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Mental Imagery, Emotion, and 'Literary Task Sets'

Clues Towards a Literary Neuroart

The Daffodils

I wandered lonely as a cloud
That floats on high o'er vales and hills,
When all at once I saw a crowd,
A host of golden daffodils,
Beside the lake, beneath the trees,
Fluttering and dancing in the breeze.

Continuous as the stars that shine
And twinkle on the milky way,
They stretched in never-ending line
Along the margin of the bay:
Ten thousand saw I at a glance
Tossing their heads in sprightly dance.

The waves beside them danced, but they
Out-did the sparkling waves in glee:
A poet could not but be gay
In such a jocund company!
I gazed- and gazed- but little thought
What wealth the show to me had brought.

For oft, when on my couch I lie
In vacant or in pensive mood,
They flash upon that inward eye
Which is the bliss of solitude;
And then my heart with pleasure fills,
And dances with the daffodils.

William Wordsworth (1770–1850)

1. Introduction

Aesthetics, as a philosophical discipline concerned with the elucidation of concepts such as 'beauty', 'inspiration', 'artistic value', 'fiction', and the like, begins with Plato, who in several of his dialogues

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discussed many of the topics now considered to pertain to aesthetics (Halliwell, 2009). What I think most baffled Plato is one of the most remarkable features of literary works of art, and lies at the heart of literary aesthetics, namely, *the power of literary works of art to produce overwhelming emotional states, and ultimately, to influence behaviour,* which Plato explicitly addressed in the tenth book of *The Republic* (Plato, 2007). Though his answer to this problem has striking similarities to mine — the relationship between mental imagery and emotion — he offers no mechanisms by which mental images are created or how mental imagery causes emotional responses. Moreover, Plato's aesthetics is founded on an outmoded theory of mind — dualism — one that is at odds with neuroscience. However, there is one aspect of Plato's proposal that I would like to stress, and that is that aesthetics as a discipline should be grounded on a clear ontology; moreover, aesthetics depends upon an explicit theory of the mind.

Humans have endeavoured to produce aesthetically pleasing objects — mainly tools, jewellery, clothing, fabrics, and paintings — since, at least, the dawn of the *Homo sapiens* lineage (Balter, 2009; Cela-Conde *et al.*, 2004; Nadal *et al.*, 2009). The paintings found in the caves of Altamira, Spain, and Lascaux, France, for example, dating as far back as 35,000 BC approximately (Pike *et al.*, 2012), show such craftsmanship that they cannot but be the work of skilfully trained artists.

In the last decade we have witnessed the emergence of a new field in aesthetic studies: *neuroaesthetics*, that is, the field of neuroscience that deals with the neuronal systems and mechanisms of aesthetic and artistic appreciation (Chatterjee, 2010; Ramachandran and Hirstein, 1999; Skov and Vartanian, 2009; Zeki, 1999). Work in neuroaesthetics has so far focused on the neuronal basis of visual (Calvo-Merino *et al.*, 2007; Cela-Conde *et al.*, 2004; 2009; Chatterjee, 2003; 2004; Di Dio *et al.*, 2007; Freedberg and Gallese, 2007; Ishai *et al.*, 2007; Kawabata and Zeki, 2004; Ramachandran, 2004; Vartanian and Goel, 2004 — see Di Dio and Gallese, 2009; Nadal *et al.*, 2008; and Zaidel, 2010, for reviews) and musical (Blood and Zatorre, 2001; Blood *et al.*, 1999; Koelsch and Siebel, 2005; Levitin, 2006; Peretz and Zatorre, 2005) aesthetics.

In this article I will offer a neurocognitive and affective model of literary aesthetics that, although highly speculative, is not only compatible with neuroscience but also expands the boundaries of neuroaesthetics into the realm of literary neuroaesthetics.

In short, my answer to Plato's perplexity is that mental imagery plays a crucial role in literary aesthetics by enhancing the emotional

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response to semantic (conceptual) processes, and by enhancing the emotional response bias to future cognitive and affective processes and, ultimately, behaviour.[1]

2. A Philosophical Framework for Neuroaesthetics

As I mentioned in the introduction, aesthetic hypotheses and theories need to be framed within an explicit theory of the mind, since they are concerned with the subjective response towards natural and artistic objects. Consider for instance the following set of statements regarding the nature of the mind and how they guide — or misguide — neuroaesthetic research:

(a) The mind is an immaterial substance that interacts with the brain (*Dualism*)
(b) The mind or mental functions are but a special kind of information processing (physical) structure — e.g. 'recurrent networks' (Churchland, 1996; Smith Churchland, 1989; Llinás, 2001)
(c) Mental functions are stuff-independent, multiple-realizable, functional states or processes (Aizawa, 2007; Aizawa and Gillett, 2009; Putman, 1960)
(d) Mental functions are properties of the whole person and not of any specific organ: 'ascription of psychological attributes to the brain is incoherent… For it makes no sense to ascribe such psychological attributes to anything less than the animal as a whole. It is the animal that perceives, not parts of its brain, and it is human beings who think and reason, not their brains' (Bennett and Hacker, 2003, p. 3)
(e) Mental functions are a *product* of brain activity; conversely, 'all of our mental phenomena are *caused* by lower level neuronal processes in the brain' (Searle, 2002, p. 57)
(f) Mental functions are molecular processes (Bickle, 2006)
(g) Mental functions are single-cell processes (e.g. *grandmother cells*)
(h) Mental functions are emergent (or systemic) brain functions (Bechtel, 2008; Bunge, 1979; 2010; Craver, 2007; Gazzaniga, 2010; Koch, 2004; LeDoux, 2003).

A few words against proposal (c) (the multiple-realizability thesis) are due here since it is now one of the most popular views among

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[1] For a similar view but in the context of emotional disorders see Holmes *et al.* (2008a,b) and Holmes and Mathews (2010).

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philosophers of mind (see Schouton and de Jong, 2007). A criticism of the other proposals will follow.

Succinctly, the multiple-realizability thesis holds that mental properties and states are stuff-independent functional states that can be actualized (realized) in different material types (physical, chemical, or biological) and structures. Since first proposed by Putnam, the thesis of the multiple realizability of mental functions (or 'psychological kinds') has been widely criticized. I will focus on two features of multiple realizability — one ontological and one epistemological — that render it incompatible with science in general and neuroscience in particular.

First, ontologically, the multiple realizability thesis is covertly dualistic. For instance, Aizawa and Gillett (2009) distinguish between two kinds of properties: *properties* and *instances of properties*, where properties 'exist in the natural world through their instances' (*ibid.*, p. 184, note 7) and 'a property instance is an entity that makes a difference to the causal powers of an individual' (*ibid.*, p. 186). Leaving aside that properties are not entities but qualities of entities, this whole distinction between *properties* and their *instances* is nothing but a revival of Plato's ontological dualism and his claim that 'form precedes substance'; that is, that properties (and things, events, etc.) exist prior to — and independently of — their material exemplars.

Second, one strong epistemological consequence of the multiple realizability thesis, that stems from the aforementioned distinction between properties and property instances, is that a true (final) explanation of a property (unlike a property instance) is material-independent (or stuff-independent), since all that matters is the causal (functional) power of a property. That is, a true explanation of a property is independent of where (in what entity) this property happens to be actualized (realized). In other words, we should be able explain action potentials without any reference to neurons, breathing without lungs, motion without moving objects, vision without brains, atomic weight without atoms, and so on. Moreover, these kinds of explanations should be the ultimate aim of science. But this is hardly what scientists are after. Scientists known that properties cannot be detached from the thing that possesses them — that is, properties are traits or qualities *of* material things. Allow me to quote this rather long passage from Craver, where he disproves the epistemology put forward by the thesis of multiple realizability:

> No neuroscientist would claim… that it makes no difference to the explanation of the action potential whether ions move across the membrane by

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> active transporters, passive diffusion, or a mechanism made of Swiss cheese (to pick a philosophically charged example). One might be entertained by building a model of the action potential out of Swiss cheese, and it would be impressive indeed if this model could reproduce the form of the action potential, but no reputable journal would publish the model, let alone allow the author to claim that it counted as an explanation of the action potential. Neurons are not made of Swiss cheese. (Craver, 2006, p. 14)

It is easy to see that the theory of mind adopted will determine what will count as a neuroaesthetic theory and also the experimental set-up to contrast neuroaesthetic hypotheses. For example, assuming that the mind is some kind of immaterial entity (or set of functions) renders neuroscience unnecessary. But even in less extreme cases, where the mind is explicitly understood as a set of brain functions, attributing mental functions to different levels of brain organization has non-trivial epistemological consequences. For example, attributing mental functions to molecular processes focuses research at the level of genes, neurotransmitters, second messengers, and the like, and treats higher-level hypotheses only as heuristic devices (Bickle, 2003; 2006). On the other hand, identifying mental functions with emergent properties of neuronal systems focuses research on the properties of neuronal assemblies and their interactions.

Here I will endorse an unabashedly materialistic framework and subscribe to the so-called psychoneural identity hypothesis; that is, I assume that every mind state or process is a state or process of the brain; or, conversely, that ‘the brain is the organ of mental processes’ (Squire and Kandel, 2000, p. 56). Note that if mental functions are processes of the brain, they cannot be understood independently of the brain, any more than respiration can be understood without the lungs or metabolism without the liver. This alone rules out any attempt to understand what the mind is independently of knowing how the brain works.

