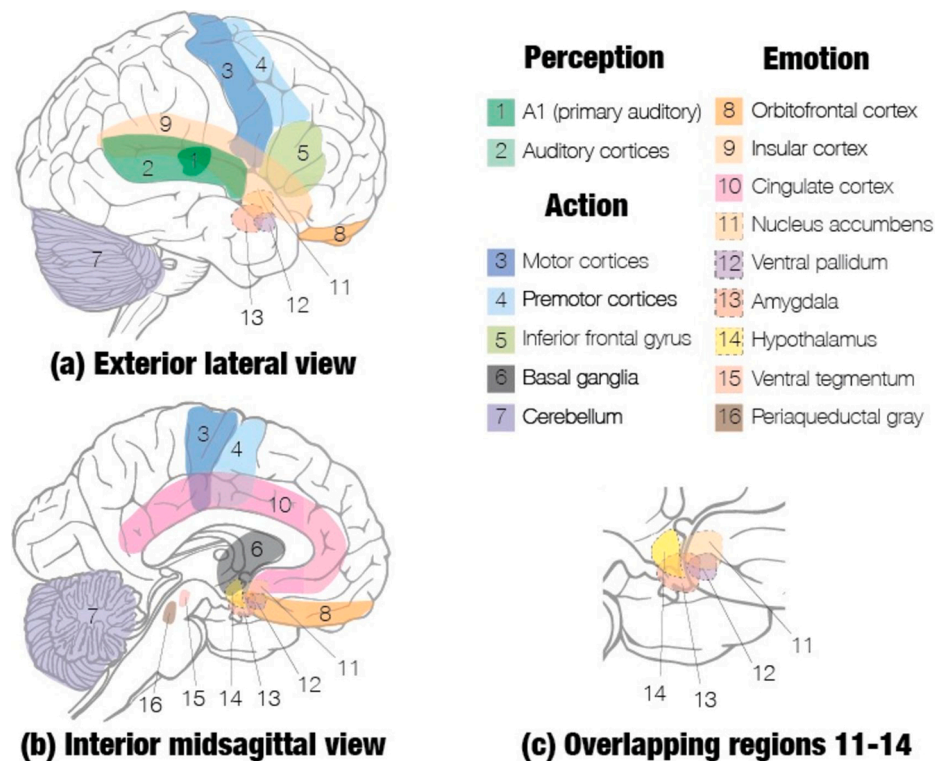


Fig. 1. Regions of the brain involved in networks relevant to music and dance.

traces that we do not know when it first appeared, but it is certainly ancient, and may have emerged as early as 1.8 million years ago (Hanna, 1987; Karpati et al., 2015; Mithen, 2011). Historically, dance has been relevant in many areas of life, with functions in religious and other rituals (Lewis, 2013; Merker et al., 2009), storytelling, imitating animals, rain-bringing (Lexová, 2012, p. 25), war dances (Merriam-Webster, 2021), and performance art.

Dance is also an important social activity. Synchronised dancing encourages social bonding, leads to feelings of inter-connectedness (Cohen and Tarr, 2015), social bonding, and elevated pain thresholds (Tarr et al., 2016, 2015). Self-other integration and the endogenous opioid system contribute to social bonding in a musical context (Tarr et al., 2014). Given the close relationship between music and dance, these mechanisms may well be involved in social bonding arising from dance (Tarr et al., 2017). By promoting social cohesion and trust, dance may have facilitated the formation of large stable social groups, and thereby contributed to our success as a species (Cohen and Tarr, 2015; Tarr et al., 2015).

Indeed, dance is often either partnered, for example in popular dance styles such as Salsa or Tango, or performed in groups. Groups of dancers can be small or large, from a few friends on a night out, to over 1000 people dancing a Charleston simultaneously (The Guinness Book of World Records, 2018), to several thousand people dancing at live concerts. Flash mobs (when a group of people gathers at a pre-ordained time in a public space to perform a, in this case dance-based, act, then disperses) of dancers can also range from small groups to the world record of over 13,000 people (The Guinness Book of World Records, 2009). Such group dancing highlights the synergetic nature of dance, with many dancers interacting in space and time to create something greater than that which any individual could achieve alone.

Dance is also frequently practised because it induces pleasure, including collective positive emotion, and because it has significant motivational and health benefits. Dance can therefore contribute significantly to *eudaimonia*; a life well-lived, a concept discussed by Aristotle and many subsequent thinkers (Haybron, 2020; Stark et al.,

2018).

The pleasurable and motivational aspects of dance seem to arise from the extended pleasure cycle which it induces. Pleasure cycles are characterised by distinct phases of wanting, liking, and satiety (Berridge and Kringelbach, 2015; Kringelbach and Berridge, 2009). In dance, the liking phase is extended compared to most sources of pleasure, and the satiation phase is weaker. This produces longer pleasure cycles, with sustained periods of positive emotion (Foster Vander Elst et al., 2021; Kringelbach and Berridge, 2017; Stark et al., 2018), and may be what induces and allows people to, quite literally, dance the night away.

1.3. The neuroscience of dance

Before dancing begins, the nervous system processes auditory and other stimuli, and instigates the various necessary preparatory processes. During dance it generates, directs, and coordinates dancers' movements, while continuing to process relevant external stimuli. Without the nervous system, dance could not occur, and the study of the neuroscience of dance is therefore essential for an adequate understanding of the subject.

Studying the neuroscience of dance can also benefit other areas of research, including: brain plasticity; brain-behaviour relationships (Karpati et al., 2015); action-perception coupling (Bläsing et al., 2012); movement-cognition integration; sensorimotor integration; advanced motor control; movement synchronisation; and neuroaesthetics. Other broader fields which can also benefit include: communication; social and physical interaction, including cooperation, trust, and social cohesion; gender studies; and health.

1.4. Dance and predictive coding

The predictive coding (PC) theoretical framework, which has advanced knowledge in diverse disciplines, is a promising tool for the study of the neuroscience of dance.

When listening to music, the brain constantly generates predictions

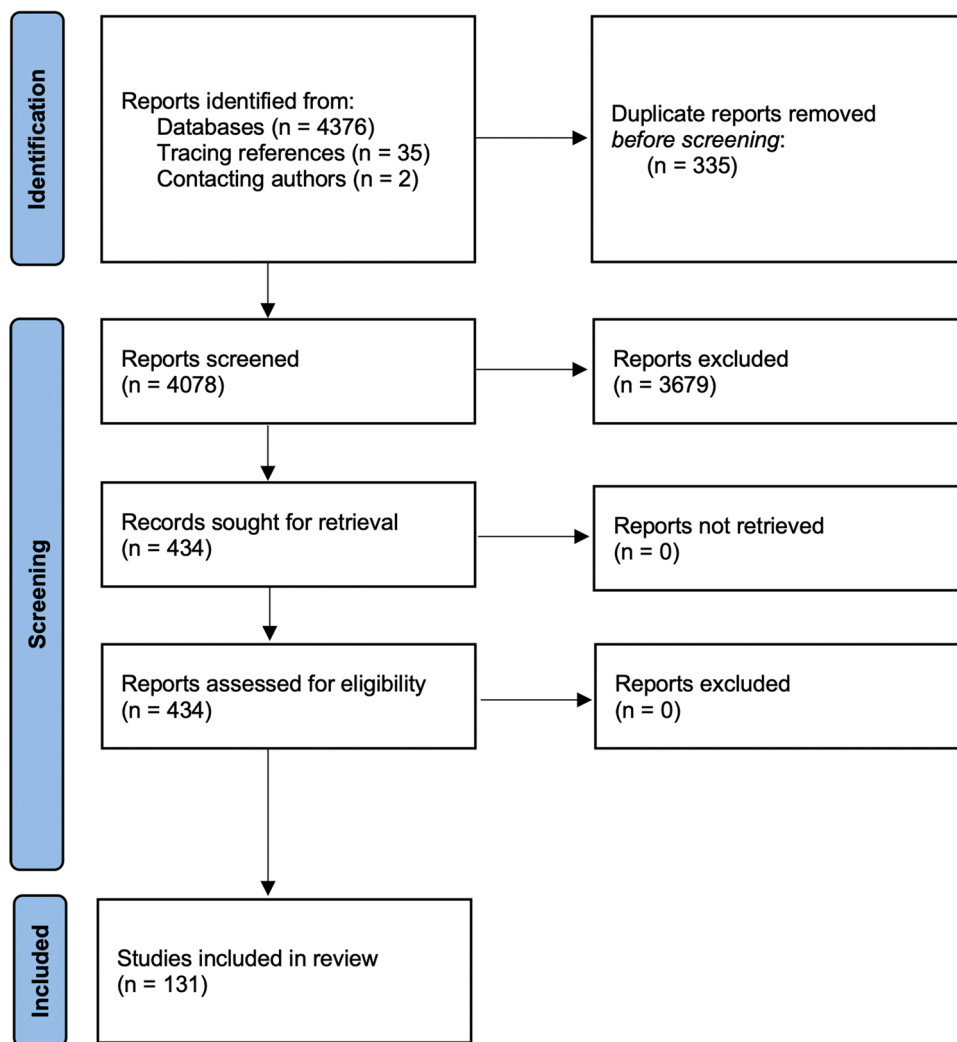


Fig. 2. PRISMA flowchart showing the number of articles at each stage of the literature search. Adapted from Page et al. (2021).

based on an underlying model, guiding our perception and actions, outlined in the predictive coding of music model (PCM) (Heggli et al., 2019; Vuust et al., 2009; Vuust and Frith, 2008). In the PCM, it is proposed that music processing, including perception, action, emotion, and learning, is an integrative, recursive Bayesian process, by which the brain attempts to minimise the prediction error between lower-level sensory input and the brain's top-down predictions (Heggli et al., 2019; Vuust et al., 2022, 2009; Vuust and Frith, 2008).

To date, PC has received relatively little attention in dance research. However, music and dance are intimately connected, and prediction is as necessary in dance as it is in music (Bläsing et al., 2012; Phillips-Silver and Keller, 2012). In dance, dancers must make predictions about the music, the position and movement of other dancers on the dance floor, and in any dance with others, they must also make predictions about the movements of the other dancers. Furthermore, in partner dancing, the leader directs the dance and communicates physical cues to the follower so that the follower can respond fluently. In the absence of choreography, the leader must plan the moves spontaneously while dancing, deciding what moves both they and the follower will perform. The leader must then perform their own moves, and communicate to the follower which moves the follower should perform. The follower must respond to cues received from the leader, which will be easier if they can make accurate predictions about the moves planned by the leader. However, they must also be ready to respond and adapt immediately if

those predictions turn out to be incorrect. The leader must also be able to react rapidly to the follower's actions, especially if they are unexpected.

Music and dance are intimately connected, and prediction is as necessary in dance as it is in music (Bläsing et al., 2012; Phillips-Silver and Keller, 2012). When listening to music, the brain constantly generates predictions based on an underlying model, guiding our perception and actions, outlined in the predictive coding of music model (PCM) (Heggli et al., 2019; Vuust et al., 2009; Vuust and Frith, 2008). In the PCM, it is proposed that music processing, including perception, action, emotion, and learning, is an integrative, recursive Bayesian process, by which the brain attempts to minimise the prediction error between lower-level sensory input and the brain's top-down predictions (Heggli et al., 2019; Vuust et al., 2022, 2009; Vuust and Frith, 2008).

Prediction in dance is therefore highly multi-modal, with relevant information not only from auditory stimuli, but also visual and haptic stimuli. We can therefore expect PC in dance to encompass auditory, visual, and haptic processes.

Given the importance of prediction in dance, and the fact that the PCM may be extended to explain the brain mechanisms of collective music-making (Vuust et al., 2022), it may help to explain the neural mechanisms of the social and interactive aspects of dance. Such a unified approach is encouraged by the existence of overlap in brain networks related to music and dance, including common regions involved in perception, action, and emotion, shown in Fig. 1.

1.5. Aims and content of this article

Innovative research has been carried out on the neuroscience of dance in recent years, but the field lacks some basic resources that would facilitate its progress.

One such missing resource is a systematic review. Several reviews have been undertaken, but with specific foci, including: (1) selected areas of the neuroscience of dance (Karpati et al., 2015); (2) a synthesis from a range of different fields including anthropology, sociology, psychology, and neuroscience (Basso et al., 2021); (3) an interdisciplinary review including neuroscientific results (Zardi et al., 2021); and (4) dance and ageing (Dominguez et al., 2021b; Muiños and Ballesteros, 2021; Nascimento, 2021; Teixeira-Machado et al., 2019; Wu et al., 2021). A broad, large-scale systematic review would help researchers to obtain a clearer view of work carried out, and to chart a productive course for future research.

Another resource which is currently lacking is a conceptual framework for researching the neuroscience of dance. Such a framework would help in the identification of fundamental elements of the field, including which phenomena to study, and how different areas relate both to each other, e.g. dance observation and dance imagery, and to relevant parts of other fields, e.g. auditory processing of music during dance observation. The lack of such a comprehensive framework can lead to insufficient awareness of the extent of the disparity of research in different areas, and insufficient integration between dance and other fields.

In this article, we therefore: (1) construct a conceptual framework (Section 3); (2) highlight the disparity of research in different areas from a numerical overview of articles in each area (outlined in Section 4.1, covered in detail in the Appendix); (3) outline the principal difficulties faced by researchers in the field (Section 4.2); (4) carry out an in-depth systematic review of individual studies, organised by the research areas outlined in the conceptual framework (Sections 4.3–4.9); (5) provide an overview of the results of the systematic review (Section 5); and (6) provide detailed suggestions for future work (Section 6). We also provide a bibliography in the Supplementary Material, in which all papers are listed by research area.

The detailed systematic review (Section 4) is tailored for established researchers interested in knowing the state of the field in depth. The overview (Section 5) is tailored for newcomers to the field, and those who wish to obtain a broad overview of the state of the field.

2. Methods

In this section, we outline the methods employed to carry out the review, including our search strategy, and the ways in which we extracted and categorised relevant results.

2.1. Search strategy

We conducted a major literature search in December 2019 and performed updating searches at intervals up to and including January 2023. Articles were identified using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses guidelines (Moher et al., 2009).

The main resources used were the NCBI database, PubMed, and Google Scholar. General search terms included “neuroscience of dance,” “neuroscience,” and “dance.” Specific search terms included “music-induced movement,” “groove,” “dance observation,” “dance/motor imagery,” “dance imagery,” “dance training,” “dance therapy,” and “dance/movement therapy.” We did not impose conditions on language or publication year.

Database searches resulted in 4376 articles. We searched through conference proceedings, and traced references backwards and forwards in the articles identified as candidates for potential inclusion, identifying 35 additional articles. We contacted researchers in the field to ask for recommendations, and identifying 2 additional articles. The removal of

duplicates reduced this to 4078. The titles and abstracts were screened for mentions of dance or related terms, reducing the number to 434. In total, 131 articles fulfilled the criteria set out in Section 2.2. These numbers are summarised in Fig. 2, adapted from Page et al. (2021).

2.2. Study eligibility

Inclusion criteria were:

- studies on dance, or on activities deemed to be sufficiently closely related to dance;
- original studies;
- not a pre-print; and
- studies containing neuroscientific results.

2.3. Data manipulation and extraction

We created a database of the 434 articles where dance or similar terms were mentioned, including the: (1) standard referencing information; (2) abstract; (3) relevant research area(s); (4) neuroimaging/stimulating techniques; (5) keywords; and (6) whether we included it.

To identify articles for inclusion, we read the abstracts and discarded those which did not meet the criteria in Section 2.2. We categorised the articles by research area, and those that dealt with more than one area were placed in multiple categories.

Within each area, we categorised the results according to the specific areas investigated in the studies (these sub-sections are not directly related to the conceptual framework). Finally, we: (1) read each article in full; (2) identified and recorded relevant neuroscientific results; (3) identified any broader relevance; and (4) used this to draft Section 4.

We used the database to extract numerical information about the articles reviewed, to assign a numerical and objective, rather than approximate and judgment-based, value to the number of studies published. To our knowledge, the only other review article in a related field in which this technique has been used is Cross et al. (2014).

Another aim of this process was to evaluate the progression of the field over time, using the number of studies published each year. This is approximate, as it does not take into account the limitations of evaluating a field solely on the number and date of studies published. These include the discrepancy in time between research being undertaken and the publication of the results, the potential disparity between the number of studies published and the number of research projects undertaken, and various other measures of the amount and importance of research activity. However, it does help to give a general idea of the development of the field. An overview of the number of studies published in each area in each year is given in Section 4.1. More detailed information is set out in the Appendix.

2.4. Ethics

All of the studies reviewed were carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was obtained for experimentation with human subjects and data was anonymised.

3. Conceptual framework

In this section, we present our conceptual framework for researching the neuroscience of dance. We delineate the framework by identifying the constituent areas of the neuroscience of dance, and the relationships between them, especially highlighting the links between music and dance.

