

Critically Evaluate the Role of Neural Structures in Sub-Serving a Specific Psychological Function.

Human faces are inherently interesting and informative visual stimuli. They possess both invariant (sex, ethnicity, age) and changeable (mood, gaze direction) types of information (Haxby et al., 2010), which are together useful for subsequent interactions. Current cognitive neuroscientific research investigates face perception by assessing how brain activity is involved in and/or necessary for the process to occur, where it occurs, and what happens if it is disrupted. *Middle-fusiform-gyrus* (also fusiform-face-area, FFA; Kanwisher et al., 1997) is fundamental to this research; the debate surrounding this region derives two classic positions: modularists contend that FFA is specifically responsive to face stimuli (Kanwisher & Yovel, 2009), whereas generalists argue that FFA is an expert of many visual categories, including faces (Gauthier et al., 2003). A contemporary group extends beyond the classic modular perspective, arguing that face perception is fulfilled by a specialist-distributed network, beyond FFA exclusively (Haxby et al., 2000). The distributed and classic-modular accounts are not incompatible; the former can be seen as an extension of the latter. This essay argues in support of Haxby et al.'s (2000) model, focusing exclusively on the *core system*, comprising of FFA, *inferior-occipital-gyrus* (occipital-face-area, OFA) and *superior-temporal-sulcus* (STS), and uses functional-magnetic-resonance-imaging (fMRI) and transcranial-magnetic-stimulation (TMS) as neurally-based evidences. Accordingly, FFA, OFA and STS fulfil complementary and distinctive roles in achieving face perception. In developmental terms, how the vast majority of humans are capable of becoming expertised in faces can be explained by innate cognitive mechanisms evolutionarily attained to ensure rich visual experience and neural maturation in facially-sensitive regions in early life (Turati, 2004; Tsao & Livingstone, 2008; Kadosh, 2011).

This essay employs two methodologies (fMRI and TMS) to evaluate three cortical structures thought to be involved in face perception: FFA, OFA and STS. Both techniques are powerful and distinctive demonstrations linking brain and behaviour. With fMRI, the underlying principle *indirectly* links change in regional cerebral blood flow and metabolism with changes to regional neural activity (Amaro & Barker, 2006). The result is a BOLD signal – a contrast agent for specific neural activations demonstrated by an image schematic. With spatial resolutions of ~3mm and temporal resolutions of ~2s, fMRI is well-balanced (Kable, 2011). However, where TMS demonstrates disruption at ~100ms for face perception (Pitcher et al., 2007), fMRI is not necessarily fast enough to verify specific brain regions involved. By contrast, TMS *directly* links electrical current on the dorsal cortical surface with *immediate* cognitive function disruption: this is visually apparent when used on motor cortex

(e.g. **Hotermans et al., 2008**). Stimulating a surface of $\sim 3\text{cm}^2$ with a depth of $< 2\text{cm}$, and with a pulse timecourse of $\sim 200\text{ms}$, TMS possesses accurate spatial and temporal resolutions, respectively (**Kable, 2011**). Hence, these methodologies are complementary: fMRI can reveal behaviourally-associated brain regions, whilst TMS can selectively disrupting those areas, to observing its behavioural deficit(s).

Haxby et al. (2000, 2010) posit the existence of a hierarchally-organised face perception network: a core system, (containing OFA, STS and FFA), which fulfils the fundamental face perception process, and an extended system, (containing external areas e.g. *amygdala*), which fulfil related-processes such as emotion perception. The model predicts that invariant information is associated with OFA and FFA; OFA fulfils early facial feature analysis, whilst FFA categorises/identifies faces. Changeable information e.g. gaze and expression are associated with STS. This essay interprets evidence to support a distributed-modular cortical network fulfilling face perception.

Haxby et al.'s (2000) first FFA prediction posits that FFA is highly sensitive to face-stimuli. **Kanwisher et al. (1997)** found in 80% of their participants reliable fMRI activation of FFA favouring faces over assorted common objects such as spoons, lions and cars, and labelled *middle-fusiform-gyrus* (FFA) to be *the* face processor. **Puce et al. (1996)**, again using fMRI, found that face stimuli evoked greater right hemispheric activation, with characteristic patterns localised to FFA (compared to letter strings, which activated *occipitofrontal* and *inferior-occipital-sulci*). Using an event-related design, faces and letterstrings were presented alternately. 12/13s gaps before/after each stimuli acted as a 'cooling period', meaning they could acquire relatively clean activation patterns resulting from a single category stimulus. However, individual stimulus responses were combined to derive overall differences, which is statistically-weaker than block design (**Kable, 2011**). However, these studies both support **Haxby et al.'s (2000)** first prediction. A second FFA prediction forecasts FFA as selectively responsive to invariant face information e.g. identity. **Tong et al. (2000)** found, again with fMRI, equally strong activation for cat, cartoon and human faces of variant image properties, equal activations for front and profile views, and negligible activation for non-face stimuli. Here, stimuli were presented one-at-a-time and randomly, but in a serial fashion according to their category e.g. blocks of faces. FFA activation to different faces and different orientations suggests that it is responsive to invariant information, thus supporting **Haxby et al.'s (2000)** second prediction. Note: **Tong et al.'s (2000)** block design meant that subtle between category differences could be optimally analysed (**Chee et al., 2003**). Although block designs can be liable to produce predictability effects, **Chee et al. (2003)** found block and event-related designs to be equally as effective to demonstrate the word-frequency-effect.