Identifying mental functions with brain processes is not enough, since not every brain process is a mental function. Neurons perform a host of processes which are not mental and are common to every cell, like maintaining homeostasis and metabolizing. Moreover, not even every complex function of a brain system, like regulating heart beat or maintaining body posture, is a mental function. In fact, I claim that only special kinds of brain processes can be identified with mental functions. In set theory terms: if M is the set of mental functions and B is the set of brain processes then $\mathrm{M} < \mathrm{B}$, which means that M is a subset of B. This is equivalent to $\{x \mid x \,\varepsilon\, \mathrm{M} \rightarrow x \,\varepsilon\, B\}$, that is, if x belongs to M

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then *x* belongs to B, but not the other way round. In particular, I identify mental functions with *systemic* or *emergent properties* of neuronal systems or 'assemblies' (Bunge, 1979; 2010; Casanova, 2010; Casanova and Tillquist, 2008; Gazzaniga, 2010; Hebb, 1949/2002; Koch, 2004; Kosslyn, 2005; LeDoux, 2003; Mountcastle, 1997 — for a history of the concept and discussions of emergence, see Bedau and Humphreys, 2008; Bunge, 2004).

This hypothesis has received support from neuropsychological and brain image studies showing that it takes large portions of the brain (or the loss of large portions of the brain) to perform (or preclude) any given mental function. Single cells have some properties which make them poor candidates as the organs of mental functions. For example, single neurons are unable to depolarize a postsynaptic neuron (Koch and Segev, 2000), and the activity of a single neuron is 'unstable [and] is not activated uniquely by one specific complicated or simple stimulus… [which means that] activation of single neurons alone cannot specify any unique information in a situation' (Sakuray, 2007, p. 251). This has been shown neurophysiologically by Sato and colleagues who recorded electrical activity from electrodes implanted in monkeys and found that, whereas inferior temporal (IT) single cells have a wide range of stimulus selectivity, IT columns have more stable object selectivity (Sato *et al.*, 2009), and by Kreiman and colleagues who showed that IT local field potentials (LFP, which measure the pooled input activity of small neuronal populations) have a stronger selectivity to complex visual stimuli than single cells (Kreiman *et al.*, 2006; see also Meyers *et al.*, 2008). Furthermore, single-cell activity was a poor predictor of LFP selectivity. Hung and colleagues (2005) arrived at similar results and calculated that the activity of a small IT population of ~100 neurons is indeed needed to decode the stimulus identity. This result is very interesting since there are approximately 80 to 100 neurons in a cortical minicolumn (Buxhoeveden and Casanova, 2002; more on cortical minicolumns below).

Interestingly, Rasch and colleagues (2009) tried to predict LFP properties from single-cell activity and concluded that while some circuit-level properties could be predicted from single-cell activity, others call for a systemic approach; in their own words: 'Circuits of neurons may show emergent properties that are not always easy to visualize by looking at individual neurons without studying their interactions' (*ibid.*, p. 13795).

In summary, though much more research is needed, there is a general consensus that the brain codes perceptual stimuli, memories, and motor actions at the level of neuronal populations (systems)

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(Kreiman, 2004; Logothetis, 2008; Quian Quiroga *et al.*, 2007; Quian Quiroga and Kreiman, 2010), and that the information processed at this level cannot be reduced to single cell processes (Liu *et al.*, 2009; Meyers *et al.*, 2008; Quian Quiroga and Panzeri, 2009; Rasch *et al.*, 2009). This does not mean that single-cell recordings are useless, but it stresses the need to complement single-cell recordings with other methods that can measure activity at the population level before jumping to any conclusion.

Within this general framework I postulate the following:

Hypothesis: at the level of the cortex the smallest unit capable of mental functions (or smallest mental unit) is the minicolumn.

The idea that the cortical minicolumn is indeed a functional or processing unit was first proposed by Spanish neuroanatomist Rafael Lorente de Nó — a former disciple of Ramón Santiago y Cajal — based purely on anatomical grounds (DeFelipe, 2005). Further support for this hypothesis came from the pioneering electrophysiological recordings of Mountcastle in the cat’s somatosensory cortex and Hubel and Wiesel’s recordings from cat’s primary visual cortex (Hubel and Wiesel, 1959; Mountcastle, 1957; see Shepherd, 2010). Since then, more and more evidence has been gathered that makes cortical minicolumns suitable candidates as the smallest processing unit of the cortex with the capacity to sustain mental functions (Buxhoeveden and Casanova, 2002; Casanova, 2010; Mountcastle, 1997; Rockland, 2010).

Anatomically, a minicolumn is a vertical organization of neurons spanning from cortical layers 2 to 6, consisting of a pyramidal core and a periphery (neuropil) of GABAergic interneurons and local synapses; each minicolumn is composed of 80 to 100 neurons and has a mean width of 60 μm (Buxhoeveden and Casanova, 2002; Casanova *et al.*, 2009; DeFelipe, 2005). (It should be mentioned, however, that minicolumnar composition and structure differ not only among species but also among different brain areas: DeFelipe, 2005; DeFelipe *et al.*, 2002.) Interestingly, each minicolumn has all cortical neuronal phenotypes, that is, both *spiny neurons* (excitatory pyramidal and stellate neurons) and *aspiny nonpyramidal neurons* (inhibitory GABAergic interneurons) are present in every minicolumn. This makes stimuli processing in any minicolumn a very complex process that involves both excitations and inhibitions in every neuron in the minicolumn. As a result, every output of a minicolumn has undergone ‘extensive localized processing’ (Buxhoeveden and Casanova, 2002,

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p. 943) before reaching its targets (for a model of the mechanisms involved see Douglas and Martin, 2004; for the role of inhibitory interneurons in minicolumnar processes see Raghanti *et al.*, 2010; for more on minicolumn anatomy see Buxhoeveden and Casanova, 2002; DeFelipe, 2005; DeFelipe *et al.*, 2002; and Jones and Rakic, 2010).

Functionally, a minicolumn can be defined by a common receptive field, common stimuli selectivity or preference, and common output properties (Hubel and Wiesel, 1977; Mountcastle, 1997). Interestingly, minicolumns have been identified in almost all mammals, including non-human primates, rodents, cats, and even dolphins (Raghanti *et al.*, 2010). Accordingly, we should endow these species with mental functions, although not necessarily with self-consciousness.

Minicolumns have very interesting properties. One extremely relevant property of minicolumns is that they are plastic; that is, they can undergo structural and functional changes due to activity-dependent processes.[2] In other words, they can learn. This property can hardly be overestimated. Firstly, because the capacity to learn has been postulated to be one of the defining properties of mental functions (Bunge, 2010) and is what distinguishes them from subcortical fixed-action circuits (Tucker *et al.*, 2000).[3] Secondly, because plasticity is driven by activity-dependent processes, cognitive and affective neuroscience cannot overlook environmental effects in brain development and function. And since the human environment is mostly artificial (cultural), C&A neurosciences should be integrated with social or cultural neuroscience (see Balcetis and Lassiter, 2010; Franks, 2010). Since the seminal works of Hubel and Wiesel (1977) on deprivation, plasticity in the primary visual cortex is a widely recognized phenomenon, so much so that it can be shown that 'rearing [a monkey] in a pattern of vertical stripes reduces the percentage of cells responding to horizontal bars [in V1]; rearing in a pattern of horizontal stripes reduces the percentage of cells responding to vertical bars; and so on' (Daw, 2004, p. 128).

Another interesting property of minicolumns is that the interplay between excitatory and inhibitory connections results in the emergence of global properties absent in single cells, like amplification of input signals, noise reduction, more robust selectivity, and the

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[2] That plasticity is a property of neuronal systems is another argument against the identification of mental functions with either single-cell or molecular processes.

[3] Significantly, minicolumns and columns have been identified in some subcortical nuclei (Rockland, 2010) and also some subcortical nuclei have been shown to have plastic properties (like the amygdala: LeDoux, 2000), so the identity mental = cortical and non-mental = subcortical does not hold.

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capacity to maintain activity in the absence or reduction of input signals (Logothetis, 2008).

Others have proposed as the smallest processing unit of the cortex not the minicolumn but a microsystem composed of bundles of apical dendrites with the underlying ‘parent’ somas — which do not always belong to the same minicolumn — and its cortical and subcortical output targets (Innocenti and Vercelli, 2010). Clearly far more research is needed to understand the daunting functional organization of the cortex.

Minicolumns, in turn, organize themselves in macro-systems called hypercolumns (Hubel and Wiesel, 1977), macrocolumns, or simply columns (Buxhoeveden and Casanova, 2002; Mountcastle, 1997; Rockland, 2010). Each column has a mean width of 300 μm to 500 μm approximately and is composed of 50 to 80 minicolumns. It should be stressed, however, that variability — within certain ranges — is a constant among both minicolumns and columns (Rockland, 2010). As for columns, it should be noted that their structure and constituents are dynamically arranged and rearranged according to task demands (Tommerdahl *et al.*, 2005).

