Review

The physiological study of emotional piloerection: A systematic review and guide for future research

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ABSTRACT

This paper provides an accessible review of the biological and psychological evidence to guide new and experienced researchers in the study of emotional piloerection in humans. A limited number of studies have attempted to examine the physiological and emotional correlates of piloerection in humans. However, no review has attempted to collate this evidence to guide the field as it moves forward.

We first discuss the mechanisms and function of non-emotional and emotional piloerection in humans and animals. We discuss the biological foundations of piloerection as a means to understand the similarities and differences between emotional and non-emotional piloerection.

We then present a systematic qualitative review ($k = 24$) in which we examine the physiological correlates of emotional piloerection. The analysis revealed that indices of sympathetic activation are abundant, suggesting emotional piloerection occurs with increased (phasic) skin conductance and heart rate. Measures of parasympathetic activation are lacking and no definite conclusions can be drawn. Additionally, several studies examined self-reported emotional correlates, and these correlates are discussed in light of several possible theoretical explanations for emotional piloerection.

Finally, we provide an overview of the methodological possibilities available for the study of piloerection and we highlight some pressing questions researchers may wish to answer in future studies.

1. Introduction

Piloerection—also known as goosebumps or goose pimples—is the contraction of small muscles at the base of hair follicles resulting in visible erection of hair. Piloerection has many different functions in various species. It serves as a form of temperature regulation in mammals (Chaplin et al., 2014; Tansey and Johnson, 2015) and also represents a method of making non-human animals appear larger in response to threat. In humans, however, piloerection also occurs in response to a wide variety of emotional stimuli. This *emotional piloerection* is not well understood and raises many interesting questions about the psychology and physiology of emotion.

The goal of this review is to provide an accessible guide to the scientific study of piloerection from both biological and psychological perspectives. Some of the research questions from these two perspectives are similar, but many diverge widely. However, they can both inform each other and it is our goal to synthesize this information to make cooperation between the two fields easier. Therefore, in this article, we provide an overview of biological foundations of non-emotional piloerection and discuss how it can be used to inform the study of emotional piloerection from a psychological perspective.

This review is organized into four main sections. First, we discuss the biological mechanisms of piloerection and introduce piloerection as a temperature regulation mechanism. In the second section, we discuss the psychology of emotional piloerection and its physiological correlates. Then we conduct a systematic review of the literature on physiological correlates of emotional piloerection. In the final section, we provide an overview of the current methodological state of the art and suggest some ideas for how researchers may move forward in this area.

1.1. A note on terminology

Many terms and various definitions are used to refer to piloerection across the literature. Several scholars have discussed the relationship between piloerection and *chills*. For example, Benedek and Kaernbach (2011, p. 320) emphasize that in "humans, the study of emotional

piloerection (i.e., goose bumps) is tightly linked to the study of chills or thrills. While piloerection actually denotes the visible erection of body hair, the phenomenon of chills or thrills usually relates to a subjective experience." Further, Craig (2005, p. 281) found that in 52 % of the cases subjective chills responses featured objective piloerection and concludes that"pilo-erection marks the occurrence of a chill, but a chill may also occur without pilo-erection.". Other researchers differentiated between *objective chills* (with piloerection) and *subjective chills* (without piloerection, (Sumpf et al., 2015). Similarly, Maruskin et al. (2012) consider *chills* as a subjective experience consisting of two higher order clusters labelled *goosetingles* and *coldshivers* that have different correlates. *Goosebumps* or piloerection are considered as part of *goosetingles* and are associated with positive affect and approach intentions (see also Bannister and Eerola, 2021, for conceptualizing different types of *chills*).

In this manuscript, we use the term *piloerection* to refer to the physical contraction of the muscles resulting in hair erection, regardless of the cause. The term *goosebump* is used when referring to piloerection colloquially—for example, when describing the experience subjectively or relying on self-reports. The term *chills* (or *frisson, thrills*) is used almost exclusively in the context of listening to music and often refers to a self-reported sensation (de Fleurian and Pearce, 2021). Based on previous definitions, we consider piloerection a subpart of the psychological construct of *chills*. Studies focusing exclusively on (musical) *chills* are therefore informative when reviewing evidence with regard to piloerection, although it is possible that such studies treated *chills* occurring without piloerection. However, one corollary goal of this paper will also be to determine the similarities and differences between *chills* and *piloerection*.

2. Non-emotional piloerection

2.1. Biological mechanisms

The mechanisms of piloerection have been well-understood since the mid-1800s. For example, in Darwin's book *The expression of emotion in man and animals* (Darwin, 1872, pp.101–103), he cites a variety of biological evidence describing piloerection in non-human animals (e.g., Lister, 1853).

In the years since, scientific evidence has further illuminated our understanding of the physiological mechanisms underlying piloerection (Chaplin et al., 2014; Glatte et al., 2019a). Presumably, both non-emotional and emotional piloerection rely on the same neurological and molecular mechanisms. In this first section, those mechanisms will be identified briefly so that they can then be applied to the understanding of emotional piloerection. Specifically, it is hoped that researchers can implement this theoretical understanding of piloerection into their research along with a focus on physiological measurement in place of relying purely on self-report.

2.2. Muscular mechanisms

Piloerection is the result of the contraction of arrector pili muscles (APM), which reside in the dermis layer of skin. APM are smooth muscle bundles between the hair follicle and the connective dermal tissue, and are connected to the bulge, the permanent portion of the hair follicle, throughout the hair cycle (Barcaui et al., 2002; Narisawa and Kohda, 1993). Multiple follicular units can share a single muscle (Poblet et al., 2002; Song et al., 2005). When the muscle contracts, the hair follicle is pulled and the hair shaft becomes erect (Hanukoglu et al., 2017; Torkamani et al., 2014). As a result, the skin bunches up and forms little bumps, increasing the surface area. The density of hair follicles also differs across bodily sites, with estimates suggesting 14 follicles per cm^2 on the calf, 17 on the thigh, 18 on the forearm, 29 on the back, and 32 on the upper arm (Otberg et al., 2004).

Most mammals have APM, with some exceptions (Chaplin et al., 2014; Starcher et al., 2005). In contrast, birds have feather muscles which are different from the APM in mammals (Homberger and Silva, 2000; Stettenheim, 1972). Thus, while the functions (e.g., increased size, temperature regulation) may be the same as that of mammals, the mechanism is not strictly identical.

2.3. Neurochemical mechanisms

The APM are innervated by the sympathetic nervous system (Hellmann, 1963). Specifically, postganglionic class C nerve fibres provide both adrenergic and cholinergic innervation to dermal organs, including the APM.[1]

The APM are generally believed to be under sympathetic control, they have α-1 adrenergic receptors (Glatte et al., 2019b), and use norepinephrine as their neurotransmitter. In short, norepinephrine is received by the receptor which begins an intracellular signalling process (Qin et al., 2011) that ultimately results in smooth muscle contraction (Carlson and Kraus, 2019). In humans, direct administration of α-1 adrenergic agonists has been observed to cause piloerection. For example, iontophoresis of phenylephrine causes piloerection (Alsene et al., 2006; Siepmann et al., 2012).

2.4. Piloerection as a temperature regulation mechanism

Thermoregulation via piloerection appears to be common in both human and non-human animals (Chaplin et al., 2014; Davenport, 1992; Herrington, 1951). In short, humans have thermoreceptors in their skin (Granovsky et al., 2005; Hensel, 1974) and throughout their body (e.g., in the gut; Villanova et al., 1997), which detect sensory inputs from temperature and pain. Some of these thermoreceptors are dedicated to either hot or cold temperatures (Campero et al., 2001).

Hairy skin is generally more sensitive to thermal information compared to hairless (i.e., glabrous) skin (Ackerley et al., 2014; Filingeri et al., 2018; Hamalainen et al., 1985) and functions as a highly sensitive organ, relaying information about touch, airflow, and other sensations. Humans have relatively little hair so, while piloerection may be useful in non-human animals to trap a layer of air around the skin (Herrington, 1951), it seems less useful in humans. It is thought that piloerection may be useful in conjunction with shivering (Parsons, 2014) particularly because shivering increases metabolism and piloerection does not (Chaplin et al., 2014; DeGroot and Kenney, 2007; Tansey and Johnson, 2015).

2.5. Relation to the sympathetic and parasympathetic nervous system

The APM are controlled by the sympathetic branch of the autonomic nervous system. The primary function of the autonomic nervous system is to adjust the body's function to changes in the external environment. For example, external threats require modifications to blood and oxygen flow by regulating smooth muscle, as in the "fight or flight" response of the sympathetic nervous system. Additionally, temperature changes require activation of sweat glands to cool the body (in humans) or to trap in a layer of heat (in non-human animals) and promote vasoconstriction (Chaplin et al., 2014; Glatte et al., 2019a).

Only a few experimental studies have been published showing deliberate induction of piloerection via direct sympathetic nerve activation (Hijazi et al., 2020). However, it is clear that piloerection occurs in response to many types of external events. These events might be purely physiological in nature, such as temperature change, or they might have a psychological component, such as a positive or negative emotional experience. In the next section, we turn to discussing the

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[1] Some cholinergic fibres were reported in the muscles in one study and are believed to represent parasympathetic fibres (Donadio et al., 2019), though they are sparse and it is unclear whether they are directly responsible for APM functioning and related to piloerection.

psychological antecedents of piloerection.

3. Emotional piloerection

Thus far, we have discussed the biological mechanisms and functions of non-emotional piloerection. In this section, we turn to discussing *emotional* piloerection, exclusively. The mystery of piloerection is that it also occurs in response to a wide variety of emotional stimuli and experiences. Presumably, when emotional stimuli cause piloerection, it does so via the same physiological mechanisms as non-emotional piloerection. However, some psychological theories make varying predictions regarding the involvement of the sympathetic nervous system (SNS) and the parasympathetic nervous system (PNS) based on the classification of the emotional antecedents.

3.1. Piloerection and human psychology

The psychological mechanisms of piloerection are not as well understood as the biological mechanisms. Piloerection is often discussed in both scientific and non-scientific media as resulting from (or co-occurring with) strong emotions, such as awe, excitement or fear; there is little evidence for or against these claims. Importantly, much of the psychological literature is concerned with a phenomenon called *chills*, which is similar to goosebumps, but does not necessarily require the hair to be visibly raised (e.g., (Maruskin et al., 2012)). As mentioned earlier, the methodologies employed to study these phenomena are extremely similar and we will therefore also consider the literature on chills when evaluating the psychological structure of emotional piloerection, well-knowing that *chills* do not necessarily need to involve objective piloerection.

3.2. Emotions in humans

Perhaps the most common cause of piloerection in humans, and the most attractive to psychological researchers, is emotional experience. (Darwin, 1872) for example, suggested that piloerection occurs in response to anger, fear, or excitement. Indeed, one of the main driving forces behind psychological research is that the environment can influence bodily responses via perceptive input and cognitive processing (Harris et al., 2015).

3.3. Positive emotions

In psychological literature, goosebumps and the chills are often claimed to have an emotional tie. For example, researchers have provided evidence that they are related to *being moved* (Benedek and Kaernbach, 2011), a predominantly positive emotional experience occurring in response to significant social events or values (Cullhed, 2019; Zickfeld, Schubert, Seibt, & Fiske, 2019; though see for example Menninghaus et al., 2015 who consider *being moved* a *mixed* emotion). Similarly, it is often believed they occur as a physiological correlate of awe (Quesnel and Riecke, 2018; Schurtz et al., 2012), typically defined as a positive emotion elicited by perceived vastness and the need for accommodation (Keltner and Haidt, 2003; though see Gordon et al., 2017 discussing a negative type of awe). However, some evidence failed to find a relationship between piloerection and awe (McPhetres and Shtulman, 2021; Zickfeld et al., 2020). They are reported to occur at the peak of the pleasure response (Salimpoor et al., 2009) and in response to strong positive emotions (Grewe et al., 2011; Maruskin et al., 2012; Sumpf et al., 2015; Wassiliwizky et al., 2015). Much of this research focuses on musical stimuli (Goldstein, 1990) though they can also occur in response to videos and virtual reality (Quesnel and Riecke, 2018; Schubert et al., 2018).