Statistically-sound designs are required to disentangle perceptually-similar perception categories (Tsao & Livingstone, 2008).

Some argue that FFA is responsive to various expertised categories (Gauthier et al., 2000). This derives from fMRI data revealing FFA activation relative to categorical expertise, with faces being strongest, other expertised and then non-expertised categories following subsequently. This may suggest a non-specific FFA; however, non-face categories may share conceptual/functional properties with faces that encourages FFA activation. Here, expert categories such as cars and birds both possess similar perceptual properties to faces e.g. up-down asymmetry, perhaps causing invalid FFA activation (Turati, 2004). Another counter argument is perceptual interference (Gauthier et al., 2003). Here, using electrophysiological methods, they found behavioural evidence demonstrating interference between the two categories, suggesting generalism. However, this interference may result from a visual processing bottleneck occurring locally to their measured N170 region – N170 is associable to FFA, but it is debateable if it *exclusively* measures this region (Pitcher et al., 2011).

FFA development has been documented by Golarai et al. (2005 - see Golarai et al., 2006). Right FFA in 7-11 year-olds was half the size of 12-16 year-olds, and 1/3 of adult size, and size was correlated with face recognition memory. This ability was domain-specific too, insofar that object recognition scores and object-sensitive cortex were matched across groups. Despite this sequence, behavioural research shows that face processing is qualitatively present by 4 years-of-age (Kanwisher et al., 2006 – see Kanwisher & Yovel, 2009). So why FFA changes (at least) twofold, even after face perception is seemingly present, is an outstanding question requiring intensive longitudinal documentation. It may be that this change links to increasing connectivity to other core system regions, such as STS and OFA. Rossion et al. (2012) using large-scale fMRI revealed six interconnected, right lateralised regions: OFA, FFA, STS, *amygdala*, *pulvinar* and *anterior-infero-temporal-cortex*. It is plausible that developmental changes in these regions results from individualised growth *and* increasing interconnectivity. A distributed-modular account is equipped to verify this claim, as it acknowledges that specific regions function as part of a functioning system (Haxby et al., 2010).

Prosopagnosia (“face: not-knowing”) is often used to demonstrate dissociations between face and other types of perception (Kanwisher, 2000). However, brain damage seldom respects anatomical boundaries, and ‘pure’ prosopagnosia is therefore rare – many prosopagnosiacs possess other recognition deficits. Neuropsychological evidence is therefore dubious at best when used in support/opposition of modularity/generalisability. However, with

TMS, researchers can now *simulate* lesions in healthy people to demonstrate modularity in the face perception network. Although deeper regions like FFA are currently inaccessible, disruption to specific locations on the dorsal surface can produce very specific face perception deficits (**Pitcher et al., 2011; Downing, 2007, 2009**). Thus, FFA cannot be the *only* face processing region, because disruption to other brain regions are implicated in the process. Models considering neural structure as connected and bi-directional are better equipped to explain how regions fulfil specific subtasks (**Haxby et al., 2010**).

Complementary to FFA function, **Haxby et al. (2000)** posit that: firstly, OFA will process invariant information *before* FFA, and secondly, will specifically focus on facial features. TMS studies by **Pitcher et al. (2007, 2009)** verify OFAs role in face perception. In **2007**, disruption at 60-100ms after target onset was shown to impair performance on perceptual discrimination tasks (presentation: stimulus-interval-target; task: was the target same/different to the previous stimulus?). Face stimuli were varied by face parts (OFAs theorised focus) or their spacing, with houses used as controls. TMS was delivered at 10Hz for 500ms concurrent with the target stimulus. No deficit occurred for house stimuli, and for face stimuli, the deficit only occurred for right OFA and not in surrounding object recognition-related areas. The performance deficit was greater for face part variation, insubstantial for their spacing – suggesting that OFA is an entry point for face processing, with an analysed representation perhaps being sent to ‘higher’ regions such as FFA. Furthering OFAs role as a preliminary face processing stage, dynamic causal modelling attests that OFA sends information to FFA (Hemond et al., 2007 – see **Pitcher et al., 2011**).