Columns and minicolumns have been identified as the functional units in a great number of processes. Here I shall mention but a few: (a) ocular dominance, orientation, and colour mini- and hypercolumns in primary cortex (Dow, 2002; Hubel and Wiesel, 1977); (b) movement orientation minicolumns in brain region V5 (DeAngelis and Newsome, 1999); (c) somatosensory mini- and macrocolumns (Mountcastle, 1997; Tommerdahl *et al.*, 2005); and (d) complex visual shapes in IT columns (Kreiman *et al.*, 2006; Sato *et al.*, 2009; Tanaka, 2003; 2004; Tanifuji, 2004; Tanifuji *et al.*, 2005; Tsunoda *et al.*, 2001). Furthermore, minicolumnar anomalies are now being identified in many psychiatric and neurodegenerative diseases such as autism, schizophrenia, Alzheimers, and dyslexia (Casanova, 2010; Casanova and Tillquist, 2008; Chance *et al.*, 2008; Di Rosa *et al.*, 2009).

Finally, minicolumns and columns are part of large-scale distributed networks (Mesulam, 1998; 2002; Rockland, 2010). Importantly, the constituents of large-scale networks — that is, the interconnected minicolumns and columns — are task- and (brain) state-dependent and change dynamically with environmental and information processing demands (McIntosh, 2007). When people think about mental functions — perception, decision making, attention, planning, feelings, consciousness, and the like — they are actually thinking about the functions of these large-scale networks.

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Taking the anatomical and functional organization of the cortex described above, I postulate the following:

Hypothesis: mental functions are both localized and distributed.

Hypothesis: mental functions have a hierarchical structure determined by the systemic (emergent) properties of minicolumns, columns, and large-scale networks.

In other words, I identify low-level mental functions with the functions of minicolumns, mid-level functions with columnar functions, and high-level functions (the traditional cognitive and emotional processes) with the functions of large-scale networks, as shown in Figure 1 below.

I must be clear on one thing: there is, currently, no scientific theory of what the mind is, or what mind functions are. Notwithstanding, the conjunction of stable selectivity and robust responses (similar to what Koch, 2004, p. 26, has termed 'explicit representation'), together with plasticity (that is, the ability to learn) seem promising candidates for defining properties of 'mindness'; and I have shown that minicolumns are the smallest unit of the cortex to have these properties.

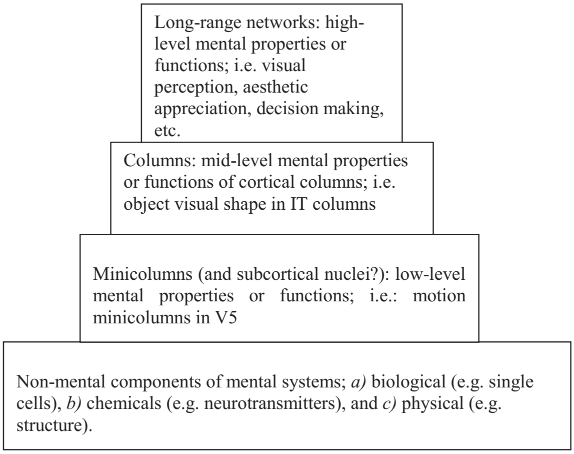

Figure 1. The relationships between levels should not be understood as causal relationships; that is, it is not that low-levels cause higher-levels (as proposed by Searle; see thesis (e) above). On the contrary, this figure portrays compositional and emergent relationships. For instance: when single cells organize themselves into minicolumns, they acquire low-level mental properties or the ability to perform low-level mental functions. In turn, when minicolumns organize themselves into columns they acquire mid-level mental functions, and so on.

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One of the main epistemological consequences of the ontological hierarchy of mental functions is that each mental level can, and should, be studied in its own right, independently of the levels above and below it. However, since mental levels are ontologically dependent upon each other, a full account of any mental function should specify the mechanism by which these functions emerge from low-level components and processes (see Craver, 2007).

3. Mental Images and Emotions: Clues Towards a Literary Neuroaesthetics

Writers and critics alike have emphasized the role of mental imagery in aesthetic appreciation and emotional excitement related to artistic literature in general and poetry in particular (Eliot, 1932); *Imagism* even made mental imagery the essence of poetry. There is also evidence that for amateur poets different kinds of mental imagery (visual, auditory, gustatory, etc.) correlate with particular emotions; for example, sexual emotions correlate better with haptic and olfactory images (Shaw, 2008).

But, what are mental images and how do they interact with emotions? Let us tackle first the nature of mental images. In short, I offer the following:

Definition: a mental image is the experience of a perceptual phenomenon (visual, somatosensory, auditory, olfactory, etc.) in the absence of sensory (‘external’) stimuli.

Metaphorically, a mental image corresponds with the experience of ‘seeing with the mind’s eye’, ‘hearing with the mind’s ears’, and the like.

Now I put forward the following:

Hypothesis: a mental image occurs when the neuronal pattern of a perceptual feature (i.e. colour, shape, taste, tone, etc.) is activated within the modality-specific cortex (i.e. visual cortex, auditory cortex, etc.) in the absence of sensory stimuli (Kosslyn, 1994; Kosslyn *et al.*, 2001; 2006).

In other words, imaging an object (or sound, or taste, etc.) and perceiving the same object (or sound, or taste, etc.) make use of the same neuronal substrate. This hypothesis has been confirmed in many modalities including audition (Kraemer *et al.*, 2005; Hubbard, 2010; Zatorre and Halpern, 2005), olfaction (Bensafi *et al.*, 2003; 2007),

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and intero- and propioception (see below). Since visual imagery is by far the most studied of mental images, I am now going to analyse the case of visual mental imagery in greater detail.

3.1. Visual Cortex and Visual Mental Imagery

Those acquainted with the visual cortex can skip this section and head straight to the next section (*3.2. The Mind's Eye*).

Humans and non-human primates are highly visual creatures. The macaque's visual cortex is comprised of 40 anatomically and functionally distinct regions that occupy about half (52%) of the total surface of the cortex. In humans, the visual cortex represents 27% of the total cortical surface, and it is composed of more than 40 distinct specialized sub-regions (Van Essen, 2004). Here we are only going to review some general properties of the visual cortex and how these properties determine many of the properties of visual mental imagery.

1) **Functional specialization**: the different visual attributes (like colour, shape, movement, texture, etc.) are processed in specialized and anatomically segregated regions of the visual cortex. For example, while visual movement is processed in area MT/V5 (Bartels *et al.*, 2008), colour is processed in subregions of V4 (Zeki and Marini, 1998), and an object's shape is processed in IT (Tanaka, 2003). Interestingly, this functional segregation is observed as early as thalamic inputs to V1, where distinct thalamic layers project to different layers of the primary visual cortex (Casagrande and Xu, 2004; Sherman and Guillery, 2001).
2) **Hierchical processing**: the visual cortex can be functionally divided into low-level, mid-level, and high-level visual areas (Farah, 2004; Ullman, 1996), defined by the capacity to process increasingly complex (abstract and global) features, probably through the integration and transformation of inputs of lower-level areas (Rolls, 2004; 2007; but see Hegdé and Van Essen, 2007, for evidence of complex shape processing already in V1). The output and input layers of the cortex can provide an anatomically-based criterion for processing hierarchies, since feedforward connections typically originate from supragranular layers (2 and 3) and terminate in layer 4, while feedback connections typically originate from infragranular layers (5 and 6) and terminate in non-granular layers (Bullier, 2004; Rockland, 2004; Ungerleider *et al.*, 2008). Likewise, the percentage of supragranular layer neurons (SLN) — from V1 to extrastriate visual

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areas — has been proposed as a criterion for assessing processing hierarchies in the cortex (Batardière *et al.*, 2002).

3) **Feedforward-feedback processing**: almost every visual area sending feedforward (afferent) projections receives a reciprocal feedback (efferent) projection (Felleman and Van Essen, 1991; Kaas, 2004; Rockland, 2004).
4) **Parallel processing**: (a) distinct visual features (shape, colour, motion, etc.) are processed in parallel systems of the visual cortex (Casagrande and Xu, 2004; Nassi and Callaway, 2009); and (b) there are at least two visual streams operating in parallel: (i) the 'dorsal/occipitoparietal' (Ungerleider and Pasternak, 2004) or 'vision-for-action' (Milner and Goodale, 2006) stream, specialized in visuomotor transformations and spatial location processing; and (ii) the 'ventral/occipitotemporal' (Kanwisher, 2004; Ungerleider and Pasternak, 2004) or 'vision-for-recognition' (Milner and Goodale, 2006), specialized in the visual properties necessary for the visual recognition of objects (i.e. shape and colour invariance). Milner and Goodale (2006) claim that it is not the kind of information that distinguishes between ventral and dorsal visual pathways (e.g. visual features *vs.* spatial information), but the transformations performed upon the visual information. In support of this idea, there is evidence of spatial information (object scale and location) in populations of IT neurons (Hung *et al.*, 2005; Schwarzlose *et al.*, 2008).
5) **Domain-specificity**: along the ventral stream, visual categories such as faces, places, and bodies are processed in specialized areas. Specifically, faces are processed in the so-called fusiform face area (FFA) and occipital face area (OFA), places in the so-called parahippocampal place area (PPA) and transverse occipital sulcus (TOS), and bodies in the so-called extrastriate body area (EBA) and fusiform body area (FBA) (Kanwisher and Yovel, 2006; Reddy and Kanwisher, 2006; Schwarzlose *et al.*, 2008). These specialized areas contrast with the activity of the lateral occipital complex (LOC) and posterior fusiform (pF) which seem to be specialized in object shape processing independently of the category of the stimuli (Grill-Spector and Mallach, 2004; Schwarzlose *et al.*, 2008; Vuilleumier *et al.*, 2002).
6) **Processing areas are storage areas**: that is, the distinct visual features are stored in the same brain areas that processed them (Slotnik, 2004). Interestingly, some forms of non-declarative

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memories are stored in areas as early as the primary visual cortex (Squire and Kandel, 2000).

