Brain Connectivity: The Feel of Blindsight

A visual subcortical pathway to the amygdala that undergoes structural plastic strengthening in blindsight has been identified in humans — neuroanatomical evidence for a pathway that might mediate rapid non-conscious processing of salient information.

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Cortically blind patients who suffer from lesions in their primary visual cortex can nevertheless make above-chance accurate guesses about the emotional properties of visually presented objects [1]. This is a puzzling phenomenon because even though visual information is not consciously available to blindsight patients, they report a sensation or a 'feeling' of perceiving within their visual blind field. It has been suggested that sensory information reaches the amygdala, a structure known to play a key role in the appraisal of the ecological importance of a stimulus, through a direct subcortical pathway that bypasses primary visual cortex [2].
One problem that has bedevilled this interpretation is that neuroscientists had, until recently, failed to demonstrate the existence of a crucial anatomical connection linking visual subcortical processing structures to the amygdala in humans. Hence, both the existence and the functional role of a subcortical visual pathway to amygdala have been subject of intense debate [3,4].
A study by Tamietto *et al.* [5], reported in this issue of *Current Biology*, shows that such an anatomical connection does indeed exist in humans. Using diffusion tensor imaging (DTI), the authors also demonstrate that, in a blindsight patient, this subcortical pathway increases its strength in the damaged, but not the intact, hemisphere (Figure 1). These new data provide compelling evidence for the idea of rapid subcortical processing, the existence of which has been disputed largely on the basis of an apparent absence of the relevant pathway.

Neuroimaging data have shown that, in healthy individuals, subliminal or 'unseen' emotional stimuli engage brain structures such as the superior colliculus, the pulvinar, and the amygdala; more so than do consciously perceived stimuli [6,7]. Importantly, amygdala activity during perceptual tasks involving emotional stimuli seems to be independent of the observers' state of attention [8], which has led to the idea of automaticity of amygdala function in environmental behavioural-relevance assessment [9]. Electrophysiological data and computational modelling provide supporting evidence for a functional role of an auditory subcortical amygdala pathway that is particularly relevant in early time periods, soon after sound onset [10]. This result highlights the importance of an expedited salience assessment in the amygdala, which enables adaptive behaviour. A validation of this result is still needed for vision.

All of these results make a strong case for the hypothesis that a rapid subcortical colliculo-pulvinar route can bypass a slower resource-dependent cortical pathway in order to access the amygdala. But as much as this pathway ought to exist in the human brain, based on compelling functional (if correlative) evidence, as well as anatomical evidence in non-human primates [11], the failure to demonstrate a structural pathway has remained a problem. In their attempt to define such a pathway, Tamietto *et al.* [5] used DTI, a non-invasive magnetic resonance-based technique that produces quantitative maps of non-isotropic water molecule displacement in brain tissues that occurs as part of the diffusion process. 'Free' water molecules diffuse randomly in all directions of space. In biological tissues, however, these molecules encounter obstacles that modulate the diffusion process, such that displacement is higher along, versus across, a fibre tract. The degree of anisotropy of the diffusion process is quantified by a numerical value, the fractional anisotropy, which is thought to reflect axonal diameter and myelination in white matter [12].

Tamietto *et al.* [5] found fibre tracts that go between the superior colliculus and the amygdala, *via* the pulvinar, in both healthy individuals and a blindsight patient with unilateral destruction of the visual cortex. Remarkably, the blindsight patient showed a significant increase in fractional anisotropy connectivity between the pulvinar and the amygdala in the damaged hemisphere. This could reflect an increased reliance on non-conscious processing, perhaps on behaviourally salient aspects of perceptual information, in the absence of an explicit perceptual experience. Interestingly, no differences were found for the colliculo-pulvinar-amygdala pathway strength between the patients' intact hemisphere and the homologous pathway in healthy individuals. However, new interhemispheric tracts emerged between subcortical structures and the opposed non-damaged primary visual cortex. Therefore, it seems that this structural plastic reorganisation is a consequence of primary visual cortex destruction.

What remains to be fully understood is the functional role of such a subcortical pathway. One notable study [13] showed that information about the low spatial frequency of an object is processed in subcortical visual structures such as the superior colliculus and the pulvinar, as well as in the amygdala. On the other hand, high spatial frequency information engages cortical visual areas. This suggests that a subcortical pathway might convey coarse information about the properties of a visual object for subsequent amygdala evaluation. Presumably, this information might reach amygdala conveniently earlier than the fine-detailed information, possibly extracted through a slow cascade of cortical processes.