Pitcher et al. (2009) demonstrated a triple dissociation in OFA, *extrastriate-body-area* (EBA) and *lateral-occipital-complex* (LOC) using discrimination tasks (same as **2007**) involving faces, bodies and novel objects. Using fMRI they first localised relevant locations with region-of-interest (RoI). RoI involves preliminary fMRI localisation, with response magnitudes subsequently measured in new conditions; therefore, regions can be studied powerfully and objectively despite individual anatomical variances (Saxe et al., 2006 – see **Kanwisher & Yovel, 2009**). TMS was then systematically applied at 10Hz for 500ms concurrent with probe stimulus presentation, with selective effects: where OFA disruption influenced face stimuli decisions, EBA influenced bodies, and LOC influenced novel objects – none of the disruptions affected participants’ discrimination of the other stimulus types. This is strongly supportive of distributed modularity: that it was shown threefold for differing perceptual categories demonstrates that selective processing of perceptual categories must occur in distinctive regions. Further it seems that subtasks involving ‘people perception’ e.g. face/body perception occur independently. However, there is the possibility that an untested

category may equally activate these neural regions as well, but **Downing (2009)** notes he has explored this possibility with colleagues (2006) and has not discovered such categories. **Pitcher et al.'s (2007, 2009)** research is supportive of **Haxby et al.'s (2000)** model because it demonstrates modularity as well as coinciding in their prediction of OFA function (e.g. OFA disruption specifically affects the perception of face-parts).

Haxby et al.'s (2000) third major prediction of core network function posits that STS responds to *changeable* attributes of faces e.g. eye gaze/expression/lip movement. **Pelphrey et al. (2005)** found, using an event-related fMRI, that STS in individuals with autistic-spectrum-disorder (ASD) was not susceptible to intention 'violation' as were healthy controls. A virtual actor's eye gaze would change when new objects entered the scene; gaze would be placed either on the object, or in open space (the latter being a violation of expected behaviour). Where ASD individuals equivalently noticed to controls regarding change in the actors' gaze, STS activation was significantly different between groups. STS was also more activated when selectively attending to eye gaze rather than to face identity, suggesting its distinctiveness from FFA. That healthy STS was associated with an unexpected intention affirms its placement as a responsive mechanism to changeable information, as predicted by **Haxby et al. (2000)**. STS has been particularly researched in ASD, due its association with atypical gaze and emotion perception (**Golarai et al., 2006**). Future insights into STS function will benefit debates surrounding ASD; enhanced clarification of anatomical differences in individuals with ASD provides a more accurate basis for better understanding the condition itself, as cognitive neuroscientific research further explores the relationship between STS and its behavioural function.

STS has also successfully been localised and disrupted using repeated TMS (rTMS). **Grossman et al. (2005)** administered a 10-minute train of repetitive low-frequency (1Hz) stimulations – (deemed to be enough to reduce excitation, this is typically used to produce longer measured effects than 10Hz stimulation) – they showed that when placed over *right* (but not left) posterior STS, the disruption impaired biological motion perception, as measured by point-light animations. This demonstrates STSs vital role in interpreting dynamic information, which has intuitive importance following face perception. Both fMRI and TMS studies substantiate the predictions of STS function in **Haxby et al.'s (2000)** model. Further, gaze and expression as sub-processes have been localised independently *within* STS, suggesting deeper modularity than originally predicted (**Engell & Haxby, 2007**). Future research should test this finding with low-frequency TMS stimulations to establish if they are dissociable via observed gaze/expression deficits. Conversely TMS may require further improvement before such an endeavour is deemed plausible.

An alternative view posits that STS activates from generic (not face-specific) stimuli conveying intention (**Golarai et al., 2006**), as evidence shows activation when simple geometric shapes convey intention (Schultz et al., 2004 – see **Golarai et al., 2006**). Other fMRI research, however, shows that STS is responsive to moving and stationary eyes and mouths, but not appreciably by moving checkerboards or contracting circles (**Puce et al., 1998**). Regardless of STSs specificity to changeable face or generic information, both views posit that STS activation is important for responding to signals important to potential behaviours *after* face perception. Although the latter would involve a revision of **Haxby et al.'s (2000)** core system, (perhaps involving STS moving to the extended system), its application to different dynamic perception types *including* face perception would still remain.

