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Preliminary report on the association between pulvinar volume and the ability to detect backward-masked facial features

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ABSTRACT

Although backward masking is a powerful experimental tool in mitigating visual awareness of facial expressions of emotion, ~20% of participants consistently report being resistant to its effects. In our previous studies, we excluded these participants from analysis as we focused on neural data in individuals who were subjectively unaware of backward-masked facial features that were presented for a brief period of time (e.g., 17 ms). Here, we shifted our focus to potential structural brain difference between aware and unaware participants. To achieve this, structural magnetic resonance imaging (sMRI) data were pooled from two recent backward masking studies of emotional faces or eye whites (Kim et al., 2016, 2010). Out of a total of 64 participants, 12 reported being subjectively aware of the masked faces or their facial features. Whole-brain, voxel-based morphometric analysis of structural MRI data yielded significantly greater volume of the posterior thalamus, including the bilateral pulvinar, for the subjectively aware versus unaware individuals. No other brain region showed significant volumetric differences between groups. The present findings offer a neuroanatomical basis for visual awareness of emotional content in the form of backward-masked facial features, which complements the known functional role of the pulvinar in such neurobehavioral processes.

1. Introduction

Backward masking is a powerful tool that experimental psychologists employ to mitigate awareness of a target stimulus, which is achieved by immediately replacing it with a mask stimulus. For example, for facial expressions of emotion, provided that the stimulus onset asynchrony between the emotional target (i.e., fearful expression) and neutral mask stimuli was sufficiently brief, most subjects reported being unaware that the target stimulus had been presented (Esteves and Öhman, 1993). This technique is often used to elucidate the neural substrates of processing visual stimuli of emotional and social salience without awareness. For example, functional magnetic resonance imaging (fMRI) studies have shown that the human amygdala is responsive to masked fearful faces, even when participants report being unaware of their presentation (Morris et al., 1998; Whalen et al., 1998; Pessoa et al., 2006; Williams et al., 2006; Kim et al., 2010). This automaticity in the brain was further accentuated when masked fearful eye whites—crude, unrefined components of fearful faces—were shown to be sufficient to evoke amygdala responses (Whalen et al., 2004; Straube et al., 2010; Kanat et al., 2015; Kim et al., 2016).

Interestingly, across multiple studies employing a backward masking paradigm to mitigate visual awareness for faces or facial features (i.e., eye whites) of fearful or happy expressions, we have consistently observed ~20% of the participants to be resistant to its effects (e.g., Whalen et al., 1998; Kim et al., 2010; Kim et al., 2016). Given a focus on implicit responding, data from these participants who are subjectively aware of the "hidden" target images are typically discarded from further analyses (e.g., Whalen et al., 1998; Etkin et al., 2004; Kim et al., 2010; Straube et al., 2010; Kanat et al., 2015; Kim et al., 2016). The rationale for this choice is based on the assumption that once the target images are seen, participants' behavior and brain activity will be significantly altered for the remainder of the experiment, since they no longer become naïve to the true purposes of the study and would likely display a fundamental shift in their response (e.g., actively searching for the target images with every mask presentation).

Although individuals who are impervious to the effects of backward masking and ostensibly hypersensitive to masked target images have been regarded as outliers in their respective experiments to date, these participants offer useful insights into understanding visual awareness. A formal investigation of these individuals is a somewhat challenging task due to the difficulty in procuring a sufficient number of subjectively aware individuals. In the present study, we attempt to address this issue

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by pooling behavioral and neuroimaging data from two independent backward masking studies (e.g., Kim et al., 2010, 2016). Of importance, we used the same experimental procedure, identical imaging parameters, and collected self-reported levels of anxiety across both studies, which facilitated the merging of the two datasets. Although a direct pooling of fMRI data is difficult due to the differences in the actual stimuli used in each experiment (full faces vs. eye whites), sMRI and behavioral data are able to circumvent this issue by providing a common measure between studies that is not susceptible to task differences.