Dance can occur in the absence of music, and some people dance while music is playing but, from their lack of synchronisation, do not seem to dance “to” it. We therefore do not aim to explain all dance with this framework.

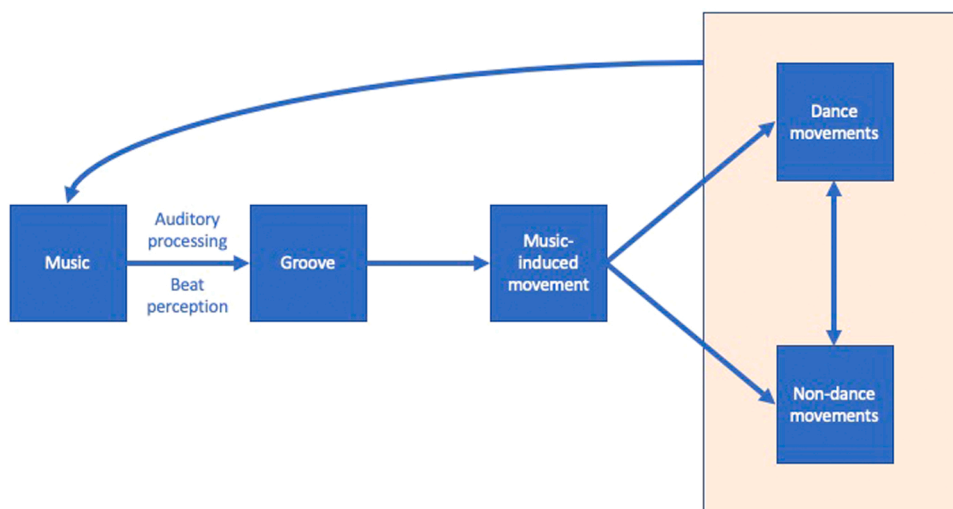


Fig. 3. Connections between music, auditory processing, beat perception, groove, music-induced movement, and dance, which are relevant to the conceptual framework.

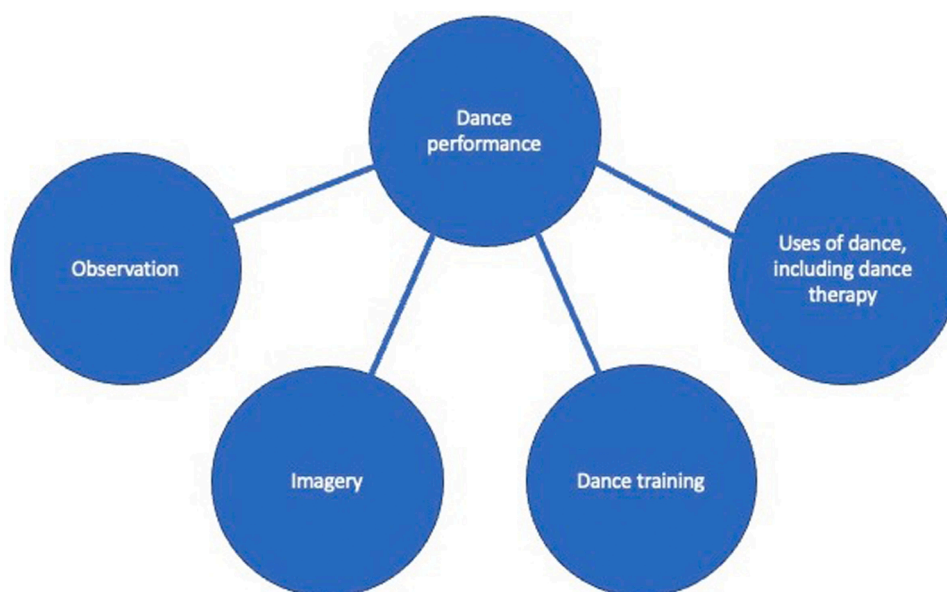


Fig. 4. Areas of dance represented in the conceptual framework: *dance performance*, the physical activity of dancing; *dance observation* by both an audience, and dancers observing themselves; *dance imagery*, when people imagine themselves dancing, either consciously or unconsciously; *dance training*; and uses of dance including *dance therapy*.

This ontological exercise is complicated by the need to create delineated categories from phenomena that are not entirely separable. The categories chosen cannot, therefore, be beyond debate, but we are confident that this framework is workable and ontologically justifiable.

3.1. The delineation of the conceptual framework

The relationship between music and dance can be considered to be bidirectional. In this framework, we do not aim to explain all aspects of this relationship, but focus on that of dance arising from music, whether heard externally or imagined internally. This focus is motivated by the fact that the field of the neuroscience of music is more advanced than the neuroscience of dance. We therefore propose to start by building on, and borrowing from, the more established field.

When music is played, *auditory processing* enables the perception of features that influence or elicit behavioural responses via a series of inter-connected phenomena, outlined in Fig. 3. Rhythm is an element of

the music of paramount importance in the context of dance, and the related process of *beat perception* facilitates precisely timed movement. Under certain conditions, auditory processing and beat perception can elicit a compelling and pleasurable desire to move, known as *groove*. If acted on, the ensuing *music-induced movement* can include both *dance* and *non-dance movements*. Such movements can have close links to music performance. For example, in dance styles such as Tap, Flamenco, or any in which body percussion plays a prominent role, the production of sound is an integral component of the dance which adds to, and becomes part of, the music.

Dance has multiple manifestations and uses, as described in the introduction, and outlined in Fig. 4. *Dance performance*—the physical activity of dancing—and *dance observation*—both by an audience and the dancers observing themselves—occur in contexts that vary in form and function. People can also imagine themselves dancing, either intentionally or unintentionally, via *dance imagery*, and some people undergo *dance training* that can vary in terms of systematicity and

intensity. Dance is often used in a therapeutic context, and such *dance therapy* can take many forms.

The constituent areas of the conceptual framework—discussed more fully below—therefore relate to the following phenomena: (1) music, and other auditory processing; (2) groove; (3) music-induced movement; (4) dance performance; (5) dance observation; (6) imagery relevant to dance; (7) dance training; and (8) dance therapy.

3.2. Music, and other auditory processing

Almost all dance occurs to music. The auditory processing of music must therefore almost always occur before, and continue while, dancing takes place. Rhythm is the most influential component of music in this context (Leisman and Aviv, 2020). The temporal patterning of sounds facilitates the coordination and pacing of body movement within and between dancers. Beat perception, the experience of isochronous pulses underlying music, which may or may not contain isochronous onsets (London, 1995), is an important element of this. Other salient non-musical sounds, such as dancers' breath or feet hitting the ground, also accompany dance, and are processed both by the dancers and any audience.

3.3. Groove

Listening to music often induces a desire to move. When the desire to move to music is pleasurable, it is often called groove (Janata et al., 2012; Senn et al., 2018; Madison, 2006). Groove is most strongly felt when music (or rhythms) has medium levels of syncopation (the appearance of a beat on a metrically weak accent, preceding a rest on a metrically strong accent (Longuet-Higgins and Lee, 1984)) (Matthews et al., 2019; Witek et al., 2014). Too little syncopation is perceived as boring, too much syncopation is felt to be too complex. A medium amount of syncopation is felt to be interesting, and creates a desire to 'fill in' the gaps with movement (Witek, 2017), stabilising an internal metrical model.

Groove plays a pivotal role in bringing about, and continuing, most dance. Music that is especially effective at doing so is described as "high-groove." Music that is only somewhat effective is described as "low-groove." Groove is a subjective sensation, but there is considerable consistency across random samples of people when they are asked to assign a degree of groove to music or rhythms (Madison, 2006; Stupacher et al., 2016). Spontaneous dance to music can therefore be considered as arising from groove, which is therefore a key factor linking music and dance.

3.4. Music-induced movement

If a desire to move to music is acted on, the result is music-induced movement. This includes non-dance movements such as wrist flexion, finger tapping, foot tapping and head bobbing, as well as organised whole-body movements which may be recognisable as dance. Music-induced movement is therefore an important factor linking music and dance.

Many neuroscientific studies have been carried out on non-dance movements to music, particularly tapping and single joint flexion. However, while these activities are informative about general sensory-motor processing, the specific relevance of such research to dance is unclear (Leisman and Aviv, 2020). For this reason, we do not include research on general music-induced movement in the review unless another aspect of the study is relevant, e.g. investigating the effects of dance training on neural activity during tapping to music.

3.5. Dance performance

Dance performance can be defined in the sense of a planned performance of either amateur or professional dancers for an audience, or in

a wider sense to denote the physical activity of dancing in any context. In this article, we use the latter definition.

There are many challenges associated with researching the neuroscience of dance performance, discussed in detail in Section 4.2. To work around these difficulties, research has been carried out on people performing activities similar to dancing, but which allow for neuroimaging. The movements investigated are necessarily different from normal dancing, and highly constrained, so the extent to which these results generalise to typical dance performance is an open question. However, when the proxy activities are directly related to dance movements, findings are likely to be informative.

3.6. Dance observation

In addition to being a social activity, dance is a visual art form, frequently meant to be observed by an audience. Moreover, dancers observe themselves dancing, and there is often a mirror in dance studios for this purpose. Both of these phenomena constitute dance observation. In dance research, dance observation is usually that of an audience observing dancers.

Dance observation can be of either live or recorded dance. Most of the studies reviewed used recorded dance. There are many reasons for this, principally that: (1) it is difficult to undertake neuroimaging in a live dance setting such as a theatre; (2) it is complex to arrange a dance performance in most laboratory settings; (3) observing recorded dance makes experimental paradigms easier to carry out and control; and (4) a great deal of dance observed is recorded, e.g. on television or online.

The study of the neuroscience of dance observation is an intrinsically informative aspect of the study of the neuroscience of dance. This is because aesthetic, cultural, health, and other benefits derive not just from the performance of dance, but also from its observation. Dance is, to a significant extent, a spectator sport. Dance observation has important functions in non-verbal communication, expressing emotions, and story-telling (Cohen and Tarr, 2015). A significant amount of communication between dancers is visual, but also occurs via coupled movement dynamics, supporting evolutionary theories of dance as a means to enable communication between and within large groups of people (Vicary et al., 2017).

The study of the neuroscience of dance observation is also valuable because it can be used as a proxy for the study of neural activity associated with dance performance, supported by the claim that action observation engages the human mirror system (Gallese et al., 1996; Grèzes and Decety, 2001; Rizzolatti and Sinigaglia, 2010). In this putative system, mirror neurons match "observed events to similar, internally generated actions" (Rizzolatti and Arbib, 1998). In other words, neural activity occurring as a result of observation of movement resembles neural activity during the performance of that same movement, suggesting an internal process of covert action simulation. While reservations have been expressed about mirror neuron theory (see e.g. Heyes and Catmur (2021); Hickok (2009)), there is partial overlap of regions of the brain involved in action imagery, observation, and execution (Hardwick et al., 2018; Morales et al., 2019; Munzert et al., 2008; Vogt et al., 2013; Wright et al., 2014), and all three tasks recruit similar premotor-parietal cortical networks (Hardwick et al., 2018). Although it is far from ideal to use dance observation as a proxy for dance performance, such results are still useful and provide something of a work-around for the technical problems associated with studying the neuroscience of dance performance directly.

3.7. Imagery relevant to dance

During dance observation by an audience, both unintentional and intentional motor imagery of the movements observed can occur, i.e. "the cognitive simulation of an action without actually executing it" (Carey et al., 2019). Different types of motor imagery include: (1) kinesthetic imagery; (2) visual imagery; (3) imagery of oneself moving;

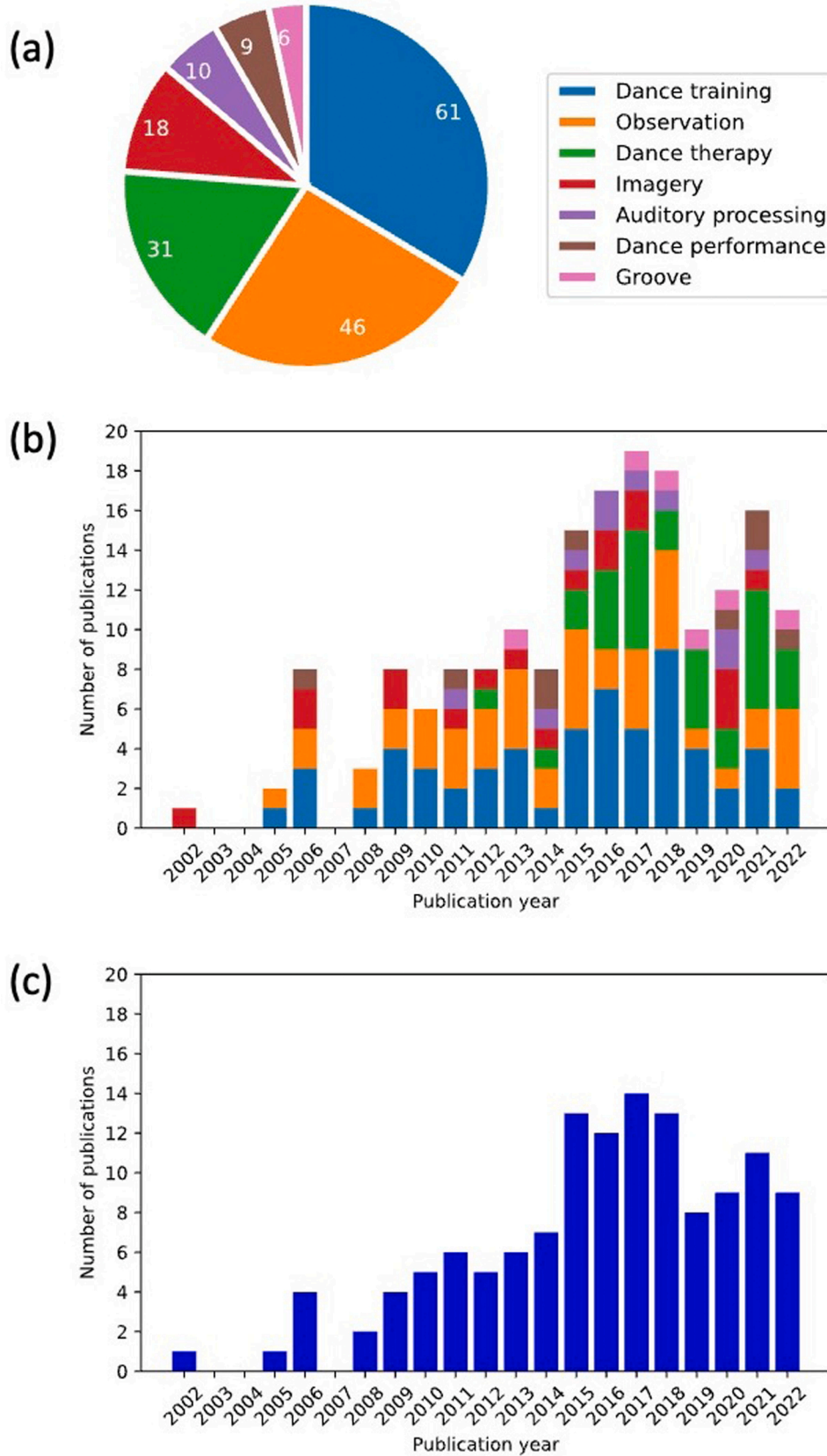


Fig. 5. (a) Total number of studies published in each area, decreasing number of studies listed clockwise. (b) Number of studies published each year in each area, listed in order of decreasing number of studies. Some studies are included in more than one area, and are therefore counted more than once in this graph. (c) Total number of individual studies published each year.

Table 1

All studies published in each area, arranged by year, are listed in order of decreasing number of studies. Also shown is the total number of unique studies published each year.

Publication year	Number of studies							Total unique studies
	Dance training	Dance observation	Dance therapy	Imagery	Auditory processing	Dance performance	Groove	
2002				1				1
2003								0
2004								0
2005	1	1						2
2006	3	2		2		1		8
2007								0
2008	1	2						3
2009	4	2		2				8
2010	3	3						6
2011	2	3		1	1	1		8
2012	3	3	1	1				8
2013	4	4		1			1	10
2014	1	2	1	1	1	2		8
2015	5	5	2	1	1	1		15
2016	7	2	4	2	2			17
2017	5	4	6	2	1		1	19
2018	9	5	2		1		1	18
2019	4	1	4				1	10
2020	2	1	2	3	2	1	1	12
2021	4	2	6	1	1	2		16
2022	2	4	3			1	1	11
Total	61	46	31	18	10	9	6	169

and (4) imagery of someone else moving. In kinaesthetic imagery, motion control is rehearsed mentally, emphasising the feeling produced by the execution of the movement (Malouin et al., 2007). In visual imagery, the execution of a motion is visualised mentally, emphasising the ideal execution of that action and how it will look (Mizuguchi et al., 2016).