3.4. Negative emotions

Piloerection has been hypothesized to be linked to negative emotions as well, stemming mostly from animal models. For example, it was proposed (Panksepp, 1995) to be linked with coldness and sadness in animals who have been separated from their caretaker (e.g., the *separation call hypothesis*). Some research has uncovered physiological patterns associated with sadness (Benedek and Kaernbach, 2011). However, other research (Wassiliwizky, Jacobsen, et al., 2017; Zickfeld et al., 2020) has failed to find evidence for the physiological patterns, expected to accompany this emotional state of sadness (Kreibig, 2010).

Though a common belief is that piloerection occurs with the emotion of fear—consider that *Goosebumps* is the title of a popular horror novel series—this has not been studied empirically. The experience of piloerection in response to fear has only been recorded using self-reported, retrospective reports of goosebumps or chills (Grewe et al., 2011; Maruskin et al., 2012; McCrae, 2007; Schurtz et al., 2012).

Going beyond the specific valence of the emotional experience, some scholars have argued that piloerection occurs in response to any strong emotional reaction or high emotionality (Bannister and Eerola, 2018; Beier et al., 2020a; Rickard, 2004). This is related to findings arguing that there are at least three different types of aesthetic chills (*warm*, *cold*, and *moving*), highlighting different types of negative and positive emotions (Bannister, 2019).

3.5. Emotions in non-human animals

Piloerection has also been observed in non-human animals in a variety of situations assumed to have an emotional component. For example, during mating rituals, when separated from others, or when in threatening situations—in some ways, these experiences are similar to those experienced by humans. Insights from these situations are often called upon when questioning the functions of piloerection in humans and form the basis of some theorising (e.g., the separation call hypothesis; Panksepp, 1995).

3.6. Mating

In non-human animals, piloerection has been observed to accompany various behaviours related to mating, including accompanying genital displays (Abbott, 1984) and mating dances in birds (Coleman et al., 2004; Nishida, 1997). Male pygmy marmosets show increased piloerection and courtship behaviours prior to their mates ovulatory period (Converse et al., 1995). Titi monkeys, which are monogamous, display higher levels of arousal, including piloerection, after being separated from their mates for prolonged periods of time (Fernandez-Duque et al., 1997).

3.7. Response to threat

In non-human animals, piloerection is used to make an animal appear larger, either to communicate or respond to a threat. In states of anger, fear, or anxiety animals experience piloerection (Masuda et al., 1999). For example, when a dog hears a knock at the door or sees something move out of the window, the hairs on its back (the "hackles") stand up. This behavior has been documented in marmosets (Abbott, 1984), night monkeys (Wright, 1978), and chimpanzees (Muller et al., 2006, 2007) when charging at or threatening other individuals. This behavior has also been noted in various species of birds (e.g., Morris, 1956; Wolovich et al., 2010; Yorzinski and Platt, 2012), but birds do not have APM; they use "feather muscles" to control their feathers. Juvenile monkeys also display increased piloerection when separated from their parents (Dettling et al., 1998).

3.8. Theoretical considerations

Several theoretical explanations have been put forth by various researchers in an attempt to explain why (certain) emotional experiences may be associated with piloerection or what function emotional piloerection serves. An overview is provided in Table 1. For simplicity, we will discuss these in terms of two sets of theories. For an in-depth discussion of these theoretical propositions as they relate to the chills in the context of music research, see de Fleurian & Pearce (2020b).

One set of theories proposes that psychological needs for social functioning activate the same mechanisms used for thermoregulation. The other set of theories proposes that emotional experience is directly tied to autonomic activation. Thus, both sets of theories propose an explicit connection between social and biological mechanisms mediated in various ways by autonomic activation. However, as you will see, these sets of theories differ in whether this would require SNS or PNS activation and in the valence of the emotions.

3.8.1. Thermoregulation

Some perspectives propose that emotions and piloerection are connected because they happen to rely on the same mechanisms used for thermoregulation. The *separation-call hypothesis* proposes that feelings of physical coldness are linked to social coldness and sadness, which elicit a piloerection response (Panksepp, 1995, 2009). According to this proposition, separation distress calls from parents and offspring have specific acoustic qualities resembling the qualities of music responsible for eliciting piloerection in humans. These acoustic qualities have been examined in past research (e.g., Bannister, 2020; Bannister and Eerola, 2018). Considering the physiological predictions, there is mixed evidence on the relationship between specific ANS responses and feelings of loneliness and sadness. A systematic review has differentiated between forms of *activating* and *deactivating* sadness, suggesting that sadness accompanied by crying shows increased SNS activity, while sadness without crying is characterized by sympathetic withdrawal (Kreibig, 2010). Previous studies have found that piloerection and crying co-occurred with increased SNS activation, though piloerection was not necessarily accompanied by crying (Wassiliwizky, Jacobsen, et al., 2017). Therefore, it remains unclear whether the separation-call hypothesis would predict increases in SNS or PNS activity.

Similarly, IJzerman et al. (2015) proposed that social attachment needs and thermoregulation are connected physiologically. That is, thermoregulation can be satisfied through social interaction (e.g., huddling, sharing food and shelter) or through solitary metabolic means. First evidence has supported the idea that physical and social warmth share similar underlying mechanisms (Inagaki and Eisenberger, 2013). Both forms are achieved via physiological mechanisms mediated by the SNS (e.g., heart rate, vasoconstriction, etc). Thus, these perspectives suggest that psychological and physiological experiences of loneliness and coldness can modulate the SNS, which can result in piloerection.

3.8.2. Emotional activation

Other theories propose that emotional functioning directly activates the autonomic nervous system (Kreibig, 2010). That is, rather than overlapping with a specific function like thermoregulation, it is possible that the experience of certain emotions could then sometimes cause piloerection directly. From these perspectives, piloerection is an indicator of "strong" emotional experiences.

One particular example is the emotion of *being moved* by music and other experiences that is often accompanied by piloerection (Schubert et al., 2018; Zickfeld, Schubert, Seibt, Blomster, et al., 2019). There is disagreement whether *being moved* represents a positive or mixed emotion, but the majority of theories agree that it is evoked by some kind of social closeness or attachment (Cullhed, 2019). It has been speculated that piloerection often co-occurs with strong instances of *being moved*, as it provides a social communicative function, signalling approach tendencies (Maruskin et al., 2012; Zickfeld, Schubert, Seibt, Blomster, et al., 2019). Supporting this notion, piloerection has been associated with social closeness (Maruskin et al., 2012; Schoeller and Eskinazi, 2019). In this vein, *being moved* (and the accompanying piloerection) might also fulfil a social thermoregulation function (IJzerman et al., 2015). There is mixed evidence with regard to the ANS correlates of *being moved*, with most theoretical and empirical contributions highlighting a co-occurrence of tonic PNS and phasic SNS activity (Mori and Iwanaga, 2021a; Zickfeld, Schubert, Seibt, & Fiske, 2019; Zickfeld et al., 2020).

Considering that piloerection can occur with a multitude of different emotional experiences, other researchers have proposed that piloerection occurs at the point when the height of emotional experience is surpassed (Grewe et al., 2009; Rickard, 2004). This was termed the *peak arousal hypothesis* (Benedek and Kaernbach, 2011). This perspective argues that piloerection can occur in response to both strong negative (e.g., sadness, fear) and positive emotional (e.g., awe, excitement, pleasure) experiences and is strongly related to increases in SNS activity. It is not completely clear, whether piloerection would occur to any peak arousal surpassing a specific threshold or whether other cognitive evaluations or appraisals need to be in place according to this view.

In contrast, another perspective relying on the interplay of emotions is *vigilance theory*, which was proposed to understand musical chills (also called *contrastive valence*; Huron, 2008). Vigilance theory proposes that listeners have an expectation about how music will progress. When listeners experience a surprising or unexpected change in the music (change in tempo, crescendo, entrance of new voices, etc), emotional and attentional systems are activated. Some research has found these changes to be associated with chills (Bannister, 2020; Beier et al., 2020a; Grewe et al., 2007a; Guhn et al., 2007). Such unexpected outcomes might lead to fear appraisals that are then resolved by considering the stimulus as *safe*. This contrast between negative and neutral/positive evaluation then results in perceiving piloerection as pleasurable. By highlighting the perception of *safeness* and secure attachment, this theory could also be considered to indirectly build on thermoregulation

Table 1
Overview of different theories explaining emotional piloerection.

Theory	Type	Elicitor	ANS	Valence	Main source
Separation call	Thermoregulation	Coldness/sadness highlighting need for social reunion	SNS/PNS	−	(Panksepp, 1995)
Being Moved	Emotional Activation/Thermoregulation	Increased social closeness/morality	SNS/PNS	+(−)	(Konečni, 2005; Zickfeld, Schubert, Seibt & Fiske, 2019)
Peak Arousal	Emotional Activation	Surpassing threshold in emotional/physiological arousal	SNS	+/−	(Benedek and Kaernbach, 2011)
Vigilance/Contrastive Valence	Emotional Activation/Thermoregulation	Contrast between fear appraisal and *safe* stimuli	SNS	+(−)	(Huron, 2008)
Knowledge Acquisition	Emotional Activation	Maximum in Dis/Similarity between Mental Representations and External World	SNS/PNS	+/−	(Schoeller, 2015)

Note: ANS = Autonomic nervous system; SNS = sympathetic nervous system; PNS = parasympathetic nervous system; − = negative valence; +/− = negative and positive valence; +(−) = predominantly positive valence.

processes.

This vigilance perspective is loosely based in an evolutionary explanation involving fight-or-flight and attention mechanisms (Bannister, 2020). Essentially, the idea is that changes in the environment require attention due to the possibility of danger. For example, increased volume is associated with approaching agents, and changes in tempo or the introduction of new sounds may signal some new danger in one's environment. Broadly, this would suggest that attention and aspects of knowledge (e.g., surprise, uncertainty) are the key experiences that would activate the SNS and yield piloerection. However, the exact mechanisms and processes have not been proposed by these theorists.

A final explanation, labelled *knowledge-acquisition* (or *knowledge-instinct*), argues that piloerection occurs when the similarity between internal mental representations and the external world reaches a maximum (either positive or negative; Schoeller, 2015). This perspective emphasizes that humans strive to acquire knowledge about the external environment and create meaningfulness. Piloerection is either expected to occur when this knowledge is acquired and fully understood or when no information is internalized. It is thereby related to both positive and negative affect depending on the amount of knowledge acquisition. Which physiological activations this perspective would predict is not straightforward. On the one hand, sudden insights, that could be considered as a full acquisition of knowledge regarding a specific phenomenon, have been related to increased SNS activity (Nam et al., 2021). On the other hand, the emotion of awe that is proposed to involve a violation of expectations (Keltner and Haidt, 2003), is associated with PNS activation (Chirico et al., 2017; Shiota et al., 2011) and is often *assumed* to be indicated by piloerection.

3.8.3. Summary

In summary, each of these theories imply that some emotional response may activate the autonomic nervous system, resulting in piloerection. While they do not make explicit predictions about the underlying physiology, these perspectives differ in many ways. First, the basic mechanism differs—that is, whether emotions directly activate the autonomic system or whether they overlap with temperature regulation mechanisms. Second, the theories differ in whether they focus on positive (e.g., calming, pleasurable) or negative (e.g., sadness, aloneness) emotions. Following this point, they also differ in whether they propose that emotional experienced activate the SNS or PNS primarily (see Table 1).

To begin to answer these questions, a review of the available literature is needed. Once we understand how emotional piloerection is working physiologically, we can work backwards and begin to understand the emotional antecedents and functions of this experience. Physiological correlates indicating SNS activation would yield evidence for the peak-arousal and vigilance explanations, whereas evidence showing PNS activation would be more in line with the separation call, being moved, or knowledge acquisition perspectives. Alternatively, piloerection may be associated with both SNS and PNS activation, or with both positively and negatively valenced experiences.

