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“Stopping for knowledge”: the sense of beauty in the perception-action cycle.

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Highlights

- -Aesthetic appreciation signals optimal perceptual learning.
- -Beauty appreciation inhibits motor behaviour to foster learning.
- -Immobility during aesthetic appreciation favors perceptual processing.
- -Correlates of aesthetic appreciation are similar across sensory and artistic domains.
- -The experience of beauty motivates to tolerate uncertainty.

ABSTRACT

According to a millennial-old philosophical debate, aesthetic emotions have been connected to knowledge acquisition. Recent scientific evidence, collected across different disciplinary domains, confirms this link, but also reveals that motor inhibition plays a crucial role in the process. In this review, we discuss multidisciplinary results and propose an original account of aesthetic appreciation (the *stopping for knowledge hypothesis*) framed within the predictive coding theory. We discuss evidence showing that aesthetic emotions emerge in correspondence with an inhibition of motor behavior (i.e., minimizing action), promoting a simultaneous perceptual processing enhancement, at the level of sensory cortices (i.e., optimizing learning). Accordingly, we suggest that aesthetic appreciation may represent a hedonic feedback over learning progresses, motivating the individual to inhibit motor routines to seek further knowledge acquisition. Furthermore, the neuroimaging and neuropsychological studies we review reveal the presence of a strong association between aesthetic appreciation and the activation of the dopaminergic reward-related circuits. Finally, we propose a number of possible applications of the *stopping for knowledge hypothesis* in the clinical and education domains.

Keywords: aesthetic appreciation; neuroaesthetic; learning; attention; processing enhancement; motor inhibition; intrinsic motivation; predictive coding.

1. Introduction

"Stopping" and "seeing" are sometimes referred to as the yin and yang of Buddhist Zen meditation. They have been considered as complementary halves of a unified whole since the publication of the Zen fundamental text “The great stopping and seeing” written by sixth-century Buddhist master Chih-i. Chinese Buddhists employed “stopping” and “seeing” to translate the Indic terms “concentration” and “insight”. "Stopping" refers to freeing oneself from clinging and craving for objects, and “seeing” is intended as “sensing and receiving” to attain insight (Chin-i, 2000). This reveals an ancient intuition linking action inhibition and sensory attunement for the sake of (spiritual) knowledge. The condition of a contemplative absorption momentarily stopping us described by meditators is something we all experience, perhaps more frequently than we think, e.g. in front of a sunset, a painting in a museum, a movie or even a moving speech at a wedding. Beauty seems to urge us to stop to let us embrace the present moment, sometimes so intensely that it can be disturbing, as in the Stendhal syndrome: “Absorbed in the contemplation of sublime beauty ... I reached the point where one encounters celestial sensations ... Everything spoke so vividly to my soul. Ah, if I could only forget. I had palpitations of the heart, what in Berlin they call 'nerves'. Life was drained from me” (Stendhal, 1959, p.271). Beside peak experiences, however, aesthetic value might be an often hidden feature of all experience (Berleant, 2015). A number of relevant questions then arise, which philosophers have attempted answering across the centuries: What is the nature of beauty? Why are we so sensitive to aesthetic value? Why did we evolve to appreciate it? What is the function of the sense of beauty in the "embodied mind" architecture? We believe that neuroaesthetics might provide novel insights into the investigation of the nature of beauty. Based on the review of philosophical theories and more recent experimental contributions in the neuroscientific domain, we will propose an original account of aesthetic appreciation (the *stopping for knowledge hypothesis*) suggesting that aesthetic perception is deeply rooted in the adaptive control and reciprocal modulation of active behavior and perceptual learning along the perception-action cycle, i.e. the circular flow of information from the environment to sensory and motor processing structures, back again to the environment, and so on (Fuster, 2004). As suggested by research reviewed in the present paper, aesthetic emotions should not be reduced to a mere decorative aspect of life experience but should instead be considered a key part of our knowledge acquisition process, enabling us to learn from the environment and behave intelligently. In this sense, aesthetic emotions might be related to our learning and adaptation ability (Perlovsky, 2010). This idea traces back to the romantic notion of "primacy of aesthetic" over reason, or even to the Greek classic philosophical tradition. Since Aristotle, much debate has been dedicated to the epistemic value of aesthetic emotions. In Aristotle's Poetics, the philosopher affirms: "to be learning something is the greatest of pleasure, not only to the philosopher but also to the rest of mankind […] The reason in delight in seeing a picture is that one is at the same time learning-gathering the meaning of things" (Tracy, 1946, p.43). Accordingly, Aristotelian aesthetics has been considered as a "learning and inference doctrine" (Tracy, 1946). In more modern times, romanticism broke with the Enlightenment rationalism tradition and with the Cartesian concept of mind/body dualism and shared the belief in a call "back to feeling" and, hence, to aesthetics. In the words of the German poet Friedrich Hölderlin (1796): "I am now convinced that the highest act of reason, by encompassing all ideas, is an aesthetic act, and that truth and goodness are siblings only in beauty" (Bernstein, 2003, p.186). The romantic re-evaluation of the senses and corporality was indeed prompted by the German philosopher Baumgarten, who is commonly considered as the founder of modern aesthetics (Rigby, 2020). Baumgarten (1735) gave to the modern investigation of the nature of beauty its actual name (*epistêmê aisthetikê,* i.e., *aesthetics*, the science of what is sensed). Hence, aesthetics was originally intended as an alternative approach to the philosophy of knowledge (Gross, 2002); in Baumgarten's words: "the science of sensory knowledge directed toward beauty" (Berleant, 2012, p.1). Although criticized by Kant, Baumgarten's aesthetics was partially borrowed by Kant and applied to sensory experience in general. As we will see below, the Kantian intuitions on the "embodied mind" (Khachouf et al., 2013; Shell, 1996) positioned aesthetics in the field of epistemology (Nuzzo, 2006), and appear still influential in the interpretation of recent experimental results from neuroaesthetic research (Chatterjee & Vartanian, 2016; Perlovsky, 2010).

In the present review, we will discuss some recent neuroaesthetic research findings in different disciplines, e.g., neuroscience, psychology, computational modeling, and philosophy. We will specifically focus on those perspectives suggesting the existence of a link between aesthetic emotions, motor inhibition and knowledge acquisition. Importantly, our investigation will include studies examining the experience of beauty driven by everyday life objects and events. In the conclusions we will extend the analysis to aesthetic experiences in interpersonal communication and their value for education and psychotherapy.

Our *stopping for knowledge hypothesis*, extending the seminal theoretical models of aesthetic appreciation by Perlovsky and Schoeller (Perlovsky & Schoeller, 2019) and Van de Cruys and Wagemans (Van de Cruys and Wagemans, 2011), has been developed on the basis of the predictive coding theory (i.e. the brain makes systematic attempts to actively infer the causes of the incoming sensory inputs and integrates these inferences in predictive models of the environment; Friston, 2010; Friston et al., 2006) and it is grounded on neuroimaging and neuropsychological evidence. We propose that the experience of beauty emerges in correspondence with an inhibition of motor behavior, able to promote a simultaneous perceptual processing enhancement. In other words, beauty can be considered as a hedonic, self-generated, feedback of optimal learning dynamics, signaling to the system to stop acting based on previously acquired knowledge in order to learn something new. To account for this model of aesthetic appreciation, as a first step we introduce the philosophical concept of *disinterested interest* and discuss recent neuroscientific evidence suggesting an anatomo-functional segregation between the circuits of *wanting* (appetitive function) and *liking* (contemplative function - § *2. Disinterested interest: liking without wanting?*). Hence, as supporting evidence of the dissociation between a goal-oriented behavior and a contemplative perception/learning-directed attitude, we review several neurophysiological studies reporting motor inhibition effects during beauty perception (§ *3. Contemplation of beauty and motor inhibition*). According to theoretical research and neuroimaging evidence, such beauty-related motor inhibition is coupled with an enhancement of the attentional focus toward sensory stimulation, promoting the concentration of processing resources on the object of the aesthetic appreciation (§ *4. Attentional enhancement during aesthetic appreciation*). Within a model directly connecting aesthetic appreciation and knowledge acquisition, this deployment of attentional resources via motor inhibition appears crucial to promote learning mechanisms, as those described by the predictive coding account. In the following chapter (§ *5. Aesthetic pleasure as a "meta-learning" feedback from predictive coding dynamics*), we describe the predictive coding theoretical framework (§ *5.1. Update of sensory predictions and associated rewards*) and the empirical evidence directly linking aesthetic appreciation with the refinement of the predictive models of sensory input (§ *5.2. How to build precise predictions? Evolutionary-based vs. experience-based modulations of perceptual learning*). In paragraph 6, we detail our *stopping for knowledge hypothesis* of aesthetic appreciation (§ *6.1. The stopping for knowledge hypothesis as a possible model of aesthetic experience*), discussing how our model may also account for apparent contradictory experimental evidence (§ 6.2. *Empathic vs un-empathic approaches of aesthetic appreciation: solving an apparent contradiction*). Finally, in the concluding remarks, we present the possible applications of our hypothesis, particularly in the context of teaching and psychotherapy (§ 7. *Conclusions and possible future applications*).

2. Disinterested interest: liking without wanting?

Some linguists argue that the word "desire" (from latin "de": away from, and "sidus": stars/constellation) originally meant "to stop contemplating stars" (Cortellazzo & Zolli, 2016). The etymology of this word somehow implies that contemplation and goal-oriented actions are two partially opposite but intrinsically connected modes of experience. This suggests the possibility of a trade-off between liking (i.e., contemplative appreciation) and wanting (i.e., the goal-oriented program to acquire/achieve an object or a desired outcome), inscribed in the way we perceive and interact with the environment. This idea, which has informed the philosophical aesthetic debate throughout the centuries, is also reflected in recent neuroaesthetic research, describing aesthetic experiences as a pleasurable cognitive process involving a focus of attention on the stimulus and the neglect of self-referred concerns and desires (i.e. *disinterested interest*; Apter, 1984; Chatterjee & Vartanian, 2014, 2016; Cupchik & Winston, 1990; Marković, 2012). *Disinterest* might enable observers to maintain a psychological distance from objects perceived as beautiful and, meanwhile, to fully embrace the "here and now" of perception (see the Distancing-Embracing model in Menninghaus et al., 2017).