Research on dance imagery is likely to be informative about neural processes relevant to dance performance and dance observation, as there is overlap between the brain regions involved in action imagery, action observation, and action execution (Hardwick et al., 2018; Morales et al., 2019; Munzert et al., 2008; Vogt et al., 2013; Wright et al., 2014).

In the studies we review, it is either stated or implied that: (1) the type of imagery is motor imagery; (2) participants imagine themselves, not others, moving; (3) participants imagine the movements consciously. Some studies employ non-dance imagery, but are relevant to dance, e.g. because participants imagined themselves walking before and after a course of Tango lessons.

3.8. Dance training

Dancing can take place without training, and frequently does. However, dancing well is a skill that can only be acquired through many hours of practice, lessons, rehearsals, etc. Furthermore, in the long term, learning to dance is inseparable from dance performance. The neurological effects of long-term dance training and those of dance performance are therefore inseparable.

3.9. Dance therapy

Dance is often used in a therapeutic context. Such dance therapy takes many forms, including traditional dance, traditional dance adapted for those with reduced mobility, aerobic dance, creative movement to music, and dance/movement therapy. The latter involves the psychotherapeutic use of movement, incorporating factors such as embodiment and creativity, to promote health and well-being, based on the interconnection of body and mind (Koch et al., 2019). For reviews of dance therapy see, e.g. (Mandelbaum and Lo, 2014; Kshtriya et al., 2015; Millman et al., 2020; Koch et al., 2019; Quiroga Murcia and Kreutz, 2012).

4. In-depth review of studies by research area

In this section, we review the individual studies in the field, categorised by the research areas identified in the conceptual framework: (1) music, and other auditory processing; (2) groove; (3) dance performance; (4) dance observation; (5) imagery relevant to dance; (6) dance training; and (7) dance therapy. As noted in Section 3.4, we do not have a dedicated section on music-induced movement in the review.

In Section 4.1, we provide graphical and tabular representations of the number of studies published in each area in each year. In Section 4.2, we discuss limitations of, and obstacles to, research in the field. In Sections 4.3 to 4.9, we summarise the results of individual studies in each area. Some studies relate to more than one area, so appear in more than one sub-section. The exception is dance training, as this would result in too much repetition. Studies pertaining to dance training and another area, e.g. dance observation, are included in the other area. Studies pertaining to dance training that are not relevant to another area are reviewed in Section 4.8.

Several studies use small sample sizes ($1 \leq n \leq 11$), and it is therefore unclear how well the results would generalise. We therefore include the number of participants when discussing these studies.

Frequency bands of brain activity (*delta* 0.5–4 Hz, *theta* 4–8 Hz, *alpha* 8–13 Hz, *mu* 8–13 Hz over the sensorimotor cortex, *beta* 13–30 Hz, and *gamma* 30–48 Hz) are italicised.

4.1. Graphical and tabular representation of the number of studies

As research varied greatly over time and by area, we have produced a tabulated chronology of the number of studies published in each area in each year. The neuroscience of dance is a growing area of research, with all but one article published since 2005. The total number of studies published in each area and each year, and the total number of unique studies published in each year, are shown in Fig. 5 and Table 1. Individual graphs of the number of studies published in each area, in each year, are set out in the Appendix.

Our search yielded 131 articles published up to and including January 2023 containing original and relevant neuroscientific results. We do not include articles published in 2023 in the numerical overview, as the last literature search was conducted in January 2023, and this would give a misleading representation of the amount of research

published in 2023.

4.2. Limitations of, and obstacles to, dance research

There are many significant obstacles to research in the field, and the studies reviewed are subject to many limitations. Most of the limitations and difficulties encountered in individual studies are set out extensively in the relevant articles. We note some striking examples when discussing individual studies, especially concerning small sample sizes ($1 \leq n \leq 11$). With a few generally applicable exceptions covered in this section, limitations specific to individual studies are not discussed further. In this section, we discuss limitations faced by researchers in the field generally.

Ecological validity presents significant obstacles to research in the field. For example, important stage elements such as backdrop changes and lighting are not reproducible in a laboratory (Dale et al., 2007). Moreover, neuroimaging while people are moving freely presents many technical difficulties. Indeed, no studies have been published to date in which dancers are scanned while performing normal, unadapted, dance.

There has been improvement in neuroimaging techniques for use when walking (EEG (Jacobsen et al., 2021) and fNIRS (Burgess et al., 2022)), but these techniques have low spatial resolution in the brain. Mobile Brain/Body Imaging (EEG combined with motion capture (Barnstaple et al., 2020)) offers promise, but no data have yet been published using this technique on dancers dancing. Significant progress has also been made using MEG sensors which allow for some movement (Boto et al., 2018). fMRI is even more restrictive as the person must be lying down, and any movement may therefore only approximate dance. This is also true of PET scanning, which has the additional disadvantage that it measures activity over relatively long intervals (on the scale of minutes), and it is therefore not possible to extract dynamic information related to fine-grained temporal processing.

Another significant difficulty is controlling for regular participation in strenuous physical activity. It can be difficult to ascertain whether results are due to: (1) dance training; (2) regular physical activity in general; or (3) some combination of the two. Some researchers have used an active control group, such as basketball players or rowers, but no “no-change” control group. This method was used in several studies on brain structure in dancers (Ermutlu et al., 2015; Meier et al., 2016; Ushiyama et al., 2010) and dance therapy (Müller et al., 2017, 2016; Narici et al., 2017; Rehfeld et al., 2018, 2017, 2015; Zilidou et al., 2018).

This approach is sensible when there is no alternative, but the interpretation of results is fraught with difficulty, especially when investigating changes over time, as it is impossible to determine what changes would have occurred without the intervention. This is particularly relevant in dance therapy for older adults, as rapid degeneration can, and often does, occur in the elderly. In two studies on dance therapy for older adults with a “no-change” control group (Qi et al., 2019; Sejnoha Minsterova et al., 2020), significant differences were observed between the two groups, and in a study with multiple groups (though none of these groups were “no-change”) (Burzynska et al., 2017b), white matter integrity declined in all groups.

Another complication of using only an active control group regards the difference in the social aspects of dancing and the other physical activities. There are important social aspects to all of them, but their character is very different, both in nature and degree.

Furthermore, the social and physical lives of people who regularly participate in physical activities, such as dance and team sports, are very different from the social and physical lives of those who do not. This difference further complicates attempts to ascertain which results relate specifically to dance, regular participation in strenuous physical activity, or the social interactions intrinsic to practising each activity.

4.3. Music, and other auditory processing

Research on music, and other auditory processing, relevant to the

neuroscience of dance has addressed: (1) preferred music; (2) metre; (3) intentionality of sound production; (4) dance training and musical training; and (5) beat perception.

4.3.1. Metre

A metre is formed of regular and recurring patterns of beat accentuations (Vuust et al., 2006). This can result in entrainment, with “synchronization of attention and/or other behaviors (especially motor behaviors) with periodic rhythms in the environment” (London, 2004). Metric structure may be present in the music, or may be imagined. The imagination of a metre is especially important for the prediction of future events in the music (Vuust and Witek, 2014). Metre is also of central importance in dance.

Metres usually constitute two, three, or four beats. Some dances, such as the Paso Doble, use a metre of two beats (binary), in which every second beat is emphasised (STRONG weak STRONG weak). Marching, which resembles dance in some ways but is not usually classified as such, is also performed to a metre of two beats. Other dances, such as the waltz, use a metre of three beats (tertiary), in which every third beat is emphasised (STRONG weak weak STRONG weak weak). Many dances use a metre of four beats (quaternary), in which every fourth beat is emphasised (STRONG weak weak weak STRONG weak weak weak). The relevant studies in this area involved: (1) imagining a metre; and (2) moving to a metre.

4.3.1.1. Imagining a metre. Listening to evenly spaced tones with identical emphasis, i.e. with no metre, has been found to elicit a sustained, periodic, neural response tuned to the beat frequency (Nozaradan et al., 2011). Decreases in *beta* band power have also been found, related to the beat, 200 ms after the beat. This was followed by an increase in power, leading to the onset of the next beat (Fujioka et al., 2015). It is likely that this increase was associated with predictive processing.

Imagining a metre when listening to such tones also affects neural activity. Imagery of either a binary metre or a tertiary metre elicited marked neuronal entrainment at the metrical frequency (Nozaradan et al., 2011). Imagery of these metres elicited a greater increase in *beta* band power on the strong beat than on the subsequent weak beat (Fujioka et al., 2015). The regions of the brain involved were: (1) the auditory and sensorimotor cortices; (2) the frontal, parietal, and inferior temporal lobes; and (3) the cerebellum (Fujioka et al., 2015). This activity may reflect timing information being translated to auditory-motor coordination.

These results are promising for research on entrainment generally, showing that music (and, by extension, dance, as they have similar periodic temporal structures) provides a useful context for the exploration of neural entrainment.

4.3.1.2. Moving to a metre. Moving to a metre affects neural activity associated with listening to it. When listening to a repeated rhythmical pattern of identical tones, neural responses to rhythms at frequencies related to the metre were significantly larger after metrical movement to it. Neural activity associated with movement to a metre appears to help internalise it, which in turn appears to improve temporal predictions relevant to the metre (Chemin et al., 2014). This is of critical importance in dance, in which dancers synchronise their movements to music.

Moving consciously to rhythms also improves temporal predictions relevant to those rhythms. These predictions were found to be encoded by the left sensorimotor cortex, through interdependent oscillations in the *beta* and *delta* bands. The oscillations originating in this region were directed towards auditory regions of the brain. During overt rhythmic movement, greater right-lateralised activity occurred in frontoparietal associative regions, related to temporal predictions. Motor regions of the brain therefore appear to play key roles in providing temporal and contextual information to sensory regions of the brain (Morillon and

Baillet, 2017).

4.3.2. Preferred music

In an EEG study, dancers and non-dancers listened to either preferred music or non-preferred music. When dancers and non-dancers listened to music they preferred, compared to music that they did not prefer, both groups had more activity in *gamma*, *beta*, and *alpha* bands. When listening to music they preferred, dancers had, compared to non-dancers, more initial event-related desynchronisation, and subsequently augmented and uninterrupted event-related synchronisation, both in the *alpha* band (Nakano et al., 2021).

The authors interpret the: (1) *gamma* activity as affective responses to, and conscious recognition of, preferred music; (2) *beta* activity as appreciation of the tempo of the preferred music, and emotional arousal related to the preference; (3) *alpha* activity as enhanced attention for cognitive functions such as memory retrieval; and (4) augmented synchronisation in the *alpha* band in dancers as being derived from motor imagery, or creative cognition generally.

4.3.3. Intentionality and temporal delay of sound production

Intentionality of sound production during performance of one's own actions affects neural activity when observing those actions. Participants were recorded performing tap dancing or hurdling (a sport "in which a runner races over a series of obstacles called hurdles, which are set a fixed distance apart" (The Editors of Encyclopaedia Britannica, 2019)). In the scanner, they were presented with point-light displays of their own actions, including the corresponding sounds. Sounds associated with tap dancing were classified as "intentionally produced" and sounds associated with hurdling were classified as "unintentionally produced." Intentionally produced sounds were associated with greater activation of posterior superior temporal gyri and the supplementary motor area. Unintentionally produced sounds were associated with greater activation of the primary auditory cortex (Heins et al., 2020a). Processing of self-generated sounds during observation of one's own actions therefore appears to depend on intentionality of sound production (Heins et al., 2020a).

Temporal delay of self-created sounds made during performance of one's own actions also affects neural activity when observing those actions. Participants observed point-light displays of themselves performing tap-dancing (intentional sounds) and hurdling (unintentional sounds), hearing the sound presented either at the original time or with a 200 ms delay (Heins et al., 2020b). When the sound was presented at the original time, for intentionally produced sounds compared to unintentionally produced sounds, there was: (1) attenuation in the primary auditory cortex; and (2) greater activity in the posterior superior temporal gyrus and supplementary motor area. When the sound was presented with a delay: (1) blood-oxygen-level-dependent response initially increased in the posterior superior temporal gyri, but quickly adapted on subsequent presentation of the stimuli; (2) activity in the supplementary motor area increased more for intentionally produced sounds; and (3) activity in the posterior superior temporal gyri was more strongly correlated with that in the supplementary motor area when the sound was delayed, than when it was reproduced with the original timing.

When self-created sounds are distorted, action evaluation may therefore be based more strongly on top-down predictions originating from the supplementary motor area (Heins et al., 2020b). This is consistent with theoretical conceptualisations of internal models in which there is disengagement from incongruent perceptual input. This facilitates endogenous action prediction based on signals from the supplementary motor area (see e.g. Ito (2008)).

During dance observation in the presence of music, greater inter-subject correlation (ISC) has been found in a left anterior region of the superior temporal gyrus (STG) involved in complex audio processing. In the absence of music, greater ISC was found in the parietal and occipitotemporal cortices and a posterior region of the STG. The difference in activity in the STG could be due to sounds made by the dancer, such as

the breath, providing an auditory signal which is more "salient" than music, in primary auditory regions of the brain (Reason et al., 2016). This study is also included in Section 4.6.1, as it is also relevant to dance observation.

4.3.4. Dance training and musical training

Dance training and musical training both affect auditory processing, including changes in neural activity related to specific musical events, and synchrony of different brain wave frequency bands (*theta*, *alpha*, *beta*, and *gamma*) across different electrodes on the scalp. Changes related to musical events can be investigated using event-related potentials such as P50, N100, and P200 responses. "P" and "N" refer to positive and negative changes in potential; the number refers to the approximate number of milliseconds after the event.

While listening to Shchedrin's *Carmen Suite*, a ballet suite arrangement of Bizet's opera, the P50 was greater in dancers when the timbre of the music changed than in musicians or controls. The N100 was larger in controls than in dancers or musicians. In dancers, this might have been a counter-effect of the greater P50 observed (Poikonen et al., 2016).

During observation of dance in the presence of music (Shchedrin's *Carmen Suite*) dancers had greater synchrony across different electrodes in the *theta* and *gamma* bands than in the absence of music. Musicians had less synchrony across different electrodes in the *alpha* and *beta* bands than in the absence of music (Poikonen et al., 2018a).

Dancers therefore appear to have enhanced pre-processing of changes in timbre in music than musicians or controls (Poikonen et al., 2016). Different neural processes seem to occur when dancers, musicians, and controls listen to music, and perception of music and dance is shaped by both dance and musical training (Poikonen et al., 2018a). The unconscious awareness of changes in timbre that dancers seem to have may help them to adapt their movements to reflect the character of the music more successfully.

4.3.5. Beat perception

Beat perception is the perception of isochronous beats in music or rhythms, which may or may not contain isochronous onsets (London, 1995).

During beat perception, activity has been observed in neural networks associated with motor timing and auditory-motor integration (Araneda et al., 2017; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010; Chen et al., 2008; Grahn and Brett, 2007; Grahn and Rowe, 2013, 2009; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014). The basal ganglia appear to perform a crucial role (Matell and Meck, 2004; Merchant et al., 2015; Teki et al., 2011), and are part of corticostriatal motor circuits which may support motor functions, and motivational functions relevant to groove (Alexander et al., 1986; Haber, 2003; Matthews et al., 2020; Todd and Lee, 2015). The putamen and the supplementary motor area also appear to be involved in beat and metre perception (Araneda et al., 2017; Q. Li et al., 2019).

Neural activity has been observed in response to a strong beat in premotor, prefrontal, and parietal regions (Bengtsson et al., 2009; Danielsen et al., 2014; Grahn et al., 2011; Grahn and McAuley, 2009; Grahn and Rowe, 2009; Grahn and Schuit, 2012; McAuley et al., 2012; Schubotz et al., 2000; Schubotz and von Cramon, 2001). The caudate forms circuits with prefrontal and parietal regions (Jarbo and Verstynen, 2015) implicated in rhythmic expectation (Trost et al., 2014).

Several motor regions of the brain are engaged when listening to music. This engagement is related to the formation of rhythmic expectations. Movement preparation also occurs when listening to music, which may be used to test rhythmic expectations (Matthews et al., 2020).

4.4. Groove

The relevant studies in this area involved: (1) groove and musical training; and (2) listening to music or rhythms with different groove

ratings.

4.4.1. Groove and musical training

Musical training has no significant effect on the degree of groove perceived when listening to high-groove or low-groove music/rhythms, or noise (Stupacher et al., 2013; Witek et al., 2014), but does affect neural responses (Matthews et al., 2020; Stupacher et al., 2017, 2013).