Using this approach, our aim in the present exploratory study was to investigate the behavioral and neuroanatomical characteristics of the subjectively aware individuals. Studies on blindsight—a condition where a person can still respond to visual stimuli despite their visual awareness being lost due to V1 damage (Weiskrantz, 2009)—suggest that because of their subjective unawareness, these patients show superior ability on certain visual tasks (Trevathan et al., 2007), not dissimilar from the "super-detectors" we examine here. In light of this line of work, the interconnected brain regions that are central to the visual pathway that include the V1, extrastriate cortex and thalamus—particularly the posterior dorsal subregion, which includes the lateral geniculate nucleus and pulvinar (Leopold, 2012)—may show volumetric differences as a function of subjective awareness. However, given the exploratory nature of the present investigation, we surveyed the volumetric properties of the whole brain. In addition, given that increased anxiety is related to threat-related attentional bias (Bar-Haim et al., 2007), and the use of fearful faces and facial features in the present study, we tested whether the subjectively aware individuals would exhibit higher levels of self-reported anxiety.

2. Materials and methods

2.1. Participants

A total of 64 participants (39 women, mean age = 19.6 ± 1.3 years) were included in the present study. Data were pooled from two recent backward masking studies that used either full faces or eye whites taken from fearful and happy expressions ($n = 37$ and $n = 27$ respectively; Kim et al., 2016, 2010). All participants were screened for past or current psychiatric illnesses (Axis I or II) using the Structured Clinical Interview for DSM-IV (First et al., 1997). No participants had any history of taking psychotropic medications. The study protocol was approved by the Committee for the Protection of Human Subjects at Dartmouth College. Prior to the experiment, written, informed consent was obtained from all participants. To assess each participant's self-reported levels of state and trait anxiety, the State Trait Anxiety Inventory Forms Y-1 and Y-2 was used (STAI-S and STAI-T respectively; Spielberger et al., 1988).

2.2. Subjective awareness

Both studies utilized a backward masking paradigm, with the goal of mitigating visual awareness to briefly presented targets (fearful/happy faces or eye whites) by immediately replacing them with masks (neutral faces or pattern images). With the exception of the type of targets (full faces vs. eye whites) and corresponding masks (photos of faces vs. black and white line drawings of faces) that were tailored to meet the specific aims of each study, the experimental procedure was identical (see the Materials and methods section of both studies for a detailed description). In brief, participants passively viewed blocked presentations of target-mask pairs, with each 18 s trial block interleaved by a fixation block of the same duration. Within each trial block, a target stimulus (fearful/happy faces or eye whites) was presented on the screen for 17 ms, which was immediately replaced by a mask stimulus (neutral face or pattern image) that was on the screen for 183 ms, followed by a fixation interstimulus interval of 300 ms. This yielded a total of 500 ms duration for each trial, which amounted to 36 trials per block. Each participant viewed 24 trial blocks, resulting in a grand total of 864 target-mask pairs. We note that in both studies, neutral faces and pattern images were used as masks in equal number of trials (432 target-mask pairs each), facilitating the pooling of the data. Importantly, participants were not informed about the backward masking procedure and thus were naïve about the existence of the hidden targets going into the experiment.

We assessed subjective awareness with post-scan interview sessions. Immediately upon exiting the scanner, we asked the participants what they thought the purpose of the study was. Then, we instructed them to describe what was presented on the screen during the fMRI scanning sessions. Next, we asked the participants to comment on any aspects of the faces and pattern images. Finally, we asked them directly if they had seen any parts of fearful or happy expressions during the fMRI scanning sessions. If any participants reported seeing any feature of fearful or happy expressions (i.e., widened eyes, teeth, smile, etc.) out of 864 total pairs, we considered them to be subjectively aware of the target stimuli.

2.3. Image acquisition

All sMRI data were collected at the Dartmouth Brain Imaging Center using the 3.0 T Philips Intera Achieva Scanner (Philips Medical Systems), equipped with an 8-channel head coil. Participants' high-resolution anatomical T1-weighted images were scanned using a magnetization-prepared rapid gradient echo sequence (MPRAGE), with 160 contiguous 1-mm thick sagittal slices (TE = 4.6 ms, TR = 9.8 ms, FOV = 240 mm, flip angle = 8°, voxel size = 1 × 0.94 × 0.94 mm).