7) **Processing areas are perceptual areas**: that is, the perception of a visual attribute depends on the activity of the specialized brain region processing that attribute. In other words, visual consciousness is distributed among the distinct visual processing areas (Koch, 2004; Rees, 2007; Zeki, 2003).

Research on the neural basis of mental imagery is a very active field; even restricting the time frame to 2005–2011, 'mental imagery' in search engines like *PubMed* returns more than 580 hits. Evidently a review of this literature is out of the scope of this article. Here, I will just mention some evidence for the general hypothesis concerning the nature of visual mental imagery; that is, that a visual mental image is the reactivation of the visual cortex in the absence of sensory stimuli.

3.2. The Mind's Eye

The first source of evidence suggesting common mechanisms and neuronal substrate between visual perception and visual imagery was psychology and psychophysics. Research has shown, among other things, that (a) visual mental images have a 3-D structure — and hence can be mentally rotated (Shepard and Metzler, 1971); (b) it takes (almost) the same time to scan a map perceptually as to scan it mentally (Borst and Kosslyn, 2008; Kosslyn, 1994); (c) visual imagery interferes with visual perception but not with perception in other modalities (Segal and Fusella, 1970); (d) visual imagery can also facilitate visual perception but not perception in other modalities (Ishai and Sagi, 1997); (e) visual mental images can be 're-inspected' to see implicit properties of the images (e.g. symmetry) (Thompson *et al.*, 2008); (f) visual mental images induce eye movements consistent with the imagined content (Brandt and Stark, 1997; Rodionov *et al.*, 2004).

Perhaps the most compelling psychological evidence comes from the research conducted by Pearson and colleagues (2008). They showed that visual imagery can disrupt 'perceptual rivalry'. 'Perceptual rivalry' occurs when two distinct images are presented simultaneously to each eye; counterintuitively, subjects do not perceive an image that is a combination of the two, but report seeing one image at a time. What Pearson and colleagues showed was that imaging one of the stimuli produced a positive bias as to which of the two images reached conscious perception. Interestingly, this effect was both

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location- and orientation-specific, suggesting that visual imagery activates retinotopically organized visual areas.

Interesting and attractive though this evidence is, it cannot single-handedly establish the neuronal systems and mechanisms involved in the generation and manipulation of mental images. With the advent of neuroimaging techniques (in particular PET and fMRI), research on the neural basis of mental imagery is now a very active field. Here, I will just mention the most relevant evidence for my purpose. I shall divide the evidence into three groups: (a) studies using brain imaging techniques; (b) neuropsychology of mental images; and (c) research on visual working memory.

3.2.1. Imaging visual images

Ganis and colleagues (2004) directly compared a perceptual task against an imagery task and found that 92% of the brain areas that showed increased activity during visual perception were also active during visual mental imagery, as measured by fMRI. More impressively, in studying the representation of visual shapes both in perception and imagery, Stokes and colleagues (2009) and Reddy and colleagues (2010) have shown that imaging simple geometrical shapes — the letters 'X' and 'O' — activates the lateral occipital complex (LOC, a brain area specialized in object shape processing independently of the category of the stimuli) in the same way as actually perceiving the shapes does. Strikingly, a neuronal network trained solely on the fMRI data obtained during the perception sessions was able to correctly classify the different shapes when presented only with the data obtained during the imagery sessions.

Brain activity related to visual shape imagery also shows domain-specificity. For instance, imaging faces or buildings activates the corresponding domain-specific processing areas: the fusiform face area (FFA) and the parahippocampal place area respectively (O'Craven and Kanwisher, 2000). This selectivity is also found at the level of single cells. Kreiman and colleagues (2000) found that a subset of medial temporal lobe (MTL) neurons that were active while the subject viewed a face were also selectively active while the subject imaged the same face; this was also shown for other visual categories. Likewise, a network trained only with the perception data could predict what visual category the subject was imaging (*ibid.*). Ishai and colleagues (2000) extended these findings by showing that imaging faces, houses, and chairs activated a distributed network of extrastriate visual areas similar to that activated during the actual perception of the stimuli itself.

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Finally, when subjects are asked to picture mental images with high spatial resolution — that is attending to highly detailed spatial features of the image — activity is observed in retinotopically organized visual areas, including the primary visual cortex (Klein *et al.*, 2004; Kosslyn and Thompson, 2003; Slotnik *et al.*, 2005). Moreover, applying TMS (transcranial magnetic stimulation) to the occipital cortex disrupts this ability (Kosslyn *et al.*, 1999). Interestingly, differences in subjective vividness of mental imagery correlate with the level of occipital activity (Cui *et al.*, 2007).

The evidence mentioned above focused on the similarity between visual mental imagery and visual perception in the so-called ventral stream (Ungerleider and Pasternak, 2004). Evidence also shows that visual imagery and perception recruit similar areas in the so-called dorsal stream as well. For instance, Trojano and colleagues (2004) showed that imaging different positions of clock hands and judging their angle amplitude selectively activates regions within the posterior parietal cortex. Also, Kaas and colleagues (2009) showed that imaging moving objects selectively activates hMT/V5+, the human homologue of primate V5 (or MT). Finally, Mazard and colleagues (2004) reviewed the literature on PET scans and showed that imagery tasks requiring the transformation and manipulation of spatial relations consistently activate dorsal stream visual areas.

3.2.2. Insulting the brain: the neuropsychology of imagery

The neuropsychology of visual imagery is open to fiery controversies. While there are well documented cases in which damage to visual cortical areas affects both perception and imagery in a similar way (Grüter *et al.*, 2009; Farah, 2000), there is also unavoidable evidence of cases where damage impairs imagery but not perception and vice versa (Bartolomeo, 2002; 2008; Dulin *et al.*, 2008; Moro *et al.*, 2008). This situation merits some remarks. First, where dissociations between imagery and perception are reported, the purported dissociations are mostly based on subjective accounts and not on objective measurements, which makes it hard to asses the data. Second, the mechanisms involved in visual imagery generation are likely to be task-dependent (Kosslyn *et al.*, 2004), a feature hardly ever considered in neuropsychological reports. Finally, differences between the mechanisms and brain areas involved in perception and imagery are expected for several reasons; while visual perception is driven by retinal input and requires a great deal of local processes (such as local depth, orientation, and luminance extraction, among many other input transformations), figure-ground segregation, colour-, motion-, and

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contours-shape extraction — to name but a few — none of these processes are required in visual imagery which relies on prefrontal cortex (PFC) signals and the reconstruction of long-term memories (Kosslyn *et al.*, 2006).

Finally, applying dynamic causal modelling to fMRI data in both a visual perception and visual imagery task, Mechelli and colleagues (2004) showed that, while in perception and imagery the same set of brain areas were active, activity in perception was driven by bottom-up signals and in imagery activity it was driven by top-down signals arising from PFC and parietal cortices.

3.2.3. Visual working memory: the top-down activation of visual areas

Working memory has been defined as the 'mechanism for short-term active maintenance of information as well as for the processing of maintained information' (Funahashi, 2007, p. 311), and it is believed to rely on top-down feedback signals from the PFC to modality-specific and motor areas (Squire and Kandel, 2000; Fuster, 2008). Visual working memory research is relevant to visual mental imagery because it shows how visual brain areas can support visual representations in the absence of external (retinal) stimulation. For instance, Harrison and Tong (2009), in a working memory task, were able to successfully identify the stimulus held in the working memory when the stimulus was not present, based solely on the fMRI activity patterns in early visual areas, suggesting that information about the identity of the stimulus was being fed from higher PFC areas to lower visual areas. Also, Meyers and colleagues (2008), with electrophysiological recordings in non-human primates, and Ranganath and colleagues (2004), with fMRI recordings in humans, found substantive evidence of stimuli-specific activity in IT (a visual area) during working memory tasks. Perhaps the most straightforward evidence of the capacity of the PFC to produce activity in visual areas in the absence of retinal stimuli is the series of experiments conducted by Tomita and colleagues (1999) on non-human primates. They showed that (a) in the absence of visual input, the PFC signal could activate single IT neurons and that this activity was content-specific; and (b) by the resection of callosal interhemispheric connections, they were able to demonstrate that IT activity was driven by PFC projections and not from visual cortico-cortical interhemispheric connections. These results have suggested a similarity between the mechanisms of short-term memory (or working memory) and the mechanism of visual

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mental imagery (Cattaneo *et al.*, 2009; Kosslyn and Thompson, 2003; Ranganath, 2006; Ranganath and D'Esposito, 2005).

So far I have reviewed some evidence in support of the hypothesis that visual mental imagery relies on the same neural tissue as visual perception (for an updated review of the evidence for and against this hypothesis and a detailed mechanism of visual mental imagery generation, see Kosslyn *et al.*, 2006). For present purposes this is highly relevant because it provides a way of explaining how mental imagery could influence emotions; namely, *through the anatomical connections between visual cortical areas and emotion processing areas*.

Although I have focused on visual imagery, there is evidence in support of similar processes in auditory (Hubbard, 2010; King, 2006; Kraemer *et al.*, 2005; Zatorre and Halpern, 2005), olfactory (Bensafi *et al.*, 2003), and motor (Porro *et al.*, 2000) imagery.