Comparative studies demonstrate dissociation between components of **Haxby et al.'s (2000)** core system. **Hoffman & Haxby (2000)**, using repetition-detection tasks and fMRI, participants were first informed whether they needed to attend to the identity or gaze of a face, (task: does the target match/differ from the previous stimulus?), with scrambled/nonsense colour images as controls. Identity was primarily associated with FFA/OFA, with gaze associated with STS and *intraparietal-sulcus*. Using block design, they revealed invariant and changeable information processing systems, one processing identity, the other, expression/gaze, as predicted by **Haxby et al.'s (2000)** model.

To summarise thus far, substantial fMRI and TMS evidence supports three discernible regions involved in face perception, which supports **Haxby et al. (2000)** core network. FFA holistically processes identity, being sensitive to generic facial stimuli; its anatomy can also be traced to face memory (**Kanwisher & Yovel, 2009; Golarai et al., 2006**). OFA is sensitive to facial features, indicative of an entry-point processor, providing information for important higher-level analyses (**Pitcher et al., 2007, 2009**). STS is sensitive to face-related social information, but may also process intention generally (**Pelphrey et al., 2005; Golarai et al., 2006**). It must be noted that face perception relies on external processes as well (**Haxby et al., 2000**). **Rossion et al. (2012)**, using fMRI, recently highlighted multiple regions involved with face perception beyond FFA, OFA and STS. This was found using ‘multi-dimensional’ stimuli e.g. faces conveying fear. It is likely that connectivity is equally important as modular functioning in face perception – **Haxby et al. (2000)** acknowledge this by theorising a bi-directional relationship within and between both core and extended networks.

Reflecting this multi-dimensional view, **Haxby et al. (2010)** have made a further distinction between maximal and significant activation in the face perception network. Where FFA/OFA and STS maximally respond to invariant/changeable information respectively, extended systems, such as *amygdala*, may respond significantly to such information. This maybe because they are susceptible to more generic attributes within stimuli, such as fear *within* a face (**Haxby et al., 2010**). This distinction may also prove helpful in supporting distributed-modularity, because counter evidences finding general expertise effects can then be better justified. It may be that non-face categories resemble faces in undetected and generic ways; for example, a frontal view of a car/house look face-like insofar that it may contain may face-like asymmetry (**Turati, 2004**). This *may* therefore activate FFA significantly, as generalists have found. However, as others have found (**Kanwisher & Yovel, 2009**), face stimuli *consistently* and maximally activate FFA over non-face stimuli.

Tsao & Livingstone (2008) assert that *all* visual stimuli possess the same problem: image changes regarding position, illumination and occlusion. **Turati (2004)** suggests that we innately possess *non-specific* perceptual constraints, such as up-down asymmetry (i.e. top-heavy facial configuration). Therefore, faces are ‘special’ because they possess salient perceptual configuration. The prediction of asymmetrical stimuli being preferred is also evidenced by **Turati (2004)**. This account may explain newborn preferences for face-like stimuli as well as biological motion (**Johnson et al., 1991; Simions et al., 2002**), and also provides an insight into adult face memory efficiency (**Farrelly & Turnbull, 2008**). Adaptive cognitive mechanisms provides a platform to explore the growth trajectories of face perception capability, and the interaction of experience and maturation (**Le-Grand et al., 2003; Kadosh, 2011**). Lastly, **Turati’s (2004)** account may account for modular cognitive development overall: for example, phonetic sensitivity, present from birth, aids fast language development in early life, and seemingly deteriorates around six-months-of-age; perhaps we possess specific mechanisms to aid modular ability foundations early on.

To conclude, face perception is our most advanced visual capability (**Haxby et al., 2010**). **Haxby et al.’s (2000)** model is a promising representation of cortical structure fulfilling face perception. Three dedicated neural systems fulfil distinctive subtasks for face perception in the core system: FFA, OFA and STS, with additional subtasks being pursued externally (**Rossion et al., 2012**). Early face perception development may be aided by specific cognitive mechanisms (**Turati, 2004**). Future directions include investigating how the face perception network operates as a system, as well as how it develops early on. **Rossion et al. (2012)** show that a systemic approach using appropriate statistical methodology reveals an extensively connected network. **Kadosh (2011)** reminds us how developmental insights into

face perception can reveal much about the nature of the neural-behavioural relationship. Echoing **Pitcher et al. (2009)**, fMRI and TMS are powerful colleagues: RoI-driven fMRI to impartially locate multiple face regions, followed by precise TMS disruption, will reveal how specific areas connect with neighbours functionally. Previous research shows how regions behave individually: how these regions interact as network members is the logical next step.

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