2.4. Voxel-based morphometry

T1-weighted images from all 64 participants were submitted to a voxel-based morphometry (VBM; Good et al., 2001) data analysis pipeline, using the VBM8 toolbox (http://dbm.neuro.uni-jena.de/vbm/) running on the Statistical Parametric Mapping software (SPM8; Wellcome Trust Center for Neuroimaging, London, UK). Images were first segmented into gray matter, white matter, and cerebrospinal fluid. Next, the segmented tissue images were spatially aligned into standard Montreal Neurological Institute (MNI) space (1.5 × 1.5 × 1.5 mm) using the diffeomorphic anatomical registration through exponentiated Lie algebra (DARTEL) algorithm implemented in SPM8. Then, in order to acquire volume information for each voxel, gray matter images were modulated with the Jacobian determinants derived from the nonlinear spatial alignment procedure. Finally, these modulated gray matter images were smoothed using a Gaussian kernel (full-width-half-maximum = 8 mm). To assess group differences in regional gray matter volume on a voxel-by-voxel basis, a general linear model (GLM) was constructed at the group level. In the GLM, intracranial volume (ICV), study group (to address the potential differences across the two studies), age, and sex were included as covariates of no interest. ICV was estimated by summing the volumes of the gray matter, white matter, and cerebrospinal fluid images derived from the segmentation step. Main group contrasts were subjectively aware > unaware group and subjectively aware < unaware group. We imposed a significance threshold of $p < 0.05$ family-wise error (FWE) corrected for multiple comparisons over the gray matter volume across the whole brain, as determined by Monte Carlo simulations ($n = 10{,}000$) implemented in *3dClustSim* (compiled in Jan 2016; Cox et al., 2017) within Analysis of Functional Neuro Images (AFNI) software (Cox, 1996). The FWE-corrected $p < 0.05$ threshold was achieved using an uncorrected $p < 0.001$, $k \geq 531$ voxels (1792 mm^3). Whole-brain VBM results at a lenient statistical threshold ($p < 0.01$, $k \geq 531$ voxels) is summarized in Supplementary Figure 1 and Supplementary Table 1. All of the VBM data and experimental variables are publicly available at NeuroVault (Gorgolewski et al., 2015)(https://neurovault.org/collections/3063/).

3. Results

3.1. Behavioral characteristics

Among the 64 participants, 52 participants were unaware (33 women, mean age = 19.5 ± 1.3 years) and 12 participants were subjectively aware (6 women, mean age = 20.3 ± 1.2 years) of the masked targets during the experiment. Although there was a trend for age differences ($t = -1.89$, $p = 0.063$), it did not reach significance ($\alpha = 0.05$). No significant group differences were observed for sex ($\chi^2 = 0.742$, $p = 0.389$). Likewise, there were no significant differences in state anxiety ($t = 0.684$, $p = 0.497$) or trait anxiety ($t = -0.183$, $p = 0.856$) between participants who were subjectively aware versus unaware. There were no significant differences in the proportion of participants who became subjectively aware between the two studies ($\chi^2 = 0.002$, $p = 0.968$). We found no evidence for any association between subjective awareness and the order of study participation (Kim et al., 2010: Spearman's $\rho = -0.024$, $p = 0.904$; Kim et al., 2016: Spearman's $\rho = -0.11$, $p = 0.517$).

3.2. Subjective awareness and pulvinar/posterior thalamus volume

Whole-brain, voxel-based morphometric analysis of sMRI data yielded significantly greater volume of the posterior thalamus, including bilateral pulvinar, for the subjectively aware vs. unaware individuals (aware > unaware group contrast; Left peak MNI −10, −28, −6; $t = 4.56$; Right peak MNI 15, −25, −2, $t = 4.42$; FWE-corrected $p < 0.05$, $k = 1336$ voxels; Fig. 1). No other brain regions displayed significant group differences.

4. Discussion

In this report, we offer preliminary neuroanatomical evidence that pulvinar/posterior thalamic volume is positively associated with individual differences in sensitivity to detecting hidden emotional content, as measured using a standard backward masking paradigm. Participants who were able to detect the very briefly presented (17 ms) masked faces or eye whites, despite having no prior knowledge of their existence, had larger pulvinar volumes compared to those who never became aware of the masked images.