The concept of *disinterestedness* was originally formulated by Kant in his oevre Critique of Judgement: "taste in the beautiful is alone a disinterested and free satisfaction; for no interest" (Hofstadter & Kuhns, 2009, p. 286). Disinterest refers to the perception of an object "for its own sake" (Menninghaus et al., 2019), prompted by a special attitude of attention toward the percept. The aesthetic attitude is thus intended as a purely contemplative, self-rewarding mode of experience, preventing the engagement in other more pragmatic attitudes (Apter, 1984; Levinson, 1992). In other words, aesthetic judgements shift the focus of attention from the extrinsic (pragmatic) to the intrinsic (aesthetic) value of the object (Marković, 2012). Kant first hypothesized that the correspondence between concepts and the world established by judgment ability brings pleasant satisfaction, independently from the satisfaction of "lower" bodily needs related to hunger or fear. In this way, according to the philosopher, we can experience beauty and the sublime (Perlovsky, 2010).

Schopenhauer further developed the Kantian notion of "disinterest". According to the German philosopher there is a clear dissociation between liking and wanting (Hofstadter & Kuhns, 2009), as aesthetic experiences free the beholders from their "will", allowing them to achieve a transitory state of *will-less* perception of the world. These momentary will-less mental states are fundamental to reorient will and update desired states in an ever-changing environment (Perlovsky, 2010).

In more recent times, Chatterjee and Vartanian (2014), two cognitive neuroscientists, reaffirmed that the engagement and pleasure induced by the contemplation of beautiful percepts is not always accompanied by the desire to possess, consume or control them in any other way (Chatterjee and Vartanian, 2016); i.e., aesthetic emotions are triggered by objects rather than outcomes (Chatterjee and Vartanian, 2016). In line with this view, other scholars (Schindler et al., 2017) postulated that aesthetic pleasure and other hedonic rewards associated with utilitarian (i.e., outcome-driven) behavior might be related to the activation of two fully dissociable neural networks (Berridge and Kringelbach, 2013, 2008). Namely, aesthetic pleasure might emerge from the activation of the liking system only, while utilitarian pleasure might emerge from the additional activation of the wanting system (Chatterjee and Vartanian, 2016; Pearce et al., 2016; Schindler et al., 2017). As we will discuss below (§ 6), aesthetic appreciation might be involved in the reciprocal modulation of these two partially functionally segregated motivational networks. Interestingly, neuroimaging studies confirmed the existence of an anatomo-functional segregation of the *liking vs. wanting* mechanisms in our brain. The subjective experience of "wanting" a reward (*appetitive motivation*) activates a widespread network involving the mesolimbic dopaminergic system (Tibboel et al., 2015), and implying the influence of emotional and motivational values on motor programs (Mogenson et al., 1980). Conversely, a small network of hot spots within the limbic system underlies the core reaction to hedonic inputs and the experience of "liking" (Berridge and Kringelbach, 2015), which is mediated by opioids and endocannabinoid activations in the ventral globus pallidus and in the nucleus accumbens (Berridge et al., 2009; Berridge and Kringelbach, 2015). Accordingly, the opioid system has been suggested as a potential neural substrate for aesthetic appreciation (Nadal, 2013), with neuroimaging research supporting this hypothesis (Yue et al., 2007). Crucially for our *stopping for knowledge hypothesis* (see below § 5 *Aesthetic pleasure as a "meta-learning" feedback from predictive coding dynamics*), directly relating aesthetic appreciation with the update of predictive representations, opioids transmission might play a fundamental role in the emergence of perceptual pleasure derived from the acquisition of novel information (Biederman and Vessel, 2006a, 2006b; Nadal, 2013). More specifically, it has been suggested that the opioid system triggers perceptual pleasure correlated to the informational value of stimuli: the release of endomorphins and the stimulation of m-opioid receptors might correlate with the informational value conveyed by stimulation (Biederman and Vessel, 2006). Coherently with this mechanism, aesthetic chills (i.e. non-thermoregulatory hedonic shivering) can be inhibited by the excitant opioid-antagonist naloxone (Goldstein, 1980) which is known to impair retention and learning performances in rats (Saha et al., 1991).

To sum up, aesthetic pleasure represents an intrinsic feedback, which, differently from other extrinsic rewards, does not motivate any craving for potential outcomes or trigger the necessary motor activation to obtain such outcomes (Chatterjee and Vartanian, 2016, 2014). Conversely, as we will argue in the next paragraphs, motor behaviour may result inhibited during aesthetic experiences, thus saving processing resources to be committed on perceptually salient beautiful stimuli (Chatterjee and Vartanian, 2016; Gallese and Guerra, 2012; Menninghaus et al., 2017).

3. Contemplation of beauty and motor inhibition

As reported in the previous paragraph, some authors argue that during an aesthetic experience the object of beauty does not serve as a tool for the satisfaction of bodily needs (Ramachandran and

Hirstein, 1999), but it is rather apprehended for its intrinsic aesthetic value only (Menninghaus et al., 2019). This *will-less* mental state of disinterested interest (see above) might emerge from the activation of the liking system, without the contribution of the wanting system, including its motor components (Chatterjee, 2014). This cognitive state should result in the inhibition of the motor component of the response to beautiful stimuli. This hypothesis is supported by behavioural research investigating the elicitation of chills by beautiful stimuli, showing that participants experience a strong relaxation during the chill episode (Bannister, 2019; Schoeller & Perlovsky, 2016). Moreover, recent neuroimaging results support the presence of motor inhibition during aesthetic experiences (relevant research related to the present hypothesis is reported in *Table 1*, second section; brain areas involved in this mechanism are presented in *Figure 1B*). In an EEG experiment, de Tommaso et al. (2008) found that the motor inhibition-related P3 component displayed greater amplitude for visual stimuli perceived as beautiful than for neutral or ugly images. In a seminal fMRI study, Kawabata and Zeki (2004) found greater activations in the primary motor cortex during the observation of ugly paintings compared to more beautiful ones. Importantly, motor activations were linearly decreasing with subjective aesthetic judgements. Similarly, Di Dio and colleagues (2007) found that the presentation of images of statues rated as ugly increased bold activations in the left motor cortex as compared to beautiful images. Moreover, the existence of a negative correlation between motor responses to sounds and their pleasantness has been recently hypothesized in the auditory domain (Brattico, Bogert, & Jacobsen, 2013). Coherently with this hypothesis, startle eye blink reactions registered with EmG were larger for unpleasant than for pleasant consonant intervals (Roy et al., 2009). More recently, our research group demonstrated the presence of a positive correlation between motor inhibition and pleasant sounds in a series of EEG experiments (Sarasso et al., 2019): more appreciated musical intervals induced slower response times in a detection task and the concomitant enhancement of the motor inhibition N2-P3 complex in a go-nogo task. N2 and P3 auditory and visual ERP components index the activation of an inhibitory mechanism targeting motor cortices (Burle et al., 2004; Dutra et al., 2018; Folstein and Van Petten, 2008; Wessel, 2017; Wessel and Aron, 2017) and reflect earlier non-motoric (targeting premotor and supplementary motor areas) and later motoric stages (targeting the primary motor cortex) of motor inhibition respectively (Angelini et al., 2015). We interpreted this evidence proposing that more attentional resources were oriented on the pleasant sensory features of musical intervals rather than on the motor response. In accordance with neurophysiological evidence collected in humans and in rodents, it has been suggested that our nervous system is equipped with a “Behavioural Inhibition System”, activated by novel, unexpected events and actively hindering behavioural responses, thus allowing the individual to re-plan an adequate motor response (Anderson et al., 2019). In other words, we suggest that the ultimate product of aesthetic experience may not be an approach reaction, but a simple enhancement of the perceptual activity per se (Kirsch, Urgesi & Cross, 2016). In the next paragraph we will discuss this hypothesis.

4. Attentional enhancement during aesthetic appreciation

The study of attentional dynamics underlying aesthetic experiences is essential to bridge the discussion of aesthetics and perception together (Nanay, 2016). In a seminal contribution, Monroe Beardsley (1981) explicitly described aesthetic appreciation as a cognitive process, suggesting that aesthetic experiences occur when attention is focused on the perceptual features of the object (Marković, 2012). Similarly, according to the philosopher Dewey, aesthetic experiences maintain the focus of the perceivers on the ever-changing present moment and thus prevent the engagement in more mechanical, routinely interactions with the environment (Stroud, 2010). In line with this theoretical framework, Menninghaus and colleague recently proposed the Distancing-Embracing model (Menninghaus et al., 2017). According to the model, the beauty-driven transient suspension of prototypical motor responses, resulting from perceivers’ absence of personal goals and environmental threats (i.e., psychological distance), makes room for a higher intensity of the felt sensations and emotions elicited by beautiful objects (i.e., embracement). This “aesthetic presence” enables observers to direct attention to the perceptual activity for its own sake, with the subjectively felt intensity of present sensation being a reward in its own right (Menninghaus et al., 2019; for a discussion of the relation between sensuous pleasure and aestehtic pleasure see) Brielmann & Pelli, 2017, 2019)

Hence, to perceive beauty, a shift in attentional deployment toward sensory input perceptual features is needed to overcome the automatic motor programming and subsequent behavior driven by semantic stimulus contents (Cupchik, 1992; Cupchik and Winston, 1996). This peculiar attentional shift has often been considered as content-dependent, i.e. produced by the inherent features of the beautiful object, as predicted by Ramachandrand's *peak shift effect* theory. Artists, for example, make use of "perceptual heuristics" which optimally engage the visual areas of the brain of the observer (and of the artist himself; Ramachandran and Hirstein, 1999). Attentional dynamics are thus essential to escape the automaticity of everyday pragmatic perceptual activity. Drawing on Tolstoy's work, Shklovsky (1965) proposed that ''the purpose of art is to impart the sensation of things as they are perceived and not as they are known". The inhibition of the object-identification habit is essential for the emergence of aesthetic experiences, or, in Beardsley's words, to adopt an "aesthetic point of view" (Breadsley, 1984). Similarly, Dewey proposed that during "transformative aesthetic experiences", fully receptive perception replaces mere recognition of objects (Girod and Wong, 2005), or other individuals (Pappas, 2008). In this sense, the aesthetic attitude reveals that phenomena are not identical to "things-in-themselves" (Perlovsky, 2010), simply affording the satisfaction of bodily instincts: any object is first of all a phenomenon (wonderfully) accessible to cognition and perception (see also the comparison of Buddhist "emptiness of objects" and Kantian "aimless purposiveness" in Perlovsky, 2010).