When listening to high-groove rhythms, musicians had greater neural activity in motor-related areas of the brain than when listening to low-groove rhythms. This effect was not observed in non-musicians (Stupacher et al., 2017). Further findings include (Stupacher et al., 2013): (1) higher corticospinal excitability in musicians than non-musicians when listening to high-groove music; (2) no difference in corticospinal excitability between musicians and non-musicians when listening to low-groove music; (3) in non-musicians, lower corticospinal excitability when listening to high-groove music than low-groove music or noise, even though they rated the high-groove clips as subjectively higher groove; and (4) in non-musicians, higher pre-pulse electromyogram activity when listening to high-groove than low-groove music.

When listening to rhythms of differing degrees of groove, musicians showed greater activity than non-musicians in some regions of the brain associated with beat-based timing and beat perception, including the caudate, right prefrontal cortex, supplementary motor area, primary and premotor cortex and primary and secondary auditory regions (Matthews et al., 2020). Listening to high-groove rhythms resulted in greater activity in several regions of the brain than listening to low-groove rhythms (Matthews et al., 2020). Regions associated with reward included: (1) the nucleus accumbens; (2) the caudate; and (3) the medial orbitofrontal cortex. Regions associated with beat-based timing included: (1) the putamen; (2) the supplementary motor area; and (3) the prefrontal and parietal cortices.

These findings show that: (1) the nervous system is more engaged when listening to high-groove music than when listening to either low-groove music or noise (Stupacher et al., 2013); (2) a combination of motor and reward regions in the brain drive the sensation of groove when listening to high-groove rhythms (Matthews et al., 2020); (3) musical training affects neural responses to high-groove and low-groove rhythms (Stupacher et al., 2017); and (4) musical training leads to stronger auditory-motor associations and greater engagement of regions of the brain involved in beat perception (Matthews et al., 2020).

4.4.2. Listening to music or rhythms with different groove ratings

Neural entrainment (the synchronisation of large-scale neural oscillations to external periodic stimuli (Thaut, 2015)) often occurs when listening to musical rhythms (Nozaradan et al., 2015).

When listening to precisely timed computer-generated rhythms, no relationship has been found between groove ratings and neural entrainment. However, when listening to rhythms performed by humans with some timing variability, rhythms with higher groove ratings elicited greater neural entrainment (Cameron et al., 2019). Furthermore, neural tracking of the beat is greater when listening to rhythms conveyed by low-frequency tones than by high-frequency tones, but only for syncopated rhythms requiring endogenous metre generation. This difference was not attributable to differences in perceived loudness (Lenc et al., 2018). This may explain why the presence of low frequencies (bass) in music increases the degree of groove perceived (Stupacher et al., 2016).

After listening to a high-groove rhythm, participants who experienced more groove felt more “clear-headed,” and performed better on an executive function task. They also had more activity in the left dorso-lateral prefrontal cortex, which could be predicted by the amount of groove experienced (Fukuie et al., 2022).

4.5. Dance performance

There are very few studies in this area, all of which differ greatly. In

this section, we therefore summarise the findings of each study without further synthesis. The relevant studies in this area involved: (1) performing Tango steps while lying supine; (2) ‘inclusive’ dance in a wheelchair; (3) performing a modern jazz dance routine; (4) playing a dance video game; and (5) performing a limited range of dance movements.

4.5.1. Performing Tango steps lying supine

In a pioneering study by Brown and colleagues, dancers performed Tango steps on an inclined surface while lying supine in a positron emission tomography (PET) scanner (Brown et al., 2006). Findings included that: (1) the anterior cerebellar vermis was involved in the entrainment of dance steps to music, compared to self-paced movement without music; (2) the right putamen was involved in dancing to a regular metric rhythm, compared to an irregular rhythm; and (3) the medial superior parietal lobule was involved in spatial guidance of leg movements.

4.5.2. ‘Inclusive’ dance in a wheelchair

Participants with cerebral palsy performed inclusive dance choreography in their wheelchairs. Compared to baseline (the absence of activation (Gusnard and Raichle, 2001)), the power spectrum was greater in *theta*, *alpha*, and *beta* bands compared to baseline. The *beta* power spectrum was greater in dance, but not in music listening (Mendoza-Sánchez et al., 2022). This study is also included in Section 4.9.1.3, as it also relevant to dance therapy.

4.5.3. Performing a modern jazz routine

Having learnt a modern jazz dance routine, 11 dance-naïve participants underwent EEG scanning immediately before and after performing the dance in the presence and absence of music. After performance in the presence of music, there was, compared to pre-performance: (1) less neural activity in the parietal cortex in the *gamma* band; and (2) more functional connectivity between frontal and temporal regions in the *theta* band. After performance in the absence of music, there was, compared to pre-performance: (1) more neural activity in frontal and occipital regions in the *alpha* band; (2) higher frequency in frontal, central, temporal, and parietal regions in the *alpha* band; (3) more connectivity between the frontal and occipital lobes in the *alpha* band; (4) less connectivity between electrodes in parietal regions in the *alpha* band; and (5) less neural activity in occipital regions in the *gamma* band. Both in the presence and the absence of music, brain activity and functional connectivity increased after the performance compared to pre-performance (Wind et al., 2020). No significant differences were found between male and female participants in either condition (Wind et al., 2021).

There therefore appears to be recruitment of working memory, attentional processing, and heightened awareness when the routine was performed in both conditions. In the absence of music, there may be a state of “relaxed wakefulness” leading to deep concentration. There may also be reduced demand for visual processing, due to the automatic nature of the dance performance, and sensory input being transformed into motoric output (Wind et al., 2020).

Significant differences were found between performance and imagery of the dance, in male participants only. Power increased after performing the dance, and decreased after imagining the dance, in: (1) posterior regions (*alpha* band) in the presence of music; and (2) central regions (*beta* band) in the absence of music. Synchronisation increased after performing the dance, and decreased after imagining the dance, between central and right temporal regions (*alpha* and *beta* bands), in the presence of music. Synchronisation increased after performing the dance in the presence of music, and decreased after imagining the dance in the absence of music, between: (1) central and right temporal regions (*alpha* and *beta* bands); and (2) right temporal and posterior regions (*alpha* and *beta* bands) (Wind et al., 2021). This study is also included in Section 4.7.4, as it is also relevant to imagery.

4.5.4. Playing a dance video game

In three studies, fNIRS was used to measure brain activity when dancers took part in a dance video game based on “Dance Dance Revolution™” (Ono et al., 2014, 2015; Tachibana et al., 2011). It was found that: (1) activity in the superior parietal lobule and superior temporal gyrus increased as a function of task difficulty (Tachibana et al., 2011); (2) after training, the mean oxygenated haemoglobin waveform changed from activity above baseline to below baseline (Ono et al., 2015); and (3) frontotemporal oxyhaemoglobin dynamics predicted performance accuracy (Ono et al., 2014).

The authors conclude that, as the dancers became more adept, they were guided more by stimulus-led bottom-up cortical activity than by cognition-led top-down cortical activity.

4.5.5. Performing a limited range of dance movements

During performance of a range of prescribed “expressive” dance movements, EEG was used to measure neural activity in 4 participants (Cruz-Garza et al., 2014). Bilateral premotor and motor cortices and dorsal parietal lobule areas were involved in these movements. It is not clear from the article, however, whether the effect was bilateral in the premotor and motor cortices or only in the premotor cortex. These results provide proof of principle that, even with a small sample size, EEG can be used to infer the expressive components of movements.

In another study, participants performed different types of bimanual movement with an experimenter: (1) improvised movements based on contact improvisation dance; and (2) choreographed movements designed to have similar motor properties. When the movements were performed with the eyes open, no differences were found in alpha power. However, when the eyes were closed, there was greater alpha activity in a posterior region during choreographed movement, compared to improvised movement (Goldman et al., 2019).

4.6. Dance observation

The relevant studies in this area involved: (1) auditory processing during dance observation; (2) observing live or recorded dance; (3) perception of dance and dance-like movements; (4) aesthetic judgements; and (5) dance training and familiarity with observed dance.

4.6.1. Auditory processing

During dance observation in the presence of music, greater inter-subject correlation has been found in a left anterior region of the superior temporal gyrus (STG) involved in complex audio processing (Reason et al., 2016). In the absence of music, greater inter-subject correlation was found in the parietal and occipitotemporal cortices and a posterior region of the STG. This study is also included in Section 4.3.3, as it is also relevant to auditory processing.

4.6.2. Live and recorded dance

In promising findings for research on dance observation, it has been found that signal-to-noise ratio in EEG signals is not compromised when participants observe: (1) recorded dance compared to still images of dance; or (2) of dance compared to landscapes (Welke and Vessel, 2022).

Neural activity associated with dance observation appears to depend on whether the dance is observed live (in-person) or recorded, and on the editing style of dance recordings.

While watching a full-length dress rehearsal of the ballet *Sleeping Beauty*, corticospinal excitability in the 4 participants decreased over the entire performance, and within each of the three acts (Jola et al., 2011). This implies that, contrary to what one might expect, motor simulation did not always occur automatically during movement observation, but that the longer the spectators watched the ballet, the less they simulated the movements.

During observation of ballet, Indian Bharatanatyam dance, and an active acting control, corticospinal excitability was larger for observation of Indian Bharatanatyam dance than either ballet or the active

acting control, but only in live observation. Corticospinal excitability was significantly greater when participants watched Indian Bharatanatyam dance live compared to watching recorded dance (Jola and Grosbras, 2013).

During observation of unedited (one static shot) and edited (additional shots of close-ups of the upper body and face, or feet) recordings, similar activity was observed in the occipital and temporal cortices. Greater inter-subject correlation (ISC) occurred, in the STG only, during observation of the unedited recording. Greater ISC occurred in the postcentral gyrus, lingual gyrus, precentral gyrus, and medial frontal gyrus during observation of the edited recording (Herbec et al., 2015). This greater ISC may arise from large changes in visual input in the edited recordings, resulting in similar eye movements. Indeed, a “close medium shot” of the type used in the edited recording is associated with such attentional synchrony (Smith, 2013).

4.6.3. Perception of dance and dance-like movements

Motion smoothness, during observation of a humanoid robot performing dance, has been found to influence several cortical networks, especially in motion-sensitive and body-sensitive visual processing areas, with little variation between participants. These networks appear to be associated with visual perception in the early phases of cognitive processing of movement. Changes in neural activity related to motion smoothness were also found in networks including the parietofrontal network and the inferior temporal region, with a large degree of variation between the participants. Several cortical networks therefore appear to be involved in the processing of motion smoothness of dance-like movements (Miura et al., 2010).

Activity related to “the global silhouette change of a dancer” has been found in the right inferior temporal gyrus (Noble et al., 2014). At times of event boundaries in the dance, activity was observed in the right inferior temporal gyrus and bilaterally in the occipitotemporal cortex. This activity may be involved in the mechanisms employed to transform visual representations of human motion into more complex action representations (Noble et al., 2014).

The visual processing of dancers moving in synchrony appears to employ two distinct neural mechanisms: (1) for perception of a group of items moving synchronously; and (2) for perception of a group of moving items with “human quality” (Alp et al., 2017). Areas of the brain usually associated with voluntary motor control also appear to be involved in the perception of apparent dance-like movement, where the apparent movement was created by showing a sequence of three different static body poses (Orgs et al., 2016).

In a study on apparent motion, twelve images of static human poses were presented, arranged such that a movement was completed every half cycle, and the apparent motion would either be perceived as fluent, or non-fluent. Neural responses at the rate of the half cycle were strongest for fluent apparent motion. Neural responses at the rate of the full cycle, and of individual image presentation, were strongest for non-fluent apparent motion. Responses at the rates of individual images, half cycle, and full cycle, were each associated with different topographies of EEG activity, indicative of: (1) processing of individual images in early visual areas; (2) processing of postures in lateralised, higher-order visual areas; and (3) perception of dynamic movement in visual and fronto-central areas, with potential motor involvement (Cracco et al., 2022).

The same images were presented again with pictures of four human bodies rather than one. Responses at the rate of the half cycle were stronger for synchronous than asynchronous movement. This effect was stronger for fluent than non-fluent sequences, and stronger for upright than inverted bodies. Movement synchrony was a more dominant effect than fluency, and the two factors interacted. Inversion of the images did not interact with movement synchrony. Responses at the rate of the full cycle were weaker during observation of: (1) synchronous vs. asynchronous movement; (2) fluent vs. non-fluent movement; and (3) upright vs. inverted bodies. In these conditions, processing of the individual images may have been a more dominant mechanism than

processing of the full cycle. Responses at the rate of individual image presentation were: (1) not affected by synchrony when fluency changed; and (2) were stronger for asynchronous movements when bodies were presented upright vs. inverted (Cracco et al., 2022).

4.6.4. Aesthetics

Dance combines auditory and visual arts, and both participation and observation are important components of it. An audience's aesthetic judgments of dance performance are therefore of great importance, and have been a focus of several studies.

Appreciation of the aesthetic aspects of dance performance appears to rely on a large cortico-subcortical network. This includes regions of the brain involved in visual processing, as well as the coding of emotional reward, such as the amygdala (fear/disgust), and the nucleus accumbens, insula, and cingulate cortex (pleasure/reward) (Candidi and Aglioti, 2015; Reybrouck et al., 2018).

Subjective emotional judgement has been found to be negatively correlated with activity in the right posterior parietal cortex (Grosbras et al., 2012). Observing movements that are difficult to reproduce and aesthetically pleasing results in greatest activity in the occipitotemporal and parietal regions of the action observation network (Cross et al., 2011). Other regions involved include the extrastriate body area (Calvo-Merino et al., 2010), bilateral occipital cortex, and right premotor cortex (Calvo-Merino et al., 2008).

Moreover, the occipital and frontal lobes appear to be involved in dance aesthetic preference of Chinese dance posture, with more activity in these regions during observation of preferred postures compared to non-preferred postures, and the right hemisphere appears to be more involved than the left in the visual aesthetic processing of Chinese dance posture (Li et al., 2022).

Familiarity of dance observed can also affect neural activity related to aesthetic judgements. When watching more familiar dance sequences, which participants found more enjoyable, neural activity associated with the aesthetic response shifted from subcortical regions, associated with dopaminergic reward processing, to posterior temporal regions, involved in processing biological motion, multisensory integration, and emotion (Kirsch et al., 2015).

There could therefore be a direct link between activity in the posterior parietal cortex activity and emotional reactions to dance (Grosbras et al., 2012); and visual and sensorimotor regions of the brain may have a role in automatic aesthetic response to dance (Calvo-Merino et al., 2008). These findings may go some way to explaining why dance is culturally universal.

4.6.5. Inter-subject correlation during dance observation

Significant inter-subject correlation has been found during dance observation. In one study, high levels of synchronised activity were found between all participants, in several regions of the brain, including frontal and somatosensory regions and the primary visual and auditory cortices (Vicary et al., 2013).

Eight subnetworks associated with dance observation have also been identified through inter-subject correlation (Pollick et al., 2018). Each subnetwork was related to different aspects of dance observation, with putative regions (and functions): (1) the parahippocampal gyrus, and medial regions of the posterior cingulate and retrosplenial cortices (visuospatial and scene processing); (2) several nodes in the right superior temporal gyrus and bilateral auditory cortex (auditory feature and complex sound processing); (3) the right and left inferior temporal gyrus with strong bilateral connections between them, and the fusiform gyrus (body motion and form processing); (4) three regions in Brodmann areas 7 and 40 in the parietal cortex (somatosensory associated processing); (5) four regions in Brodmann areas 17, 18, and 19 in the occipital cortex (visual feature processing); (6) the left and right precuneus (hub processing and default mode); (7) several regions in the parietal and frontal cortices, almost exclusively in the left hemisphere (attention and frontoparietal control); and (8) bilateral regions in the frontal cortex in the

premotor cortex and supplementary motor area, and a region of the primary somatosensory cortex in the postcentral gyrus (motor cognition).

The activity in subnetworks 1, 2, 3, 4, 5, and 8 was attributed to the processing of motor and sensory aspects of the dance performance. The activity in subnetworks 6 and 7 did not appear to relate to either the physical properties of the dance or action understanding, but rather to complex emotional or cognitive processing.

4.6.6. Dance training and familiarity with observed dance

Neural activity associated with dance observation can change as a result of dance training. Changes have been found to occur in: (1) corticospinal excitability; (2) brain wave activity; and (3) neural activity in specific brain regions and networks. Furthermore, when people observe a performance of specific dance choreography, it has been shown that neural activity is affected by whether the observed choreography has been learnt. This change varies as a function of the age of the observer.

4.6.6.1. Corticospinal excitability. Corticospinal excitability has been found to correlate with experience of dance, and can be increased by visual experience alone. It has been suggested that, when spectators observe movements for which they have visual experience, they covertly simulate them, and that motor resonance during dance observation can be heightened by empathic abilities (Jola et al., 2012).

4.6.6.2. Brain wave activity. In dancers, musicians, and a control group who did not have any significant dance or musical training (controls), there was less synchrony across different electrodes in the *alpha* band when they observed rapid dance movements than when they observed choreographed, almost motionless, action (Poikonen et al., 2018b).