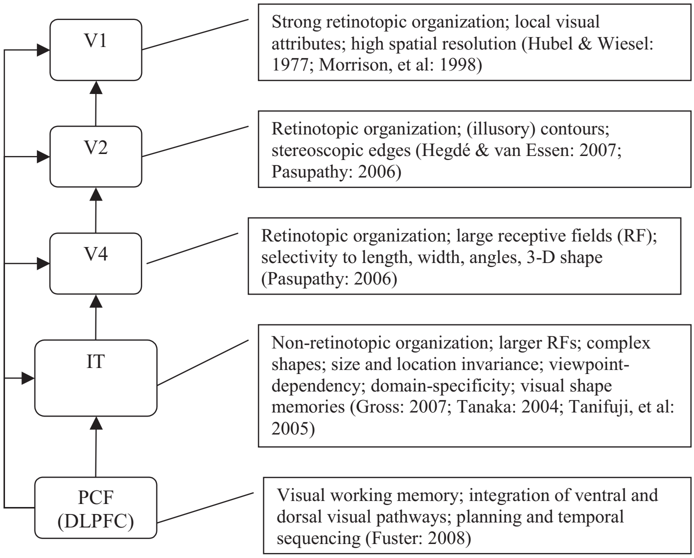

Figure 2. A schematic representation of the brain areas involved in the generation of visual mental imagery of visual shapes in the ventral stream (parietal areas are not represented here). Arrows represent the direction of activity.

3.2. The Interactions between Visual Mental Imagery and Emotions

In this article I propose that in the anatomical and functional connections between modality-specific cortices and emotional processing

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areas lies one of the keys to understanding literary aesthetics. Previously I have dealt with mental imagery and its neural basis (particularly, visual mental imagery). Here I am going to specify what I understand by ‘emotion’. Unfortunately, neuroscientific research on emotions, though rapidly growing, is as yet not as advanced as the research on our perceptual systems, and there is no clear consensus on how to define an emotion. Notwithstanding, many agree upon the following blueprint:

Emotion Scheme: an emotion consists of the following processes: (a) an appraisal process whereby a stimulus is categorized according to its survival value and/or goal; and (b) a coordinated system of bodily (visceral and motor), brain (i.e. attention), and behavioural responses, which are more or less stereotyped.

In other words, each emotion can be characterized by a set of bodily (both autonomic and behavioural) and cognitive states (Damasio, 2003; Ledoux, 1996; 2003; Panksepp, 1998). Finally, an emotion must be distinguished from its conscious perception, or feeling. Explicitly:

Definition: a feeling is the conscious perception (or awareness) of an emotional response (Adolphs and Heberlein, 2002; Damasio, 2003; LeDoux, 1996).

This distinction between emotion and feeling — homologous to that between sensation and perception — stresses the fact that there can be emotional responses without a conscious feeling, and the fact that there are neural structures necessary for the triggering of an emotional response but not for its conscious perception. For example, while the amygdala is necessary for danger detection (Freese and Amaral, 2009) and the related fear response (LeDoux, 1996), it might not be necessarily involved in the feeling of fear (Anderson and Phelps, 2002; Damasio *et al.*, 2000).

Regarding the neural basis of emotions, theories can be grouped along a continuum with, at one end, (a) the theory that all emotions are the function of the same brain system and particular emotions being but different states (coded by valence and arousal levels) of the same system; and at the other end, (b) the theory that each particular emotion is the function of an independent neural circuit specialized in that particular emotion.

I propose the following:

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Hypothesis: there are specialized neuronal systems for some emotions (like the so-called basic emotions, e.g. fear) with different degrees of activity (coded by valence and arousal levels) of that system yielding related emotional responses (e.g. terror or horror). Still other emotions emerge from the interactions between different emotional systems (e.g. pride).

This means that there is not an 'emotional organ' or 'emotional centre' whose function is to produce the whole range of human emotions; moreover, emotional responses are the functions of systems and not individual brain areas, and so to talk of the amygdala as the 'fear centre' or the nucleus accumbens as the 'pleasure centre' is misleading (for the system involved in fear, see LeDoux, 2000; for the system involved in hedonic/pleasure response, see Berridge and Kringelbach, 2008). This should be taken into account when trying to extrapolate the findings regarding a particular emotion to other emotions. For instance, while an intact insula is necessary for feeling disgust (Ibañez *et al.*, 2010) and recognizing disgust in others (Wicker *et al.*, 2003), it seems that an intact insula is not necessary for recognizing other emotions (Adolphs *et al.*, 2003).

Each emotional system can be thought of as a vertical hierarchical organization, spanning from low-level, fixed-action, mesencephalic (brainstem) and diencephalic (thalamus and hypothalamus) brain areas (involved in visceral and somatic control, reflexes and stereotyped behaviours), to higher-level, plastic, corticolimbic brain areas (Liotti and Panksepp, 2004; Tucker *et al.*, 2000).

In general, the brain areas believed to participate in some emotional responses and their purported functions are:[4]

(a) *Amygdala*: involved in danger detection, the triggering of fear-related responses, and the formation and consolidation of emotional (fearful), non-conscious memories (Dalgleish, 2004; Fellous *et al.*, 2003; Freese and Amaral, 2009; Hamann, 2009;

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[4] Though I will not deal with laterality of function here, some commentaries are needed. According to popular knowledge, the right hemisphere is the brain's emotional hemisphere, while the left hemisphere is the cognitive one; even Kane (2004) put forward the hypothesis that poetic language is a right-hemisphere function (see also Holland, 2009). Though not entirely wrong, this view is an oversimplification. Emotions are whole-brain processes and as such involve both hemispheres. What is true is that different aspects of the emotional responses (and feelings) are lateralized (Demaree *et al.*, 2005). For example, the right hemisphere is biased towards processing negative emotions (e.g. sadness; the reverse is true of the left hemisphere), more readily identifies emotional face-expressions, and is more involved in arousal and motivation (Liotti & Panksepp, 2004). Most probably, the emotional responses to literary works of art, both in reading and creating, involve interactions between both hemispheres.

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LaBar and Cabeza, 2006; LeDoux, 1996; 2003; LeDoux and Sciller, 2009).

(b) *Hypothalamus and brainstem nuclei*: triggering and regulation of autonomic responses, including visceral, hormonal, motor, and neuromodulatory (Adolphs and Heberlein, 2002; Amin *et al.*, 2005; Blessing, 2002; Cools, 2008; Cools *et al.*, 2007; Damasio, 1999; 2003; Lledo, 2002).

(c) *Anterior cingulate cortex*: integrates the motivational value of a stimulus with the organism's bodily and cognitive state; involved in pain perception, emotional-cognitive conflicts, error detection, and memory (Beckmann *et al.*, 2009; Price, 2002).

(d) *Insula*: integrates complex (multimodal) sensory information with the set of visceral responses associated with those stimuli. Implicated in interoception (the feeling of one's viscera), self-reflection, the feeling of disgust, autonomic functions, and mood (Damasio, 2003; Ibañez *et al.*, 2010; Jabbi *et al.*, 2008; Modinos *et al.*, 2009; Mufson *et al.*, 1997). Craig (2010) claims that the seemingly heterogeneous activities of the insula can be understood if one considers the insula as the interoceptive cortex, with a caudal to rostral organization, from primary interoceptive areas to association ones, much like the visual cortex.

(e) *Somatosensory cortices*: involved in propioceptive (the feeling of one's body) and emotional feelings (Adolphs *et al.*, 2003).

(f) *Orbitofrontal cortex (OFC)*: integrates complex sensory (perceptual) and emotional information in a task- or goal-dependent manner. Involved in regulation of autonomic responses, decision-making, hedonic and reward experiences, and short-term memory of emotional values (Kringelbach, 2005; Wallis, 2007a). Interestingly, the OFC is the only neocortical area with reciprocal connections to the mesencephalon, which allows it to control autonomic functions (Damasio, 2003).

Importantly, all of these regions are anatomically connected and functionally integrated with modality-specific cortices and can thus influence imagery processes, either directly — through direct connections — and/or indirectly — through the release of neuromodulators (monoamines, hormones, neuropeptides, etc.).

In summary, I propose the following model of interactions between visual mental imagery and emotions (see Figure 3). Although I focus on visual imagery, a similar model can be put forward for the other modalities.

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(i) From mental images to emotions: the excitatory route. The activation of visual brain areas through descendent (top-down) projections from PFC causes activity in emotional brain areas through the ascendant (bottom-up) connections between the visual cortex and the different emotional areas.

(ii) From emotions to mental images: the modulatory route. The emotional state of the organism modulates (facilitates or inhibits) the activity in visual processing areas. In particular, both the quality (i.e. the definition of detail) and the content (i.e. what is visualized) are modulated by the emotional state of the organism. This modulation can be achieved through distinct parallel processes: (a) direct projections from the amygdala, orbitofrontal cortex, and ventromedial prefrontal cortex to the dorsolateral prefrontal cortex (involved in visual working memory), the inferior frontal gyrus (involved in semantic retrieval), and ventral stream processing areas (LeDoux and Sciller, 2009; Kensinger, 2009; Vuilleumier, 2009); (b) direct projections from the insula to visual association areas (particularly in the anterior inferior temporal cortex, TEm) and PFC (Mufson *et al.*, 1997); and (c) diffuse modulatory projections from monoaminergic nuclei to PFC and visual cortex. Other modulatory routes are expected.