At a neurophysiological level, the *absorption* (a condition of amplified attention that fully engage the subject's perceptual resources; Tellegan and Atkinson, 1974) associated with aesthetic experiences should imply a modulation of responses to aesthetic stimuli along the neural perceptual hierarchy, similar to those underlying exogenous end endogenous attentional modulations, i.e. more pronounced neural responses to attended stimuli (Nadal, 2013). Indeed, increased neural responses in sensory areas during aesthetic appreciation were found in a plethora of fMRI studies (Calvo-Merino et al., 2008; Cupchik et al., 2009; Koelsch et al., 2006; Munar et al., 2009; Vartanian & Goel, 2004). For example, Vartanian and Goel (2004) reported increased bilateral activity in the occipital gyrus following the presentation of more appreciated paintings. According to these authors, enhanced activations in visual areas reflect attentional engagement, which in turn triggers aesthetic appreciation (see *Table 1*, first section, for a summary of relevant research; brain areas involved in attentional enhancement are represented in *Figure 1B* – see also § 5 for further specification of aesthetic appreciation as hedonic feedback of perceptual/learning dynamics). Notably, increased activations in the left parietal cortex, which is involved in spatial attention deployment (Corbetta and Shulman, 2002), were found to positively correlate with aesthetic appreciations (Kawabata and Zeki, 2004). Furthermore, a beauty-related enhancement of neurophysiological indexes of perceptual processing was confirmed by EEG studies across different sensory modalities (Sarasso et al., 2020; Sarasso, et al., 2019). In Sarasso et al. (2020), we demonstrated an amplification of early components of the event-related response originating from primary visual cortex (C1 component) for more appreciated abstract images. Early and middle-latency components of the VEP, such as C1 and N1, have been suggested to reflect the attentional up-weighting of visual inputs according to their estimated signal-to-noise ratio (i.e. precision) via modulations of the synaptic gain of pyramidal cells (Brown and Friston, 2012). Moreover, alpha oscillation event-related desynchronization (ERD), which is recognized as an index of attentional amplification (Klimesch, 2012; Pfurtscheller et al., 1994), was more pronounced after the presentation of more appreciated images (Sarasso et al., 2020). More specifically, alpha ERD has been shown to dynamically modulate the neural gain in sensory areas (see Sigala et al., 2014 for a review). However, one EEG study (Handy et al., 2010) evidenced a seemingly opposite result, showing that early components of the visual ERP were enhanced during the perception of disliked images. Handy et al. (2010) found significant effects of negative evaluation on the amplitudes of the P100/N170 complex (150–200 ms), and the occipital N2/P2 complex (200–400 ms), with decreased central/parietal P100 and increased N170, increased frontal/central N2 and decreased parietal/occipital P2 amplitude. The authors interpreted this evidence suggesting that disliked images (commercial logos) were processed as more attentionally arousing due to an *emotional negativity bias* (Ito and Cacioppo, 2000). However, this effect rather than being selectively related to aesthetic judgements, may be directly linked with the different emotional/semantic valence associated with the logo images.

Furthermore, attentional enhancements and the related boost in processing efficiency for more appreciated stimuli was also evidenced by behavioral data (Mather, Clewett, Sakaki, & Harley, 2016; Sarasso et al., 2019b; Spehar et al., 2015) and subjective fluency ratings (Carbon and Albrecht, 2016; Reber et al., 2004, 1998; Reber and Schwarz, 2001). Accordingly, in Sarasso et al. (2020) we found that the detection of targets embedded in more appreciated backgrounds (the same that elicited enhanced early attention related VEP responses) was faster, suggesting that enhanced activation in early sensory areas correlate with increased attentional engagement and perceptual performances during aesthetic appreciation (Kirsch et al., 2016; Leder and Nadal, 2014; Nadal, 2013). Similarly, Reppa & McDougall (2015) found that the aesthetic appeal of icons facilitates performance efficiency in a visual search of a target icon among distractors only when the target icon was complex, abstract or unfamiliar and thus harder to locate among distractor icons. In sum, the positive effect of aesthetic appeal on performances (faster response times) in a visual search task is more apparent under challenging conditions, probably because of the presence of a ceiling effect preventing aesthetic appeal to influence performances in the localization of simple, concrete and familiar icons.

Even though the increased activity in cortical regions related to sensory processing resulting in enhanced attention has often been attributed to beautiful objects perceptual features, it may also be driven by endogenous (top-down) attentional modulations due to aesthetic evaluation “per se” (i.e., context-dependent attentional shifts; see *Figure 1*). For example, increased cortical activations were found by comparing aesthetic vs. more pragmatic evaluation tasks (Kirk, 2008). A context of stimulation regarded by the perceiver as *artistic* may induce similar effects: Lacey et al. (2011) showed that activations in visual areas were greater when participants viewed pictures they regarded as artworks than when they viewed stimuli depicting identical content but not regarded as artworks (but see also Pelowski et al., 2017; Spee et al., 2018). These results are coherent with findings suggesting a functional dissociation between aesthetic/affective and cognitive/pragmatic judgements, as evidenced by different EEG waveforms in the two tasks (Brattico et al., 2010; Höfel and Jacobsen, 2007; Jacobsen et al., 2006).

To sum up, in the previous paragraphs, we reported multidisciplinary data showing that the attentional amplification observed during aesthetic appreciation may be induced either by stimulus features (i.e., content-dependent) or by contextual factors, such as the experimental task (context-dependent). Overall, aesthetic appreciation seems to be consistently related to an up-weighting of sensory input (i.e., *prediction errors*, see § 5.2). This effect is exactly opposite to the neuromodulatory process underlying sensory attenuation (i.e., the attenuated neurophysiological responses following sensory stimulation induced by one's' own movement; Brown et al., 2013; Limanowski et al., 2018; Voss et al., 2006). During sensory attenuation, attention is withdrawn from the consequences of the movement, thus reducing sensory gain, so that movement may access to all the necessary processing resources to fully develop (Brown et al., 2013). On the contrary, sensory gain results amplified during aesthetic appreciation, as strongly suggested by the neuroimaging results reviewed above.

Altogether, this evidence raises a relevant question: why does aesthetic appreciation correlate with attentional amplification? The relation between attentional amplification and aesthetic emotions can be better understood within the predictive coding framework, as we will argument in the next paragraph.

5. Aesthetic pleasure as a "meta-learning" feedback from predictive coding dynamics

5.1. Update of sensory predictions and associated rewards

As we anticipated in the introduction, starting with Aristotle, aesthetic experiences have been described in terms of "learning and inference" (Tracy, 1946). This hypothesis fits well with recent neurocomputational accounts of cognition and perception, which describe the mind as an inferential predictive process based on optimal Bayesian learning (Friston, 2010), and somehow suggest that the sense of beauty is something more than a superfluous pleasurable corollary of ordinary cognition. Although in more recent times the original principles and programmes of Baumgarten aesthetics have been mostly neglected (Gross, 2002) in favour of a detailed investigation of the perception and creation of art, contemporary neuroaesthetics and experimental aesthetics are revitalizing the scientific interest toward the relation between aesthetic appreciation and knowledge acquisition (Perlovsky, 2014; Perlovsky & Schoeller, 2019; Sarasso, et al., 2019; Schmidhuber, 2009; Schoeller & Perlovsky, 2016; Van de Cruys & Wagemans, 2011). In general, such theories claim that aesthetic emotions, at both conscious and unconscious levels, regulate and guide everyday learning processes, i.e. the natural reflex that humans have to track and anticipate patterns in experience and the ability to generalize on the basis of observed redundancies (Schoeller, 2015b). Similarly to the original Aristotelian intuition (Perlovsky, 2006; Schoeller, 2019; Schoeller et al., 2018; Schoeller & Perlovsky, 2015), aesthetic emotions might be envisaged as promoters of the, specifically human, appetence for novelty for the seek of coherence and logical simplicity (Schoeller, 2015b) along the hierarchy of representations of the world, from low-level to more abstract cognitive models, up to, e.g., the meaning of life (Levine & Perlovsky, 2008; Perlovsky, 2006b; Schoeller, 2015b).

In this paragraph, we will summarise the evidence supporting the existence of a link between aesthetic pleasure and perceptual learning, intended as the update of environment mental predictive representations to account for new sensory inputs (Chetverikov & Kristjánsson, 2016; Schmidhuber, 2009; Schoeller & Perlovsky, 2016; Van de Cruys & Wagemans, 2011). This process of adaptation is fundamental for an optimal learning of the statistical regularities detectable in the stochastic and ever-changing environment; it is necessary to better predict and interact with the outer world (den Ouden et al., 2012); and it is also central to the formation and update of memories (Krawczyk et al., 2017). We believe that the link between aesthetic pleasure and perceptual inference can be better understood within the Predictive Coding (from now on, *PC*) account of cognition derived from the "free energy principle" (Friston, 2010). PC claims that the sensory system is actively engaged in predicting upcoming sensory input rather than being a passive processor of information. Mental representations can be considered as predictions, encoded as probabilistic hierarchical generative models of the causes of sensations. Higher levels in the hierarchy contextualize lower levels, and lower levels provide evidence for higher levels. Increasingly higher-level beliefs represent increasingly complex abstract states of the world at increasingly broader time scales.