When non-dancers observed ordinary, small, movements in silence, synchrony in the *theta* and *gamma* bands was greater than when they observed a still figure, and when they observed "vast energetic" dance movements to music, synchrony in the *alpha* and *beta* bands decreased, compared to listening to music with no visual stimulus (Poikonen et al., 2018a).

During dance observation, in dancers the power of both the *alpha* and *beta* bands was significantly lower than during observation of a visual baseline. This was not found when dancers observed everyday movements, nor in non-dancers (Orgs et al., 2008; Poikonen et al., 2018b). During observation of multimodal, naturalistic dance, dancers had greater *theta* synchrony in frontocentral regions than musicians or controls (Poikonen et al., 2018b).

When ballet dancers observed a familiar ballet sequence, they showed higher individual *alpha* peak frequency, greater *alpha* desynchronisation, and greater task-related *beta* power than dancers of other genres, or non-dancers. Dance observation was also associated with greater neural plasticity than observation of everyday actions, with possible translational benefits to attentional and sensorimotor networks (Di Nota et al., 2017).

During observation of dance movements, choreographed such that the dancers would find them familiar but would not have direct motor experience of them, dancers had a larger N400 effect and smaller late positivity amplitude compared to rest. The regions involved were the frontoparietal network, the limbic system, and regions of the brain associated with processing the body and face. This effect was not observed in non-dancers (Orlandi et al., 2017).

When dancers and non-dancers watched videos depicting ballet steps: (1) in both dancers and non-dancers there was a posterior N2 component, which was larger in dancers than in controls; (2) in dancers, there was engagement of bilateral inferior and middle temporal regions; and (3) dancers showed early P2 and larger P300 responses in both hemispheres (Orlandi and Proverbio, 2019). When participants were shown "effortful" or "effortless" ballet steps: (1) both groups had a greater late positivity effect in posterior regions when they observed

“effortful” compared to “effortless” steps; (2) this greater late positivity effect showed greater engagement of frontoparietal regions in dancers than in non-dancers, and greater engagement of occipitotemporal visual regions in controls; and (3) a larger P300 effect was observed in the frontal regions of dancers when they observed “effortful” compared to “effortless” steps, which was not observed in non-dancers (Orlandi et al., 2020b).

Comparing ballet dancers with sign-language users observing either dance or sign language sequences, both groups showed stronger synchronisation, in frontal regions, to the stimuli with which they had expertise. In occipital regions, no difference was found. Stimulus tracking therefore does not appear to depend on language-specific prediction mechanisms, but instead on domain-general expertise (Brookshire et al., 2021).

Desynchronisation of *mu* brain wave activity can be used as a correlate for action simulation. Larger amounts of weekly practice of contact improvisation (a dance style “in which small groups use physical contact and transferred weight to fluently and jointly move together without choreography” (Goldman et al., 2019)) predicted greater *mu* rhythm desynchronisation during action observation of dance or non-dance actions. More weekly practice of choreographed dance also showed a trend towards greater *mu* rhythm desynchronisation, but with a smaller effect size. This maximal desynchronisation was found in regions posterior to the motor cortex in both groups. Practising improvisation, as opposed to contact improvisation, did not predict any differences in *mu* rhythm desynchronisation. The authors concluded that the amount of time spent practicing contact improvisation, as opposed to other dance styles, predicted greater motor simulation in the brain during action observation (Goldman et al., 2019).

Machine learning was used to classify participants as dancers or non-dancers based on brain wave activity. The most useful component for this classification, during observation of movements specific to Tango, was found to be connectivity in the *theta* band (73% accurate classification). During rest, the most useful component for classification was found to be *mu* connectivity (100% accurate classification) (Amoruso et al., 2022).

These findings show that: (1) both dance training and musical training affect the brain wave activity of people who observe dance; (2) dancers appear to have faster stimulus processing and subsequent recognition; (3) there appears to be increased sensitivity of the occipitotemporal cortex in dancers for the encoding of the kinematics of bodily motion; (4) cortical communication is increased in dancers when they watch dance; and (5) this increase is related to the observation of dance and to complex internal cognitive and emotional processes.

4.6.6.3. Activity in specific brain regions and networks. When movement is observed, the action observation network (AON) is preferentially engaged if the movement is more familiar (Diersch et al., 2013). In dance observation, activity in the AON varies depending on the amount of dance experience (Amoruso et al., 2014; Burzynska et al., 2017a; Calvo-Merino et al., 2005; Cross et al., 2006, 2009b; Gardner et al., 2015; Jang and Pollick, 2011; Jola et al., 2013; Orgs et al., 2008; Pilgramm et al., 2010), and type of familiarity, e.g. physical or solely visual (Calvo-Merino et al., 2006, 2005; Cross et al., 2009a; Jang and Pollick, 2011; Jola et al., 2012). Variation has been found when comparing: (1) dancers; (2) non-dancers with little experience of viewing dance; and (3) non-dancers with a great deal of experience of viewing dance (Jang and Pollick, 2011), and when comparing dancers observing moves they perform versus moves they only observe (Calvo-Merino et al., 2006, 2005; Cross et al., 2009a; Jola et al., 2012). Functional connectivity of the AON also appears to be altered in dancers (Burzynska et al., 2017a).

As familiarity with dance observed increases, activity has been found to increase in the left middle temporal gyrus, inferior parietal lobule, and inferior frontal gyrus. During observation of videos rated as being more familiar, bidirectional attenuation of effective connectivity was

found between parietal and temporal nodes of the AON. These results support a predictive coding model of the AON, with preferential engagement of the AON during observation of familiar movements (Gardner et al., 2015).

During observation of dance, greater activity has been found in the brains of dancers than in the brains of non-dancers in: (1) the premotor cortex (PMC) (Calvo-Merino et al., 2006, 2005; Cross et al., 2009b, 2006; Pilgramm et al., 2010); (2) the inferior parietal lobule (Calvo-Merino et al., 2005; Cross et al., 2006); (3) the middle and posterior superior temporal gyrus (Jola et al., 2013); (4) the right primary somatosensory cortex; the right temporoparietal cortex; and (4) the left retrosplenial cortex (Jang and Pollick, 2011). Jang and Pollick (2011), however, found less activity in the PMC in dancers than in non-dancers.

Dancers and experienced dance viewers had greater activity than non-dancers during dance observation, in the right temporoparietal and left retrosplenial cortices. Experienced dance viewers had less activity in the right primary somatosensory cortex than dancers, but more activity bilaterally in the PMC. In the primary somatosensory cortex, this may be caused by overlearning, or may be a result of neurological or task constraints. Dance training appears to result in a reorganisation of the network of brain regions used during dance observation (Jang and Pollick, 2011).

When dancers observed movements from their own repertoire, there was more activity in the PMC (Calvo-Merino et al., 2005), especially the right ventral PMC (Cross et al., 2009a), than when they observed movements they did not perform but with which they had visual familiarity. Premotor, parietal, and cerebellar activity were all greater when the dancers observed movements of the same style usually performed by people of their own sex (Calvo-Merino et al., 2006). When expert dancers observed familiar dance movements (Calvo-Merino et al., 2005), they showed more activity in regions of the brain generally associated with the human mirror system than when they observed unfamiliar dance movements. Motor experience of dance movements has also been found to modulate activity in the inferior parietal lobule and ventral PMC in both dancers and non-dancers, supporting the theory that motor vocabularies are stored within these regions of the brain (Cross et al., 2006).

Anticipatory activity in a fronto-parietal-occipital network appears to enable expert dancers to anticipate and discriminate earlier than non-dancers when observing dance (Amoruso et al., 2014). Dancers appear to have a greater degree of motor simulation than non-dancers when they observe dance than non-dancers, with stronger de-synchronisation of the motor cortex (Bläsing et al., 2012).

4.6.6.4. Age, and observing learnt choreographies. Age and experience have both been shown to affect neural activity associated with dance observation, and the two factors interact.

During observation of learnt dance, young adults have been found to have more distinct patterns of activity than adolescents in visual cortices (Sumanapala et al., 2018). During observation of familiar figure skating movements, older adults have been found to have greater recruitment of visual regions, the hippocampus, and the caudate, than younger adults (Diersch et al., 2013).

Neural activity during observation of a performance of a choreographed dance is affected by the ways in which the choreography has been learnt. In Kirsch et al. (2018); Kirsch and Cross (2015); Sumanapala et al. (2018), ‘auditory training’ involved listening to the soundtrack of a dance music video, ‘visual training’ involved watching the dance sequence with concurrent auditory input, and ‘physical training’ involved physically practising the dance sequence with concurrent auditory and visual input.

During observation of learnt dance movements, activity in the AON has been found to differ if the movements were learnt through visual training or physical training (Sumanapala et al., 2018). Furthermore: (1) the more types of learning used to learn an action, the greater the

activity in the AON when observing it; and (2) the better the participant was at performing the action, the stronger the neural response, especially in the PMC (Kirsch and Cross, 2015).

Different patterns of neural activity have been observed in younger adults (18–23 years old) and older adults (55–69 years old) when they observed a dance sequence after learning it, compared to before learning it, through either visual or physical training (Kirsch et al., 2018).

During observation of the dance sequence after learning via visual training, younger adults had no increased neural activity, and had decreased activity in several regions of the right hemisphere, including the fusiform gyrus, postcentral gyrus, and middle temporal gyrus. Older adults had increased neural activity in the right precuneus, and no decreased activity.

During observation of the dance sequence after learning via physical training, younger adults had no increased neural activity, and had decreased neural activity in: (1) the amygdala; (2) the middle occipital gyrus; and (3) regions associated with sensorimotor processing, including the left paracentral lobule, postcentral gyrus, right precentral gyrus, and inferior temporal gyrus. Older adults had increased activity in the right precuneus, as after visual training, as well as decreased activity in the right superior lobule, right inferior parietal lobule, and right thalamus.

Physical training resulted in greater group differences between younger and older adults in the change in neural activity during observation before and after training. The only significant group difference was found in the left inferior parietal lobule, in which younger adults had less activity than older adults.

Visual and motor regions of the brain therefore appear to contain experience-specific representations of learnt motor actions, with a similar pattern of activity in younger and older adults. Young adults may also have processing efficiency gains which older adults lack, and visual training effects are different on a neural level in the two groups. This difference may be a way of exploiting different mechanisms, compensating for age-related decline in attentional and visual processing.

4.7. Imagery relevant to dance

The relevant studies in this area involved: (1) dance training and experience; (2) familiarity with the choreography; (3) imagery with eyes open or eyes closed; (4) imagery in the presence or absence of music; and (5) modelling an individual's neural activity during dance imagery.

Some of the studies reviewed in this section deal with non-dance imagery, such as walking, but are nonetheless included because they pertain both to movement imagery and dance; e.g. when participants imagined themselves walking before and after a course of dance training (Sacco et al., 2006).

4.7.1. Dance training and experience

Activity occurs in the AON in both dancers and non-dancers when they imagine themselves dancing (Burzynska et al., 2017a; Hökelmann and Blaser, 2009).

When an expert Salpuri dancer (a traditional Korean shamanic dance, originally performed to appease evil spirits) imagined her dance performance there was, compared to the resting state: (1) more neural activity in the *alpha* band; (2) more neural activity in the *theta* band in the frontal midline; (3) more global field power; and (4) less generalised frequency and spatial complexity (Park et al., 2002). When an expert break-dancer imagined dancing to familiar music, there was less activity in Heschl's gyrus and more activity in the supplementary motor area, than when he imagined dancing to unfamiliar music (Olshansky et al., 2015). As these studies only present data on one subject, it is unclear how well the results would generalise. However, several larger-scale studies have also been undertaken.

After a one-week course in which healthy participants learnt to dance Tango, when participants imagined themselves walking, activity increased in premotor areas and the supplementary motor area, and

activity decreased in the right posterior region of the brain (Sacco et al., 2006). It therefore appears that, after training, the role of visual imagery decreased in favour of kinaesthetic imagery.

When professional dancers imagined themselves performing improvised dance, they had more *alpha* activity and exhibited greater right-hemispheric *alpha* synchronisation than novice dancers. Neither of these effects was observed when they imagined themselves dancing a waltz (Fink et al., 2009).

During imagery of non-dance movements, individual *alpha* peak frequency of ballet dancers was faster than that of dancers of other genres, and non-dancers. All groups showed: (1) significant desynchronisation relative to baseline when they imagined themselves performing non-dance movements; and (2) more desynchronisation when they imagined themselves performing dance movements than when they imagined themselves performing non-dance movements. The authors concluded that: (1) complex dance imagery recruits greater cognitive resources than the imagery of everyday, non-dance, movements; (2) dance imagery may be a more important factor than non-dance imagery in driving neural plasticity in action networks; and (3) the results corroborate and extend the evidence for the plasticity of *alpha* and *beta* activity during imagery, dependent on experience (Di Nota et al., 2017).

During imagery of "effortful" and "effortless" ballet steps, maximum peak amplitude in neural activity 400–550 ms after imagery was greater in anterior regions of the brain in dancers than in non-dancers. The difference had a centroparietal distribution in dancers and a frontal distribution in non-dancers. Non-dancers had more engagement of prefrontal regions than dancers, and dancers had more engagement of occipitotemporal and bilateral sensorimotor areas than non-dancers. In non-dancers, the maximum peak amplitude was more negative in response to effortful than effortless movements (Orlandi et al., 2020a). It would therefore appear that: (1) non-dancers experienced more cognitive demands than dancers; and (2) the imagery of complex actions recruited visuomotor simulation processes in dancers, but not in non-dancers.

During observation and simulation of another dancer's movements, regions of the brain involved were found to include: (1) the inferior parietal lobule; (2) cingulate and supplementary motor areas; (3) the superior temporal sulcus; and (4) the premotor cortex. In the inferior parietal lobule and ventral premotor regions, this activity was modulated by dancers' ratings of their ability to perform the observed movements, and by their motor experience (Cross et al., 2006). This result supports the theory that motor vocabularies are stored within these two regions of the brain.

During imagery of performing either moving dance sequences or static dance postures, dancers had more activity in the left retrosplenial cortex, and less activity bilaterally in the premotor cortex and the right orbitofrontal cortex, than non-dancers. Dancers had less activity in the right temporal pole than experienced dance viewers. Dancers and experienced dance viewers had more activity than non-dancers in the left retrosplenial cortex. In the right orbitofrontal cortex, experienced dance viewers had more activity than non-dancers, who had more activity than dancers. Experienced dance viewers had less activity in the right temporal pole than dancers or non-dancers. Cognitive processes therefore appear to enhance the perception of dance actions in experienced dance viewers, but not in non-dancers (Jang and Pollick, 2011).

4.7.2. Familiarity with the choreography

Imagining specific dance choreography appears to be associated with distinct patterns of neural activity (Bar and DeSouza, 2013, 2016; DeSouza and Bar, 2012; Di Nota et al., 2016). These studies all used small sample sizes: (Bar and DeSouza, 2013), $n = 11$; (Bar and DeSouza, 2016; DeSouza and Bar, 2012), $n = 10$.

Professional ballet dancers learnt specific dance choreography and underwent fMRI scanning while imagining the movements they were learning, with musical accompaniment. When they imagined the movements, activity in a network of brain regions, including the

bilateral auditory cortex and supplementary motor area, initially increased (7 weeks from the start) then decreased (34 weeks from the start) (Bar and DeSouza, 2013, 2016; DeSouza and Bar, 2012). This reduction was not observed in the basal ganglia (caudate nucleus), which may therefore have been involved in learning the choreography (Bar and DeSouza, 2013).

Changes in activity also occurred in sub-regions of the lateral occipitotemporal cortex, specifically: (1) the lateral occipital cortex; (2) the extrastriate body area; and (3) the MT+ motion area (this area overlaps substantially with the extrastriate body area). All three sub-regions were more activated during dance observation than during imagery, and all were activated bilaterally during the viewing task at the end of the (34 weeks from the start). Significant increases in activity over the entire study were observed only in the left lateral occipital cortex, and only during imagery of the unlearned choreography (Di Nota et al., 2016).

Neural activity initially increased as the choreography was learnt, then decreased, following the typical inverted-U shape expected when learning takes place. It may therefore be possible to determine the timing of learning sensorimotor tasks using neuroimaging (Bar and DeSouza, 2013).

4.7.3. Imagery with eyes open or closed

During dance imagery with eyes open or eyes closed, significant differences have been found in *alpha* power in different brain regions. During imagery with eyes open, *alpha* power was significantly higher in all areas except the left temporal regions. With eyes closed, *alpha* power was lower relative to baseline in the occipital and right parietal regions of the brain. Moreover, with eyes open, participants were less able to imagine the dance than when their eyes were closed (Di Nota et al., 2014).