An intriguing finding is that electrophysiological responses to visual stimuli have a similar latency in both pulvinar and visual cortex, which seems to be at odds with the idea of a temporal advantage furnished by a subcortical pathway. However, it might be that similar latencies in

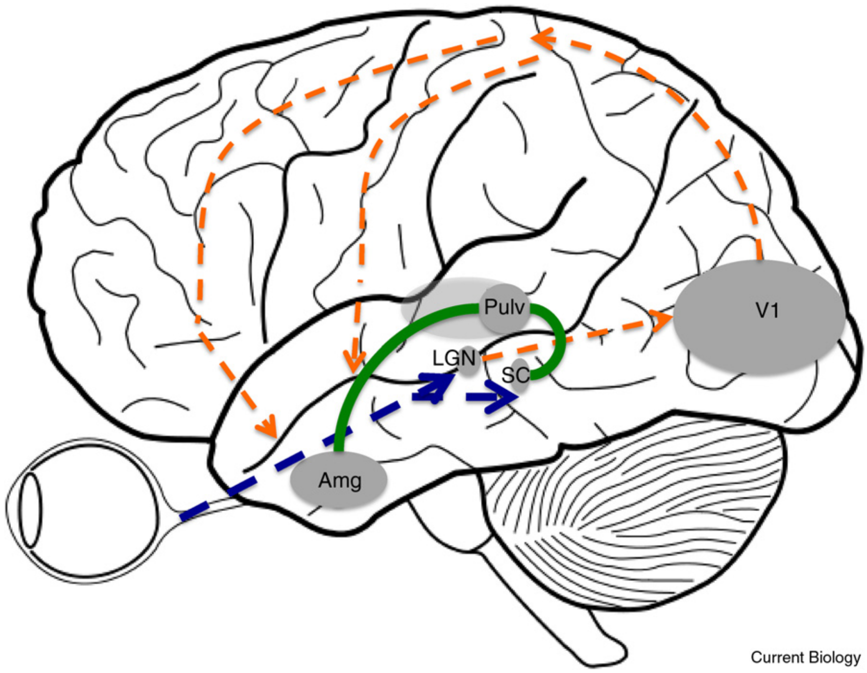

Figure 1. Roadmap to amygdala.

Tamietto *et al.* [5] provide neuroanatomical evidence for a subcortical pathway (in green) linking the superior colliculus (SC), the pulvinar (Pulv), and the amygdala (Amg). This pathway undergoes structural plastic strengthening in the damaged hemisphere of a blindsight patient. Cortical visual routes to amygdala (in orange) involve brain areas such as the lateral geniculate nucleus (LGN) and the primary visual cortex (V1). Visual inputs from the retina are displayed in blue.

different areas trigger behavioural responses at different points in time. Indeed, objects presented to the visual blind field evoke faster involuntary facial muscular activity (perhaps mediated by the pulvinar) than objects presented in the non-damaged visual field of blindsight patients [14].

In proposing a functional role for a subcortical route to amygdala there is an implicit assumption that a colliculo-pulvinar pathway involves feedforward processes. This remains an open question though, which the Tamietto *et al.* [5] study cannot address, given the non-directional nature of DTI measurements. Another point worth mentioning is that the results of Tamietto *et al.* [5] do not rule out ideas of multiple cortical pathways to amygdala [3], although it is not clear whether alternative pathways are useful in the absence of conscious perception.

Most functional neuroimaging studies have found amygdala enhancement for fear-related, as compared to happy or neutral stimuli [1,13]. Consequently, the putative role of this subcortical visual pathway to amygdala has been linked to an evolutionary advantage in the context of threat. Nonetheless, it has been shown that amygdala activity is associated with reliable guesses of the emotional content of facial expressions in blindsight, irrespective of the type of emotion [1]. This suggests that such a subcortical pathway is not restricted to fear, and perhaps one could even question whether it is specific to emotion. Instead, this pathway could speed up extraction of the general ecological relevance of a scene or an event. In keeping with the suggested behavioural salience detector role for the amygdala [15], it is likely that this subcortical pathway provides a shortcut for environmental inputs whose relevance can be quickly assessed by the amygdala. The relevance or salience of these inputs might well have to do with their reward significance [16], their novelty, or maybe their quirkiness [10,17].

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http://dx.doi.org/10.1016/j.cub.2012.06.012