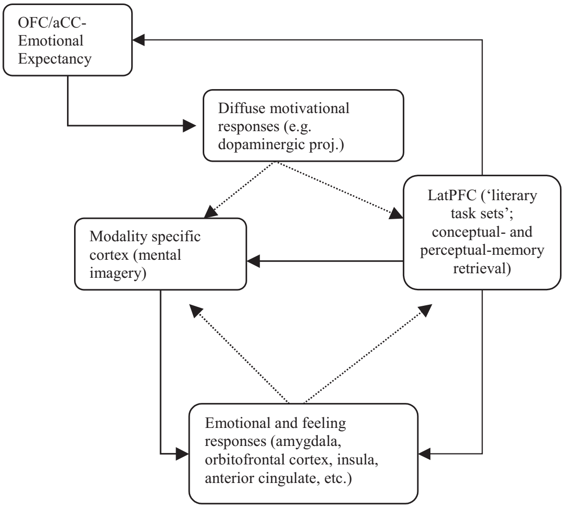

Figure 3. The schematic imagery-emotion 'loop'. The filled lines represent excitatory connections. The dotted lines represent modulatory connections.

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4. Probing the Model

Unfortunately, neuroscientific research on literary aesthetics is non-existent, so there is no direct evidence to test our proposed model. Nevertheless, it can be tested indirectly, mainly through research on the interactions between mental imagery and emotion (the excitatory route of our model), and between emotions and visual perception (the modulatory route of our model); regrettably, evidence for these processes is also scarce.

Two necessary observations before I continue. First, while stressing the relevance of the interactions between mental imagery and emotions for the aesthetic experience associated with literary works of art, I want to underscore the fact that many other processes not mentioned here are surely involved in literary aesthetics, like linguistic rhythm and music, linguistic innovation, agreement between the meaning of the poem (or novel, etc.) and the worldview of the reader, autobiographical experiences, and cultural and social factors, to name but a few. If I have not dealt with these other phenomena here, it is because we know little about the neural basis of these processes and they are therefore poor candidates on which to found a literary neuroart. Phenomena as complex as aesthetic experiences are the result of the interactions between many brain networks and processes; in their complexity lie both joy and tears for scientists. Secondly, the importance of the interactions between imagery and emotions should be understood in the broader context of what I shall call ‘literary task sets’. *Task sets* are sets of abstract rules that guide behaviour and information processing according to task demands, context, and expectations (Bunge and Wallis, 2008; Wallis, 2007b). These sets, probably the function of regions in the most anterior and lateral parts of the prefrontal cortex, coordinate perceptual, mnemonic, attentional, cognitive, and emotional resources in order to guide behaviour toward a desirable goal or purpose. I postulate that the reading of literary works of art is guided by ‘literary task sets’ — learned through experience and/or education — that guide emotional and cognitive expectations that coordinate attention, (conceptual and perceptual) memory retrieving processes, etc. according to literary genres, authors, titles, and the like. Through their influence on expectations, ‘literary task sets’ are crucial components of the pleasure that we find in reading (Kringelbach *et al.*, 2008). Some consequences of the existence of ‘literary task sets’:

(a) Distinct ‘literary task sets’ might tap into the imagery-emotion network differently, or might focus attention on a different type of process altogether — like syntactic creativity or conceptual depth.

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One example might clarify this point. In analysing these verses by tango songwriter Tagle Lara: '¿Dónde están aquellos hombres y esas chinas, / Vinchas rojas y chambergos que Requena conoció?' (Where are those men and chinas,[5] / Red headbands and wide-brimmed hats that Requena knew?)[6] Borges praises the interrogative tone imposed on grief (Borges, 1999a). But why in the first place should we read these verses in a mournful tone, as though expressing some kind of grief? Borges imposed on the poem his knowledge of tango (his 'tango-literary task set') that states that tango lyrics often express sorrowful emotions and that we should read the lines in a mournful tone. (If we are reading these verses in silence, the mournful tone is a special kind of auditory imagery! Which illustrates the influences of emotional expectancy on imagery processes, as if postulated by the modulatory route.)

(b) The existence of these 'literary task sets' might also explain why, although visual mental imagery is apparent in reading descriptions, mapping, problem solving, following verbal instructions, and the like, no particular emotion is evoked. I claim that this might happen because the 'task set' for these tasks inhibits, or simply diverts attention from, the mental image-emotion associations.

(c) One way to prove the existence of literary task sets might be this: have three sets of people read the same sentence — e.g. 'He was waiting at the corner'. One group is told that this is the beginning of a crime story; another group, that it is the beginning of a love story; and the third is told to pay attention to potential semantic mistakes. I predict the following differences: (i) while in groups one and two mental imagery activity should be apparent, no such activity can be expected in the third group; (ii) while more amygdala activity is to be expected in the first group, more insular activity can be expected in the second group (Bartels and Zeki, 2004); and (iii) differences in the pattern of frontoparietal activity should be observable in all three groups (for differences in frontoparietal activity between trained and untrained viewers of cubists paintings, see Wiesmann and Ishai, 2010).

(d) The existence of 'literary task sets' has one major important epistemological consequence that I would like to stress: the search for one model that explains the gamut of our emotional reactions independently of literary genre and styles is unlikely to succeed. Different genres and styles demand different task sets, and so expect different reading strategies and reactions from the reader. It might be the case

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[5] The wife or mistress of a gaucho.

[6] My translation

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that for some literary genres mental imagery plays a small part in the aesthetic experience (think of John Cayley's P=r=o=g=r=a=m=m=a=t=o=l=o=g=y or Jessica Smith's *Manifist*), while in others mental imagery is essential to the aesthetic and artistic reaction (think of *Imagism*). See Figure 3.

Let us go back to where we left off. One interesting piece of evidence for our model comes from studies assessing the relationship between the emotional value of a stimulus and the so-called startle response. The startle response is an automatic reaction to a sudden and unexpected stimulus; commonly, it is tested by the application of air puffs to the eye and measuring the magnitude of the eye blink. This response has been shown to be modulated by attention, emotional state, context, and semantic meaning (Herbert *et al.*, 2006), and that this modulation might arise from the activity of the thalamus, anterior cingulate cortex, orbitofrontal cortex, cerebellum, and somatosensory cortices (Neuner *et al.*, 2009). Miller and colleagues (2002) have shown that the magnitude of the startle response can also be modulated by the emotional content of a visual mental image. That visual mental imagery can positively modulate the magnitude of the startle response suggests that mental imagery has a causal effect over emotional brain areas. Moreover, Han and colleagues (2008) and Ritz and colleagues (2002) have shown that visual mental imagery with emotional content (particularly fearful imagery) can bring about changes in respiration rates, suggesting that mental imagery can modulate physiological responses as well. Finally, Holmes and colleagues (2005; 2008b)have shown that subjects report higher levels of anxiety when asked to image the content of a text describing a stressful situation than when simply asked to process the same description conceptually.

In their single-unit recordings in the MTL (medial temporal lobe), Kreiman and colleagues (2000) found that visual mental imagery of faces, houses, and chairs did produce activity in the amygdala.

Taken together, these studies suggest that visual mental imagery can positively alter a subject's emotional state, and that this new emotional state has behavioural and cognitive consequences, as proposed by the 'excitatory route' in our model.

As regards the 'modulatory route', Borst and Kosslyn (2010) offer the only direct evidence for my hypothesis. In their experiment they show that the prior presentation of fearful stimuli (faces) can either facilitate or impair the mental visualization of words, depending on whether the subjects had to pay attention only to the global shape of words or if they had to pay attention to particular details, respectively.

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Notwithstanding, there is robust evidence to show that the emotional value of a stimulus can effectively modulate the activity in visual cortical areas by enhancing its responses to emotional stimuli (Adolphs, 2004; Sabatinelli *et al.*, 2007; Pourtois and Vuilleumier, 2006; Vuilleumier and Driver, 2007). This emotional modulation of visual areas is greater on high-level visual areas — like TE (IT) and LOC, areas known to process global object shapes — and it is thought to arise from feedback projections from the amygdala, probably from the deep nuclei: basal, lateral, and accessory basal nuclei (Freese and Amaral, 2009; Vuilleumier, 2009). Moreover, the amygdala also projects profusely to the PFC — both to its dorsolateral and orbital components — which, as mentioned earlier, is a crucial component of working memory and the system involved in the generation of mental images (Dolan, 2007; Schaefer and Gray, 2007). Interestingly, the amygdala, through the central nucleus, projects to cholinergic nuclei in the basal forebrain, which in turn projects to a number of frontal, parietal, and sensory cortices, with the effect of enhancing processing in these areas. Koch (2004) argues that if there is any single neurotransmitter that can be linked to consciousness, it might be the cholinergic system, due to its widespread projections throughout the cortex. Moreover, activity in the amygdala itself is modulated by hormones (Rodrigues *et al.*, 2009) and monoamines (LeDoux and Sciller, 2009), which is in keeping with the role of monoamines, like dopamine and serotonin, in the modulation of cognition, mood, emotion, and motivation (Amin *et al.*, 2005; Cools *et al.*, 2007; 2008; Dayan and Huys, 2009).