It is important to make it clear that the present findings do not indicate that the pulvinar is the locus of subjective visual awareness in the brain. Rather, our data suggest that greater pulvinar volume is linked to an increased likelihood that rapidly presented visual information will reach the level of subjective awareness. Considering the findings from the phenomenon of blindsight—the ability to respond to visual cues, despite the loss of subjective awareness to their presence due to damage to V1 (Sanders et al., 1974; Weiskrantz et al., 1974)—it is clear that V1 is critical to the emergence of subjective visual awareness in humans, as it contributes to a link between subjective visual awareness and visually guided performance (Azzopardi and Cowey, 1997). Furthermore, work in the cat visual system has shown that the pulvinar receives projections

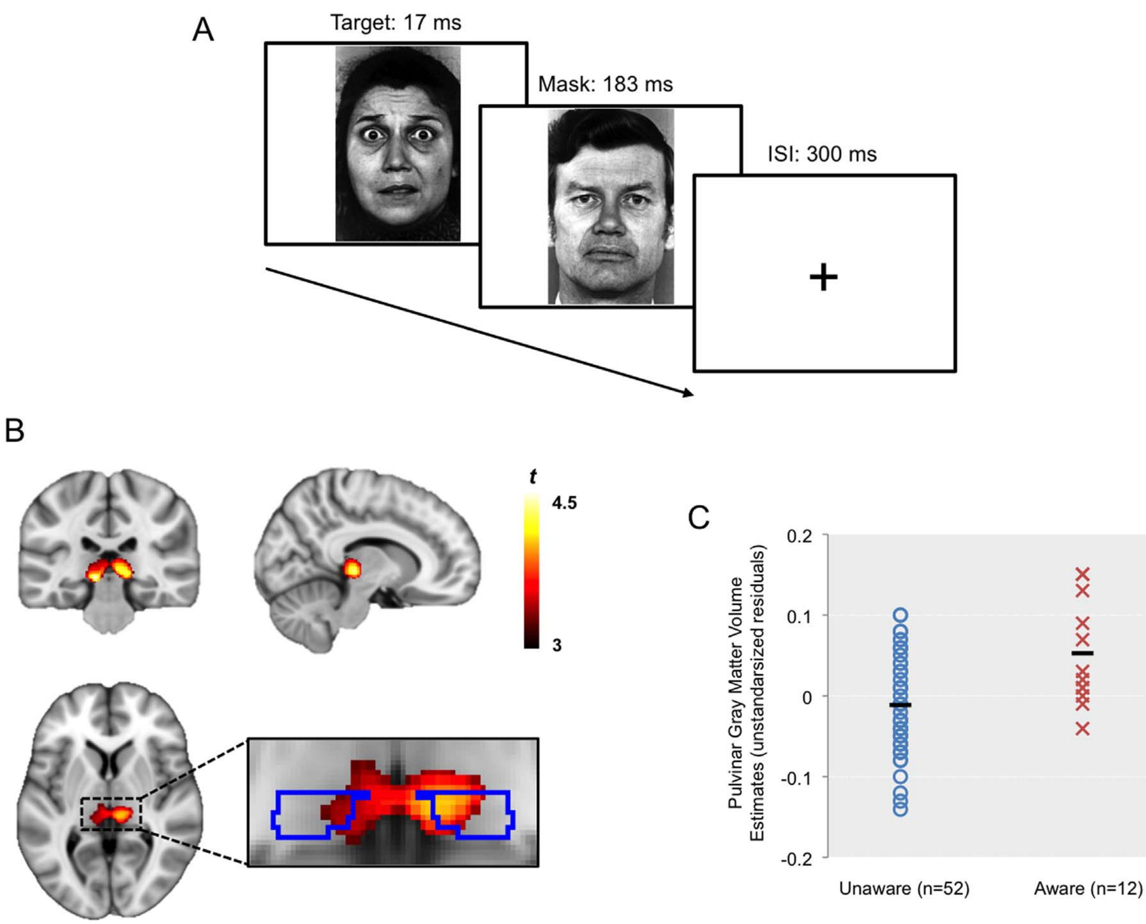

Fig. 1. (A) A sample trial from a backward masking paradigm (Kim et al., 2010). A target image was presented briefly, and then was immediately replaced by a mask image, followed by a fixed interstimulus interval. Out of a total of 864 trials, if the participant reported seeing at least one target image, that individual was categorized as being subjectively aware. (B) Whole-brain VBM results (FWE-corrected $p < 0.05$) highlighting significantly greater pulvinar/posterior thalamic gray matter volume, in subjectively aware versus subjectively unaware groups (i.e., aware > unaware group contrast). The blue lines depict the border of the anatomically defined bilateral pulvinar from the Talairach Daemon database atlas, implemented in the WFU PickAtlas toolbox (Lancaster et al., 2000; Maldjian et al., 2003). (C) Gray matter volume estimates of the pulvinar, extracted from the significant voxel clusters, summarized for each group. Unstandardized residuals of pulvinar volume estimates, after accounting for ICV, experiment, age, and sex, were used to plot the data. Black lines denote the mean for each group.

from the superior colliculus (Sherman and Guillery, 2002) and possibly the optic tract (Chalupa et al., 1972), suggesting potential anatomical pathways along which this 'unaware' visual information may be computed in parallel with 'aware' visual pathways. It follows then that the enlarged pulvinar in our data may reflect an increased capacity for detecting briefly presented masked stimuli, which is subsequently passed on to V1 where the visual information eventually reaches subjective awareness.

In addition to projections to V1, the pulvinar directly projects to the extrastriate cortex, which is an important pathway that enables the processing of visual signals without awareness (Shipp, 2003). Similarly, a retino-collicular-pulvinar pathway has been suggested to be the basis for an early threat detection system that does not require subjective awareness, which feeds information to other brain regions including the amygdala (Morris et al., 1999; Davis and Whalen, 2001; LeDoux, 2007; Burra et al., 2017; Gerbella et al., 2017). Indeed, the pulvinar has been shown to be functionally coupled with the amygdala in response to visual signals (e.g., fear-conditioned faces, fearful faces or eye whites) that have not reached subjective awareness (Morris et al., 1999; Liddell et al., 2005; Troiani et al., 2014; Kanat et al., 2015), a relationship that likely echoes the underlying extensive anatomical connections between the two structures (Tamietto et al., 2012). The present neuroanatomical data support and further extend the known functional role of the pulvinar in processing visual information by showing that the volumetric variability of the pulvinar may also be informative in explaining the individual differences in sensitivity toward hidden, emotionally charged visual stimuli that would ultimately contribute to the emergence of subjective awareness.