4.7.4. Imagery in the presence or absence of music

Having learnt a modern jazz dance routine, 11 dance-naïve participants underwent EEG scanning immediately before and after imagining themselves performing the dance in the presence and absence of music (Wind et al., 2020).

After performance in the presence of music, there was, compared to pre-performance: (1) more neural activity in temporal and parietal regions in the *theta* band; and (2) less connectivity between central and parietal regions in the *beta* band. In addition to the conscious perception and processing of music, visualisation of body movements in space may therefore also have taken place during imagery of the performance.

After performance in the absence of music, there was, compared to pre-performance: (1) stronger neural activity in the *alpha*, *beta*, *gamma*, and *theta* bands, predominantly in frontal, central, and parietal regions; (2) greater connectivity between frontal and temporal regions in the *alpha* band; (3) less connectivity between frontopolar-central, frontal-frontal, and frontal-central regions in the *beta* band; and (4) greater connectivity between frontopolar and parietal regions in the *gamma* band.

After imagery in the absence of music, signal power decreased in male participants, and increased in female participants, in: (1) posterior regions (*theta* band); and (2) posterior and left temporal regions (*gamma* band). Furthermore, synchronisation decreased in male participants, and increased in female participants, between: (1) central and left temporal regions (*theta* band); (2) left temporal and posterior regions (*theta* band); (3) left temporal and posterior regions (*alpha* band); (4) frontal and right temporal regions (*beta* band); and (5) left and right temporal regions (*beta* band). Synchronisation decreased between left and right temporal regions (*alpha* band) in both male and female participants (Wind et al., 2021).

Significant differences were found between performance and imagery of the dance, in male participants only. Power increased after performing the dance, and decreased after imagining the dance, in: (1) posterior regions (*alpha* band) in the presence of music; and (2) central regions (*beta* band) in the absence of music. Synchronisation increased

after performing the dance, and decreased after imagining the dance, between central and right temporal regions (*alpha* and *beta* bands), in the presence of music. Synchronisation increased after performing the dance in the presence of music, and decreased after imagining the dance in the absence of music, between: (1) central and right temporal regions (*alpha* and *beta* bands); and (2) right temporal and posterior regions (*alpha* and *beta* bands) (Wind et al., 2021). This study is also included in Section 4.5.3, as it is also relevant to dance performance.

4.7.5. Modelling an individual's neural activity during dance imagery

Individual models were constructed based on participants' descriptions, and self-ratings of various characteristics, of imagery of 20 common scenarios, including dance. Using an individual's model to predict neural activity during imagery gave better results than using another person's model, highlighting the importance of conducting research on both individuals and groups (Anderson et al., 2020).

4.8. Dance training

Both short- and long-term dance training lead to significant changes in brain structure and neural activity, including, in particular, neural activity during dance performance, imagery, and dance observation. We have already reviewed research on the effect of dance training on such neural activity in each of the relevant sections. In this section, we review the remaining literature. The relevant studies in this area involved: (1) neural activity; (2) changes in brain structure; and (3) corticomuscular coherence.

4.8.1. Neural activity

The relevant studies in this area involved: (1) disrupting neural activity; (2) resting state neural activity; (3) *beta* power; and (4) neural activity associated with leading/following/mutual adaptation.

4.8.1.1. Disrupting neural activity. When participants learnt folk dances using augmented reality, they performed better and had more similar results within the group when tDCS was applied before each session of learning. The anode was placed over midline central brain regions to facilitate primary motor cortex function. The cathode was placed on the forehead (Kico and Liarokapis, 2022).

4.8.1.2. Resting state neural activity. (Barnstaple and DeSouza, 2019) Dancers have also been found to have significantly higher resting state amplitudes than fast ball sports athletes in the *alpha* and *beta* bands, and than controls in the *alpha* band (Ermutlu et al., 2015). In a small-scale study ($n = 4$), participation in a one-hour dance class modulated resting state *alpha* activity in the frontal cortex (Barnstaple and DeSouza, 2019).

Expert ballroom dancers have been found to have lower amplitude of low-frequency fluctuation than novice dancers in the left lingual gyrus. Expert dancers had greater amplitude of low-frequency fluctuation than novice dancers in the: (1) left middle temporal gyrus; (2) bilateral pre-central gyrus; (3) bilateral inferior frontal gyrus; (4) left postcentral gyrus; (5) left inferior temporal gyrus; (6) right middle occipital gyrus; (7) right superior temporal gyrus; and (8) left middle frontal gyrus. Expert dancers also had more neural activity in sensorimotor regions than novice dancers, and functional alterations in frontal-temporal and frontal-parietal connectivity. These changes may well reflect the acquisition of skills needed for dancing such as attentional control, action perception, and movement adjustment (Lu et al., 2018).

Professional Chinese classical dancers have also been found to have increased amplitude of low-frequency fluctuation compared to controls in the: (1) left superior occipital gyrus; (2) right cuneus; and (3) left calcarine fissure and surrounding cortex (calcarine). The professional dancers also had greater fractional amplitude of low-frequency fluctuation and regional homogeneity in the right calcarine than controls. This

indicates increased spontaneous activity in these regions of the brain (Wen et al., 2022).

4.8.1.3. Beta power. Dancers have been found to have greater power in the *beta* band during a musical recall task, and preferred faster musical tempi than non-dancers. Dancers were also more extraverted than non-dancers, but exhibited a higher melancholic score, which is associated with introversion. The authors therefore concluded that dancers need more stimulation, and that they obtain this from faster, more energetic, music (Jin et al., 2021).

4.8.1.4. Neural activity associated with leading/following/mutual adaptation. Many styles of dance, such as Tango, Waltz, and Salsa, are partner dances. One dancer “leads,” directing both people’s movements, and the other “follows,” responding to the leader’s cues. The acquisition of the skills needed for each role is therefore an important element of dance research. However, the inclusion of two interacting people poses even greater challenges to research than encountered in single-person studies.

A few researchers have nevertheless devised innovative experiments which enable some neuroscientific investigation of partner dancing. Leading/following/mutual adaptation paradigms were investigated using limited hand and wrist movements similar to those performed when dancing (Chauvigné et al., 2018, 2017; Chauvigné and Brown, 2018). The participant, lying supine in an fMRI scanner, engaged in bimanual contact with an experimenter outside the scanner. The experimenter was experienced in both leading and following in partner dancing. The participant and experimenter performed movements of the wrist and metacarpophalangeal joints. The participants always had to move their hands actively.

This research is also relevant to the field of joint action. For example, van der Wel and colleagues showed that increasing force assists coordination by amplifying haptic information (van der Wel et al., 2011). Increased force may be helpful for the follower in the context of improvised partner dancing, although other factors, such as tension in the arms, also contribute. For a general introduction to joint haptic interaction, see e.g. van der Wel et al. (2021).

Leading involved regions of the brain associated with motor planning, action monitoring, sequencing, navigation, and error correction. Following involved regions of the brain associated with proprioception, somatosensation, motion tracking, outcome monitoring, and social cognition. Mutual adaptation was associated with more activity in regions of the brain associated with social reward and mentalising than when either leading or following (Chauvigné et al., 2018).

Neural activity during leading and following was found to be enhanced by prior expertise in the respective roles. Moreover, task-specific regions of the brain tended to be positively correlated with the level of expertise in the role (Chauvigné and Brown, 2018).

More activity occurred in motion area MT+/V5 when dancers followed than when they led, although this region is usually thought to be responsible for processing visual motion. It may be that this region responds to force-cue based motion during joint haptic interaction, especially when a follower is responding to haptic cues from a leader (Chauvigné et al., 2017).

It therefore appears that: (1) leading and following are associated with activity in different regions of the brain; (2) training in one role can selectively enhance role-related brain activity; and (3) regions of the brain associated with motor planning and working memory are important in motor improvisation. There may therefore be advantages to learning both leading and following on a cerebral level, especially in a therapeutic context.

4.8.2. Changes in brain structure following dance training

Brain structure is affected by dance training. Whole brain volume appears to be unaffected (Burzynska et al., 2017a; Niemann et al., 2016;

Wen et al., 2022), as does total volume of: (1) the whole brain; (2) grey matter; (3) white matter; (4) and cerebrospinal fluid (Wen et al., 2022). However, associations have been found between dance training and: (1) white matter in specific areas; (2) grey matter in specific areas; (3) diffusivity and coherence; (4) cortical thickness; and (5) functional connectivity.

4.8.2.1. White matter. Dancers have been found to have lower white matter volume than non-dancers in regions of the brain including: (1) both corticospinal tracts; (2) both internal capsules; (3) the corpus callosum; and (4) the left anterior cingulum. Negative correlation has been observed between the age at which dance training started and white matter volume in the internal capsule. Positive correlation has been observed between the age at which dance training started and white matter volume in: (1) the left precentral gyrus; and (2) the corpus callosum (Hänggi et al., 2010).

Fractional anisotropy in white matter underlying the left and right premotor cortex has been found to be lower in dancers than in an active control group (Nigmatullina et al., 2015).

4.8.2.2. Grey matter. Negative correlation has been found between the age at which dance training started and grey matter volume, in the right premotor cortex (Hänggi et al., 2010). Comparing dancers and slackliners (people who walk “along a rope or a narrow piece of strong fabric that is stretched above the ground between two points, less tightly than a tightrope” (Cambridge Dictionary, 2021)), dancers had: (1) lower grey matter volumes in the anterior hippocampal formation and parts of the parieto-insular vestibular cortex; and (2) higher grey matter volumes in the posterior hippocampal formation, as well as bilaterally in the lingual and fusiform gyri. In both dancers and slackliners, there was: (1) negative correlation between the amount of time spent training and grey matter volume in the right anterior hippocampal formation; and (2) positive correlation between the amount of time spent training and grey matter volume in the right posterior hippocampal formation. The lower volume in the right anterior hippocampal formation may be a result of long-term suppression of destabilising vestibular input. The higher volume in the posterior hippocampal formation may be a result of greater use of visual cues for balance. It therefore appears that, in the hippocampus, there is spatial separation of visual and vestibular processes (Hüfner et al., 2011). However, in a study on older active women, no difference was found in hippocampal volume in non-professional senior dancers compared to a non-sedentary control group (Niemann et al., 2016).

Dancers have been found to have lower grey matter volume than non-dancers in: (1) the left premotor cortex; (2) the supplementary motor area; (3) the putamen; and (4) the superior frontal gyrus (Burzynska et al., 2017a). Dancers have been found to have higher grey matter volume than non-dancers in: (1) the right hippocampus; (2) the parahippocampal gyrus; (3) the insula; and (4) the cingulate motor cortex. Variations in grey matter volume also occurred bilaterally within the cerebellum (Dordevic et al., 2018), and dancers have been found to have more grey matter volume than handball players in regions of the brain involved in the control of the feet (Meier et al., 2016).

Experienced ballroom dancers have been found to have higher empathic concern scores than controls. These scores were positively correlated with the volume of grey matter in the subgenual anterior cingulate cortex (Wu et al., 2023).

Anisotropy has been found to be affected by dance training, with dancers having lower anisotropy in the corticospinal tract than non-dancers (Burzynska et al., 2017a) and lower fractional anisotropy than handball players in the fibres connecting regions of the brain involved in the control of foot and hand areas (Meier et al., 2016).

4.8.2.3. Diffusivity and coherence. Dancers have been found to have more diffusivity and less coherence in sensorimotor pathways than

musicians (Giacosa et al., 2016). Dancers have also been found to have greater radial diffusivity than musicians, especially in descending motor pathways. This was found in all regions of the brain, but most notably in the right hemisphere, and was negatively correlated with the age at which dance training started (Giacosa et al., 2019).

4.8.2.4. Cortical thickness. Dancers have been found to have a trend-level significantly thinner cortex than non-dancers (Porat et al., 2016), but in superior temporal areas both dancers and musicians have both been found to have greater cortical thickness than controls (Karpati et al., 2017).

Dancers have also been found to have lower correlation between cortical thickness in the left dorsolateral prefrontal cortex and mean cortical thickness across the whole brain. This was associated with better performance on a dance video game task, implying that the dorsolateral prefrontal cortex was structurally decoupled in dancers and might have been more affected by training than other regions of the brain (Karpati et al., 2018).

4.8.2.5. Functional connectivity. Altered functional connectivity has been found in dancers in several studies (Burzynska et al., 2017a; G. Li et al., 2019; Li et al., 2015; Wu et al., 2023).

Compared to non-dancers, expert ballroom dancers appear to have: (1) altered functional connectivity between the inferior frontal gyrus and temporal/parietal regions (Lu et al., 2018); greater functional connectivity between the thalamus and the frontal pole, positively correlated with dance skill (Burzynska et al., 2017a); and (3) greater connectivity between the subgenual anterior cingulate cortex and the occipital gyrus, positively correlated with empathic concern and number of years dancing with one dance partner (Wu et al., 2023).

Dancers had enhanced connections of the action observation network (AON) to regions involved in: (1) sensory interpretation/body image (inferior parietal lobule); (2) and somatosensory association (supramarginal gyrus). Dancers had attenuated connections of the AON to regions of the brain involved in: (1) face and body recognition (fusiform gyrus); (2) visual perception of the human body and parts of the body (lateral occipitotemporal cortex/extrastriate body area); and (3) visual perception (occipital pole) (Burzynska et al., 2017a).

Dancers have been found to have significantly greater functional connectivity than non-dancers in: (1) the precentral gyri; (2) postcentral gyri; and (3) bilaterally in the putamen; and between: (1) the middle cingulate cortex and the bilateral putamen; and (2) the precentral and the postcentral gyri. Dancers may therefore have better functional integration in the cortico-basal ganglia loops governing motor control and integration (Li et al., 2015).

Function of the insular subnetwork, associated with empathic ability, of both dancers and musicians has been found to be better than the mean of a large random sample. Enhanced functions included higher-level cognitive control (dorsal anterior insula subnetwork), affective evaluation (ventral anterior insula subnetwork), and interoceptive sensorimotor representation (posterior insula subnetwork) (G. Li et al., 2019).

4.8.2.6. Conclusions regarding changes in brain structure in dancers. The changes observed in diffusivity coherence in sensorimotor pathways (Karpati et al., 2017) may arise from greater efficiency in the crossing of fibre pathways. The changes observed in functional connectivity (Burzynska et al., 2017a; G. Li et al., 2019; Li et al., 2015) may reflect: (1) the improved empathic ability of dancers; (2) improved sensorimotor function; and (3) facilitation of the integration of internal and external information.

Long-term dance training appears to be associated with changes in brain structure, notably cortical thickness and plasticity of grey matter and white matter, especially in regions of the brain associated with motor and auditory functions. This is important as neuroplasticity plays a major role in recovery from brain injury, may reverse adverse effects

associated with neurodegenerative diseases (Nahum et al., 2013), and cognitive decline due to old age occurs in conjunction with grey matter atrophy (Ramanoël et al., 2018). These results are highly relevant to the use of dance in a therapeutic context, discussed in Section 4.9.

4.8.3. Corticomuscular coherence

In ballet dancers and weightlifters, less corticomuscular coherence was found than in controls, especially in the muscles of the lower limbs. In controls, there was significantly more coherence in muscles further from the centre of the body than in muscles closer to the centre of the body. Oscillatory coupling between the sensorimotor cortex and motor neurons therefore appears to be affected by long-term training (Ushiyama et al., 2010). Given the marked differences between weightlifting and dancing, and the similar results found for both groups, the difference in coherence appears to relate generally to regular, strenuous, physical activity.

4.9. Dance therapy

Diverse health conditions can be positively affected by dance therapy. These include broad groups of motor disorders, brain injury, neurodegeneration, (Barnstaple and DeSouza, 2019; Batson et al., 2014; Brown et al., 2006; Burzynska et al., 2017b; Kullberg-Turtiainen et al., 2019; Leisman and Aviv, 2020; López-Ortiz et al., 2019; Müller et al., 2017; Patterson et al., 2018; Shanahan et al., 2015; Zilidou et al., 2018), a wide range of mental health conditions (Barnstaple and DeSouza, 2019; Koch et al., 2014, 2019; Lee et al., 2015; Malá et al., 2012; Margariti et al., 2012; Martin et al., 2016; Millman et al., 2020; Ventouras et al., 2015). Dance therapy can also have a range of psychological benefits (Hanna, 2017; Palo-Bengtsson et al., 1998), and modulate hormonal levels (Christensen et al., 2017; Quirogo Murcia et al., 2009).

Relevant neuroscientific studies in this area involved: (1) benefits for specific health conditions; and (2) benefits for older adults.

4.9.1. Benefits for specific health conditions

In several studies, the effects of dance therapy on a cerebral level have been investigated for specific health conditions, building on studies focusing on physical measures such as balance and cognitive tests.