These modulatory influences of amygdala over association visual areas, multimodal and amodal areas (like the PFC and attention-related parietal areas) also alter memory processes. Kensinger and colleagues (2007) have shown that people are better at recalling stimuli with negative emotional valence than neutral ones, and that they were able to remember more details of emotional than neutral objects. Interestingly, they found that these emotional effects on memory correlated with an enhancement of activity in the right fusiform gyrus (rFf) during visual encoding of the stimuli, and that this enhancement was mainly driven by amygdala projections. The rFf is part of the inferior temporal cortex (IT), and it is believed to process and store specific exemplars of visual object shapes, while the left Ff is associated with general, categorial object encoding (Garoff *et al.*, 2005).

The visual cortex — as early as the primary visual cortex or V1 — receives a wealth of connections from basal forebrain and mesen-

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cephalic nuclei, so it is no wonder that its activity is modulated by the overall state of the organism (Daw, 2004; Morrison *et al.*, 1998).

Another way in which emotion can modulate activity in visual cortical areas is indirectly, through its modulation of attention. That attention modulates activity in the visual cortex is well proven (Reynolds and Chelazzi, 2004). Emotional states guide attentional resources and thus also influence activity in the visual cortex (Pourtois and Vuilleumier, 2006; Vuilleumier and Driver, 2007). (For an updated review of the influences of emotions on perception, memory, attention, and working memory see Kensinger, 2009.)

Another source of evidence comes from brain image experiments showing that simulating a feeling — that is, self-provoking a feeling in the absence of emotional stimuli — activates the same cortico-limbic brain areas as during an actual, emotion-driven, feeling (Damasio *et al.*, 2000; Jabbi *et al.*, 2008). In particular, Damasio and colleagues found activity in subcortical nuclei (involved in autonomic responses; pons, midbrain, hypothalamus), amygdala, and cortico-limbic areas (involved in the high-level integration of bodily information with cognitive processes; insula, cingulated cortex, and OFC). Whether actual body information (as measured by activity from the sympathetic nervous system and the gastrointestinal system), or only simulated (imaged) body states (through insula and somatosensory cortices activity) influence the degree of vividness of emotional imagery is an issue currently under debate (Vianna *et al.*, 2009).

Finally, Kiefer and colleagues (2007) have shown that the emotional state of the subject influences the semantic system, making it easier to recall semantic information with an emotional content that matches the subject's actual emotional state.

All this evidence, added to the well-established influence of emotion in decision making processes (Damasio, 2003; Wallis, 2007a), suggests that emotion has powerful influences over perceptual, motor, and cognitive processes.

Although this evidence is at best indirect, it can nevertheless be taken to support — albeit weakly — my model of the two routes of activity.

5. Towards a Literary Neuroaesthetics

In this article I have strived to offer a plausible answer to one of most salient problems in literary aesthetics; namely, *how do literary works of art produce overwhelming emotional states, and ultimately, influence behaviour*? At the same time I have shown that literary neuroaesthetics is not only possible but actually necessary.

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I have founded my model on two general principles:

(a) *Mental functions are the functions of neuronal systems*. Moreover, I have proposed that mental functions are the functions of cortical minicolumns (and subcortical nuclei), columns, and long-range neuronal networks.

(b) *Mental imagery contributes to aesthetic effects by enhancing the emotional response of conceptual processes*[7] (that is, our symbolic knowledge of categories of objects and events).

I would like to add a third principle that has remained implicit throughout this article but is a direct consequence of the philosophical system presented above; namely:

(c) *The content of a literary work of art exists only in the brain of the reader*. In other words: a text (any text, even this one) is but a series of ink blots on a sheet of paper; it is only when a brain interprets these ink blots as words and ascribes to them both a conceptual (or semantic) meaning and mental images that literature comes to life.

Even though my model is openly speculative, it is open to empirical experimentation, since it is not only subject to, but ultimately founded on, neuroscientific research. Furthermore, my model also suggests both behavioural and neuroscientific predictions that can be tested. Here are only some of the open questions promoted by my model; I invite readers to deduce more of their own and scientists to devise ways to put them to the test:

(a) The emotional response to a literary work of art should be correlated with the ease with which its content can be imaged, which in turn correlates with an enhancement of activity in both modality-specific and emotional brain areas.

(b) It is known that subjects differ in their capacities to produce mental images of the different modalities. Subjects with an ease for generating visual but not auditory mental images, or olfactory but not haptic (tactile) images (measured by the degree of activity in

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[7] Another way in which mental imagery could affect literary aesthetics is that mental imagery makes explicit information not stored in conceptual (or semantic) format. For example, while trying to answer whether your elementary teacher wore glasses or not, you will most probably generate a visual mental image of him/her and 'look for' the glasses on his/her face. That is, though the fact that your teacher wore glasses or did not is stored in your brain, this piece of information has not been coded conceptually but perceptually (Kosslyn *et al.*, 2006). Moreover, mental images are crowded with details not easily expressed by words.

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the respective modality-specific cortices), will prefer those literary works of art that tap into their imagery capacities.

(c) As they are involved with the processing and recognition of letters and words, fovea-processing cortices are not available for visual mental imagery. Thus, while reading, visual mental imagery must rely on peripheral visual cortices. I call the images thus formed 'gist imagery', and hypothesize that this is the kind of visual image most commonly involved in reading; it takes a great deal of practice to be able to overturn this situation. Moreover, I conjecture that the degree of emotional arousal caused by visual mental imagery depends on the degree of the involvement of fovea-processing cortices in the representation of visual mental imagery, and the more fovea-processing cortices are engaged in visual mental imagery, the more reading mistakes one is prone to make. I also conjecture that the visual mental imagery associated with a particular literary work of art would be more emotionally arousing during post-reading recall since fovea-processing cortices can be more easily recruited.

(d) Some literary effects might be explained by the manner in which they engage the mental imagery system. For example, some of the appeal of the figure of speech called 'hyperbaton' (a variation of the normal order of words in a sentence) might stem from the fact that it poses an 'imagery configuration problem' since one cannot anticipate the final appearence of the image until one reconstructs the normal order of the sentence. I conjecture that readers experience pleasure when they solve this imagery problem.

(e) Chatterjee (2004) argues that some neuropsychological deficits — in particular visual impairments — alter artistic productions. I propose that the same holds for literary aesthetic appreciation. For instance, deficits in visual imagery generation might alter aesthetic preferences to a more conceptual type of literary work of art than a visually imaginative one. Also, emotional deficits should bias aesthetic preferences.

(f) Readers commonly describe their reactions to literary works of art in terms of bodily experiences, like 'my heart was pounding', 'I couldn't breathe', and the like. When attempting to describe the feeling a good poem or verse induced in him, Borges frequently spoke of 'physical pleasure' or 'physical commotion' (Borges, 1999b), and in Nabokov's short story, *A Forgotten Poet,* the poems of the main character are described as locating 'the sensorial effect of true poetry right between one's shoulder

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blades' and 'to make poetry splutter and scream instead of twittering' (Nabokov, 2002). My model suggests that such expressions might be more than just metaphors. Moreover, my model offers an explanation for such physical feelings in the projections from modality-specific cortices (involved in the generation of mental images) to somatosensory and interoceptive cortices in the case of emotional imagery, and/or the activation of the motor cortex (and mirror neuron system) in the case of motor imagery (see Freedberg and Gallese, 2007).

(g) Persinger and colleagues showed that during activities involving verbal creativity and intense emotional states, subjects usually experience the feeling of the presence of another self, and that this phenomenon might be due to an enhancement in burst-firing in the right hemisphere, particularly in the right MTL and temporal lobe (Johnson and Persinger, 1994; see also Kane, 2004; for the hypothesis that this enhanced activity in the right temporal lobe is influenced by genetic factors and childhood trauma see Brooks Platt, 2007). Remarkably, Blanke and colleagues (2002) were able to experimentally induce out-of-body experiences (OBEs, the sense of one's own body to be physically detached from the physical body) by electrically stimulating the right hemisphere's angular gyrus and somatosensory cortices in a temporal-lobe epileptic patient (for a review on OBEs, see Blanke and Arzy, 2005). My model also predicts these results, since the angular gyrus (or temporoparietal junction) and somatosensory cortices have been shown to be involved in visual and emotional (somatosensory) imagery, respectively (Kosslyn *et al.*, 2006) (for the network of occipital, temporal, parietal, and frontal brain areas involved in the representation of one's own body and the body of others, which could be involved in somatosensorial mental images, see Berlucchi and Aglioti, 2010).

These predictions — and many others — can be tested with an array of different techniques, from neuropsychological tests and questionnaires, to more hi-tech techniques, ranging from GSR (galvanic skin response), TMS (transcranial magnetic stimulation), to brain imaging techniques like PET and fMRI.

Though my model is restricted to the impact of mental imagery on emotion, and vice versa, and its purported role in literary aesthetics, it can easily be integrated with other models in neuroaesthetics to cover other aesthetic phenomena. In particular, Chatterjee (2003) proposed a model of visual aesthetics preference, where he claims that what

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differentiates visual aesthetics from other visual processes (like visual recognition, for example) is the involvement of emotional feedback to visual processing areas and decision-making processes by which the subject judges the aesthetic appeal of the work based on (a) the perceptual characteristics of the visual image, and (b) the emotional arousal and reward value. Nadal and colleagues (2008) reviewed the neuroaesthetic literature and identified several areas whose activities might be attributed to the processes identified by Chatterjee. In particular, they propose that the medial orbitofrontal cortex and dorsolateral prefrontal cortex might be involved in the decision-making process; the medial orbitofrontal cortex activity might reflect the emotional and reward value associated with the painting, while dorsolateral prefrontal cortex activity might reflect decision-making processes based on the perceptual information, in keeping with other proposed models of decision-making (Wallis, 2007a). Interestingly, Kawabata and Zeki (2004) found that the activity of a section of the orbitofrontal cortex correlates with the subjective scale of beauty while the subjects watched and rated paintings, independently of the picture's genre. They termed this orbitofrontal section, the 'beauty spot' (*ibid.*). Moreover, Ishai (2007) also found activity in the OFC that correlated with subjective ratings of facial attractiveness. It is easy to see how our model could be accommodated in Chatterjee and Nadal's framework.