The present neuroanatomical findings could be better understood when considering the known functional role of the pulvinar in visual processing and attention. Of particular relevance, evidence from human and monkey lesion studies and animal electrophysiology research suggest that the pulvinar plays an important role in fast processing of visual information, filtering distractions, and integrating visual information (see Saalmann and Kastner, 2011 for review). The pulvinar connects the visual cortex with the superficial layers of the superior colliculus (Berman and Wurtz, 2010; Lyon et al., 2010), which receive direct input from the retina. It follows then this retino-collicular-pulvinar pathway likely represents a fast processing stream that bypasses the lateral geniculate nucleus (Berman and Wurtz, 2010), which laid out the foundation for the aforementioned fMRI studies of autonomic threat processing that employed the backward masking paradigm. Lesion studies clearly demonstrated the role of the pulvinar in filtering distractions, as patients who sustained pulvinar damage displayed impaired task performance when distracters were present, but not when the target stimulus was shown by itself (Snow et al., 2009). Moreover, patients with unilateral pulvinar lesions were found to have deficits in attaching visual feature with spatial information in the contralesional visual field, as these patients would often fail to integrate color information with the appropriate letter when multiple letters are presented simultaneously (Ward et al., 2002). The functional role of the pulvinar outlined in these studies sheds light on how it may contribute to the emergence of subjective awareness towards very briefly presented, masked images. For example, we could speculate that the pulvinar would facilitate the processing of the target by filtering the mask, which in turn increases the likelihood that the target information reaches visual awareness. That being said, since the exact nature of the association between the volumetric properties of the pulvinar and its function is still largely unknown, such speculation must be made with caution.

Behaviorally, we found no evidence for self-reported anxiety levels facilitating the detection of masked facial expressions or eye whites, replicating the report from a previous backward masking study that explicitly tested for differences in anxiety based on awareness (Etkin et al., 2004). Given that elevated anxiety levels are associated with increased attentional bias toward threat and threat-related facial expressions (Mogg and Bradley, 1999; Fox, 2002; see Bar-Haim et al., 2007 for meta-analysis), the converging null findings from the Etkin et al. (2004) study and the present data suggest that the ability to detect hidden images in a backward masking context is less susceptible to the influences of anxiety, compared to experimental paradigms that focus on manipulating visuospatial attention.