It's important to disentangle the method of physiological activation because a single action can be differentially associated with different physiological patterns depending on other factors, such as the valence of experience. For instance, in a recent study two different type of chills (*vigilance chills* and *social chills*) showed different ANS correlates (Bannister and Eerola, 2021).

However, it's also worth considering that different theories of emotions make different predictions. For example, (social) constructionist perspectives suggest that specific emotions should *not* map on to physiological activation patterns one-to-one (Siegel et al., 2018) and we should instead be focusing on classes of experiences. On the other hand, identifying specific physiological patterns has been a focus of much emotion research (Kreibig, 2010). Many researchers may see piloerection as a possible indicator of some specific emotional state, but an overview of the evidence is needed before any conclusions can be drawn.

4. Systematic review: the physiological correlates of emotional piloerection

Thus far, we have discussed the biological and psychological causes and functions of piloerection. Further, there are different theoretical explanations for why emotions may cause piloerection. However, no systematic review has been conducted so far (though see de Fleurian & Pearce, 2020a for a systematic review on musically evoked chills). Thus, it is difficult to determine the consistent and inconsistent correlates of piloerection without a birds-eye view of the literature.

The goal of this review is not to identify average effect sizes or evaluate statistical significance; meta-analysis has issues that are often insurmountable, especially with small sample sizes (Vosgerau et al., 2019). Rather, the goal here is simply to collate the studies and provide an overview of 1) the research that has been conducted, 2) the measures that are being used most and least often, and 3) the most consistent physiological correlates of emotional piloerection. Following this, we can move forward and determine the outstanding questions and how those questions should be answered.

4.1. Method

4.1.1. Procedure

We conducted two independent literature searches on PsycARTICLES and PsycINFO. The first author performed a first search in summer 2020 using the keywords "Piloerection OR goosebump* OR chills AND physiolog*" on PsycARTICLES. On PsycINFO, the terms "physiological arousal OR physiological psychology OR physiological correlates" (from their pre-specified list of phrases) were selected in place of *physiolog**. The first author also searched on *PsyArXiv* but uncovered no additional articles that met the inclusion criteria. The second author performed an additional independent search on the 5th of November 2021 using the same keywords as in the first search, but adding *horripilation, frisson,* and *goose pimples*.

Results were pre-screened by each author independently and relevant articles were downloaded and further examined according to the criteria described below. Throughout the review process, any additional eligible articles were included and are noted as "other sources". This protocol was not preregistered, though we report all articles found in the Supplementary Material and reasons for exclusion (see Tables S1-S2). The PRISMA flow chart is depicted in Fig. 1 and the summary of the final included articles is presented in Table 2.

4.1.2. Eligibility

A study was included if it 1) examined human participants, 2) used psychological stimuli to attempt to elicit piloerection/chills/goosebumps, and 3) reported the co-occurrence of piloerection/chills/goosebumps and any physiological indicators. Studies which did not include other objective physiological indicators were excluded along with studies that were designed to investigate other correlates. For example, Zickfeld et al. (2020) examined the physiological correlates of kama muta so, while piloerection was observed sometimes, the stimuli were not specifically designed to elicit piloerection. Finally, qualitative studies were also excluded as these could not quantitatively assess physiological data.

4.2. Results

4.2.1. Screening

The first search identified 1268 articles ($n = 1216$ PsycINFO, $n = 42$ PsycARTICLES, $n = 10$ other sources). In total, 79 articles were retained after screening, resulting in 75 articles after duplicates removed. The second search identified 706 articles and retained 57 full-text articles after excluding 19 duplicates (both searches retained 97 individual full-
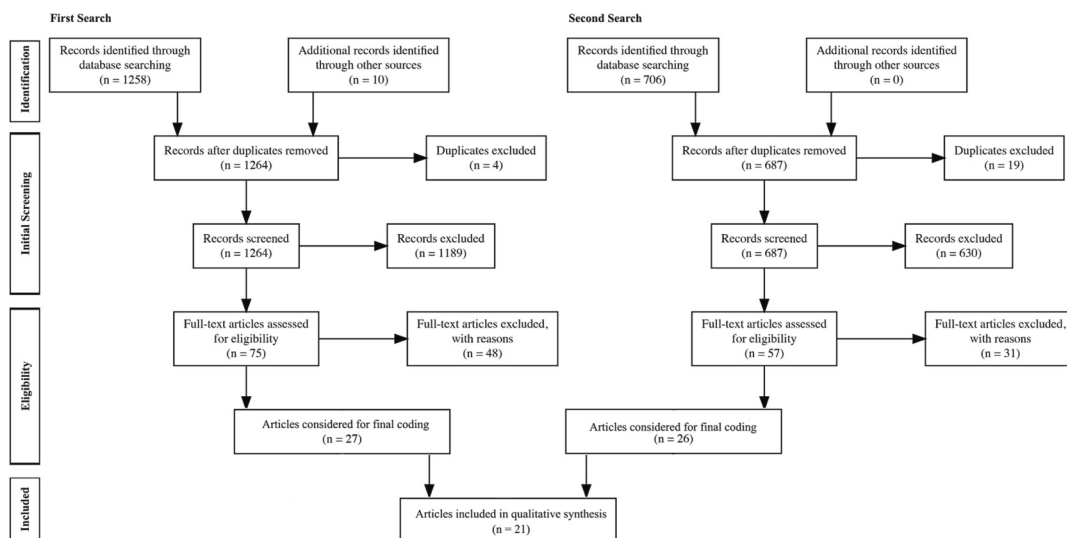
Fig. 1. PRISMA diagram depicting the search and review process.

text articles). Of all articles, the same 32 articles were retained by both searchers and the authors reached the same decision for final inclusion in all except one instance (Cohen's kappa = 0.93). After full-text screening, the first author coded 27 articles from the first search and the second author coded 26 articles from the second search. A total of 30 different articles were coded across both searches. We realized after coding that of these 30 articles four articles used skin conductance responses to validate chills (a self-reported chill was only defined as such if it occurred with an electrodermal response), four articles did not employ stimuli to induce chills specifically, and one article focused mostly on ASMR responses. Therefore, 21 final articles were retained and coded from both searches. Overall, the authors indicated the same coding in 86 % of all instances (same codes in 111 out of 129 instances) for these 21 articles. Differences in coding were resolved through discussion.

The final review included 24 studies from 21 articles. An overview is provided in Table 2. For each study, we searched through the article to find a report of the relevant physiological measure. Physiological measures were grouped into cardiovascular, electrodermal, respiratory, temperature-related, and *other* changes based on previous studies (e.g., Siegel et al., 2018). We recorded the outcome of the piloerection/chills condition in contrast to a baseline or control condition. We recorded whether effects were statistically significant or not and if yes, whether they showed in increase or decrease in the specific physiological measure.[2] Finally, we summarised the self-reported emotions measures from each study in Table 3.

Note. The total number of screened articles does not reflect the sum of both searches since both searchers may include the same article. Since we only recorded full-text articles assessed in the first search, we are not able to quantify the total amount of articles across both searches. Note that the final number of studies included is k = 24.

4.2.2. Study details

Articles were recently published ranging from 2001 to 2021 in publication year and included small sample sizes ranging from a total of 10 to 95 participants ($M = 38.25$, $SD = 19.07$). Such small sample sizes might severely limit the effects one is able to obtain with a high power. As an example, a sample size of 40 will be sensitive for detecting correlation effects at $r = 0.52$, or between-subjects differences (e.g., in an experiment with two groups of 20) of $d = 1.17$ given a power of 95 % (and an alpha level of 0.05). These effects are very large—much larger than the average psychological effect (Funder and Ozer, 2019; Gignac and Szodorai, 2016)—and small samples inflate effect sizes (Button et al., 2013; Ioannidis, 2008; Rochefort-Maranda, 2017). As a result, it is likely that some associations are spurious (or may even have been missed) due to the sample size.

4.2.3. Stimuli

The most popular stimuli used was music ($k = 21$); though four studies used music in combination with some other stimuli (mainly film clips). One study used video stimuli, one used poetry, one used the recall of emotional events, and auditory, tactile, and gustatory stimuli.

4.2.4. Type of construct

The majority of studies ($k = 21$) focused on chills or different variants thereof. For instance, Bannister & Eerola (Bannister and Eerola, 2021) differentiated between *social* and *vigilance chills* and Sumpf et al. (Sumpf et al., 2015) distinguished between chills with and without piloerection. Only five studies focused on piloerection specifically.

4.2.5. Piloerection measure

Overwhelmingly, studies relied on self-reported chills ($k = 23$). Only five studies measured piloerection objectively; four of those also included a self-report measure.

Physiological correlates.

4.2.6. Cardiovascular changes

As can be seen in Table 2, the majority of studies ($k = 16$) included some type of cardiovascular measure. In all instances, heart rate was assessed, pulse volume amplitude in three instances, and flattened emotionality in one article. In eleven of those instances, the study reports an increase in heart rate. This was observed in eight out of 12 studies using self-reported chills; and in 3 out of 4 studies using objective piloerection measures. Sumpf et al. (2015) provided a direct comparison between self-reported chills with and without piloerection and found a significant increase in heart rate only for responses including objective piloerection. The other cardiovascular measures show mixed results. For example, three studies report pulse volume amplitude; two reported a

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[2] We acknowledge that this approach has some drawbacks, as a study might uncover a strong effect size (and potentially practical significant effect) that is not statistically significant due to low power and a small sample size (which is common for physiological studies). However, the majority of studies did not report effect sizes, so focusing on them might have resulted in more exclusions. Further, most studies have similar sample sizes, so power (and therefore effect size cutoff) can be expected to be similar. Also note that a statistically non-significant effect does not equal the absence of an effect (Lakens et al., 2018).

Table 2

Physiological correlates of emotional piloerection as identified through a systematic review of the literature. (+) indicates that piloerection or chills was associated with a stat. Significant increase in that measure; (−) indicates that piloerection or chills was associated with a significant decrease in that measure; (ns) indicates that piloerection or chills was associated with no statistically significant change in that measure; SR = self-report; HR = heart rate; PVA = pulse volume amplitude; BVP = blood volume pulse; Eκ = flattened emotionality; SCL = skin conductance level; SCR = skin conductance response; RR = respiratory rate; RD = respiratory depth; ST = skin temperature; EMG = electromyography; corr = corrugator supercilii; zyg = zygomaticus major.

Study details				DV		SR	Cardiovascular			Electrodermal		Respiratory		Temperature	Other
Author(s)	Year	N	Stimuli	Type	Objective Piloerection	SR	HR	PVA/BVP	Eκ	SCL	SCR	RR	RD	ST	
Bannister & Eerola	2018	24	Music	Chills		X				+	+				
Bannister	2020	40	Music	Chills		X					+				
Bannister & Eerola	2021	44	Music	Vigilance Chills		X				+	+			−	
Bannister & Eerola	2021	44	Music	Social Chills		X				ns	ns			ns	
Benedek & Kaernbach	2011	50	Music/Film	Piloerection	Goosecam	X	ns	ns		ns	+	ns	+		
Blood & Zattore	2001	10	Music	Chills		X	+			ns[a]			+	ns	+ (EMG)
Craig	2005	32	Music	Chills/Piloerection	Observation					+[a]				ns	
Grewe et al	2009	95	Music	Chills		X	+			+	+	ns			
Grewe et al	2011	36	Pictures/Music/Sounds/Tactile/Gustatory/Recall	Chills		X	ns/+[b]				+	ns			
Guhn et al	2007	27	Music	Chills		X	ns				+				
Laeng et al	2016	52	Music	Chills		X									+ (pupil diameter)
Mori & Iwanaga	2014	32	Music	Chills		X				+	+	ns			
Mori & Iwanaga	2015 (Study 2)	32	Music	Chills		X					+				
Mori & Iwanaga	2017	32	Music	Chills		X	ns			+	+	ns	+		
Mori & Iwanaga	2021 (Study 1)	20	Music	Chills		X	+				+	+			
Mori & Iwanaga	2021 (Study 2)	34	Music	Chills		X	ns				+	+			
Polo	2017	71	Music	Chills		X	+				+				
Salimpoor et al	2009	26	Music	Chills		X	+	−		+		ns		ns	
Salimpoor et al	2011	10	Music	Chills		X	+	−		+		+		−	
Starcke et al	2019	39	Music	Chills		X	+			−					
Sumpf et al	2015	58	Music/Film	Chills w/o Piloerection		X	ns		ns			ns			
Sumpf et al	2015	58	Music/Film	Chills w Piloerection	Goosecam	X	+		+						
Wassiliwizky & Jacobsen et al	2017a	25	Videos	Piloerection	Goosecam	X	+				ns	ns			+ (corr); ns (zyg)
Wassiliwizky & Koelsch et al	2017b	27	Poems	Piloerection	Goosecam	X	+				+				+ (corr); ns (zyg)

N is reported before any exclusions.