Predictions are formed through experience and adapt to account for the mismatches (prediction errors) between the incoming input and prior expectations. Such process of prediction adaptation is designed to minimize the uncertainty (states of surprise) associated with the context of stimulation (Feldman & Friston, 2010; Friston, 2010; Friston et al., 2006). The representation of the current state of the world (the internal generative model) which can best explain the sensory input is selected and guides our perception (e.g., associating each input with a specific weight according to its relevance) and our actions (e.g., planning and executing an adequate motor behavior). Along the neural hierarchy, predictions are generated and transmitted from higher associative areas to lower levels (top-down transmission), where they are compared with incoming inputs (bottom-up transmission). The working hypothesis is that these predictions (i.e. prior beliefs) suppress/inhibit, or "explain away", the processing of the sensory inputs that are coherent with them within the lower areas, leaving only the mismatches (i.e. prediction errors) to propagate upward. In this way, the detection of a mismatch between prior predictions and current sensory evidence may inform the plastic process responsible for the update of predictions. Attentional resources can thus be mainly directed to unpredicted stimuli that have not been satisfactorily explained, and carry information which could still be potentially learnable (Baldi and Itti, 2010; Itti and Baldi, 2009). Moreover, as we will see in more detail, and importantly for our account of aesthetic appreciation, attention constantly and dynamically balances the relative influence of prior beliefs and incoming sensory evidence on belief updating across the entire hierarchy and between sensory modalities. This is accomplished by weighting the ascending prediction errors by their relative expected precision (Adams et al., 2013; Feldman & Friston, 2010). Interestingly, this process of adaptation of generative models may be related to emotional and motivational components. Joffily and Coricelli (2013) hypothesized a correlation between positive and negative emotional valence attributed to the stimuli and the degree of sensory surprise over time, with a positive valence associated to a decrease of surprise. In their words: "pleasure is elicited in the transition from a state of high to low surprise" (page 8). This might constitute the implicit motivation pushing individuals toward the pursuit of minimizing uncertainty through action or plasticity (i.e. adaptation of sensory predictive representations) and constitutes and important "meta-learning" function. Similarly, other authors proposed that the brain generates an intrinsic reward when it recognizes learning progresses (i.e., a decline in prediction errors over time), allowing the individual to spontaneously engage in perceptual activities reducing (learnable) uncertainty while avoiding random (unlearnable) or overlearned inputs (Biederman & Vessel, 2006b; Gottlieb, 2012; Oudeyer, Kaplan, & Hafner, 2007). Van de Cruys and Wagemans (2011b) suggest that positive aesthetic emotions will be triggered by a shift from a highly arousing and attentional demanding stimulation context - characterized by the incongruence between perceptual inputs and preexisting models of the causes of sensations - to a situation where perceptual prediction errors are successfully "explained away" by the update of the generative model. When listening to music, for example, we constantly and automatically generate predictions about the future evolution of the musical theme, which are resolved within the next few musical events. Musicians, consciously or unconsciously, provide us the opportunity to test and re-establish our predictions, thus continuously engaging us in resolving uncertainty over such predictions (Koelsch et al., 2019). According to this model, aesthetic pleasure is experienced when the perceiver has succeeded in reinstating predictability (solving the prediction error), thus moving from an initial situation of higher unpredictability that captures our attention (higher prediction errors), to a final state of the generative models' refinement (higher predictability). Within this framework, pleasure intensity correlates with the degree of prediction updating (with more intense pleasure in response to a greater updating; *Figure 1A*). Mathematically, the perception of beauty correlates with the derivative of the learning curve (i.e. the speed of learning, Schoeller et al., 2018), and emerges when the system reaches a local peak in the similarity between sensory inputs and representations of the world (Perlovsky, 2010; Schmidhuber, 2009; Schoeller et al., 2018). This corresponds to a decline in prediction errors after an initially arousing growth of them (*Figure 1A*; Van de Cruys & Wagemans, 2011), which is also consistent with the general computational account of emotions in relation to the rate of growth of prediction errors proposed by Joffily and Coricelli (2013).

Therefore, aesthetic emotions or, rather, their anticipation, may serve as an intrinsic motivational state (Murayama et al., 2010; Oudeyer et al., 2016; Schmidhuber, 2010) favoring learning from the environment (Perlovsky, 2014; Perlovsky & Schoeller, 2019; Schmidhuber, 2009; Schoeller & Perlovsky, 2016). The (expected) subjective perception of beauty might implicitly motivate the observer to focus on those inputs leading to the highest learning progress, given the current state of its predictive models, while avoiding stimuli that are overlearned or purely random (Schmidhuber, 2010; Van de Cruys, 2017). In more simple terms, the sense of beauty makes us curious of novelty (Berlyne, 1971; Schoeller, 2015; Schoeller & Perlovsky, 2016; Van de Cruys, 2017), as we will further discuss in paragraph 5.3.

5.2. How to build precise predictions? Evolutionary-based vs. experience-based modulations of perceptual learning

Model updating does not exclusively depend on the current state of predictive models based on individual previous experience (unpredicted novel *vs* predicted acquired inputs). The degree to which predictive models are updated by sensory inputs (and consequently aesthetic value according to our *stopping for knowledge hypothesis*) also relies on some *aprioristic* factors, phylogenetically and ontogenetically based (Van Beers et al., 2002). Indeed, bottom-up signals (i.e. prediction errors) are multiplied by adaptive weights, or long-term memory traces, that can be tuned by learning from the environment. These experience-based expectations help to focus attention upon salient (e.g. precise) stimulus features, that are expected in a given environment and to which our sensory systems are tuned (Grossberg, 2019). More specifically, the nervous system associates different sensory inputs (prediction errors) with different *weights*, indicating their level of contribution to the refinement of the generative predictive models. Such weights are attributed according to the estimated precision (corresponding to the signal-to-noise ratio) of the specific sensory input (Brown & Friston, 2012; Feldman & Friston, 2010; Lecaignard et al., 2018; Quiroga-Martinez, 2018). Stimuli interpreted by the nervous system as more precise (with higher signal-to-noise ratio), are up-weighted via modulations of the synaptic gain of cells that convey sensory information (Brown & Friston, 2012; Kanai et al., 2015). Conversely, stimuli interpreted as less precise are down-weighted, ensuring that only the more reliable sensory signals drive learning and behavior. Apparently, this mechanism of prediction error precision weighting is not only affected by individuals' previous experience (Ronga et al., 2017), but also follows some kind of universalistic trends, shared by most individuals. As an example, in the context of the multisensory integration necessary to guide motor behavior (such as grasping), as human beings we tend to rely more on visual input (considered as more precise) as compared to proprioceptive input (Van Beers et al., 2002). Interestingly, even for aesthetic appreciation, we can observe some generalized trends. For example, within the auditory domain, consonant musical intervals are generally more appreciated than dissonant ones (Bowling et al., 2017; McDermott et al., 2010; Pallesen et al., 2005). Some authors suggested that this preference may also be ascribed to estimated input precision (Sarasso, et al., 2019; Tabas et al., 2019). It has been shown that bird vocalizations as well as human voices are often composed of consonant sounds and that vocal similarity explains the aesthetic preference for consonance (Bowling et al., 2017). In accordance with this view, it is possible that the human nervous system might be specifically tuned by evolution to process such input (Crespo-Bojorque & Toro, 2016; González-García et al., 2016;

Toro & Crespo-Bojorque, 2017; Tramo et al., 2006; Zentner & Kagan, 1996). This may represent a possible explanation of the greater precision estimation granted to consonant rather than dissonant sounds (Bowling and Purves, 2015). Interestingly, a very similar mechanism (a correlation between input precision estimation and shared tendencies of aesthetic appreciation) may also be observed in vision, when considering the aesthetic judgements in response to different spatial frequency distributions of visual input resembling natural signals (Sarasso et al., 2020; Spehar et al., 2015, 2003). This said, our *stopping for knowledge hypothesis* of aesthetic appreciation, directly linking aesthetic pleasure with learning and motor processes, might account both for individual preferences (associated with the *experience-based* update of predictive models) and for generalized aesthetic trends (related to the *evolutionary-based* estimation of different inputs' precision).

5.3. How beauty makes us curious: aesthetic value and the "knowledge instinct".

The *stopping for knowledge hypothesis* is in agreement with previous models of aesthetic pleasure. Schoeller and Perlovsky (2016), e.g., grounded their model of aesthetic experiences (the *Perlowsky-Schoeller theory*) within the process of knowledge acquisition. In their view, aesthetic emotions (i.e., the sense of beauty) are the motivations subtending the update processes through which mental representations are modified. Humans are intrinsically motivated to "explain" the incoming sensory input through the maximization of the similarity between representations and novel information (De-Wit, Machilsen, & Putzeys, 2010; Friston, 2010). According to some authors, the need for "understanding" is so crucial that it is tied to an inborn mechanism driving it, the so called "knowledge instinct" (Perlovsky, 2010; Perlovsky, 2006b, 2006c, 2006a; Perlovsky & Schoeller, 2019; Schoeller & Perlovsky, 2016), independently from the satisfaction or dissatisfaction of other instincts (Perlovsky, 2010). The core idea of the "knowledge instinct" (i.e. the drive to minimize the difference between mental models and the world) has been treated in the psychological and neuroscientific domain as curiosity, cognitive dissonance, a need for knowledge or prediction errors minimization since the 1950s (Harlow, Harlow, & Meyer, 1950; Festinger 1957; Cacioppo & Petty 1982; Friston, 2010). Within this framework, whenever a predictive model is successful in maximizing the similarity between sensory inputs and the corresponding representations of the world, the "knowledge instinct" is satisfied and a positive aesthetic emotion arises (Schoeller & Perlovsky, 2016), followed by a momentary relaxation of the drive for knowledge (Schoeller et al., 2018). This is reminiscent of Berlyne's idea (Berlyne, 1971), suggesting that the beholder gets aesthetically rewarded as a result of reduced arousal corresponding to the relief of curiosity. Hence, aesthetic appreciation involves a relief of uncertainty following an act of exploration prompted by curiosity. Kubovy (1999), similarly described the emotions leading to the "pleasure of the mind" as the ability to interpret and thus resolve the violation of an expectation. Biederman and Vessel's (2006b) also described perceptual pleasure as an information-acquisition mechanism that rewards us for learning about the environment. Crucially, and in line with this hypothesis, informational value "per se" was found to correlate with the activation of dopamine-rich midbrain reward-related structures (Schwartenbeck et al., 2016). Coherently, activations in the same structures are also usually found to correlate with aesthetic appreciation (Blood & Zatorre, 2001; Kawabata & Zeki, 2004; Vartanian & Goel, 2004) and aesthetic judgments (Cela-Conde et al., 2004; Jacobsen et al., 2006). Other authors proposed that the same circuits might underlie the human ability to appreciate the intrinsic value of beautiful objects (Ishizu & Zeki, 2013; Kawabata & Zeki, 2004). Through a DTI and probabilistic tractography study (Sachs et al., 2016), it has been shown that aesthetic emotions triggered by music are related to the structural connectivity between associative auditory cortices and the frontal reward-related areas (such as the anterior insula and the medial prefrontal cortex; for a review of functional connectivity studies supporting this evidence refer to Reybrouck et al., 2018). Mnecke and colleagues, in a very elegant study exploring the aesthetic appreciation of atonal music and its relation with learning mechanisms, suggested that the dopaminergic activity may mediate the reward generated in response to representational models' refinement (Mencke et al., 2019). As indicated by seminal studies in non-human primates, such dopaminergic activity, is observed selectively in correspondence to a certain degree of uncertainty, whereas is lacking when the upcoming input is completely predictable (Fiorillo et al., 2003). In other words, this dopaminergic-based reward may represent the intrinsic motivation to acquire new information (Ferreri et al., 2019; Koelsch, 2010), thus helping the individual to tolerate the risk deriving from uncertainty, to focus on learning-oriented activities (Cheung et al., 2019; Gold et al., 2019a; 2019b; Koelsch et al., 2019; Mencke et al., 2019). For a summary of the relevant research showing an involvement of the frontal reward-related network in aesthetic appreciation see *Table 1*, section 3 (see also *Figure 1B* for a representation of the brain areas involved).