Overall, we were limited to testing for potential effects of self-reported state and trait anxiety on subjective awareness due to the experimental design of the original studies. Despite the null correlation between anxiety and subjective awareness of the masked stimuli, there may be other trait characteristics that predict this outcome. For example, existing work suggests that autism spectrum scores correlate with increased acuteness of spatial visual perception ability (Robertson et al., 2013), although the "acuteness" of perception in the current study is across short intervals of time rather than small intervals of space. Future investigations should aim to comprehensively assess other behavioral characteristics that may distinguish individuals who become subjectively aware versus those who did not. Specifically, future work could aim to assess if those with high attentional capacities are better at detecting masked stimuli. Similarly, and in an effort to define the behavioral characteristics that correlate with the ability to detect hidden images, future studies would benefit from investigating whether people with extraordinary face recognition ability—sometimes referred to as super recognizers—are more likely to be able to detect masked faces. Such studies would help expand our understanding of whether the ability to detect hidden stimuli is an attentional ability, or attributable to another process such as practice effects.

Future work should address the following caveats of the current study. First, the present data were limited to visual awareness toward faces or facial features of emotional expression—specifically those of fear and happy. As such, whether or not the association between pulvinar volume and subjective awareness could be generalized to other categories of affect, or non-facial or non-emotional stimuli remains to be seen. Next, we focused on sMRI data because pooling fMRI data presents difficulties due to the heterogeneous types of target stimuli being used in the respective original studies (full faces vs. eye whites). In addition, a comparison of fMRI data between subjectively aware versus unaware individuals is confounded by the likelihood that the observed brain activity patterns would reflect fundamentally different processes between the groups (e.g., those who become aware will start to expect and actively search for other hidden images, thus changing the underlying brain systems that may be involved). Finally, the present study included a relatively small number of subjectively aware individuals, as they were relatively uncommon, despite pooling the data from two independent studies. Thus, due to the preliminary nature of the present study, it is important for the present findings to be followed up with better-powered, preregistered studies. Because only a minority of randomly sampled participants was subjectively aware of the masked stimuli, there is a need for future investigations that are explicitly designed to collect data from these individuals. For example, future studies would benefit from a two-stage approach in which participants are first identified as being subjectively aware or unaware in a backward masking experiment, and then are subsequently tested for group differences in behavioral and neural characteristics. This approach would make it possible to investigate the neural signatures for these potentially divergent processes. Such a strategy would be especially suitable for functional neuroimaging investigations, because a direct comparison of brain activity patterns between the subjectively aware versus unaware participants from a backward masking paradigm that were used to identify awareness in the first place (such as the fMRI data in Kim et al., 2010, 2016) is suboptimal, as discussed above.

To summarize, the present data highlight the neuroanatomical characteristics of individuals who are resistant to the effects of a backward masking procedure by demonstrating subjective awareness of the masked images. Specifically, the volume of the pulvinar was positively correlated with individual differences in the subjective sensitivity toward hidden emotional faces or eye whites, such that a larger pulvinar corresponded to increased likelihood of detecting the masked images. Given the known functional role of the pulvinar in visual information processing, enlarged volume of the pulvinar in these relatively uncommon individuals may represent an increased capacity for detecting a visual signal feature that exists at the fringe of awareness.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2017.10.034.