In two studies neuroscientific data was collected for one participant (Batson et al., 2014; Kullberg-Turtiainen et al., 2019), and several others were conducted on a small scale ((Barnstaple and DeSouza, 2019) $n = 4$, (Margariti et al., 2012) $n = 11$, (Ventouras et al., 2015) $n = 8$). Although the results of these studies are promising, a great deal more research is necessary to draw meaningful and reliable conclusions.

The relevant studies in this area involved: (1) Parkinson's disease; (2) depression and schizophrenia; and (3) cerebral palsy.

4.9.1.1. Parkinson's disease. After taking part in a dance intervention, an individual suffering from Parkinson's disease had significantly increased network connectivity between the basal ganglia and cortical areas involved in motor function, especially the premotor cortex (Batson et al., 2014). After another dance intervention, an individual who had suffered a traumatic brain injury showed recovery in three subnets of the default mode network, with clearest improvement in the right occipito-parieto-temporal subnet (Kullberg-Turtiainen et al., 2019).

After a different dance intervention, individuals suffering from Parkinson's disease had significant delays in: (1) onset time and duration of activity of the tibialis anterior muscles; and (2) onset time in the medial gastrocnemius muscles. All of these muscles are in the lower leg. In both the leg and trunk, significant delays were found in onset time in antagonist and agonist muscles, with a significant reduction in antagonist duration (McKay et al., 2016). As people with Parkinson's disease typically have normal, or earlier than normal, automatic postural response in agonist muscles (Dimitrova et al., 2004), and earlier than normal response in antagonist muscles (Carpenter et al., 2004;

Dimitrova et al., 2004), these results are promising.

4.9.1.2. Depression and schizophrenia. In individuals suffering from depression, participation in a one-hour dance class modulated resting state alpha activity in the frontal cortex (Barnstaple and DeSouza, 2019). In a depressive/psychotic psychiatric population, resting state activity in the alpha state increased following a dance intervention (Margariti et al., 2012).

In individuals suffering from schizophrenia, a potentiation effect (the persistent strengthening of synapses following recent activity) was observed after the dance intervention in: (1) inter-hemispheric connectivity in frontal areas; (2) the attenuation of inter-hemispheric connectivity of left frontal and right central areas; and (3) bilaterally in the intra-hemispheric connectivity of frontal and central areas (Ventouras et al., 2015).

4.9.1.3. Cerebral palsy. Participants with cerebral palsy performed inclusive dance choreography in their wheelchairs. Compared to baseline, the power spectrum was greater in *theta*, *alpha*, and *beta* bands. The *beta* power spectrum was greater in dance, but not in music listening (Mendoza-Sánchez et al., 2022). This study is also included in Section 4.5.2, as it is also relevant to dance performance.

4.9.2. Benefits for older adults

The effects of dance therapy in older adults have been investigated in several studies, with positive outcomes on physical measures such as balance tests and cognitive tests. Several studies have also been carried out on the effects of dance therapy on a cerebral level.

In several articles (Müller et al., 2017, 2016; Narici et al., 2017; Rehfeld et al., 2018, 2017, 2015) it appears, but is not explicitly stated, that data was used from the same study. In several other articles (Baniquet et al., 2017; Burzynska et al., 2017b; Ehlers et al., 2017; Mendez Colmenares et al., 2021), it is stated that data is used from the same clinical trial NCT01472744 (available at ClinicalTrials.gov). In this trial, there were four groups: (1) dancing; (2) walking; (3) walking and nutritional changes; and (4) an active 'stretching and toning' control group.

One study was conducted on adults with mild cognitive impairment (Qi et al., 2019), one study was conducted on adults on a spectrum from healthy to suffering from mild cognitive impairment (Kropacova et al., 2019), and the other studies were conducted on healthy adults.

The relevant studies in this area involved: (1) neural activity during walking, networks, and information flow; (2) amplitude of low-frequency fluctuation; (3) functional connectivity; (4) neuroplasticity; and (5) brain volume and structure.

4.9.2.1. Neural activity during walking, networks, and information flow.

Video-game-based dance and balance/stretching programs were both found to significantly reduce oxygenation in the pre-frontal cortex during acceleration while walking. In the left pre-frontal cortex, the dance intervention had a larger effect (Eggenberger et al., 2016).

Older adults who undertook a different dance intervention had, compared to an active control group: (1) "improved optimal network performance as estimated by the small-world property"; (2) better information flow; and (3) functional reorganisation of network nodes (Zilidou et al., 2018).

4.9.2.2. Amplitude of low-frequency fluctuation. The effect of dance therapy was investigated for older adults with mild cognitive impairment, comparing a dance therapy group and a "no-change" control group who received only their usual care. The amplitude of low-frequency fluctuation was compared to a baseline of no activation. After three months, participants in the dance group exhibited significantly increased amplitude of low-frequency fluctuation compared to baseline in the bilateral frontotemporal, entorhinal, anterior cingulate,

and parahippocampal cortices (Qi et al., 2019).

4.9.2.3. Functional connectivity. The effects of education and cognitive reserve ("how flexibly and efficiently the individual makes use of available brain resources" (Bigler and Stern, 2015)) on resting-state functional connectivity changes occurring as a result of dance interventions have been investigated in two studies (Mitterová et al., 2021a, 2021b).

Participants in the dance group had greater connectivity between the dorsal attention network and the anterior default mode network after the intervention, with no effect of education. Changes in resting state functional connectivity were only found in the dance group. Participants with 15 or more years of education had significantly greater resting state functional connectivity of the sensorimotor network, which was correlated with improved physical fitness. Cognitive reserve did not correlate with any changes (Mitterová et al., 2021a).

After the intervention, participants with: (1) lower cognitive reserve had greater dwell time and coverage in a dynamic resting state implicated in bottom-up information processing after the intervention; (2) greater cognitive reserve had greater coverage in a different dynamic resting state implicated in top-down information processing (Mitterová et al., 2021b).

After participation in clinical trial NCT01472744, it was found that: (1) in the dance group, there were no gains in cardiorespiratory fitness or executive function related to the intervention; (2) in the dance group, there was no relationship between gains in executive function and modularity; and (3) in the other groups where gains were observed in executive function, higher baseline modularity was positively related to these gains, even after controlling for baseline executive function, age, and in-scanner motion (Baniquet et al., 2017).

In another study it was found that, after the dance intervention: (1) resting state functional connectivity was significantly greater within regions of interest in the frontoparietal network; (2) regions of interest in the default mode network showed greater integration with regions of interest in other networks; and (3) more leisure time spent taking part in moderate physical activity after the intervention was associated with greater resting state functional connectivity within the frontoparietal network (Balbim et al., 2021).

Compared to a "no-change" control group, it has also been found that participation in a dance intervention resulted in a significant increase in resting state functional connectivity in the default mode network, as well as between networks including: (1) cerebellar and visual/language networks; (2) visual and language/default mode networks; and (3) insulo-opercular and right frontoparietal/frontoparietal control networks. The latter was associated with improved scores in attention and executive function (Balazova et al., 2021).

4.9.2.4. Neuroplasticity. As noted in Section 4.8.3, dance training appears to improve neuroplasticity. This is highly relevant for dance therapy because neuroplasticity plays a major role both in healing and protecting the brain (Nahum et al., 2013; Ramanoël et al., 2018).

It has been found that only dancing, and not a control activity, was associated with: (1) increased levels of neurotrophic factors associated with neuroplasticity (Rehfeld et al., 2018). It has also been found that neuromuscular junction damage, assessed by serum measurements of c-terminal peptide agrin fragment, was reduced by recreational dancing over six months, but not by a control activity (Narici et al., 2017).

The ratio of calibrated T1- to T2-weighted images (T1w/T2w) provides qualitative information on the distribution of myelin in the brain (Ganzetti et al., 2014). After participation in clinical trial NCT01472744, the dance and aerobic walking interventions resulted in positive changes in late-myelinating regions in T1w/T2w, in direct contrast to widespread decreases in T1w/T2w observed in the active control group. Regions of white matter that are vulnerable to ageing therefore appear to retain some plasticity, which can be induced by

aerobic exercise training (Mendez Colmenares et al., 2021).

4.9.2.5. Brain volume and structure. Dance and an active control activity have both been found to increase volume in the hippocampus (Rehfeld et al., 2017). Compared to those in an active control group, participants in a dance group had: (1) larger increases in brain volume, and in more areas, including the sensorimotor cortex, insula, cingulate cortex, and corpus callosum (Rehfeld et al., 2018); (2) increased volume in the parahippocampal region (Müller et al., 2017), the left dentate gyrus and the right subiculum (Rehfeld et al., 2017); (3) increased grey matter volume in frontal and temporal regions, including the parahippocampal gyrus and the precentral gyrus (Müller et al., 2016), left precentral gyrus (Müller et al., 2017), and the anterior and medial cingulate cortex (Rehfeld et al., 2015); and (4) increased white matter volume in the corpus callosum and in both the right and left frontal lobes (Rehfeld et al., 2015).

In older adults at increased risk of dementia, social dancing appears to promote hippocampal plasticity more than a treadmill-walking intervention. At the end of a 6-month study, less atrophy was observed in this region in the dance group (Blumen et al., 2022b, 2022a). However, in a study on older, active, women, no difference was found in either whole-brain volume, or in hippocampal volume, in non-professional senior dancers compared to a non-sedentary control group (Niemann et al., 2016).

After participation in clinical trial NCT01472744, it was found that: (1) there was no relationship between psychosocial measures and changes in the volume of the brain regions measured (the amygdala, the prefrontal cortex, and the hippocampus); (2) participants who had a larger amygdala at baseline experienced greater reductions in loneliness and this was due to greater reductions in stress; (3) participants who had a larger amygdala at baseline experienced greater reductions in stress and that this was due to greater increases in social support; and (4) there were no group differences in these pathways (Ehlers et al., 2017).

Hippocampus-to-cortex volume ratio can be used as a marker of the distribution of neurofibrillary tangles in the brain, and of brain atrophy specific to people with Alzheimer's disease. The baseline ratio was not associated with changes in any cognitive domain measured, nor with cognitive changes on the tasks. There was an effect, associated with participation in the dance intervention, on executive functions across a range of participants, from healthy through to those with mild cognitive impairment. This was not dependent on the magnitude of pathology in the brain related to Alzheimer's disease (Kropacova et al., 2019).

Participation in a 4-month long dance intervention was found not to affect hippocampal volume in healthy older adults. However, the authors concluded that more research is needed, using more cognitively demanding and longer interventions (Guzman et al., 2021).

After participation in a dance intervention, compared to a "no-change" control group, there were no significant differences in changes to white matter microstructure between the two groups. After the dance intervention, associations were found between improved physical fitness and changes in diffusion tensor imaging measures in the superior longitudinal fascicle, the corticospinal tract, and the white matter skeleton (Sejnoha Minsterova et al., 2020).

After participation in clinical trial NCT01472744, white matter integrity declined over six months across most regions of the brain in all groups. In those undertaking more moderate-to-vigorous physical activity, less decline occurred in prefrontal white matter. Increased fractional anisotropy in the fornix was observed in the dance group (Burzynska et al., 2017b).

Participants who undertook a dance intervention had significant thickening of the cortex in the lateral occipital, right inferior temporal, and fusiform regions; radial and mean diffusivity increased significantly in various white matter tracts (Rektorova et al., 2020).

These results are particularly interesting regarding the older population investigated in these studies, as both grey and white matter in

various regions of the brain are positively correlated with IQ (Haier et al., 2004, 2010; Schmithorst et al., 2005), and the decline in cognitive function associated with ageing occurs in conjunction with grey matter atrophy (Ramanoël et al., 2018).

5. Overview of research to date

In this section, we provide a brief overview of the findings discussed in Section 4, particularly for newcomers in the field, or those who wish to obtain a broad picture of the current state of research. The areas which, in our view, constitute the field of the neuroscience of dance are: (1) music, and other auditory processing; (2) groove; (3) dance performance; (4) dance observation; (5) imagery relevant to dance; (6) dance training; and (7) dance therapy.

Our search yielded 131 articles containing original and relevant neuroscientific results published up to and including January 2023. This is a growing area of research, and several review articles with specific foci have been published in recent years (Basso et al., 2021; Dominguez et al., 2021b; Karpati et al., 2015; Muñoz and Ballesteros, 2021; Nascimento, 2021; Teixeira-Machado et al., 2019; Wu et al., 2021; Zardi et al., 2021).

Research carried out to date is very unevenly distributed. Some areas have received little attention: 6 articles deal with the neuroscience of groove; 9 with dance performance; and 10 with auditory processing relevant to dance. Other areas, however, have received much more attention: 46 articles deal with dance observation; 61 with dance training.

The plethora of studies on dance observation and dance training compared to the other areas is probably due to the relative facility of conducting such studies, as they face far fewer technical hurdles. Population sampling for studies on dance observation is also less restrictive, as participants do not require training, and do not have to be able to dance.

5.1. Music, and other auditory processing

Several motor regions of the brain related to the formation of rhythmic expectations are engaged when listening to music. Movement preparation also occurs when listening to music, which may be used to test rhythmic expectations (Matthews et al., 2020).

Imagining a metre, when listening to evenly spaced tones with no metre, results in neuronal entrainment at the metrical frequency (Nozaradan et al., 2011). Activity in the *beta* band may reflect the translation of timing information to auditory-motor coordination (Fujioka et al., 2015). Moving to a metre helps internalise it, and improves relevant temporal predictions (Chemin et al., 2014). Motor regions of the brain appear to play key roles in providing temporal and contextual information to sensory regions of the brain (Morillon and Baillet, 2017).

When self-created sounds are distorted, action evaluation may be based more strongly on top-down predictions than from bottom-up information (Heins et al., 2020b). It has been postulated that differences in neural activity found during dance observation in the presence or absence of music could be due to sounds made by the dancer, such as the breath, providing an auditory signal which is more "salient" than music (Reason et al., 2016).

Dancers appear to have enhanced pre-processing of changes in timbre in music compared to either musicians or controls (Poikonen et al., 2016). Different neural processes seem to occur when dancers, musicians, and controls listen to music, and perception of both music and dance is shaped by both dance and musical training (Poikonen et al., 2018a). The unconscious awareness of changes in timbre that dancers seem to have may help them to adapt their movements to reflect the character of the music more successfully.

5.2. Groove

Groove, the pleasurable sensation of wanting to move to music, appears to be driven by a combination of reward and motor regions in the brain (Matthews et al., 2020), and this may be linked to the long pleasure cycles experienced when dancing.

Musical training affects neural responses when listening to high-groove music or rhythms, low-groove music or rhythms, or noise (Matthews et al., 2020; Stupacher et al., 2017, 2013). Neural entrainment is positively correlated with groove experienced when listening to rhythms performed by humans, but not when listening to computer-generated rhythms (Cameron et al., 2019). Listening to rhythms conveyed by low-frequency tones results in greater neural tracking of the beat (Lenc et al., 2018), which may explain why the presence of low frequencies (bass) in music increases the degree of groove perceived (Stupacher et al., 2016).

5.3. Dance performance

Despite the difficulties faced by research on the neuroscience of dance performance, a few studies have been carried out, and it appears that a network of brain regions is involved (Karpati et al., 2015).

Different regions of the brain appear to be involved in: (1) the entrainment of dance steps to music; (2) moving legs in dance step patterns to a regular metric rhythm, compared to an irregular rhythm; and (3) spatial guidance of leg movements (Brown et al., 2006).

In participants with cerebral palsy performing “inclusive” dance choreography in their wheelchairs, the power spectrum was greater in *theta*, *alpha*, and *beta* bands compared to baseline (Mendoza-Sánchez et al., 2022).

The performance of a modern jazz dance routine appears to affect neural activity in the *alpha* and *gamma* bands, and to recruit working memory, attentional processing, and heightened awareness (Wind et al., 2020). Significant differences have been found between dance performance and dance imagery, but in male participants only. These differences were found in both power and synchronisation in several EEG bands, and also had a spatial component (Wind et al., 2021), and further highlight the need for caution when using dance imagery as a proxy for dance performance.

As dancers become more adept at a dance video game, they appear to be guided more by stimulus-led bottom-up cortical activity than by cognition-led top-down cortical activity (Ono et al., 2014, 2015; Tachibana et al., 2011). In a study using movements based on either contact improvisation dance or choreographed dance, it was found that, when the eyes were closed, there was greater alpha activity in a posterior region during choreographed movement, compared to improvised movement (Goldman et al., 2019).

However, the activities used to date only approximate dance. In addition to the technological constraints there is therefore some doubt about the degree to which these results are translatable to dance performance, as discussed in Section 4.2.

5.4. Observation

Training in dance performance, training in music performance, and exposure to dance through observation, all affect neural activity associated with dance observation, notably the strength of perception-action coupling (Beatriz Calvo-Merino et al., 2010; Sevdalis and Keller, 2011).