The enhanced sensory activations encoding perceptual learning (Biederman and Vessel, 2006a) might trigger activity in the cortical and sub-cortical hedonic hotspots (Lacey et al., 2011; Nadal, 2013), which in turn would generate perceptual pleasure (which is a necessary condition for the perception of beauty; Brielmann & Pelli, 2019) and might represent an hedonically marked feedback over successful perceptual-learning dynamics (Chetverikov and Kristjánsson, 2016; Winkielman et al., 2003; Winkielman and Cacioppo, 2001).

The relation between aesthetic emotions, knowledge acquisition and meaning-making (including emotional meaning; Panksepp, 1995) is further suggested by studies investigating aesthetic chills (Pelowski et al., 2017; Sachs et al., 2016; Schindler et al., 2017; Schoeller, 2015; Schoeller & Perlovsky, 2016). Generally, chills correspond to emotional peaks (Grewe et al., 2009); in the case of aesthetic chills, these might underly the satisfaction of the knowledge instinct (Pelowski et al., 2018; Schoeller et al., 2018) following an insight (Lasher et al., 1983) and a momentary relief (phenomenologically perceived as relaxation) of the information drive (Schoeller et al., 2018; Schoeller & Perlovsky, 2016). Indeed, as we mentioned earlier, pharmacological studies confirmed that chills activate the opioid knowledge-acquisition system (Goldstein, 1980; Pearce and Wiggins, 2012; Spee et al., 2018). The relation between chills and knowledge acquisition is also suggested by the fact that aesthetic chills are inhibited by incoherent primes preceding the chill-eliciting stimulation. This evidence demonstrates that the aesthetic experience is strongly dependent on meaning-making (Schoeller & Perlovsky, 2016). Moreover, after repeated exposures to the same musical stimuli, chills cease to be evoked (Grewe et al., 2007a, 2007b), thus further indicating the strong relation between aesthetic emotions and knowledge-acquisition.

Our *stopping for knowledge hypothesis* might represent a novel approach to the study of the evolution or update of aesthetic preference of individuals across their lives. If it's true that we like what we are learning from, this might explain not only differences in aesthetic preferences across individuals, but also individual changes across time. It has been previously suggested that novelty, surprise, an optimal level of arousal and continuous development are crucial for appreciation of works of art (Berlyne, 2006). We all change our preference according to our experience. As an example, experienced listeners usually prefer more complex music (Geringer, 1982; Mencke et al., 2019) such as free jazz and aesthetic preferences generally narrow over time. In other words, music might simply become too predictable to engage the attention of experienced listeners and trigger perceptual learning, which in turns would induce aesthetic appreciation.

Although, as reviewed in this paragraph, aesthetic pleasure has been extensively described in terms of self-generated rewards and intrinsic motivation to learn, the hypotheses regarding the function of aesthetic self-signaling (i.e. why do we actually need to experience beauty consciously?) remain controversial. A tentative answer is provided in the next paragraph analyzing the role of aesthetic emotions in balancing between exploratory and exploitative needs driving behaviour via attentional modulations (weighting of prediction errors and prior predictive models) and motor inhibition.

6. Moving towards vs. "being moved". Aesthetic appreciation and the Free Energy Principle

6.1. The *stopping for knowledge hypothesis* as a possible model of aesthetic experience

As discussed in the previous paragraphs, aesthetic experiences have been demonstrated to couple with: *a*) an increased attentional orientation towards the perception of objects rather than towards finalized actions; *b*) pleasure-independence from "pragmatic" outcomes; *c*) successful perceptual learning dynamics (i.e., update of predictions to account for novelty). A graphic representation of our proposed hypothesis is presented in *Figure 1A*.

Can we explain this evidence with a unitary model of aesthetic experiences? We think that theories linking aesthetic emotions to the predictive coding dynamics like our *stopping for knowledge hypothesis* can do so (see also the *prediction error account for aesthetic emotions*; Van de Cruys & Wagemans, 2011b and the *Perlovsky-Schoeller theory;* Perlovsky & Schoeller, 2019). As stated by the "free energy principle", the minimization of sensory uncertainty can be achieved either by interacting with the environment or via the dynamic update of the representation of the state of the world (Friston, 2010). In other words, (reward-seeking) action and (ambiguity-resolving) perception might be considered as two intertwined components of the perception-action cycle, both minimizing sensory uncertainty (Friston et al., 2016; Klyubin et al., 2005). On the one hand, PC minimizes sensory uncertainty updating beliefs to account for predictive errors (Friston, Kilner, & Harrison, 2006); on the other hand, action provides an alternative way to minimize predictive errors, by sampling sensory data in a way that corresponds to the predicted/desired sensory outcomes (Pezzulo et al., 2018). When we act we generate a prediction of the "desired" sensory outcome expected to result from action, and we fulfill this prediction by executing the intended movement. By doing so, we suppress a predictive error signal (indicating the mismatch between current and desired states of the world) that would otherwise emerge (Adams et al., 2013; Brown et al., 2013; Friston, 2010). Pragmatic action thus reduces the difference between the current and the goal states (Pezzulo et al., 2018) that are defined by prior expectations (here indicating the desired outcome of the action; Friston et al., 2015). Accordingly, it was observed that neurons in midbrain reward-related areas encode the expected value attributed to the cues anticipating the actual gain/loss outcome (Enomoto et al., 2011; Roesch et al., 2007; Schultz et al., 1997). The dopamine-mediated mismatch signals between current and expected final sensory goal states characterize environmental stimuli with subjective appetitive value (i.e. utility, in economic terms; Schultz, 2016), weighted according to the precision associated to the expected goal state (i.e. the certainty of its occurrence following finalized action; Pezzulo et al., 2018). These activations inform a broader motivational-network, control actions and plans and influence the amount of effort that the system is willing to tolerate for obtaining an expected extrinsic reward (Nicola, 2010; Schelp et al., 2017). Learning through perception or explorative behavior, instead, is more concerned with the intrinsic epistemic value of belief update (Friston et al., 2016).

According to the free-energy principle, agents select behavioural plans which maximize both expected utility (i.e. extrinsic value)- by acting to modify the environment and information gain (i.e. belief update)-, or intrinsic epistemic value- through perceptual learning (Friston et al., 2015, 2016, 2017). According to this framework, therefore, both action and perception minimize sensory uncertainty. However, given the fact that attention is a limited resource, the most profitable strategy results, from time to time, in directing attention either at maximizing stimulus epistemic (i.e. informational) intrinsic value or at maximizing extrinsic value based on prior expectations (Cohen et al., 2007; Gottlieb, 2012). In the words of Biederman and Vessel (2006b): “infovore [i.e., eager of information] behavior is activated only when other motives are not engaged. When people are trying to satisfy a need for food, are avoiding harm or are otherwise involved in some goal-oriented behavior, then the infovorous instincts take a less active role”. But what is the mechanism that leads us to choose to direct the attention toward learning through perception *vs* toward goal-oriented action?

Given a specific context of stimulation (which might as well be determined by the perceptual features of the stimuli itself) where the individual is prompted to adopt an attitude oriented towards knowledge rather than self-utility, the perception of beauty might serve as a feedback signaling the fluency of learning dynamics (Sarasso, et al., 2019). In other terms, during aesthetic experiences the optimal strategy to restore homeostasis and avoid surprising states consists in reducing prediction errors by adapting the invalidated predictions, while inhibiting appetitive or avoidance behavior, which in contrast reduces prediction errors through the interaction with the environment by changing the actual state of things (Van de Cruys, 2017). In this sense, metaphorically speaking, we experience beauty when, instead of moving, we are moved by experience (Menninghaus et al., 2015).

The trade-off between attention to goals vs. novel sensory inputs (i.e. exploration vs. exploitation) is central to the PC theory, i.e. it results from formal Bayes optimal accounts of behaviour (Brown et al., 2013) which is governed and controlled, via attentional modulations and motor inhibition, by both the entropy and expected utility of future states (Kaplan & Friston, 2018; Schwartenbeck et al., 2013). For instance, on the one hand, movement would not be possible if the brain was not able to attenuate sensory inputs during self-initiated actions (i.e., sensory attenuation: Adams et al., 2013; Brown et al., 2013). On the other hand, it was shown that sensory surprise, and the consequent update of sensory predictions, triggers the activation of a "global suppression network" (Wessel and Aron, 2017) responsible for motor inhibition, and the slowing of motor output (Dutra et al., 2018). This inhibitory mechanism, based on the activation of the subthalamic nucleus (STN) of the basal ganglia, the pre-supplementary motor area and the inferior frontal cortex, extends beyond motor suppression and also affects cognition (e.g. it disrupts working memory; Wessel et al., 2016). Sensory surprise potentiates motor inhibition via a non-selective temporary suppression of motor activity, finalized to overcome current stimulus-to-response mappings and to update predictions about the sensory environment and action consequences (Dutra et al., 2018). Crucially, according to previous research, the activity of the fronto-basal "global suppression network" is indexed by the amplitude of N2 and P3 auditory and visual ERP components (Burle et al., 2004; Dutra et al., 2018; Folstein and Van Petten, 2008; Wessel, 2017; Wessel and Aron, 2017), the same components that we found 1) to be enhanced for more appreciated sounds and 2) to correlate with slower response times and successful movement inhibition (Sarasso et al. 2019). Moreover, the fronto-basal "global suppression network" mainly overlaps with cortical and sub-cortical areas activated by aesthetic appreciation (see *Figure 1*).