References

Azzopardi, P., Cowey, A., 1997. Is blindsight like normal, near-threshold vision? Proc. Natl. Acad. Sci. USA 94 (25), 14190–14194.
Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., 2007. Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. Psychol. Bull. 133 (1), 1–24.
Berman, R.A., Wurtz, R.H., 2010. Functional identification of a pulvinar path from superior colliculus to cortical area MT. J. Neurosci. 30 (18), 6342–6354.
Burra, N., Hervais-Adelman, A., Celeghin, A., de Gelder, B., Pegna, A.J., 2017. Affective blindsight relies on low spatial frequencies. *Neuropsychologia*. http://dx.doi.org/10.1016/j.neuropsychologia.2017.10.009.
Chalupa, L.M., Anchel, H., Lindsley, D.B., 1972. Visual input to the pulvinar via lateral geniculate, superior colliculus and visual cortex in the cat. Exp. Neurol. 36 (3), 449–462.
Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Comput. Biomed. Res. 29 (3), 162–173.
Cox, R.W., Chen, G., Glen, D.R., Reynolds, R.C., Taylor, P.A., 2017. FMRI clustering in AFNI: false-positive rates redux. Brain Connect. 7 (3), 152–171.
Davis, M., Whalen, P.J., 2001. The amygdala: vigilance and emotion. *Mol. Psychiatry* 6 (1), 13–34.
Esteves, F., Öhman, A., 1993. Masking the face: recognition of emotional facial expressions as a function of the parameters of backward masking. Scand. J. Psychol. 34 (1), 1–18.
Etkin, A., Klemenhagen, K.C., Dudman, J.T., Rogan, M.T., Hen, R., Kandel, E.R., Hirsch, J., 2004. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. Neuron 44 (6), 1043–1055.
First, M.B., Spitzer, R.L., Gibbon, M., Williams, J.B.W., 1997. Structured Clinical Interview (SCID) for DSM-IV Axis 1 Disorders. American Psychiatric Association, Washington DC.
Fox, E., 2002. Processing of emotional facial expressions: the role of anxiety and awareness. Cogn. Affect. Behav. Neurosci. 2 (1), 52–63.
Gerbella, M., Caruana, F., Rizzolatti, G., 2017. Pathways for smiling, disgust and fear recognition in blindsight patients. *Neuropsychologia*. http://dx.doi.org/10.1016/j.neuropsychologia.2017.08.028.
Good, C.D., Johnsrude, I.S., Ashburner, J., Henson, R.N., Friston, K.J., Frackowiak, R.S., 2001. A voxel-based morphometric study of ageing in 465 normal adult human brains. Neuroimage 14 (1), 21–36.
Gorgolewski, K.J., Varoquaux, G., Rivera, G., Schwartz, Y., Ghosh, S.S., Maumet, C., Sochat, V.V., Nichols, T.E., Poldrack, R.A., Poline, J.-B., Yarkoni, T., Margulies, D.S., 2015. NeuroVault.org: a web-based repository for collecting and sharing unthresholded statistical maps of the human brain. Front. Neuroinf. 9, 8. http://dx.doi.org/10.3389/fninf.2015.00008.
Kanat, M., Heinrichs, M., Mader, I., van Elst, L.T., Domes, G., 2015. Oxytocin modulates amygdala reactivity to masked fearful eyes. Neuropsychopharmacology 40 (11), 2632–2638.
Kim, M.J., Loucks, R.A., Neta, M., Davis, F.C., Oler, J.A., Mazzulla, E.C., Whalen, P.J., 2010. Behind the mask: the influence of mask-type on amygdala response to fearful faces. Soc. Cogn. Affect. Neurosci. 5 (4), 363–368.
Kim, M.J., Solomon, K.M., Neta, M., Davis, F.C., Oler, J.A., Mazzulla, E.C., Whalen, P.J., 2016. A face versus non-face context influences amygdala responses to masked fearful eye whites. Soc. Cogn. Affect. Neurosci. 11 (12), 1933–1941.
Lancaster, J.L., Woldorff, M.G., Parsons, L.M., Liotti, M., Freitas, C.S., Rainey, L., Kochunov, P.V., Nickerson, D., Mikiten, S.A., Fox, P.T., 2000. Automated Talairach atlas labels for functional brain mapping. Hum. Brain Mapp. 10 (3), 120–131.
LeDoux, J.E., 2007. The amygdala. Curr. Biol. 17 (20), R868–R874.
Leopold, D.A., 2012. Primary visual cortex, awareness and blindsight. Annu. Rev. Neurosci. 35, 91–109.