[a] Electrodermal measure not specified (GSR).

[b] + for some stimuli, ns for the majority.

decrease, and one found no statistically significant effect.

4.2.7. Electrodermal changes

Nearly all of the studies included a measure of electrodermal activity: ten studies included a skin conductance level (tonic) measure, 16 studies included a skin conductance response (phasic) measure, and two studies did not specify the exact type of electrodermal measure. Fourteen out of the 16 studies report a significant increase in phasic electrodermal activity and seven out of ten studies report a significant increase in tonic activity. This is the most consistent correlate identified through this analysis: both self-reported chills and objectively recorded piloerection were associated with an increase in (phasic) electrodermal response around the time period of the incident. Bannister and Eerola (2021) reported evidence that phasic activity differed for specific types of chills, with *social chills* showing no significant effect with regard electrodermal responses. It is unclear whether these responses also involved piloerection though.

4.2.8. Respiratory & temperature changes

Of the 11 studies measuring respiration rate, three showed a significant change, but the majority of eight reported no statistically significant effect. For respiration depth, all three studies reported a statistically significant increase. Five studies explored temperature related changes and found no statistically significant effect in four instances and a decrease in one study. Note, that skin temperature measurements were performed at different locations (e.g., finger, palmar surface, left upper arm) and therefore might not be comparable, as there has been found different degrees of variability in temperature (e.g., Zaproudina et al., 2008).

4.2.9. Other changes

Additionally, facial electromyography measures in two studies revealed an increase in corrugator but not increase in zygomaticus activity. One study—(Blood and Zatorre, 2001) found an increase in muscle contractions, but did not report the location of EMG measurement. Finally, another study reported an increase in pupil diameter (Laeng et al., 2016).

Mori and Iwanaga (2014) also looked at the influence of resting respiratory sinus arrhythmia and inter-beat intervals on subsequent chills, finding that these measures, typically indicating PNS activation,

Table 3
Self-reported emotions associated with chills and goosebumps according to study.

| Author | Year | Valence & arousal | | | High arousal | | | | | | | | | |
| | | | | | Negative valence | | | | | | | Positive valence | | |
		Valence	Pleasantness	Arousal	Agitated	Alertness	Anxiety	Fear	Nervous	Perturbed	Tense	Amused	Emotional intensity	Energetic
Bannister & Eerola	2018										ns		+	ns
Bannister	2020				ns				ns					ns
Bannister & Eerola	2021												nr	
Benedek & Kaernbach	2011	ns		ns										
Blood & Zatorre	2001		nr										nr	
Craig	2005					+	−				−			
Grewe et al	2009	+		+										
Grewe et al	2011	-/+[c]	nr	+/ns[d]									nr	
Guhn et al	2007													
Laeng et al	2016													
Mori & Iwanaga	2014	+		ns										
Mori & Iwanaga	2015	+		+									+	
Mori & Iwanaga	2017	+		+				+						
Mori & Iwanaga	2021 (S1)	ns		+										
Mori & Iwanaga	2021 (S2)	nr		ns										
Polo	2017													
Salimpoor	2009	+		+										
Salimpoor	2011													
Starcke	2019													
Sumpf et al	2015	+								ns	+	+	+	+
Wassiliwizky & Jacobsen	2017a													
Wassiliwizky & Koelsch	2017b													

Note: ns = not significant; nr = not reported. Categorization of emotion terms with regard to valence and arousal based on (Barrett, 2004; Feldman Barrett and Russell, 1998).

a For vigilance chills.
b For social chills.
c Positive for music, negative for sounds and pictures.
d Positive for music, ns for sounds and pictures.

predict the experience of self-reported chills negatively. These findings should be explored further in future research.

Finally, three studies investigated neural correlates (Blood and Zatorre, 2001; Salimpoor et al., 2011; Wassiliwizky, Koelsch, et al., 2017). Though this was not the intended focus of the present review, neural correlates represent an area of interest for future investigations and those reports may be useful as a starting point.

4.3. Discussion

This systematic review revealed that emotional piloerection (or goosebumps or the chills), as investigated in 24 studies (and 21 articles), co-occur with an increase in electrodermal, most commonly phasic activity, and heart rate. We also observed frequent non-significant effects for respiratory rate and skin temperature changes. In summary, the evidence points towards emotional stimuli activating the SNS. However, direct evidence for or against PNS activation has not been adequately tested: only one study (Mori and Iwanaga, 2014) investigated *resting* respiratory sinus arrhythmia, an index believed to indicate PNS activity. In addition, all three studies showed a significant increase in respiratory depth, which has been related to increased PNS activity. We can mainly indirectly infer decreased PNS activation due to findings of increased cardiovascular and electrodermal activity.

Notably, we did not observe any systematic differences between piloerection and (subjective) chills. This might be due to the fact that the majority of chills studied also involved instances of piloerection or that the physiological basis of both responses is rather similar. More specific evidence could only be derived from one study exploring the difference between chills with or without piloerection (Sumpf et al., 2015), mainly observing a difference in cardiovascular activity.

4.3.1. Indicators of SNS versus PNS activation

The studies included in this review identified mostly indicators of SNS activation; only one study looked at more direct indicators of PNS activation (Mori and Iwanaga, 2014) which were however resting RSA and IBI. In addition, three studies reported measuring respiratory depth,[3] which has been associated with increases in heart rate variability (Laborde et al., 2017), but there is not enough evidence to make any conclusive statements. Thus, as mentioned previously, emotional piloerection seems to be associated with (phasic) SNS activation. However, limited conclusions can be drawn concerning PNS activity.

Researchers may benefit from a focus on PNS activation because experiences associated with goosebumps are often believed to be calming (Mori and Iwanaga, 2014) and are associated with positive, low-arousal emotions (Chirico et al., 2017; Shiota et al., 2011).

4.3.2. Emotional antecedents

Regarding emotional antecedents, there is not enough research available to evaluate the specific emotions associated with the occurrence of emotional piloerection. Emotional adjectives were not measured in every study and, where they were, the adjectives used varied widely. The summary of emotions across studies is provided in Table 3.

4.3.3. Discrete emotions

Many studies considered the emotion of *being moved* as indicative of

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[3] The consistent finding on respiratory depth seems noteworthy, as it might suggest that breathing plays an important role in the experience of piloerection or chills. However, it should be highlighted that there are too few studies assessing respiratory depth and previous self-report findings focusing on voluntarily generated piloerection found no association of breathing with producing piloerection (Heathers et al., 2018; Katahira et al., 2020).

| High arousal | | | | Low arousal | | | | | | | | | | |
| Positive valence | | | | Negative valence | | | Positive valence | | | | | | | |
Enjoyment	Happy	Inspiring	Joy	Powerful	Melancholic	Sad	Affection	Awe	Being moved	Calm	Nostalgia	Relaxing	Sentimental	Tender
nr	ns	ns		ns		ns			+	ns				
ns			ns			ns	ns		ns		ns		ns	ns
nr								+[a]	+[b]					
									+					
	+					+				ns				
									ns					
									ns					
	+	+			+	+				ns				+

emotional piloerection (Bannister and Eerola, 2021; Benedek and Kaernbach, 2011; Mori and Iwanaga, 2017, 2021a; Wassiliwizky, Jacobsen, et al., 2017) providing some theoretical evidence for the perspective that piloerection is tightly linked to this emotional experience. However, only a few studies asked participants to report discrete emotions, and these emotions varied across studies (Bannister, 2020; Egermann et al., 2011; Sumpf et al., 2015). Further, there are other studies in which self-reported emotions were collected (Park et al., 2019; Rickard, 2004; Salimpoor et al., 2009) but correlations with chills were not reported because the study focused on other aspects. As a result, it is premature to determine any consistent correlations between subjective emotions, piloerection, and ANS activation.

Six studies reported associations between emotional piloerection and *being moved*. Two of these found a positive relationship, three no statistically significant relationship, and one defined a specific chill type based on being moved reports. This provides only weak evidence that emotional piloerection would be specifically tied to experiences of *being moved*.

Similarly, two out of four studies reported positive associations between sadness and emotional piloerection, also providing limited evidence for the *separation call* account. In general, emotional piloerection was positively related to experiencing a variety of emotional episodes (see Table 3), suggesting that this bodily reaction is not specific to any emotion.

Different theories of emotions make different predictions about how and why emotions may be related to autonomic activation. For example, social constructionist perspectives suggest that specific emotions should *not* map on to physiological activation patterns one-to-one (Siegel et al., 2018), meaning that piloerection should not be associated with any one specific emotion (speaking against the separation call, being moved, and contrastive valence perspectives). In contrast, classical theories of emotion propose that individual emotions would have specific patterns of physiological activation identifying them (Barrett et al., 2007). This means that piloerection should be associated with some specific emotions more frequently than others (e.g., being moved, awe, sadness). Future research will be needed to navigate between these perspectives.

4.3.3.1. Valence. Putting aside discrete emotions, these studies can tell us something about the qualities of emotions. For example, one study reported that negatively valenced music elicited arousal *and* piloerection, while positively valenced music elicited piloerection only (Grewe et al., 2007b).

Eleven studies included a self-report measure of valence (or *pleasantness*; with higher scores indicating *pleasantness*; Table 3), of which seven reported positive associations, one reported a negative association, and the remainder did not report statistically significant associations (or did not report any associations). This could be considered evidence that stimuli eliciting chills or piloerection is positively valenced. Such an observation would speak against the separation call hypothesis and more for the being moved and contrastive valence accounts.

Alternatively, there may not be a specific valence of emotional experience associated with piloerection as suggested by the peak arousal or knowledge acquisition theories. Kreibig (2010) noted that *surprise* does not have a clear valence connotation, yet it is associated with a skin conductance response and an increase in heart rate. More systematic research on (objective) measures of valence in response to emotional piloerection is needed.

4.3.3.2. Arousal/emotional intensity. Finally, we observed that thirteen studies measured self-reported arousal or emotional intensity. For arousal, these reported a positive association with emotional piloerection in six out of nine cases, a negative relationship in one, and statistically non-significant findings for the remaining two. For emotional intensity, this showed a positive association with emotional piloerection in three studies and the specific association was not reported in the remaining three cases. These findings partly replicate the physiological data showing that emotional piloerection occurs in response to increased SNS activity and lending partial support to the *peak arousal* and *contrastive valence* perspective.

4.3.4. Measurement objectives

It must be noted again that the majority of the published research did not objectively measure piloerection. Instead, most research measured self-reported goosebumps or chills response. At the same time, it should be emphasized that there is quite a lot of similarity in the physiological

correlates between the studies investigating *chills* and *piloerection*. Thus, despite evidence that subjective measures show only weak relations to objective measures of piloerection (Benedek and Kaernbach, 2011; McPhetres and Shtulman, 2021), the two phenomena demonstrate similar SNS activity providing some further evidence that they might be strongly related phenomena (Maruskin et al., 2012) or that the majority of subjective chills responses studied also included some actual piloerection responses.