Others have advanced theoretical accounts for a convergence between literary studies and neuroscience, but I am not convinced by them. For example, Massey, in his book *The Neural Imagination*, despite what the title might suggest, only pays lip service to neuroscience, as he concludes that 'It is probably futile to seek a physiological explanation for a problem in aesthetics' (Massey, 2009, p. 128) since subjective aesthetic experiences are scientifically irreducible.

Norman Holland's *Literature and the Brain* (2009) is indeed a captivating and thought-provoking book. His attempt to bridge the gap between neuroscience and literary theory is meritorious and he addresses many of the most troubling problems in literary aesthetics. In particular, I found his hypothesis of the 'willing suspension of disbelief' as a consequence of the prefrontal cortex inhibiting behavioural planning intriguing and clearly open to neurocognitive research. However, I do not see his neuropsychoanalytic theory as a promising framework for neuroart, primarily because Holland is not clear about what the relationship between the mind and the brain is. For example, in one passage Holland distinguishes between brain processes and mind functions (p. 17) — when, as we have seen, the latter are but a special kind of the former; and in another passage, he speaks of the

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mind as if it were a thing (p. 19) and not a collection of special brain functions. This confusion leads the author very close to dualism, which he tries to avoid, as when he claims that 'By relating psychoanalytic inferences about unconscious processes to neurological inferences about the brain, neuropsychoanalysts are beginning to show that various psychoanalytic entities (like libido, repression, word-representation, or superego) *function as* brain systems' (p. 21, italics added). Incidentally, to my knowledge, psychoanalytic concepts such as Id, ego, superego, repression, libido, and the like, have not received any neuroscientific validation, as Holland claims (p. 19); unfortunately he does not provide bibliographical references to support his assertion.

To conclude, two epistemological concerns about Holland's proposal. First, his neuropsychoanalytic method consists of combining free associative talk 'with the neurons and neurotransmission that neurology examines' (*ibid.*, p. 19), which is, at best, a highly debatable strategy. Secondly, Holland adheres to epistemological phenomenology — what he refers to as 'non-controversial relativism' — that is, the thesis that holds that all we can ever know are our perceptions: the world out there will always remain 'unknowable' (p. 33), which is contrary to the goals of scientific research in general, and neuroscience in particular.

At this point one question becomes pressing: can we reduce aesthetics (in the sense of the science of art) to neuroaesthetics?

Let me say a few things about the term neuroaesthetics itself first. Regrettably, neuroaesthetics has inherited the ambiguity that affects the term aesthetics, since it has been defined both as the 'neuroscience of beauty appreciation' (Chatterjee, 2010; Nadal *et al.*, 2008; 2009; Skov and Vartanian, 2009) and the 'neuroscience of art appreciation' (Di Dio and Gallese, 2009; Freedberg and Gallese, 2007; Kawabata and Zeki, 2004; Ramachandran, 2004; Ramachandran and Hirstein, 1999; Zeki, 1999), which includes but is not restricted to artistic beauty.

Here I propose to retain the term *neuroaesthetics* for the study of the neuronal systems and mechanisms of beauty appreciation, and to define *neuroart* as 'the study of the neuronal systems and mechanisms of art appreciation'. I will offer here only two arguments to support my proposal (for related arguments and the proposal of a 'neuroartsology', see Brown and Dissanayake, 2005):

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(a) The idea that artists should pursue beauty is false from an historical point of view. Moreover, one only needs to see what passes today as art to notice that it does not even hold for contemporary art. Liu's sculpture *Indigestion II* (a giant two-metre turd), Damien Hirst's *The Physical Impossibility of Death in the Mind of Someone Living* (a tiger shark preserved in formaldehyde in a vitrine, and sold for millions of dollars), and Tracey Emin's *My Bed* (her actual bed, unmade, littered with objects such as used condoms, her slippers, cigarette butts, and the like); all three considered contemporary masterpieces, and a far cry from what one might consider beautiful works of art (some might not even consider them art at all!) The same point can be made about contemporary literary works of art (see Scott Helmes' *Poems 1972–1997*). I cannot make the distinction between art and beauty more clearly than Gunnery Sergeant Hartman, screaming to Private Gomer Pyle in Stanley Kubrick's *Full Metal Jacket*: 'You're so ugly you could be a modern art masterpiece.'

(b) Artistic appreciation involves knowledge of the properties of the materials used (Gombrich, 1961/1984). In the case of artistic literature, trained readers take pleasure in the writer's linguistic skills (the way he/she uses adjectives, disobeys syntactic rules, imitates certain speaking traits, his/her vocabulary, and so on), independently of the conceptual (semantic) content. No such knowledge is necessary for judging a face or landscape as beautiful.

As regards the question of whether neuroart covers the whole of aesthetics, my answer is negative for, at least, the following reasons:

(i) As I said at the beginning, the brain's mental systems are plastic, that is, they undergo functional and structural changes due to experience. Since humans develop in a cultural environment, our brain's functional architecture is shaped by our cultural experiences (Singer, 2006). In consequence, cognitive and affective neuroscience should be integrated with sociology and social psychology (for the importance of plasticity in the development of human culture and vice versa, see Changeux, 2005). There is neuroimaging evidence that the neuronal systems and mechanisms involved in (a) cognitive processes such as perception, attention, language, music processing, and number representation and mental calculation, (b) emotional processes, (c) mental attribution (the so-called 'theory of mind'), and (d) self representation and self awareness, are all shaped by cultural factors, supporting the emergence of the field of 'transcultural neuroimaging'

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(Han and Northhoff, 2008). Furthermore, 'literary task sets' are learned, and so are parts of our cultural background and heritage.

(ii) Art, like every cultural institution, is subject to cultural conventions which cannot be explained solely in neurocognitive and affective terms, and which call for sociological research. In particular, not only what counts as art, but also what we value in artistic objects is culturally determined (as we have seen above, beauty might not be a value in contemporary art). As an analogy, think about marriage. When we — born in a 'western' culture — think of good marriages we tend to think of love, fidelity, and even legal obligations. None of these properties make sense in other cultures (e.g. arranged marriages) or in past times (e.g. political marriages in Middle Age Europe). Thus, if we attempt to search for the 'neural basis of marriage' we must take these cultural differences into account (had neuroscience existed in the eighteenth century, no one would have looked for the neural basis of marital love!) The same holds for art in general and literature in particular. What we praise in a poem or novel is deeply influenced by our cultural upbringing and cultural environment. Even what we understand as art is culturally determined. Consequently, any attempt to define art in purely psychological or neurocognitive terms (like Ramachandran, 2004, and Ramachandran and Hirstein, 1999) is ill-conceived and misleading. Notice, however, that this does not invalidate neuroart — as I have tried to argue in this article; it simply shows that neurocognitive models of art appreciation cannot in and of themselves distinguish between the great and the bogus in art, nor what kinds of images and emotions one culture encourages in literature and art. In summary, neuroart will be limp if it is kept separate from sociology and social psychology; the same holds, incidentally, for neuroethics, neuroeconomics, neurolaw, and the like.

6. Conclusions

Research into the neuronal systems and mechanisms involved in art appreciation is a very young discipline. The review of Nadal and collegues (2008) only included neuroimaging experiments (though one, Cela-Conde *et al.*, 2004, also included non-artistic pictures of objects as stimuli), and the review of Di Dio and Gallese (2009) only added seven more, which clearly shows that more research in neuroart is called for. In particular, no neuroscientific experimental research has been carried out on literary neuroart.

T.S. Eliot distinguished between the aesthetic effect of Dante and Shakespeare in that Dante's effect was based mainly on the qualities

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of his visual images (which facilitates reading Dante's poetry in translations without much loss), while Shakespeare's requires a thorough knowledge of English, since enjoyment of his work is based more on how he says things than on what he says (Eliot, 1932). The same holds for many other poets besides Dante and Shakespeare. My model clearly aims at Dante-like literary works of art; neurocognitive models explaining Shakespeare-like effects are sorely needed.

From the second half of the twentieth century, literary studies have been dominated by philosophies not just alien to, but violently against, science (Selden *et al.*, 2005). If not, they have regarded brain studies unnecessary — in the worst case — or merely anecdotic (as in cognitive poetics, see Richardson and Steen, 2002; Lakoff and Turner, 1989; Turner, 1996). I hope to have proved them wrong. I also hope this article motivates researchers to conduct experiments into literary neuroart.

Unless my model is altogether disproven, what was once held as the most 'spiritual' and least 'material' of human capacities — literary pleasure — is in fact deeply rooted in the structure and functions of the brain, *pace* Tallis (2008). Moreover, much of literary pleasure might stem from the functioning of the same brain areas that allow us to perceive the outside world and respond emotionally to it.

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