In summary, why does our brain self-signal aesthetic value? The answer might reside in the control of behavior via action inhibition. In this sense, the experience of beauty might constitute a mental state signalling to the nervous system to refrain from acting impulsively while focusing on current sensory inputs in order to learn something new. According to this view, and coherently with neuroimaging data, aesthetic appreciation is deeply rooted in the perception-action cycle. However, why aesthetic emotions are consciously perceived remained an open question, since the whole described *stopping for knowledge* mechanism could function automatically (i.e., at an implicit, bottom-up level), without resorting to a conscious hedonic feedback. Even though the conscious nature of beauty is not the focus of the present review, we may speculate that knowledge acquisition is so crucial for survival that human beings, throughout evolution, developed a redundant mechanism acting simultaneously both at an explicit and implicit level. Reminiscent of Berlyne's ideas on aesthetics, curiosity and explorative behaviour (Berlyne, 1971), our hypothesis posits that, in everyday life, as in front of a work of art, aesthetic appreciation might subserve the dynamic content and context-dependent control of exploitative and explorative behaviour.

6.2. Empathic vs un-empathic approaches of aesthetic appreciation: solving an apparent contradiction

This apparent 'un-empathic' correlation between motor inhibition and aesthetic appreciation might appear to be in opposition with other more "empathic" hypotheses, suggesting the involvement of the mirror neuron system during aesthetic appreciation, such as the "embodied simulation" hypothesis (Gallese, 2017a; Gallese and Guerra, 2012; Gallese and Sinigaglia, 2011; Stamatopoulou, 2017), Menninghaus' notion of "being moved" (Menninghaus et al., 2015) and the notion of synchrony with others mind (Schoeller et al., 2018). These perspectives advance that aesthetic appreciation may be induced by mirror system activation (Gallese, 2018, 2017b), underlying the empathic resonance with the emotional content of works of art and interpersonal communication (Menninghaus et al., 2015). In our view, however, the *stopping for knowledge hypothesis* and the above-mentioned *emphatic approaches* are not mutually exclusive. Gallese and colleagues propose that, to achieve aesthetic pleasure, artworks should induce a potentiation of the mirroring mechanisms that are normally active in daily life (Gallese, 2017b; see also *Table1*, first section). In their view such potentiation may be obtained only via motor inhibition: “immobility, that is, a greater degree of motor inhibition, probably allows us to allocate more neural resources, intensifying the activation of bodily-formatted representations, and in so doing, making us adhere more intensely to what we are simulating” (Gallese, 2017b, p.48).

In other words, the trade-off between perception and action, that we hypothesize to be involved in aesthetic appreciation, does not imply a clear-cut double dissociation between functional activations subtending action and perception. Conversely, it describes a specific kind of interaction between perceptual and motor neural processes, as also discussed by previous theoretical and empirical accounts (Schütz-Bosbach and Prinz, 2007). On the one hand, it is well known that mirror activations in predominantly motor and premotor areas encode motor programs as well as perceptual information (Gallese et al., 1996; Keysers et al., 2010). On the other, as predicted by the ideomotor theory (suggesting that actions are represented by their perceivable consequences: Shin, Proctor, & Capaldi, 2010), sensory areas participate in action programming and in the monitoring of movement consequences (Kühn et al., 2010; Limanowski et al., 2018).

In accordance with previous models of aesthetic emotions (Cross and Ticini, 2012; Gallese and Guerra, 2012; Gallese and Sinigaglia, 2011; Jeffers, 2010; Kirsch et al., 2016; Massaro et al., 2012), during perception/learning-oriented aesthetic appreciation, we also expect a correlation between aesthetic pleasure and the amount of (mirror) activation in pre-motor areas, likely responsible for empathic resonance. At the same time, we expect to record a certain degree of motor inhibition, which is essential for preventing unintentional imitation during action observation and empathic resonance (Hari et al., 2014). In sum, the *stopping for knowledge hypothesis* can also be applied to the aesthetic response to the perception of emotional content (e.g. emotional resonance in music perception; Panksepp, 1995; Panksepp & Bernatzky, 2002). In this case, motor inhibition and the concomitant enhancement of empathic/resonance mechanisms reduces the uncertainty regarding the content of others’ mind through the update of predictive representations, thus leading to aesthetic pleasure (Schoeller et al., 2018).

In conclusion, the *stopping for knowledge hypothesis* claims that the perception of beauty serves as an intrinsic motivation toward learning (Friston et al., 2017; Oudeyer, Gottlieb, & Lopes, 2016; Schwartenbeck et al., 2018) and is deeply rooted in the relation between perception and action. This mechanism may be interpreted as a sort of self-generated reward, necessary to better cope with sensory uncertainty (i.e. the mismatch between current and expected events), which is the driving force of learning and memory updating (Agres, Abdallah, & Pearce, 2018; Krawczyk et al., 2017). When attentionally arousing surprising stimuli induces a mismatch between sensory inputs and representations, aesthetic emotions might intervene in the perception-action cycle and signal to the system the opportunity to refrain from acting based on prior knowledge in order to facilitate learning from the environment. In other words, aesthetic emotions would belong to the realm of knowledge-oriented (Perlovsky & Schoeller, 2019) epistemic emotions (see Muis, Chevrier, & Singh, 2018 for a review), no less than surprise, curiosity and confusion (Berlyne, 2006; Brun & Kuenzle, 2008; Schoeller, 2015; Schoeller & Perlovsky, 2016; Van de Cruys, 2017).

7. Possible future applications

In this review we suggest that, in the case of aesthetic appreciation sensory prediction errors are up-weighted and trigger enhanced perceptual learning, while attention is diverted from mismatches between current and desired goal states and movement is inhibited. The sense of beauty might be fundamental to dynamically adjust the point of balance between action and perception of informationally profitable stimuli, thus motivating the search for learning progresses and enabling us to avoid automatic reactions and tolerate transient states of sensory uncertainty, which are the driving force of perceptual learning and memory updating. On the basis of this consideration, we speculate that aesthetic emotions are fundamental for our intelligent behaviour, enabling us to escape the automaticity of acquired behaviour, to better “attune” to reality and others’ mind. Moreover, the ability to tolerate uncertainty and ambiguity during aesthetic appreciation might explain the mitigation of cognitive interference shown by highly appreciated consonant music (Masataka and Perlovsky, 2013). Indeed, it has been suggested that the fundamental function of music is to help mitigating cognitive dissonance and avoid discarding conflicting knowledge (Masataka and Perlovsky, 2012a, 2012b). Tolerating uncertainty has a fundamental evolutionary relevance, for it allows us to reconcile cognitive dissonance without the need of devaluing knowledge. Otherwise, language and culture would have been probably discarded by evolution (Masataka and Perlovsky, 2013, 2012b, 2012a). Future studies should address whether this evolutionary function is extended to aesthetic appreciation in general or limited to specific sensory domains, such as music perception.

The *stopping for knowledge hypothesis* posits that movement inhibition during aesthetic emotions is functional to perceptual learning. We are now capable of computing the magnitude in the update of predictive representations (i.e. the informational value of stimuli), and thus quantify the correlation between subjective and objective (e.g. aesthetic chills) measures of aesthetic appreciation, behavioural and neurophysiological indexes of motor inhibition and information theoretic indexes of perceptual learning. This twofold relation should be empirically tested by future studies investigating the role of immobility in favouring knowledge seeking. Future research should also address the issue of the neurocognitive mechanisms leading to conscious vs. unconscious aesthetic emotions and how such mechanisms can be modulated by interoceptive awareness (Schoeller, 2019). It has been suggested that aesthetic emotions mostly lay below the radar of conscious awareness during learning processes (Perlovsky & Schoeller, 2019; Schoeller, 2019); but when do they become conscious and for what purpose? A possible answer to this question is that aesthetic emotions cross the consciousness border every time a change in the mental representation of the world reach such an importance or saliency as to affects the cognitive system as a whole and transform behaviour at the top of the cognitive hierarchy (Schoeller, 2019). Future studies should test this prediction by employing stimuli inducing learning at different levels of the sensory and cognitive hierarchy. Moreover, the role of interoceptive awareness in the emergence of learning- oriented aesthetic emotions is not clear yet. However, there is wide consensus over the fact that the somatic reception and response to perceptual stimuli are an essential part of aesthetic sensibility (Berleant, 2015). Enhanced interoception (by means of technology, rehabilitation and other contextual/relational factors boosting ascending bodily signals) might lower the consciousness threshold of aesthetic emotions and potentiate the subtended learning mechanisms (Perlovsky & Schoeller, 2019; Schoeller, 2019). Future developments in neuroaesthetics should address this issue by modulating interoceptive awareness in a controlled way during aesthetic appreciation.