4.3.5. Theoretical considerations revisited

Above, we discussed five types of theories: separation-call, being moved, peak arousal, contrastive valence, and knowledge acquisition. These theories also differed in the valence of the emotions and the specific ANS activity associated with emotional piloerection. As mentioned earlier, the main body of literature suggests that emotional piloerection shows an increase in SNS activation as indexed by increased heart rate and (phasic) electrodermal activity. This finding would mainly provide support for the peak arousal and contrastive valence explanations. However, two studies (Wassiliwizky, Jacobsen, et al., 2017; Wassiliwizky, Koelsch, et al., 2017) measuring valence via facial EMG observed only significant increases in corrugator activity, typically associated with negative valence, but not increased zygomaticus activity during emotional piloerection. This observation would speak against the contrastive valence perspective, though the amount of evidence is limited with only two out of 24 studies testing fEMG. Similarly, self-reported pleasantness ratings showed positive correlations with emotional piloerection in the majority of studies, which might provide evidence against the separation call hypothesis. Another observation supporting a peak arousal account would be the fact that several studies theoretically define chills by increases in physiological arousal (Beier et al., 2020a; Colver and El-Alayli, 2016; Egermann et al., 2011; Grewe et al., 2007a). In these studies, a self-reported chill response is only considered as valid if it also occurs with a skin conductance response. Similarly, the fact that piloerection has been associated with a range of positive and negative emotions (see Table 3) would further support the peak arousal hypothesis.

However, there are two main shortcomings in the present literature which preclude any clear conclusions. In the studies reviewed here, researchers have focused almost exclusively on indicators of SNS activation and have employed specific PNS measures less frequently. Thus, there is not enough evidence to adequately compare these perspectives based on the physiological correlates available in the published literature. It is indeed possible that emotional piloerection involves a co-activation of the SNS and PNS, thereby providing support for the remaining theoretical perspectives. Additionally, as discussed above, there is not enough evidence to come to conclusions about emotional antecedents. Nevertheless, this review can provide us with a host of information about the research that has been conducted. Particularly, this review can tell us about the useful indicators of SNS activation, emotional qualities, measurement objectives, and can help to identify future directions.

5. The future of piloerection research

The information reviewed thus far is intended to be a comprehensive but accessible overview of the current knowledge of piloerection. We have discussed evidence on the biological mechanisms and functions of piloerection and have outlined the available evidence concerning its psychological mechanisms. Digesting the above information yields many interesting and exciting questions. Additionally, there are some important limitations that must be considered. Therefore, the goal of this section is to outline the pressing questions for future goosebumps research and to provide an overview of how one can study the phenomenon.

5.1. What are the pressing questions?

It is clear that the remaining questions concern the explicit physiological similarities and differences between non-emotional and emotional piloerection. For example, the biological function of the arrector pili muscle is quite well understood, as are the ways in which body processes temperature-related information. Yet, this system is somehow co-opted by cognitive and perceptual information. Thus, we expect that the one fruitful future research will be attempting to identify the biological mechanisms underlying the psychological experience. Below we outline a few interesting questions, which we hope spark ideas in interested researchers.

5.1.1. Voluntary goosebumps

Darwin (1872), while having noted the apparent non-conscious function of piloerection, could not help but notice that the arrector pili muscles also seem to be under the control of voluntary muscles simultaneously. Much more recent research has also remarked on this puzzlement (Grewe and Kopiez, 2010; Heathers et al., 2018; Katahira et al., 2020a; Muzik et al., 2018): humans should not be able to control the autonomic system consciously.

However, it is worth considering that some animals can exhibit piloerection in ways that seem to be voluntary. For example, birds can also raise their feathers for self-cleaning (Homberger and Silva, 2000) and several aspects of peacock courtship rituals appear to be purposeful and complex (Dakin et al., 2016; Dakin and Montgomerie, 2009). The ability to piloerect for mating displays or to make themselves appear larger in response to a threat also seems to have purposeful elements (Morris, 1956; Yorzinski and Platt, 2012).

The ability of some humans to consciously piloerect suggests even more similarity between humans and non-human animals. Humans are, of course, mammals, so perhaps a vestigial system remains in some humans. In depth study of the people who are able to voluntarily control piloerection may provide answers to these questions (Benedek et al., 2010; Heathers et al., 2018; Katahira et al., 2020b).

5.1.2. Chills and piloerection

As noted previously, most of the research has been conducted by asking people to self-report chills or goosebumps. Some research finds that self-reports are much more frequent than objective piloerection (McPhetres and Shtulman, 2021). Yet, according to the systematic review above, chills seem to be associated with a similar pattern of physiological correlates. Are chills just unobserved instances of piloerection? What are the neurological mechanisms of chills and how are they different from observable piloerection? Does piloerection include more subjective components (e.g., tingling in the spine, chills) than what has previously been considered? Future research can begin to answer these questions.

5.1.3. Directionality

One important question relates to the direction of the relations between perception and physiology. Organisms take in information about the world through sensory organs, and that information influences how the organism functions. Indeed, emotions are posited to interrupt systematic processing and reorder priorities (Simon, 1967): when one visually perceives a threat, one's body responds accordingly. However, this also suggests that emotions can influence perceptions (Zadra and Clore, 2011) because an object in the environment must be evaluated in context of the current situation—an evaluation partly determined by one's emotional and physiological state. A classic issue in psychology is the concept of *embodiment*: the idea that aspects of cognition are shaped by bodily functions much in the same way that cognition shapes bodily functions (Harris et al., 2015).

Accordingly, some research has suggested that artificially inducing piloerection creates the feeling of surprise in research subjects (Fukushima and Kajimoto, 2012). Other researchers have "embodied"

certain physiological signals and created a wearable suit which communicates the experience of awe and piloerection (Neidlinger et al., 2019). One possible avenue for future research may be to explore exactly how piloerection is connected to perceptions by considering these alternative directionalities.

5.1.4. Emotional correlates

As discussed above, identifying the emotional antecedents of piloerection is an aim of much research. Different theoretical perspectives on emotions propose oppose possibilities: that specific emotions may or may not show a one-to-one relation with physiological activation patterns. Given the mixed evidence from the review above, future research should try to include consistent measures of discrete emotions in order to address this question.

Some research regarding piloerection and emotions is quite well developed but would not have been included in this review because it did not involve other physiological measures. A future systematic investigation could investigate a broader set of studies focusing only on emotional correlates. Such a task is outside the scope of the present review but may yield more information on self-reported emotions.

5.1.5. Genetic candidates and neurochemical mechanisms

Some of the neurochemical mechanisms of how piloerection functions have been identified. However, these mechanisms have not been investigated in emotional piloerection. That is, it remains unclear whether emotional piloerection works through the same or different pathways—this is an important area for future research to explore. There are several resources which provide an overview of the genetic mechanisms involved in piloerection, and this research has identified some specific receptors that may be involved. However, this research is still in progress (e.g., Fujiwara et al., 2011; Guipponi et al., 2007; Rouillard et al., 2016).

Additionally, the known innervation pathways imply that specific neurotransmitters will be involved at certain stages of the physiological response (e.g., norepinephrine as discussed by Laeng et al., 2016). Thus, future research can investigate whether these pathways are the same in both non-emotional and emotional piloerection, as well as in voluntary and non-voluntary piloerection. Such an investigation could use in situ or in vitro measurements of neurotransmitters, hormones, or other biosignals such as nerve conduction.

5.2. How do we study emotional piloerection?

In order to begin to answer the above questions, we must have a standardised and reproducible methodology and analytic procedure. In this regard, the study of piloerection from a psychological perspective can be optimized. In this section we discuss some limitations with past research, as well as some methodological strengths.

5.2.1. Limitations

A first step in understanding *how* one can study emotional piloerection is to understand where the shortcomings are. We first identify and briefly discuss two shortcomings before moving on to discuss methodologies.

5.2.1.1. Limitations of the available evidence.
The psychological literature on emotional piloerection suffers from some important limitations. First, there is very little research to begin with. As can be noted in the systematic review, above, there were only 24 studies that investigated physiological correlates and fit our criteria. Only five of those measured piloerection objectively, and those five studies varied in terms of methodology (e.g., the camera devices were constructed independently, analysis procedures and computation decisions vary, the stimuli were different). Thus, while there is some evidence to rely on, this area of research is almost entirely nascent.

Of the research that does exist, there is little standardisation in terms of methodology. For example, despite the availability of various objective measurements of piloerection (to be discussed below), the majority of research has examined self-reported chills.

A final limitation is that researchers in biological psychology and psychophysiology have been slow to implement open and transparent practices (Mayo-Wilson et al., 2021). See for example the TOP factor scores, which evaluates journals on their implementation of eight transparency standards (https://topfactor.org/journals). Tools like preregistration and norms around sharing data, code, and materials will only improve the quality of research on this topic and we encourage researchers to adopt these practices.

5.2.1.2. Limited uptake of biological theory.
An additional shortcoming is that the psychological literature has incorporated very little evidence or theory from the biological literature. Despite the fact that humans are animals and share common ancestors and biology, psychological studies on piloerection occur almost entirely in isolation from other bodies of theory. For example, self-reported goosebumps are often discussed in terms of broad social and emotional theories (e.g., awe, being moved) or are very loosely connected to "evolutionary explanations" (e.g., vigilance, fight-or-flight). It is unclear how well such perspectives relate to the biological processes occurring. Clearly, an interesting question is how human perception and cognition influence physiological processes. To answer this question will require the synthesis of evidence and theories from multiple areas of research.

5.2.2. Measurement

Several options for the objective measurement of piloerection exist. However, all of these options are used relatively infrequently and all of them lack more efficient standardisation and reproducibility in the workflow. Thus, one issue for future research to alleviate will be to standardise an efficient and reproducible workflow.

5.2.2.1. Goosecam.
Benedek et al. (2010) designed a MatLab program (*Gooselab*; http://www.goosecam.de/gooselab.html) and recording device (*Goosecam*), which analyses video of a subject's skin for the visual occurrence of goosebumps. This is the most widely adopted measurement system (e.g., Katahira et al., 2020b; McPhetres and Shtulman, 2021; Quesnel and Riecke, 2018; Sumpf et al., 2015; Wassiliwizky, Jacobsen, et al., 2017; Wassiliwizky, Koelsch, et al., 2017; Zickfeld et al., 2020). In general, it is quite simple and affordable. The program has recently been updated for more recent versions of MatLab.[4]

However, the workflow is flexible and is not entirely reproducible. Based on private communications with researchers who have implemented this software, large variations in equipment use, methodological choices, and analytic decisions are made. Thus, many authors are using very different protocols despite the same method. This means that 1) it is difficult for naïve researchers to adopt this protocol without training, and 2) it is unclear exactly how much this variation affects research results and conclusions.

5.2.2.2. Location of the recording device.
Researchers have recorded the occurrence of piloerection at several bodily locations. Most researchers (Benedek and Kaernbach, 2011; McPhetres and Shtulman, 2021; Quesnel and Riecke, 2018; Sumpf et al., 2015; Zickfeld et al., 2020) placed the camera on the non-dominant forearm or visually observed the arm (Craig, 2005). Wassiliwizky and colleagues (Wassiliwizky, Jacobsen, et al., 2017; Wassiliwizky, Koelsch, et al., 2017) placed the camera on the leg above the calf muscle. One study reports that chills and/or goosebumps are most likely to occur on the legs (Wassiliwizky et al.,

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[4] The most stable release working on at least up to MatLab 2021 can be found at: https://github.com/DurhamARC/gooselab.

2015), but this has not been tested empirically using objective measures.

While it seems premature to us to make any specific recommendations with regard to measurement methods or placement locations, it should be noted that recording the forearm with the Goosecam has been the most frequently used approach. Similarly, self-report evidence on voluntarily generated goosebumps suggest that piloerection was experienced most frequently on the arms (Heathers et al., 2018). Future studies would need to systematically compare different measurement approaches or placement locations in order to investigate the most valid option to measure piloerection objectively.