The neuroscience of dance observation is affected by dance training, including corticospinal excitability (Jola et al., 2012), and brain wave activity (Di Nota et al., 2017; Orgs et al., 2008; Poikonen et al., 2018a,

2018b). Dancers appear to have faster processing and subsequent recognition of dance, with enhanced visuomotor resonance processes, and refined action processing (Orlandi and Proverbio, 2019; Orlandi et al., 2017, 2020b).

There is strong evidence that dance training enhances the action observation network (Amoruso et al., 2014; Burzynska et al., 2017a; Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009b; Diersch et al., 2013; Gardner et al., 2015; Jang and Pollick, 2011; Jola et al., 2012, 2013; Orgs et al., 2008; Pilgramm et al., 2010). The action observation network is associated with empathy (Jospe et al., 2020, 2018), enabling us to infer information about others’ actions and intentions (Caspers et al., 2010; Cross et al., 2009b; Gardner et al., 2015), improve prediction of their future behaviour (Blakemore and Frith, 2005; Falck-Ytter et al., 2006; Hamilton, 2013; Hamilton and Grafton, 2006) and plan appropriate responses. These abilities are of prime importance in social interactions, and therefore in the formation and maintenance of social groups. This supports evolutionary theories of the importance of dance, and the theory that dance has had a significant role in enhancing our interpersonal skills (Basso et al., 2021).

5.5. Imagery relevant to dance

Significant differences in neural activity have been found in dancers and non-dancers during motor imagery (Burzynska et al., 2017a; Cross et al., 2006; Di Nota et al., 2017; Fink et al., 2009; Hökelmann and Blaser, 2009; Jang and Pollick, 2011; Olshansky et al., 2015; Park et al., 2002; Sacco et al., 2006). Non-dancers appear to experience greater cognitive demand than dancers (Orlandi et al., 2020a) and dancers recruit more kinaesthetic imagery than visual imagery (Sacco et al., 2006).

Dance imagery appears to be a greater driver of neural plasticity than non-dance motor imagery (Di Nota et al., 2017). During imagery of dance choreography that was being learnt, activity initially increased, then decreased, in a network of brain regions, following the usual pattern of throughout learning (Bar and DeSouza, 2013, 2016; DeSouza and Bar, 2012).

Significant differences have been found between dance performance and dance imagery, but in male participants only. These differences were found in both power and synchronisation in several EEG bands, and also had a spatial component (Wind et al., 2021), and further highlight the need for caution when using dance imagery as a proxy for dance performance.

5.6. Dance training

Both short- and long-term dance training lead to significant changes in brain structure (Burzynska et al., 2017a; Dordevic et al., 2018; Giacosa et al., 2016, 2019; Hänggi et al., 2010; Hüfner et al., 2011; Karpati et al., 2017, 2018; G. Li et al., 2019; Li et al., 2015; Meier et al., 2016; Nigmatullina et al., 2015; Porat et al., 2016), as well as in neural activity during, particularly: (1) dance performance; (2) imagery, and (3) dance observation. Dance training also appears to affect resting state neural activity (Barnstaple and DeSouza, 2019; Ermutlu et al., 2015; Lu et al., 2018), function and cortical plasticity of the sensorimotor system (Lu et al., 2018), and neural activity during musical recall (Jin et al., 2021).

Total brain volume appears to be unaffected by dance training (Burzynska et al., 2017a), but there is evidence that both white matter and grey matter volumes in specific brain regions are affected by dance training (Burzynska et al., 2017a; Dordevic et al., 2018; Hänggi et al., 2010; Hüfner et al., 2011; Meier et al., 2016; Nigmatullina et al., 2015). Long-term dance training is also associated with changes in cortical thickness and the plasticity of grey matter and white matter, especially

in regions of the brain associated with motor and auditory functions (Burzynska et al., 2017a; Dordevic et al., 2018; Hänggi et al., 2010; Meier et al., 2016; Nigmatullina et al., 2015). As discussed in Sections 4.8.3 and 4.9.2, this is important because of the role played by neuroplasticity in healing and protecting the brain.

5.7. Dance therapy

In most studies on the neuroscience of dance therapy (24 out of the 31 studies reviewed), the potential benefits for older adults have been investigated. There is therefore a great deal of scope for further research in dance therapy for specific health conditions.

Dance therapy has been found to affect resting state *alpha* activity (Barnstaple and DeSouza, 2019; Margariti et al., 2012) and a potentiation effect has been found in several regions of the brain in individuals suffering from schizophrenia (Ventouras et al., 2015).

In healthy older adults, dance therapy has been found to have beneficial effects on functional connectivity (Balbim et al., 2021; Baniqued et al., 2017; Mitterová et al., 2021a, 2021b) and increase neuroplasticity (Mendez Colmenares et al., 2021; Narici et al., 2017; Rehfeld et al., 2018). Increases in brain volume have been observed in many regions following dance therapy (Müller et al., 2017, 2016; Rehfeld et al., 2018, 2017, 2015; Rektorova et al., 2020). White matter integrity has also been found to decline less rapidly in prefrontal regions when people undertake more moderate-to-vigorous physical activity (Burzynska et al., 2017b).

The results of these studies show that, while dance therapy is far from being a panacea, the neuroscientific research that does exist corroborates the results of studies on physical measures, specifically that dance therapy: (1) is an effective method of supporting patients suffering from a broad range of health conditions; (2) has great potential to counteract age-related cognitive decline and for a broad range of health conditions; and (3) is better suited for counteracting age-related cognitive decline than monotonic physical exercise.

6. Suggestions for future work

Much valuable research has been carried out on the neuroscience of dance. However, as is to be expected in a relatively new field, much remains to be done. In this section we identify some gaps in the field, and suggest ways to address them.

6.1. The uneven distribution of research

The uneven distribution of research is immediately apparent from Fig. 5. For example, 9 articles have been published on the neuroscience of dance performance, which is the core activity of the field. Only 6 articles have been published on the neuroscience of groove directly relevant to dance and 10 on the neuroscience of auditory processing directly relevant to dance. However, 61 studies have been published on the neuroscience of dance training. We recommend that future work focus on these less well researched areas, especially dance performance.

6.2. The interactive and collective aspects of dance

This area has hardly received any attention to date. This is surprising, given that dance is intrinsically a highly interactive and collective group activity with important social aspects, with a great deal of interaction between dancers both on and off the dance floor. In all dances in the presence of other people, interaction occurs between a dancer and everyone in their vicinity on the dance floor. In partner dances,

interaction occurs both within the couple and between couples on the dance floor. In group dances, strong interaction occurs between all members of the group dancing together. Moreover, people who dance together regularly often become friends. Interaction between dancers is therefore a critical aspect of dancing. However, almost all research to date has focused on individuals. The only studies which, to our knowledge, have included neuroscientific research on interactive aspects of dance are those conducted by Chauvigné and Brown (2018); and by Chauvigné et al. (2017, 2018).

We therefore suggest that more research be conducted in this area, especially on aspects of dance such as communication, social entrainment, and interpersonal synchronisation. Such research would be of considerable interest in other fields, e.g. in providing valuable information on the predictive and social interaction mechanisms of the brain, and aiding in the development of more accurate neuroscientific models of interpersonal interaction.

6.3. The correlational nature of research to date

Almost all research to date has been correlational, employing principally fMRI, fNIRS, EEG, or MEG. We suggest that it would be helpful for more causative research to be carried out, employing transcranial stimulation such as transcranial magnetic stimulation, or transcranial alternate/direct current stimulation. This would allow the investigation of effects, relevant to dance, of modulating activity in specific regions of the brain. This could aid in the establishment of clear causal, not merely correlational, links between activity in certain regions of the brain, and behavioural measures relevant to dance.

6.4. Groove

Listening to music can often induce a pleasurable desire to move (groove), and acting on this desire can result in dance. Since groove is a key factor linking music and dance, it would be useful if research in this area included both music and dance.

Neuroscientific research to date in these areas has included musicians and non-musicians (see e.g. Matthews et al. (2020); Stupacher et al. (2017, 2013)) but has not yet included dancers, dance, or any dance-related activities. It would therefore be beneficial to all relevant fields to explore this connection further, and include dancers in future studies. For example, studies similar to those already undertaken could be carried out with the addition of a group of dancers, or neuroimaging could be undertaken during observation of similar dance choreographies accompanied by high-groove or low-groove music.

6.5. Dance performance

There are still many technical difficulties associated with researching dance performance. However, we suggest that more research be undertaken in this area, possibly using fNIRS, EEG, and Mobile Brain/Body Imaging (a neural scanning technique employing wireless mobile EEG to enable scanning of moving participants, combined with motion capture, described in (Barnstaple et al., 2020)). With recent advances in technology, it may also soon be possible to research the neuroscience of dance training in real time, e.g. by conducting neural scanning during a dance class. At the time of writing, there are at least two studies on dance performance in preparation, one by Marieke Van Vugt's group at the University of Groningen and the other by José Contreras-Vidal's group at the University of Houston.

6.6. Observation

Research on dance observation has mostly used recorded dance. Much dance observation undertaken as a pastime is of recorded dance, such as watching videos online, but dance observation also commonly takes place live. Neural activity during dance observation has been found to depend on whether the dance observed is live or recorded, as well as the editing style of recorded dance (Herbec et al., 2015; Jola et al., 2011; Jola and Grosbras, 2013). More research on the observation of live dance would therefore be valuable, and if recorded dance is used, the editing must be considered carefully.

6.7. Dance therapy

Many studies have been carried out on the physiological and behavioural benefits of dance therapy, but relatively few on neurological changes. Most of the studies to date (24 out of the 31 studies reviewed) are on older adults, rather than for specific health conditions. Some work with neuroscientific measurements is in the process of being planned, e.g. dance therapy for patients with schizophrenia (Li et al., 2021), and for older adults with mild cognitive impairment (Dominguez et al., 2021a). However, there is still a great deal of scope for further research on neurological changes associated with dance therapy for specific health conditions.

Further research on the neuroscience of dance generally, as well as dance therapy specifically, could also help to improve the future design and implementation of dance therapy interventions (Millman et al., 2020), e.g. by providing more information about the specific ways in which dance therapy affects the brain, such as its effects on neuroplasticity, reconfiguration of neural networks, and the emergence of compensatory neural mechanisms. The implementation of larger studies, and more research on the neuroscience of dance therapy for specific health conditions, would be particularly beneficial.

Ideally, comparable dance interventions would be used. Precise documentation of the dance intervention should also be included in any published work. We also recommend that both an active control group and a “no-change” control group be included whenever possible.

7. Conclusion

In recent years, much innovative research has been carried out on the neuroscience of dance. However, the field lacks some basic elements, rendering it difficult to carry out research in the field and progress research in it. In this article, we therefore provide a guide to researching the neuroscience of dance, in the form of a conceptual framework and systematic review.

In the conceptual framework, we highlight the links between music, auditory processing, groove, music-induced movement, and dance. We also outline the principal activities related to dance. We therefore categorise research on the neuroscience of dance as follows: (1) music, and other auditory processing; (2) groove; (3) dance performance; (4) dance observation; (5) imagery relevant to dance; (6) dance training; and (7) dance therapy, and review the literature in Sections 4 and 5.

Some of the links between different areas outlined in the conceptual framework have not yet been well explored. For example, there is very little research related to dance and dancers in the fields of either music or groove. We therefore make suggestions for future work on these connections, as well as detailed suggestions for research in other areas and the field generally, in Section 6.

Research on the neuroscience of dance is a promising platform for understanding the function of the human brain in naturalistic contexts,

especially relating to social interaction and communication, affect, art, health, pleasure, and motivation. A better understanding of how the brain responds to dance training, and dance therapy, also has potential to inform our understanding of neuroplasticity in old age and illness. Further research in the field generally has potential to improve our understanding of the importance and uses of dance, as well as improving our understanding of the human condition.

Author contributions

OFVE carried out the research and wrote the initial draft under the guidance of NHDF and MLK. PV provided advice about structure and content at various stages of drafting. PK provided expertise on linking the neuroscientific results to behavioural research. All authors edited the final version of the review and approved the final manuscript.

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Competing interest

There are no competing interests to declare.

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Appendix

Numerical overview of the studies reviewed

Studies containing results relevant to music in the context of the neuroscience of dance are assigned to categories of: (1) auditory processing; and (2) groove. We do not include research on beat perception in the numerical data. Although this research is relevant to the neuroscience of dance, and we include a brief overview of a selection of that research, it is not sufficiently relevant to merit detailed consideration.

The total number of studies published in each area in each year, and the total number of unique studies published in each year, are shown in Fig. 5 and Table 1. The number of studies published in each area are shown individually, by year, in Fig. 6. The graphs are arranged in order of decreasing number of studies in each area. We do not include articles published in 2023 in the numerical overview, as the last literature search was conducted in January 2023, and this would give a misleading representation of the amount of research published in 2023.

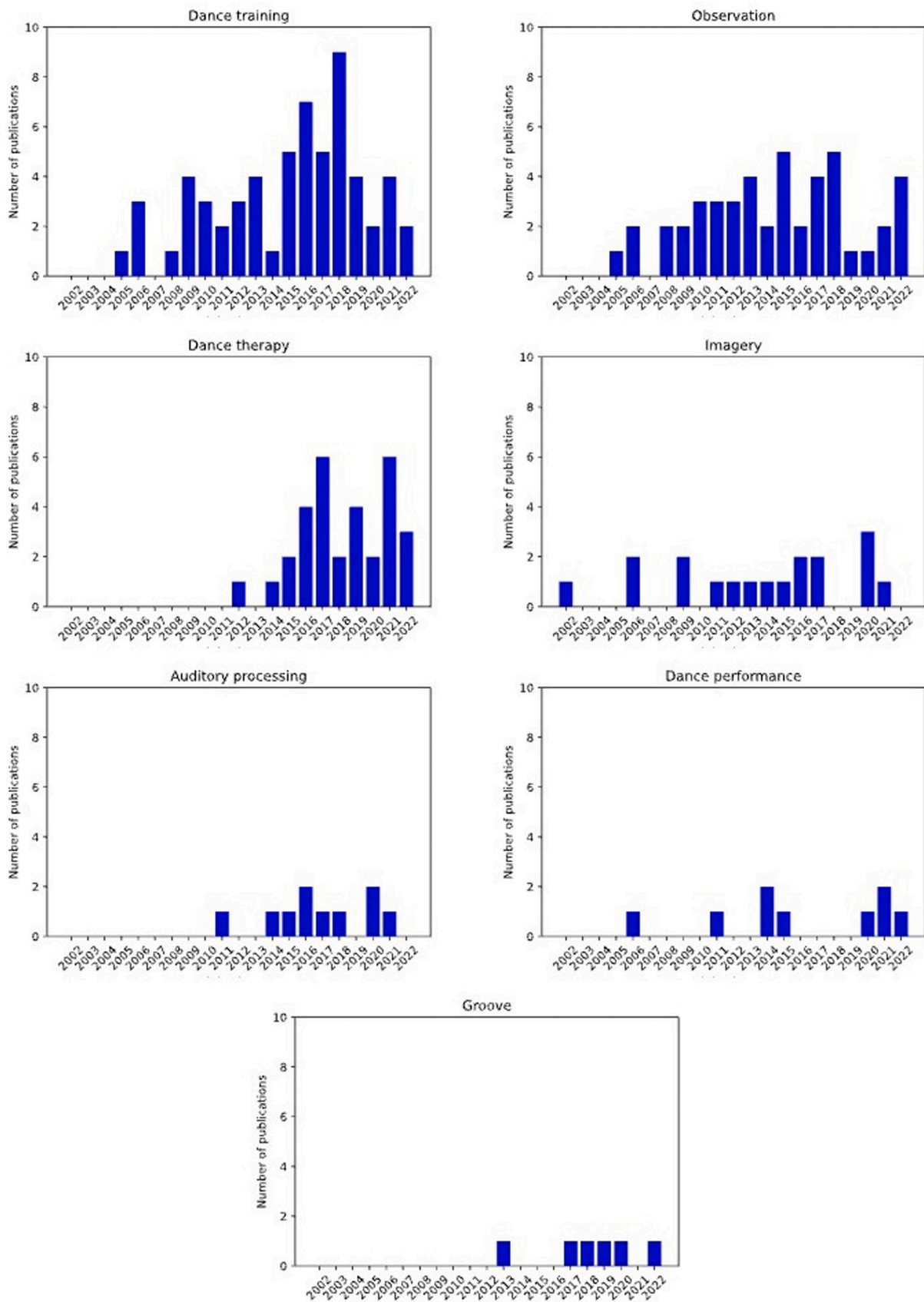


Fig. 6. Number of studies published each year in: dance training; dance observation; dance therapy; imagery; auditory processing; dance performance; groove.

Supplementary material

Supplementary material associated with this article can be found in the online version at [doi:10.1016/j.neubiorev.2023.105197](https://doi.org/10.1016/j.neubiorev.2023.105197).

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