The fact that the aesthetic value of sensory experience may modulate perceptual learning and memory retrieval [see Lehmann & Seufert (2018) for a recent review] is also interesting for its potential applications in learning and plasticity-oriented activities, such as teaching (Girod and Wong, 2005), neurological rehabilitation, or psychotherapy (Francesetti, 2012, 2019; Spagnuolo Lobb, 2018; Roubal et al., 2017). Leading psychotherapists like Gustav Jung, Wilfred Bion (Schmidt, 2019), James Hillman (1989) and Donald Meltzer (1988) have recognized the neglected value of aesthetic emotions in therapy. As an example, Gestalt therapy poses the perception of beauty and the full availability of the senses of the therapist at the heart of its therapeutic approach (Francesetti, 2015, 2012). Drawing from a Deweyan perspective (Bloom, 2011), Gestalt therapy might be considered a fully-fledged evaluative process (Perls, Hefferline & Goodman, 1994; p. 65-66) following intrinsic aesthetic criteria (the appreciation of a beautiful *Gestalt*; Francesetti, 2012, 2019; Spagnuolo Lobb, 2013). According to Gestalt therapy, when assuming an aesthetic attitude (i.e. an attitude oriented to an *Aesthetic relational knowledge;* Spagnuolo Lobb, 2018), also referred to as aesthetic diagnosis (Roubal et al., 2017), the therapist is able to tolerate sensory, emotional and relational uncertainty (Francesetti, 2019a) without escaping it, which is considered an essential sensory and relational competence for therapy (Spagnuolo Lobb, 2018). “This aesthetic element of beauty makes a very difficult situation tolerable”, in the words of Wilfred Bion (Schmidt, 2019; p. 79). Such aesthetic attitude to consciously experience emotional states in the relational field is often partially missing in psychopathology (i.e. emotion states and the experience of an emotion are dissociated; Francesetti et al., 2020) and it can thus represent a desirable outcome of psychotherapy (Francesetti, 2012, 2015). The therapist works primarily on himself and on modulating his attentional attitude in the pursuit of this goal (Francesetti, 2019a, 2019b). Therapists might therefore fruitfully exploit the enhancement of emotional sensibility characterizing aesthetic perception (Berleant, 2015). Preliminary results in empirical aesthetics research already support this intuition. Indeed, aesthetic chills have been considered as a universal marker of openness to experience (McCrae, 2007; Silvia and Nusbaum, 2011), enhance altruism (Fukui and Toyoshima, 2014) and might be triggered by mechanisms such as shared experience and empathic resonance (Bannister, 2019; Schoeller et al., 2018), which reduce the uncertainty regarding other people's contents of mind (Schoeller et al., 2018). In simple terms, within a relational context, the experience of beauty might favour a deeper understanding of others' mind (Pelowski et al., 2018; Schoeller et al., 2018) through the emotional resonance (Fuchs and Koch, 2014; Gallese, 2007) between minds. Indeed, in the words of Pelowski et al. (2018), chill-eliciting "emotional resonance" states (Pelowski et al., 2017) are characterized by low discrepancy between predictive representations and the world because, at the peak of aesthetic experiences, uncertainty is reduced to its (local) minimum (Pelowski et al., 2018). According to our hypothesis, however, such final low-discrepancy outcome must necessarily follow an initial state of increased uncertainty brought by empathic resonance (see *Figure 1*), subjectively felt as the emergence of a novel emotion. Accordingly, it was found that chill-eliciting scenes involve radical changes in the relations among characters (Schoeller & Perlovsky, 2016). Altogether, this evidence suggests that aesthetic emotions might follow the satisfaction of the (relational) knowledge instinct, which urges us to minimize uncertainty in the relational domain through emphatic resonance (Schoeller et al., 2018). Future studies should further investigate the role of aesthetic emotions in motivating toward prosocial behaviour, learning of culture and collective narratives (Schoeller, 2019) and the attunement with others mind, i.e. the relation between natural curiosity and empathy (Schoeller et al., 2018). As we have discussed above, this is especially interesting in the case of psychotherapy, where the therapeutic alliance and outcome is grounded on interpersonal synchrony (Wheatley et al., 2012), i.e. the coupling or attunement between the patient and the therapist mind (Francesetti, 2019b; Gallese et al., 2007; Koole and Tschacher, 2016; Tschacher et al., 2017).

In the domain of education and learning research, following Dewey's model of transformative experiences (Stroud, 2010), aesthetic emotions have been already considered as a relevant factor in determining students' engagement in learning activities (Girod and Wong, 2005; Mastandrea et al., 2019; Parrish, 2009; Uhrmacher, 2009). As we have previously suggested, the investigation of the relation between learning and beauty perception should not be limited to the domain of low-level sensory processing but should also embrace higher-level abstract cognitive domains, such as mathematical insight, language acquisition and science learning (e.g. mathematical beauty; Schoeller, 2015a, 2015b; Schoeller & Perlovsky, 2015). Indeed, among scientists, physicists, such as Albert Einstein, intuited that the first test of a scientific theory is its beauty (McAllister, 1999). The efficacy of an aesthetic orientation in motivating students' engagement has been already demonstrated with ecological case studies (Girod and Wong, 2005), but still needs to be further tested by more controlled experimental protocols. Finally, computational models of aesthetic emotions subtending learning in humans need yet to be tested in automatic machine learning research (Moerland et al., 2018), which aims at developing AI that are intrinsically motivated to engage in efficient learning activities (Kaplan & Oudeyer, 2004; Oudeyer et al., 2007).

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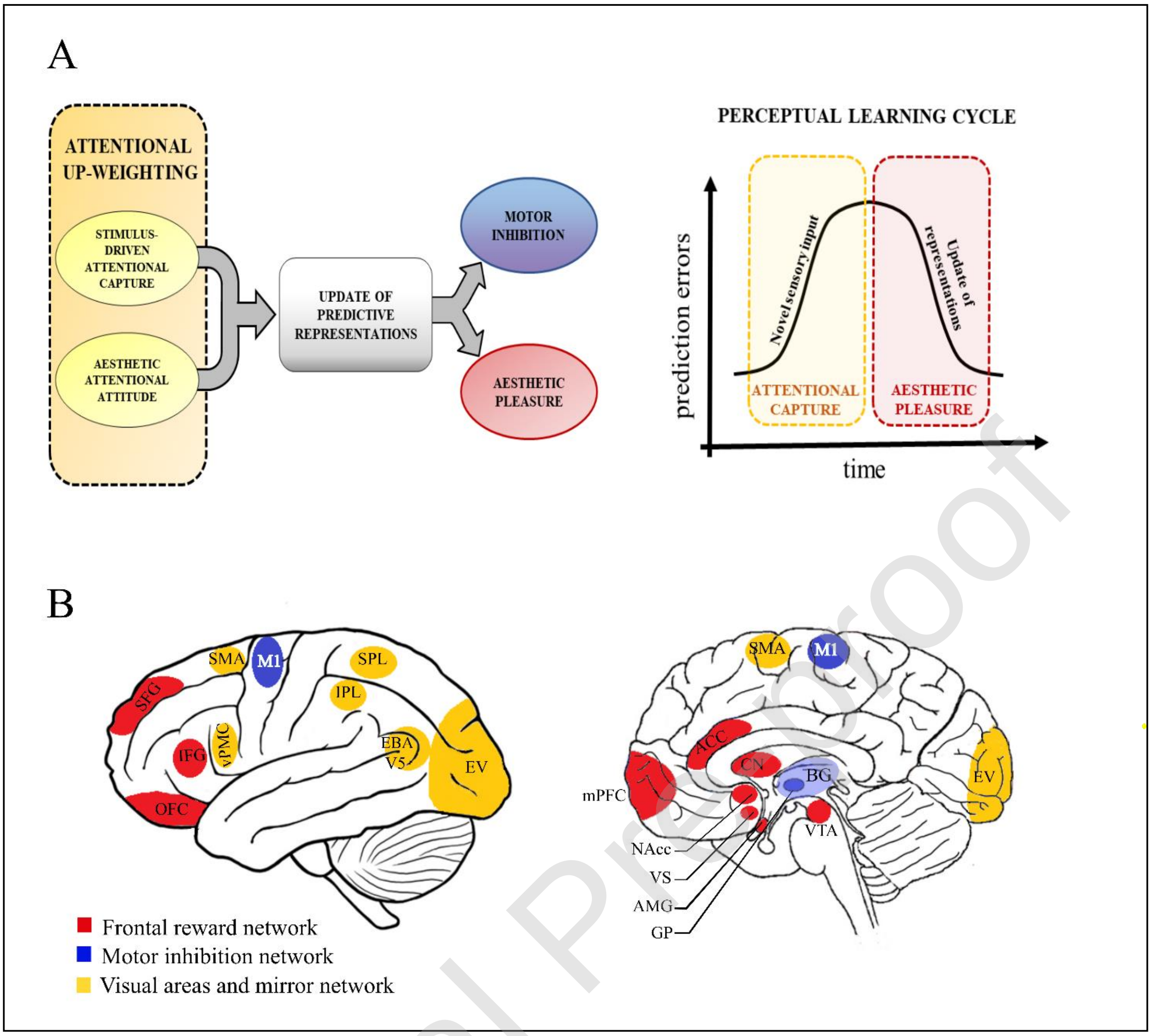

Fig.1. A) *Left Panel*: schematic representation of our *stopping for knowledge hypothesis* for aesthetic appreciation. Content or context-driven attentional up-weighting of sensory inputs (i.e. prediction errors) correlates with the magnitude of the update of predictive representations along the neural hierarchy. This in turn triggers both an aesthetic hedonic feedback and motor-inhibition via the engagement of a fronto-basal ganglia "global suppression network" (Wessel et al., 2016). *Right panel*: relationship between the evolution of sensory uncertainty (indexed by prediction errors), attentional dynamics and aesthetic pleasure along a single perceptual learning cycle. **B)** Distribution of brain areas constituting the network involved in aesthetic appreciation, based on the experimental results summarized in *Table 1*. This widespread network is composed of brain regions whose activation positively or negatively correlates with aesthetic appreciation. We color-coded regions according to their hypothesized role in aesthetic appreciation. *In red*: areas which underly the emergence of a positive hedonic feedback; *in dark and light blue*: areas responsible for motor inhibition during aesthetic appreciations; *in yellow*: areas correlated with enhanced sensory and mirror activations in response to stimuli judged as more beautiful.

SMA= Supplementary Motor Area; EV= Early Visual areas (V1,V2,V3); V5= extrastriate visual area (BA 19); vPMC= ventral Pre Motor Cortex; IPL= Inferior Parietal Lobule; EBA= Extrastriate Body Area; SPL= Superior Parietal Lobule; mPFC= medial Pre Frontal Cortex; VS= Ventral Striatum; AMG= amygdala; GP= Globus Pallidus; BG= Basal Ganglia; NAcc= Nucleus Accumbens; OFC= Obrbito Frontal Cortex; ACC= Anterior Cingulate Cortex; CN= Caudate Nucleus; VTA= Ventral Tegmental Areas; SFG= Superior Frontal Gyrus; IFG= Inferior Frontal Gyrus.