5.2.2.3. Image-based measurement. Similar to the goosecam, Uchida et al. (2018) describe a program which analyses changes in skin texture (e.g. the sulcae cutis) by means of a greyscale conversion. This has not yet been applied in any experimental research and attempts to contact the authors to access the code have not been successful.

5.2.2.4. Flexible skin sensor. Kim et al. (2014) describe a flexible skin capacitor which detects piloerection. While promising and technologically feasible, this device has not been used in any experimental research, nor has it been cited in any applied research articles.[5] However, another flexible skin sensor is in development which allows for distinguishing phasic changes based on the presence of piloerection (Jing et al., 2022).

5.2.2.5. Stimuli. After having determined how one will measure piloerection, it is important to be able to elicit it consistently. As noted in Table 2, researchers use a variety of stimuli to elicit the chills and piloerection—the most commonly used is music. However, there are many types of stimuli that are believed to elicit piloerection and an important goal of future research will be to narrow down the characteristics of the stimuli.

For example, Panksepp (1995) posits that specific acoustic qualities and dynamics may cause piloerection because of their similarity to distress calls of wild animals. A few studies describe in-depth analyses of the stimuli used in their research (Beier et al., 2020b; Guhn et al., 2007; Mori and Iwanaga, 2021b; Quesnel and Riecke, 2018; Wassiliwizky, Jacobsen, et al., 2017). However, future research could benefit from continued anlaysis of the visual and acoustic characteristics of effective stimuli.

Additionally, most of the research allows subjects to select their own stimuli from a pre-determined list or to provide their own stimuli, claiming that this helps increase the chance of observing piloerection (Craig, 2005). A few papers examine this (e.g., Benedek and Kaernbach, 2011; Mori and Iwanaga, 2021a; Wassiliwizky, Koelsch, et al., 2017) and report no differences in the effectiveness of the stimuli. However, no studies have been designed with the express purpose of testing this hypothesis. Such a study design would be complicated and invokes many related questions: are participants able to identify powerful stimuli on their own? Can participants choose from a pre-determined list? Does the participant need to be completely naïve to the stimuli? Additionally, a very large set of stimuli will be needed in order to generalise across the specific characteristics inherent in the stimuli. On the other hand, other researchers note that the familiarity of the stimuli is not related to its ability to induce goosebumps (Colver and El-Alayli, 2016; Grewe and Kopiez, 2010).

6. Conclusion

To date, a range of interesting research has uncovered details about the causes and mechanisms of emotional piloerection. However, many questions still remain. The most pressing of these questions regard the similarities and differences of non-emotional and emotional piloerection. We suggest here that a focus on the underlying biology and physiology of emotional piloerection will yield interesting and useful insights into the study of emotion.

Particularly, researchers should focus on including measures of PNS activation and self-reported measures of emotion in order to distinguish between possible theoretical explanations. Additionally, neurochemical mechanisms have not been investigated and can yield additional insight into the connection between psychology and physiology.

There are many tools available to researchers who wish to study this interesting phenomenon; we have outlined them here. Simultaneously, there is much work to be done to ensure that the tools are easy to implement and the work is reproducible. We hope that this review serves as a foundation for future research in this area.

CRediT authorship contribution statement

Jonathon McPhetres: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Janis H. Zickfeld:** Formal analysis, Investigation, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare no conflicts of interests.

Data availability

Data is available on the linked OSF page

Data availability

Coding criteria and search result data are available at https://osf. io/mx6yd/.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ijpsycho.2022.06.010.

References

Abbott, D.H., 1984. Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. Am. J. Primatol. 6 (3), 169–186. https://doi.org/10.1002/ajp.1350060305.

Ackerley, R., Saar, K., McGlone, F., Backlund Wasling, H., 2014. Quantifying the sensory and emotional perception of touch: differences between glabrous and hairy skin. Front. Behav. Neurosci. 8 (FEB), 1–12. https://doi.org/10.3389/fnbeh.2014.00034.

Alsene, K.M., Carasso, B.S., Connors, E.E., Bakshi, V.P., 2006. Disruption of prepulse inhibition after stimulation of central but not peripheral α-1 adrenergic receptors. Neuropsychopharmacology 31 (10), 2150–2161. https://doi.org/10.1038/sj.npp.1300989.

Bannister, S., 2019. Distinct varieties of aesthetic chills in response to multimedia. PLoS ONE 14 (11). https://doi.org/10.1371/journal.pone.0224974.

Bannister, S., 2020. In: A Vigilance Explanation of Musical Chills? Effects of Loudness and Brightness Manipulations, 3, pp. 1–17. https://doi.org/10.1177/2059204320915654.

Bannister, S., Eerola, T., 2018. Suppressing the chills: effects of musical manipulation on the chills response. Front. Psychol. 9, 2046.

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[5] Multiple attempts to contact the authors to gain further details about the device have not been successful.

Bannister, S., Eerola, T., 2021. Vigilance and social chills with music: evidence for two types of musical chills. Psychol. Aesthet. Creat. Arts Advance online publication. https://doi.org/10.1037/aca0000421.

Barcaui, C.B., Piñeiro-Maceira, J., De Avelar Alchorne, M.M., 2002. Arrector pili muscle: evidence of proximal attachment variant in terminal follicles of the scalp. Br. J. Dermatol. 146 (4), 657–658. https://doi.org/10.1046/j.1365-2133.2002.04541.x.

Barrett, L.F., 2004. Feelings or Words? Understanding the content in self-report ratings of experienced emotion. J. Pers. Soc. Psychol. 87 (2), 266–281. https://doi.org/10.1037/0022-3514.87.2.266.

Barrett, L.F., Mesquita, B., Ochsner, K.N., Gross, J.J., 2007. The experience of emotion. Annu. Rev. Psychol. 58, 373–403. https://doi.org/10.1146/annurev.psych.58.110405.085709.

Beier, E.J., Janata, P., Hulbert, J.C., Ferreira, F., Beier, E.J., Janata, P., Hulbert, J.C., Ferreira, F., 2020. Psychology of Aesthetics, Creativity, and the Arts Do You Chill When I Chill? A Cross-cultural Study of Strong Emotional Responses to Music Do You Chill When I Chill? A Cross-cultural Study of Strong Emotional Responses to Music.

Beier, E.J., Janata, P., Hulbert, J.C., Ferreira, F., Beier, E.J., Janata, P., Hulbert, J.C., Ferreira, F., 2020. Psychology of Aesthetics, Creativity, and the Arts Do You Chill When I Chill? A Cross-cultural Study of Strong Emotional Responses to Music Do You Chill When I Chill? A Cross-cultural Study of Strong Emotional Responses to Music.

Benedek, M., Kaernbach, C., 2011. Physiological correlates and emotional specificity of human piloerection. Biol. Psychol. 86 (3), 320–329. https://doi.org/10.1016/j.biopsycho.2010.12.012.

Benedek, M., Wilfling, B., Lukas-Wolfbauer, R., Katzur, B.H., Kaernbach, C., 2010. Objective and continuous measurement of piloerection. Psychophysiology 47 (5), 989–993. https://doi.org/10.1111/j.1469-8986.2010.01003.x.

Blood, A.J., Zatorre, R.J., 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. Proc. Natl. Acad. Sci. 98 (20), 11818–11823. https://doi.org/10.1073/pnas.191355898.

Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14 (5), 365–376. https://doi.org/10.1038/nrn3475.

Campero, M., Serra, J., Bostock, H., Ochoa, J.L., 2001. Slowly conducting afferents activated by innocuous low temperature in human skin. J. Physiol. 535 (3), 855–865. https://doi.org/10.1111/j.1469-7793.2001.t01-1-00855.x.

Carlson, A.B., Kraus, G.P., 2019. In: Physiology, Cholinergic Receptors. StatPearls, pp. 2–6.

Chaplin, G., Jablonski, N.G., Sussman, R.W., Kelley, E.A., 2014. The role of piloerection in primate thermoregulation. Folia Primatol. 85 (1), 1–17. https://doi.org/10.1159/000355007.

Chirico, A., Cipresso, P., Yaden, D.B., Biassoni, F., Riva, G., Gaggioli, A., 2017. Effectiveness of immersive videos in inducing awe: an experimental study. Sci. Rep. 7 (1), 1–11. https://doi.org/10.1038/s41598-017-01242-0.

Coleman, S.W., Patricelli, G.L., Borgia, G., 2004. Variable female preferences drive complex male displays. Nature 428 (6984), 742–745. https://doi.org/10.1038/nature02419.

Colver, M.C., El-Alayli, A., 2016. Getting aesthetic chills from music: the connection between openness to experience and frisson. Psychol. Music 44 (3), 413–427. https://doi.org/10.1177/0305735615572358.

Converse, L.J., Carlson, A.A., Ziegler, T.E., Snowdon, C.T., 1995. Communication of ovulatory state to mates by female pygmy marmosets, Cebuella pygmaea. Animal Behaviour 49 (3), 615–621. https://doi.org/10.1016/0003-3472(95)80194-4.

Craig, D.G., 2005. An exploratory study of physiological changes during "chills" induced by music. Music. Sci. 9 (2), 273–287. https://doi.org/10.1177/102986490500900207.

Cullhed, E., 2019. What evokes being moved? Emot. Rev. 12 (2), 111–117. https://doi.org/10.1177/1754073919875216.

Dakin, R., Montgomerie, R., 2009. Peacocks orient their courtship displays towards the sun. Behav. Ecol. Sociobiol. 63 (6), 825–834. https://doi.org/10.1007/s00265-009-0717-6.

Dakin, R., McCrossan, O., Hare, J.F., Montgomerie, R., Kane, S.A., 2016. Biomechanics of the Peacock's display: how feather structure and resonance influence multimodal signaling. PLoS ONE 11 (4), 1–25. https://doi.org/10.1371/journal.pone.0152759.

Darwin, C., 1872. The Expression of Emotion in Man and Animals. John Murray, Albermarle Street.

Davenport, J., 1992. Anatomy and physiology of endotherms. In: Animal Life at Low Temperature. Springer, pp. 88–109.

DeGroot, D.W., Kenney, W.L., 2007. Impaired defense of core temperature in aged humans during mild cold stress. Am. J. Physiol. Regul. Integr. Comp. Physiol. 292 (1) https://doi.org/10.1152/ajpregu.00074.2006.

Dettling, A., Pryce, C.R., Martin, R.D., Döbeli, M., 1998. Physiological responses to parental separation and a strange situation are related to parental care received in juvenile Goeldi's monkeys (Callimico goeldii). Dev. Psychobiol. 33 (1), 21–31. https://doi.org/10.1002/(SICI)1098-2302(199807)33:1<21::AID-DEV3>3.0.CO;2-U.

Donadio, V., Incensi, A., Vacchiano, V., Infante, R., Magnani, M., Liguori, R., 2019. The autonomic innervation of hairy skin in humans: an in vivo confocal study. Sci. Rep. 9 (1), 1–7. https://doi.org/10.1038/s41598-019-53684-3.

Egermann, H., Sutherland, M.E., Grewe, O., Nagel, F., Kopiez, R., Altenmüller, E., 2011. Does music listening in a social context alter experience? A physiological and psychological perspective on emotion. Music. Sci. 15 (3), 307–323.

Feldman Barrett, L., Russell, J.A., 1998. Independence and bipolarity in the structure of current affect. J. Pers. Soc. Psychol. 74 (4), 967.

Fernandez-Duque, E., Mason, W.A., Mendoza, S.P., 1997. Effects of duration of separation on responses to mates and strangers in the monogamous titi monkey

(Callicebus moloch). Am. J. Primatol. 43 (3), 225–237. https://doi.org/10.1002/(SICI)1098-2345(1997)43:3<225::AID-AJP3>3.0.CO;2-Z.