Liddell, B.J., Brown, K.J., Kemp, A.H., Barton, M.J., Das, P., Peduto, A., Gordon, E., Williams, L.M., 2005. A direct brainstem-amygdala-cortical ‘alarm’ system for subliminal signals of fear. Neuroimage 24 (1), 235–243.
Lyon, D.C., Nassi, J.J., Callaway, E.M., 2010. A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. Neuron 65 (2), 270–279.
Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI datasets. Neuroimage 19 (3), 1233–1239.
Mogg, K., Bradley, B.P., 1999. Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. Cogn. Emot. 13 (6), 713–740.
Morris, J.S., Ohman, A., Dolan, R.J., 1998. Conscious and unconscious emotional learning in the human amygdala. Nature 393 (6684), 467–470.
Morris, J.S., Ohman, A., Dolan, R.J., 1999. A subcortical pathway to the right amygdala mediating “unseen” fear. Proc. Natl. Acad. Sci. USA 96 (4), 1680–1685.
Pessoa, L., Japee, S., Sturman, D., Ungerleider, L.G., 2006. Target visibility and visual awareness modulate amygdala responses to fearful faces. Cereb. Cortex 16 (3), 366–375.
Robertson, C.E., Kravitz, D.J., Freyberg, J., Baron-Cohen, S., Baker, C.I., 2013. Tunnel vision: sharper gradient of spatial attention in autism. J. Neurosci. 33 (16), 6776–6781.
Saalmann, Y.B., Kastner, S., 2011. Cognitive and perceptual functions of the visual thalamus. Neuron 71 (2), 209–223.
Sanders, M.D., Warrington, E.K., Marshall, J., Weiskrantz, L., 1974. “Blindsight”: vision in a field defect. Lancet 1 (7860), 707–708.
Sherman, S.M., Guillery, R.W., 2002. The role of the thalamus in the flow of information to the cortex. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 357 (1428), 1695–1708.
Shipp, S., 2003. The functional logic of cortico-pulvinar connections. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358 (1438), 1605–1624.
Snow, J.C., Allen, H.A., Rafal, R.D., Humphreys, G.W., 2009. Impaired attentional selection following lesions to human pulvinar: evidence for homology between human and monkey. Proc. Natl. Acad. Sci. USA 106 (10), 4054–4059.
Spielberger, C.D., Gorsuch, R.L., Lushene, R.E., 1988. STAI-Manual for the State Trait Anxiety Inventory, 3rd ed. Consulting Psychologists Press, Palo Alto, CA.
Straube, T., Dietrich, C., Mothes-Lasch, M., Mentzel, H.J., Miltner, W.H., 2010. The volatility of the amygdala response to masked fearful eyes. Hum. Brain Mapp. 31 (10), 1601–1608.
Tamietto, M., Pullens, P., de Gelder, B., Weiskrantz, L., Goebel, R., 2012. Subcortical connections to the human amygdala and changes following destruction of the visual cortex. Curr. Biol. 22 (15), 1449–1455.
Trevathan, C.T., Sahraie, A., Weiskrantz, L., 2007. Can blindsight be superior to ‘sighted-sight’? Cognition 103 (3), 491–501.
Troiani, V., Price, E.T., Schultz, R.T., 2014. Unseen fearful faces promote amygdala guidance of attention. Soc. Cogn. Affect Neurosci. 9 (2), 133–140.
Ward, R., Danziger, S., Owen, V., Rafal, R., 2002. Deficits in spatial coding and feature binding following damage to spatiotopic maps in the human pulvinar. Nat. Neurosci. 5 (2), 99–100.
Weiskrantz, L., 2009. Blindsight. Oxford University Press, Oxford, UK.
Weiskrantz, L., Warrington, E.K., Sanders, M.D., Marshall, J., 1974. Visual capacity in the hemianopic field following a restricted occipital ablation. Brain 97 (4), 709–728.
Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., Jenike, M.A., 1998. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. J. Neurosci. 18 (1), 411–418.
Whalen, P.J., Kagan, J., Cook, R.G., Davis, F.C., Kim, H., Polis, S., McLaren, D.G., Somerville, L.H., McLean, A.A., Maxwell, J.S., Johnstone, T., 2004. Human amygdala responsivity to masked fearful eye whites. Science 306 (5704), 2061.
Williams, L.M., Liddell, B.J., Kemp, A.H., Bryant, R.A., Meares, R.A., Peduto, A.S., Gordon, E., 2006. Amygdala-prefrontal dissociation of subliminal and supraliminal fear. Hum. Brain Mapp. 27 (8), 652–661.