Tab.1. Neuroimaging correlates of aesthetic appreciation. The table reports neuroimaging findings suggesting a correlation between aesthetic appreciation (i.e. beauty ratings) and a) attention-related enhancement of sensory and mirror neural activity – corresponding to the yellow-shaded area of the model represented in *Figure 1A* and referring to the brain regions in yellow in *Figure 1B*; b) motor inhibition of automatic response – corresponding to the blue-shaded area of the model represented in *Figure 1A* and referring to the brain regions in blue in *Figure 1B*; c) engagement of the dopaminergic frontal reward network – corresponding to the red-shaded area of the model represented in *Figure 1A* and referring to the brain regions in red in *Figure 1B*. SMA= Supplementary Motor Area; V5/MT+= extrastriate visual area (BA 19); vPMC= ventral Pre Motor Cortex; IPL= Inferior Parietal Lobule; EBA= Extrastriate Body Area; SPL= Superior Parietal Lobule; mPFC= medial Pre Frontal Cortex; NAcc= Nucleus Accumbens; OFC= Obrbito Frontal Cortex; ACC= Anterior Cingulate Cortex, CN= Caudate Nucleus; VTA= Ventral Tegmental Areas; SFG= Superior Frontal Gyrus; STG= Superior Temporal Gyrus; IFG= Inferior Frontal Gyrus.

Correlates of Aesthetic Appreciation	ID	Study	Method	Stimuli	Significant findings
Increased sensory and mirror activation	1	Coburn et al., 2020	fMRI	Architectural interiors	Bold activations in primary visual areas (lingual gyrus, cuneus) covaried with different dimensions (hominess, fascination, coherence) of aesthetic rating of interiors.
	2	Sarasso et al., 2020	EEG	Abstract 1/f noise images	The amplitude of early attention-related sensory components of the visual evoked potential (C1, N1) correlated with subjective aesthetic judgements.
	3	Belfi et al., 2019	fMRI	Paintings	Modulation of activity in the lateral visual network (lateral occipitotemporal, ventral occipitotemporal, and parietal visual regions) by aesthetic appreciation (continuous aesthetic pleasure ratings) during the initial transient response to paintings.
	4	Sarasso et al., 2019	EEG	Musical intervals	Increased amplitude of the early attention-related N1/P2 complex of the auditory evoked potentials for more appreciated musical intervals.
	5	Di Dio et al., 2016	fMRI	Paintings with natural and human content	Aesthetic judgments of paintings correlated with perceived dynamism and involved a motor-resonance component processed by the cortical motor system, through the activation of parietal and premotor areas.

	6	Boccia et al., 2015	fMRI	Artworks and non-artworks	Positive aesthetic experiences, compared with negative ones (i.e. liked vs. disliked pictures), induced enhanced activity in the SMA, which is considered as part of the mirror neurons system (Molenberghs et al., 2009), as well as in the occipito-temporal areas of face processing.
	7	Flexas et al., 2014	fMRI	Paintings	Responses to beautiful paintings, compared to ugly ones, showed increased activity in the superior occipital gyrus.
	8	Vartanian et al., 2013	fMRI	Images of curvilinear vs. rectilinear interior spaces	Activation in a distributed network including the the middle occipital gyrus covaried in relation to beauty ratings.
	9	Zeki and Stutters, 2012	fMRI	Kinetic abstract configurations	The level of V5/MT+ activation was positively correlated with aesthetic preference for simple abstract kinetic visual configurations.
	10	Cross et al., 2011	fMRI	Dance movements	The positive relation between liking and sensorymotor experience (i.e. familiarity with observed movements) is encoded by activity in the occipitotemporal and parietal regions of the action observation/simulation network (PMC and IPL).
	11	Calvo-Merino et al. 2010	TMS	Body forms	Inhibitory rTMS delivered over both left and right EBA reduced aesthetic sensitivity for body stimuli.
	12	Cela-Conde et al. 2009	MEG	Abstract and figurative paintings, pictures of urban and natural landscapes	The presentation of beautiful vs. non-beautiful images induced increased activity in parietal (IPL, SPL) and somatomotor areas (BA 3,4,6, 43), which, according to the authors, might underlie heightened spatial and somatosensory perception.
	13	Calvo-Merino et al. 2008	fMRI	Dance movements	Activity in EBA and in the vPMC was modulated by subjective liking for observed dance movements.
	14	Koelsh et al., 2006	fMRI	Pleasant and unpleasant music	Pleasant contrasted to unpleasant music showed activations in the rolandic opercular areas, possibly reflecting the activation of mirror-functions that serves the formation of (premotor) representations of pleasant auditory information.

	15	Vartanian and Goel., 2004	fMRI	Paintings	Activation in bilateral occipital gyri and bilateral fusiform gyri increased in response to increasing preference.
Motor inhibition	4	Sarasso et al., 2019	EEG	Musical intervals	Aesthetic judgements positively correlated with response times in a detection task. The motor inhibition-related N2 and P3 components were enhanced for more appreciated intervals.
	16	Nakamura and Kawabata., 2015	tDCS	Abstract paintings	Inhibiting neural excitability in the mPFC by applying cathodal tDCS over the frontal pole with anodal (excitatory) tDCS over the left primary motor cortex diminished the experience of beauty but not ugliness ratings.
	7	Flexas et al., 2014	fMRI	Paintings	Stimuli took longer to be classified as beautiful than as ugly.
	8	Vartanian et al., 2013	fMRI	Images of curvilinear vs. rectilinear interior spaces	Beauty ratings covaried in relation to activity in the globus pallidus, which is responsible for motor inhibition (Chu et al., 2015) and is part of the fronto-basal ganglia "global suppression network"(Wessel et al., 2016; Wessel and Aron, 2017)
	17	Ishizu and Zeki., 2011	fMRI	Visual stimuli	The comparison between beautiful and ugly visual stimuli showed that the latter enhanced the activation of the left somato-motor area.
	18	De Tommaso et al., 2008	EEG	Abstract images and paintings	The motor inhibition-related P3 component amplitude was greater for beautiful images preceding a motor response than for neutral or ugly images. Furthermore, response times were slower after the presentation of beautiful images.
	19	Roy et al., 2008	EMG	Music	The startle blink reflex registered by the EMG showed increased amplitude and shorter latency while listening to unpleasant music, as compared to pleasant music.

	20	Di Dio et al., 2007	fMRI	2D images of sculptures	Negatively evaluated images (contrasted with positively evaluated images) determined the activation of the primary motor region.
	21	Jacobsen et al., 2006	fMRI	Symmetric vs non-symmetric abstract images	Participants needed significantly more time for beautiful than for non-beautiful judgments.
	22	Kawabata and Zeki., 2004	fMRI	Paintings	The fMRI comparison between ugly versus beautiful stimuli highlighted an increase in bilateral activation of the primary motor cortex.
Engagement of the reward network	3	Belfi et al., 2019	fMRI-continuous ratings	Paintings	Increased activity in different basal ganglia subregions (NAcc, putamen, caudate and pallidum) during the perception of highly-rated images.
	24	Cattaneo et al., 2019	tDCS	Paintings	Enhancing the excitability in the mPFC, which is part of the mesocorticolimbic dopaminergic reward system (Tzschentke, 2000), via anodal tDCS, led participants to judge paintings as more beautiful than following sham tDCS.
	6	Boccia et al., 2015	fMRI	Images of artworks and non-artworks	Liked vs. disliked pictures induced enhanced activity in frontal network encompassing the OFC, insula and ACC.
	7	Flexas et al., 2014	fMRI	Paintings	Responses to beautiful paintings showed increased activity in the cingulate cortex compared to ugly ones.
	25	Salimpoor et al., 2013	fMRI	Music clips	When listening to preferred music the NAcc increased its connectivity with the STG, OFC, amygdala, PFC, ACC, and IFG.
	26	Ishizu and Zeki., 2013	fMRI	Paintings	Increased activity in the OFC during the perception of paintings valued as beautiful.
	27	Bohrn et al., 2013	fMRI	Written texts	Positive parametrical effects of beauty were found in the ACC and in the caudate body.
	8	Vartanian et al.; 2013	fMRI	Images of curvilinear vs. rectilinear interior spaces	Activation in the SFG, which was shown to index the magnitude of rewards (Vassena et al., 2014), covaried in relation to beauty ratings.

	28	Salimpoor et al., 2011	fMRI-PET	Music	Increased dopaminergic transmission in the CN occurred during the anticipation of a musical chill, and increased dopaminergic transmission in the NAcc during the chill itself.
	17	Ishizu and Zeki., 2011	fMRI	Visual and musical stimuli	Activity in the mOFC is proportional to the declared intensity of beauty experiences: the activity was parametrically modulated within the mOFC, for both visual and musical stimuli.
	29	Kirk et al., 2009	fMRI	Images of buildings	Aesthetic ratings positively correlated with BOLD activations in the OFC and NAcc
	14	Koelsh et al., 2006	fMRI	Music	Pleasant vs. unpleasant music contrasts showed activation of the ventral striatum
	30	Menon and Levitin, 2005	fMRI	Music	Listening to pleasant music modulated activity in NAcc and the VTA. Effective connectivity showed significant VTA-mediated interaction of the NAcc with the hypothalamus, insula, and OFC.
	22	Kawabata and Zeki, 2004	fMRI	Paintings	Beautiful stimuli induced increased activity in the reward-related OFC.
	15	Vartanian and Goel., 2004	fMRI	Paintings	Activation in right CN decreased in response to decreasing preference, and the activation in the left cingulate sulcus increased in response to increasing preference.
	31	Brown et al., 2004	fMRI	Pleasant music	Activation of the ventral striatum in addition to the sub callosal cingulate cortex while listening to pleasant musical pieces contrasted with a resting condition.
	32	Blood and Zatorre, 2001	PET-EMG	Own selected and control music	Activations positively correlated with chills intensity in left ventral striatum, bilateral insula, right OFC, ACC