Filingeri, D., Zhang, H., Arens, E.A., 2018. Thermosensory micromapping of warm and cold sensitivity across glabrous and hairy skin of male and female hands and feet. J. Appl. Physiol. 125 (3), 723–736. https://doi.org/10.1152/japplphysiol.00158.2018.

de Fleurian, R., Pearce, M.T., 2021. Chills in music: a systematic review. Psychol. Bull. 147 (9), 890.

Fujiwara, H., Ferreira, M., Donati, G., Marciano, D.K., LInton, J.M., Sato, Y., Hartner, A., Sekiguchi, K., Reichardt, L.F., Watt, F.M., 2011. The basement membrane of hair follicle stem cells is a muscle cell niche. Cell 144 (4), 577–589. https://doi.org/10.1161/CIRCULATIONAHA.110.956839.

Fukushima, S., Kajimoto, H., 2012. Facilitating a surprised feeling by artificial control of piloerection on the forearm. In: ACM International Conference Proceeding Series. https://doi.org/10.1145/2160125.2160133.

Funder, D.C., Ozer, D.J., 2019. Evaluating effect size in psychological research: sense and nonsense. Advances in Methods and Practices in Psychological Science 2 (2), 156–168. https://doi.org/10.1177/2515245919847202.

Gignac, G.E., Szodorai, E.T., 2016. Effect size guidelines for individual differences researchers. Personal. Individ. Differ. 102 (November 2016), 74–78. https://doi.org/10.1016/j.paid.2016.06.069.

Glatte, P., Buchmann, S.J., Hijazi, M.M., Illigens, B.M.W., Siepmann, T., 2019a. Architecture of the cutaneous autonomic nervous system. Front. Neurol. 10 (September), 1–11. https://doi.org/10.3389/fneur.2019.00970.

Glatte, P., Buchmann, S.J., Hijazi, M.M., Illigens, B.M.-W., Siepmann, T., 2019b. Architecture of the cutaneous autonomic nervous system. Front. Neurol. 970.

Goldstein, A., 1990. Thrills in response to music. Physiol. Psychol. 8 (2), 126–129.

Gordon, A.M., Stellar, J.E., Anderson, C.L., McNeil, G.D., Loew, D., Keltner, D., 2017. The dark side of the sublime: distinguishing a threat-based variant of awe. J. Pers. Soc. Psychol. 113 (2), 310.

Granovsky, Y., Matre, D., Sokolik, A., Lorenz, J., Casey, K.L., 2005. Thermoreceptive innervation of human glabrous and hairy skin: a contact heat evoked potential analysis. Pain 115 (3), 238–247. https://doi.org/10.1016/j.pain.2005.02.017.

Grewe, O., Kopiez, R., 2010. Chills in Different Sensory Domains: Frisson Elicited by Acoustical, Visual, Tactile and Gustatory Stimuli. https://doi.org/10.1177/0305735610362950.

Grewe, O., Nagel, F., Kopiez, R., Altenmüller, E., 2007. In: Emotions Over Time: Synchronicity and Development of Subjective, Physiological, and Facial Affective Reactions to Music, 7, pp. 774–788. https://doi.org/10.1037/1528-3542.7.4.774 (4).

Grewe, O., Nagel, F., Kopiez, R., Altenmüller, E., 2007b. Emotions over time: synchronicity and development of subjective, physiological, and facial affective reactions to music. Emotion 7 (4), 774–788. https://doi.org/10.1037/1528-3542.7.4.774.

Grewe, O., Kopiez, R., Altenmüller, E., 2009. The chill parameter: goose bumps and shivers as promising measures in emotion research. Music. Percept. 27 (1), 61–74. https://doi.org/10.1525/mp.2009.27.1.61.

Grewe, O., Katzur, B., Kopiez, R., Altenmüller, E., 2011. Chills in different sensory domains: frisson elicited by acoustical, visual, tactile and gustatory stimuli. Psychol. Music 39 (2), 220–239. https://doi.org/10.1177/0305735610362950.

Guhn, M., Hamm, A., Zentner, M., 2007. Physiological and musico-acoustic correlates of the chill response. Music. Percept. 24 (5), 473–484. https://doi.org/10.1017/CBO9781107415324.004.

Guipponi, M., Tan, J., Cannon, P.Z.F., Donley, L., Crewther, P., Clarke, M., Wu, Q., Shepherd, R.K., Scott, H.S., 2007. Mice deficient for the type II transmembrane serine protease, TMPRSS1/hepsin, exhibit profound hearing loss. Am. J. Pathol. 171 (2), 608–616. https://doi.org/10.2353/ajpath.2007.070068.

Hamalainen, H.A., Warren, S., Gardner, E.P., 1985. Differential sensitivity to airpuffs on human hairy and glabrous skin. Somatosens. Motor Res. 2 (4), 281–302. https://doi.org/10.3109/07367228509144569.

Hanukoglu, I., Boggula, V.R., Vaknine, H., Sharma, S., Kleyman, T., Hanukoglu, A., 2017. Expression of epithelial sodium channel (ENaC) and CFTR in the human epidermis and epidermal appendages. Histochem. Cell Biol. 147 (6), 733–748. https://doi.org/10.1007/s00418-016-1535-3.

Harris, L.R., Carnevale, M.J., D'Amour, S., Fraser, L.E., Harrar, V., Hoover, A.E.N., Mander, C., Pritchett, L.M., 2015. How our body influences our perception of the world. Front. Psychol. 6 (JUN), 1–10. https://doi.org/10.3389/fpsyg.2015.00819.

Heathers, J.A.J., Fayn, K., Silvia, P.J., Tiliopoulos, N., Goodwin, M.S., 2018. The voluntary control of piloerection. PeerJ 2018 (7), 1–20. https://doi.org/10.7717/peerj.5292.

Hellmann, K., 1963. The isolated pilomotor muscles as an in vitro preparation. J. Physiol. 169 (3), 603–620. https://doi.org/10.1113/jphysiol.1963.sp007283.

Hensel, H., 1974. Thermo receptors. Annu. Rev. Physiol. 36, 233–249.

Herrington, L.P., 1951. The role of the piliary system in mammals and its relation to the thermal environment. Ann. N. Y. Acad. Sci. 53 (3), 600–607.

Hijazi, M.M., Buchmann, S.J., Sedghi, A., Illigens, B.M., Reichmann, H., Schackert, G., Siepmann, T., 2020. Assessment of cutaneous axon-reflex responses to evaluate functional integrity of autonomic small nerve fibers. Neurol. Sci. 41 (7), 1685–1696. https://doi.org/10.1007/s10072-020-04293-w.

Homberger, D.G., Silva, K.N.D.E., 2000. Functional microanatomy of the feather-bearing integument: implications for the evolution of birds and avian flight. Am. Zool. 40 (4), 553–574. https://doi.org/10.1093/icb/40.4.553.

Huron, D., 2008. Sweet Anticipation: Music and the Psychology of Expectation. MIT Press.

IJzerman, H., Coan, J.A., Wagemans, F.M., Missler, M.A., van Beest, I., Lindenberg, S., Tops, M., 2015. A theory of social thermoregulation in human primates. Frontiers in Psychology 6. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4404741/.

Inagaki, T.K., Eisenberger, N.I., 2013. Shared neural mechanisms underlying social warmth and physical warmth. Psychol. Sci. 24 (11), 2272–2280.

Ioannidis, J.P.A., 2008. Why most discovered true associations are inflated. Epidemiology 19 (5), 851–859. https://doi.org/10.1097/EDE.ObO.

Jing, Q., McPhetres, J., Kar-Narayan, S., 2022. Development of a Flexible Skin Sensor. Manuscript in Preparation.

Katahira, K., Kawakami, A., Tomita, A., Nagata, N., 2020a. Volitional control of piloerection: objective evidence and its potential utility in neuroscience research. Front. Neurosci. 14 (June), 1–10. https://doi.org/10.3389/fnins.2020.00590.

Katahira, K., Kawakami, A., Tomita, A., Nagata, N., 2020b. Volitional control of piloerection: objective evidence and its potential utility in neuroscience research. Front. Neurosci. 14, 590.

Keltner, D., Haidt, J., 2003. Approaching awe, a moral, spiritual, and aesthetic emotion. Cognit. Emot. 17 (2), 297–314. https://doi.org/10.1080/02699930302297.

Kim, J., Seo, D.G., Cho, Y.H., 2014. A flexible skin piloerection monitoring sensor. In: Proceedings of IEEE Sensors, pp. 847–850. https://doi.org/10.1109/ICSENS.2014.6985132.

Konečni, V.J., 2005. The aesthetic trinity: awe, being moved, thrills. Bull. Psychol. Arts 5 (2), 27–44.

Kreibig, S.D., 2010. Autonomic nervous system activity in emotion: a review. Biol. Psychol. 84 (3), 394–421. https://doi.org/10.1016/j.biopsycho.2010.03.010.

Laborde, S., Mosley, E., Thayer, J.F., 2017. Heart rate variability and cardiac vagal tone in psychophysiological research–recommendations for experiment planning, data analysis, and data reporting. Front. Psychol. 8, 213.

Laeng, B., Eidet, L.M., Sulutvedt, U., Panksepp, J., 2016. Music chills: the eye pupil as a mirror to music's soul. Conscious. Cogn. 44 (Supplement C), 161–178. https://doi.org/10.1016/j.concog.2016.07.009.

Lakens, D., Scheel, A.M., Isager, P.M., 2018. Equivalence testing for psychological research: a tutorial. Adv. Methods Pract. Psychol. Sci. 1 (2), 259–269. https://doi.org/10.1177/2515245918770963, 2515245918770963.

Lister, J., 1853. Observations on the muscular tissue of the skin. J. Cell Sci. 1 (4), 262–268.

Maruskin, L.A., Thrash, T.M., Elliot, A.J., 2012. The chills as a psychological construct: content universe, factor structure, affective composition, elicitors, trait antecedents, and consequences. J. Pers. Soc. Psychol. 103 (1), 135–157. https://doi.org/10.1037/a0028117.

Masuda, Y., Suzuki, M., Akagawa, Y., Takemura, T., 1999. Developmental and pharmacological features of mouse emotional piloerection. Experimental Animals 48 (3), 209–211. https://doi.org/10.1538/expanim.48.209.

Mayo-Wilson, E., Grant, S., Supplee, L., Kianersi, S., Amin, A., DeHaven, A., Mellor, D., 2021. Evaluating implementation of the transparency and openness promotion (TOP) guidelines: the TRUST process for rating journal policies, procedures, and practices. Res. Integrity Peer Rev. 6 (1), 9. https://doi.org/10.1186/s41073-021-00112-8.

McCrae, R.R., 2007. Aesthetic chills as a universal marker of openness to experience. Motiv. Emot. 31 (1), 5–11. https://doi.org/10.1007/s11031-007-9053-1.

McPhetres, J., Shtulman, A., 2021. Piloerection is not a reliable physiological correlate of awe. Int. J. Psychophysiol. 159, 88–93.

Menninghaus, W., Wagner, V., Hanich, J., Wassiliwizky, E., Kuehnast, M., Jacobsen, T., 2015. Towards a psychological construct of being moved. PLoS One 10 (6), e0128451.

Mori, K., Iwanaga, M., 2014. Resting physiological arousal is associated with the experience of music-induced chills. Int. J. Psychophysiol. 93 (2), 220–226.

Mori, K., Iwanaga, M., 2017. Two types of peak emotional responses to music: the psychophysiology of chills and tears. Sci. Rep. 7 https://doi.org/10.1038/srep46063.

Mori, K., Iwanaga, M., 2021a. Being emotionally moved is associated with phasic physiological calming during tonic physiological arousal from pleasant tears. Int. J. Psychophysiol. 159, 47–59.

Mori, K., Iwanaga, M., 2021. Being emotionally moved is associated with phasic physiological calming during tonic physiological arousal from pleasant tears. International Journal of Psychophysiology 159 (December 2020), 47–59.

Morris, D., 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour 9 (2), 75–113.

Muller, M.N., Thompson, M.E., Wrangham, R.W., 2006. Male chimpanzees prefer mating with old females. Curr. Biol. 16 (22), 2234–2238. https://doi.org/10.1016/j.cub.2006.09.042.

Muller, M.N., Kahlenberg, S.M., Thompson, M.E., Wrangham, R.W., 2007. Male coercion and the costs of promiscuous mating for female chimpanzees. Proc. R. Soc. B Biol. Sci. 274 (1612), 1009–1014. https://doi.org/10.1098/rspb.2006.0206.

Muzik, O., Reilly, K.T., Diwadkar, V.A., 2018. "Brain over body"–a study on the willful regulation of autonomic function during cold exposure. NeuroImage 172 (February), 632–641. https://doi.org/10.1016/j.neuroimage.2018.01.067.

Nam, P., Paromita, P., Chu, S.L., Chaspari, T., Woltering, S., 2021. Moments of insight in problem-solving relate to bodily arousal. The. J. Creat. Behav. 55 (4), 1004–1014. https://doi.org/10.1002/jocb.504.

Narisawa, Y., Kohda, H., 1993. Arrector pili muscles surround human facial vellus hair follicles. Br. J. Dermatol. 129 (2), 138–139. https://doi.org/10.1111/j.1365-2133.1993.tb03515.x.

Neidlinger, K., Toussaint, L., Dertien, E., Truong, K.P., Hermens, H., Evers, V., 2019. Emotional prosthesis for animating awe through performative biofeedback. In: Proceedings - International Symposium on Wearable Computers. ISWC, pp. 312–317. https://doi.org/10.1145/3341163.3346939.

Nishida, T., 1997. Sexual behavior of adult male chimpanzees of the Mahale Mountains National Park, Tanzania. Primates 38 (4), 379–398. https://doi.org/10.1007/BF02381879.

Otberg, N., Richter, H., Schaefer, H., Blume-Peytavi, U., Sterry, W., Lademann, J., 2004. Variations of hair follicle size and distribution in different body sites. J. Investig. Dermatol. 122 (1), 14–19. https://doi.org/10.1046/j.0022-202X.2003.22110.x.

Panksepp, J., 1995. The emotional sources of "Chills" induced by music. Music. Percept. 13 (2), 171–207. https://doi.org/10.2307/40285693.

Panksepp, J., 2009. Brain Emotional Systems and Qualities of Mental Life: From Animal Models of Affect to Implications for Psychotherapeutics.

Park, K.S., Hass, C.J., Fawver, B., Lee, H., Janelle, C.M., 2019. Emotional states influence forward gait during music listening based on familiarity with music selections. Human Movement Science 66 (September 2018), 53–62. https://doi.org/10.1016/j.humov.2019.03.004.

Parsons, K., 2014. Human Thermal Environments: The Effects of Hot, Moderate, and Cold Environments on Human Health, Comfort, and Performance. CRC Press.

Poblet, E., Ortega, F., Jiménez, F., 2002. The arrector pili muscle and the follicular unit of the scalp: a microscopic anatomy study. Dermatol. Surg. 28 (9), 800–803. https://doi.org/10.1046/j.1524-4725.2002.02038.x.

Qin, K., Dong, Chunmin, Wu, G., Lambert, N.A., 2011. Inactive-state preassembly of Gq-coupled receptors and gq heterotrimers. Physiol. Behav. 176 (1), 139–148. https://doi.org/10.1016/j.physbeh.2017.03.040.

Quesnel, D., Riecke, B.E., 2018. Are you awed yet? How virtual reality gives us awe and goose bumps. Front. Psychol. 9 (NOV), 1–22. https://doi.org/10.3389/fpsyg.2018.02158.

Rickard, N.S., 2004. Intense emotional responses to music: a test of the physiological arousal hypothesis. Psychol. Music 32 (4), 371–388.

Rochefort-Maranda, G., 2017. Inflated effect sizes and underpowered tests: how the severity measure of evidence is affected by the winner's curse. J. Philos. Stud. https://doi.org/10.1007/s11098-020-01424-z. January.

Rouillard, A., Gundersen, G., Fernandez, N., Wang, Z., Monteiro, C., McDermott, M., Ma'ayan, A., 2016. The Harmonizome: A Collection of Processed Datasets Gathered to Serve and Mine Knowledge About Genes and Proteins.

Salimpoor, V.N., Benovoy, M., Longo, G., Cooperstock, J.R., Zatorre, R.J., 2009. The rewarding aspects of music listening are related to degree of emotional arousal. PLoS ONE 4 (10). https://doi.org/10.1371/journal.pone.0007487.

Salimpoor, V.N., Benovoy, M., Larcher, K., Dagher, A., Zatorre, R.J., 2011. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. Nat. Neurosci. 14 (2), 257–264. https://doi.org/10.1038/nn.2726.

Schoeller, F., 2015. Knowledge, curiosity, and aesthetic chills. Front. Psychol. 6, 1546.

Schoeller, F., Eskinazi, M., 2019. Psychologie du frisson esthétique. Psychol. Fr. 64 (3), 305–312.

Schubert, T.W., Zickfeld, J.H., Seibt, B., Fiske, A.P., 2018. Moment-to-moment changes in feeling moved match changes in closeness, tears, goosebumps, and warmth: time series analyses. Cognit. Emot. 32 (1), 174–184. https://doi.org/10.1080/02699931.2016.1268998.

Schurtz, D.R., Blincoe, S., Smith, R.H., Powell, C.A.J., Combs, D.J.Y., Kim, S.H., 2012. Exploring the social aspects of goose bumps and their role in awe and envy. Motiv. Emot. 36 (2), 205–217. https://doi.org/10.1007/s11031-011-9243-8.

Shiota, M.N., Neufeld, S.L., Yeung, W.H., Moser, S.E., Perea, E.F., 2011. Feeling good: autonomic nervous system responding in five positive emotions. Emotion 11 (6), 1368–1378. https://doi.org/10.1037/a0024278.

Siegel, E.H., Sands, M.K., Van Den Noortgate, W., Condon, P., Chang, Y., Dy, J., Quigley, K.S., Feldman Barrett, L., 2018. Emotion fingerprints or emotion populations? A meta-analytic investigation of autonomic features of emotion categories. Psychol. Bull. 144 (4), 343–393. https://doi.org/10.1037/bul0000128.

Siepmann, T., Gibbons, C.H., Illigens, B.M., Lafo, J.A., Brown, C.M., Freeman, R., 2012. Quantitative pilomotor axon reflex test: a novel test of pilomotor function. Arch. Neurol. 69 (11), 1488–1492. https://doi.org/10.1001/archneurol.2012.1092.

Simon, H.A., 1967. Motivational and emotional controls of cognition. Psychol. Rev. 74 (1), 29–39. https://doi.org/10.1037/h0024127.

Song, W.C., Hu, K.S., Koh, K.S., 2005. Multiunit arrector pili muscular structure as a variation observed by using computer-based three-dimensional reconstruction. Cell Tissue Res. 322 (2), 335–337. https://doi.org/10.1007/s00441-005-0018-y.

Starcher, B., Aycock, R.L., Hill, C.H., 2005. Multiple roles for elastic fibers in the skin. J. Histochem. Cytochem. 53 (4), 431–443. https://doi.org/10.1369/jhc.4A6484.2005.

Stettenheim, P., 1972. Avian anatomy: integument. Part II. Avian Biol. 2, 1–63.

Sumpf, M., Jentschke, S., Koelsch, S., 2015. In: Effects of Aesthetic Chills on a Cardiac Signature of Emotionality, pp. 1–16. https://doi.org/10.1371/journal.pone.0130117.

Tansey, E.A., Johnson, C.D., 2015. Recent advances in thermoregulation. Adv. Physiol. Educ. 39 (3), 139–148. https://doi.org/10.1152/advan.00126.2014.

Torkamani, N., Rufaut, N.W., Jones, L., Sinclair, R.D., 2014. Beyond goosebumps: does the arrector pili muscle have a role in hair loss? Int. J. Trichol. 6 (3), 88–94. https://doi.org/10.4103/0974-7753.139077.

Uchida, M., Akaho, R., Ogawa-Ochiai, K., Tsumura, N., 2018. Image-based measurement of changes to skin texture using piloerection for emotion estimation. Artif. Life Robot. 24 (1), 1–7. https://doi.org/10.1007/s10015-018-0435-0.

Villanova, N., Azpiroz, F., Malagelada, J.R., 1997. Perception and gut reflexes induced by stimulation of gastrointestinal thermoreceptors in humans. J. Physiol. 502 (1), 215–222. https://doi.org/10.1111/j.1469-7793.1997.215bl.x.

Vosgerau, J., Simonsohn, U., Nelson, L.D., Simmons, J.P., 2019. 99% impossible: a valid, or falsifiable, internal meta-analysis. Journal of Experimental Psychology. General 148 (9), 1628–1639. https://doi.org/10.1037/xge0000663.

Wassiliwizky, E., Wagner, V., Jacobsen, T., Menninghaus, W., 2015. Art-elicited chills indicate states of being moved. Psychol. Aesthet. Creat. Arts 9 (4), 405–416. https://doi.org/10.1037/aca0000023.

Wassiliwizky, E., Jacobsen, T., Heinrich, J., Schneiderbauer, M., Menninghaus, W., 2017. Tears falling on goosebumps: co-occurrence of emotional lacrimation and emotional piloerection indicates a psychophysiological climax in emotional arousal. Front. Psychol. 8 (FEB), 1–15. https://doi.org/10.3389/fpsyg.2017.00041.

Wassiliwizky, E., Koelsch, S., Wagner, V., Jacobsen, T., Menninghaus, W., 2017. The emotional power of poetry: neural circuitry, psychophysiology and compositional principles. Soc. Cogn. Affect. Neurosci. 12 (8), 1229–1240. https://doi.org/10.1093/scan/nsx069.

Wolovich, C.K., Evans, S., Green, S.M., 2010. Mated pairs of owl monkeys (Aotus nancymaae) exhibit sex differences in response to unfamiliar male and female conspecifics. Am. J. Primatol. 72 (11), 942–950. https://doi.org/10.1002/ajp.20858.

Wright, P.C., 1978. Home range, acitivity pattern, and agonistic encounters of a group of night monkeys (Aotus trivirgatus) in Peru. Folia Primatol. 29, 43–55.

Yorzinski, J.L., Platt, M.L., 2012. The difference between night and day: antipredator behavior in birds. J. Ethol. 30 (2), 211–218. https://doi.org/10.1007/s10164-011-0318-5.

Zadra, J.R., Clore, G.L., 2011. Emotion and perception: the role of affective information. Wiley Interdisc. Rev. Cogn. Sci. 2 (6), 676–685. https://doi.org/10.1002/wcs.147.

Zaproudina, N., Varmavuo, V., Airaksinen, O., Närhi, M., 2008. Reproducibility of infrared thermography measurements in healthy individuals. Physiol. Meas. 29 (4), 515.

Zickfeld, J.H., Schubert, T.W., Seibt, B., Blomster, J.K., Arriaga, P., Basabe, N., Blaut, A., Caballero, A., Carrera, P., Dalgar, I., Ding, Y., Dumont, K., Valerie, G., Gracanin, A., Gyenis, R., Hu, C.P., Kardum, I., Lazarevic, L.B., Mathew, L., Alan, P.F., 2019. Kama muta: conceptualizing and measuring the experience often labelled being moved across 19 nations and 15 languages. Emotion 19 (3), 402–424. https://doi.org/10.1037/emo0000450.

Zickfeld, J.H., Schubert, T.W., Seibt, B., Fiske, A.P., 2019. Moving through the literature: what is the emotion often denoted being moved? Emot. Rev. 11 (2), 123–139. https://doi.org/10.1177/1754073918820126.

Zickfeld, J.H., Arriaga, P., Schubert, T.W., Seibt, B., 2020. In: Tears of Joy, Aesthetic Chills and Heartwarming Feelings: Physiological Correlates of Kama Muta, pp. 1–26. https://doi.org/10.1111/psyp.13662.