

Temporal-nasal asymmetry of rapid orienting to face-like stimuli

Przemyslaw Tomalski, Mark H. Johnson and Gergely Csibra

Recent work suggests that a subcortical visual route may mediate rapid orienting towards faces in the visual periphery. We now demonstrate that this orienting bias towards faces shows a temporal-nasal visual field asymmetry of responses, supporting the view that it is mediated by extrageniculate pathways. Upright schematic face-like pattern elicited faster behavioural responses than inverted one in the temporal but not in the nasal hemifield of each eye. This effect occurred for saccades but not for manual responses. The presence of a similar asymmetry of the orienting bias in newborns supports the role of extrageniculate pathways in face detection in both neonates and adults. *NeuroReport* 20:1309–1312 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Centre for Brain and Cognitive Development, School of Psychology, Birkbeck, University of London, London, UK

Correspondence to Dr Przemyslaw Tomalski, PhD, Centre for Brain and Cognitive Development, School of Psychology, Birkbeck, University of London, Malet Street, London WC1E 7HX, UK
Tel: +44 20 7631 6327; fax: +44 20 7631 6587; e-mail: tomalski@mac.com

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Introduction

Faces are difficult to ignore: they more effectively capture spatial attention than other objects [1] and elicit visual orienting in adults and neonates alike. Simple face-like patterns (Fig. 1a), consisting of a bright oval and three dark blobs corresponding to the eyes and mouth, elicit preferential orienting in human newborns only when presented upright [2,3]. Recently, we have demonstrated that orienting towards such face-like patterns can also be detected in adults [4]. Therefore, the preference for the unique configuration of elements and contrast information of faces in both neonates and adults supports continuity in face-biasing mechanisms in the human brain throughout the life span.

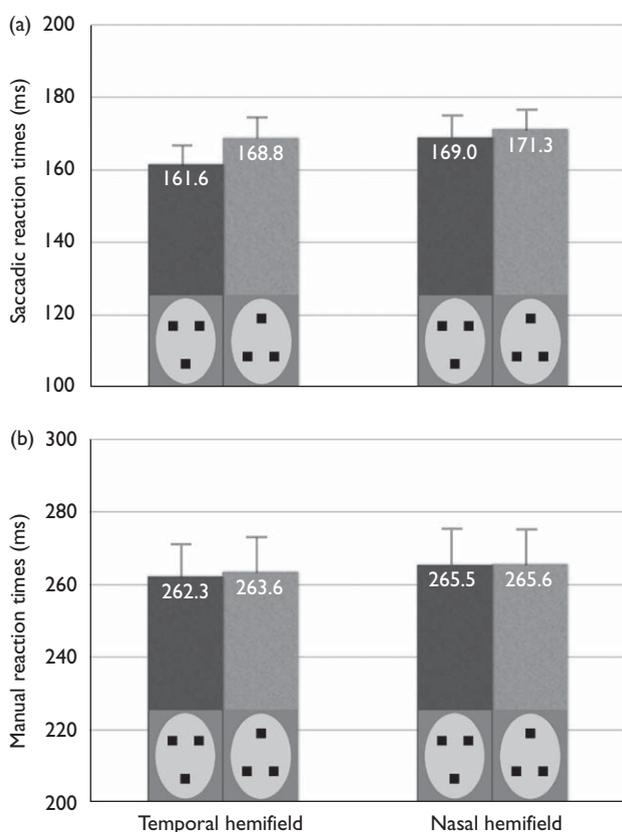
The neural basis of the preferential orienting to faces effect remains unknown. We have hypothesized that a putative ‘quick-and-dirty’ subcortical visual pathway might mediate orienting to faces and face-like patterns [4]. This hypothesis follows the proposal of a subcortical face detection pathway, which is active from birth and enables rapid detection of socially relevant stimuli, especially in the visual periphery [5]. It has been argued that subcortical structures, such as the superior colliculus (SC) and the pulvinar (that receive direct retinal input independently of the main visual relay through the lateral geniculate nucleus) might provide a route for rapid processing, facilitating fast and coarse processing of magnocellular visual input and possibly modulating fine-grained processing at higher levels of visual cortex [5,6].

To date, evidence of face sensitivity along this subcortical pathway has been found in both healthy and brain-injured

adults. Emotional facial expressions can be detected and processed in the absence of visual awareness by blind-sight patients who suffered damage to their primary visual cortex [7,8]. Further, in healthy adults undetected (masked or suppressed by binocular rivalry) fearful faces evoke correlated activity of the SC, pulvinar and amygdala, which is dissociated from the cortical processing through the ventral visual stream [9,10].

In this study we investigated whether preferential overt orienting to upright face-like patterns is mediated by the extrageniculate visual pathway and, in particular, by the visual input to the SC. Using our overt orienting task [4], we tested whether the preferential orienting effect displays a signature of the contribution of the extrageniculate pathway: temporal-nasal visual field asymmetry.

The asymmetry between the temporal and the nasal half of the visual field of each eye arises from the biased representation of the visual fields in the SC, favouring the temporal half [11–13]. The influence of this asymmetry of retinal projections has been shown for visual orienting behaviour. Typically, this effect is tested by occluding one eye and presenting stimuli exclusively to the other eye in the periphery on either side. The visual hemifield that corresponds to the side of the working eye is the temporal hemifield (projecting from the nasal hemiretina to the opposite SC), whereas the other hemifield is the nasal hemifield (projecting from the temporal hemiretina to the same side SC). A bias to make saccades towards stimuli in the temporal hemifield and a temporal hemifield advantage in terms of saccadic reaction times (SRTs) has been found [14,15], as has a similar

Fig. 1

(a) Average saccadic reaction times in Experiment 1 and (b) manual reaction times in Experiment 2 in response to upright and inverted schematic face-like patterns in the temporal and the nasal hemifield. Error bars represent standard error of mean.

asymmetry for the reflexive orienting of attention [16–18]. These asymmetries have also been observed in human newborns [19]. The existing evidence indicates that temporal-nasal asymmetry in responding to achromatic stimuli reflects the activity of the extrageniculate pathway through the SC to the pulvinar and extrastriate cortex. This is also supported by a neuroimaging study showing greater activation of the SC after the stimulation of the contralateral temporal than nasal hemifield [20]. Importantly, no parallel hemifield difference was found for the lateral geniculate nucleus or cortical areas V1–V3.

Methods

Participants

Two independent samples of 12 right-handed volunteers took part in the study. Each group completed either Experiment 1 (seven females; mean age 26.9 years, age range 21–41 years) or Experiment 2 (seven males; mean age 25.8 years, age range 18–38 years). Five additional volunteers were excluded owing to ocular artefacts. All participants had normal or corrected-to-normal

eyesight, and were asked to sign an informed consent. The study received ethical clearance from the relevant local committee.

Apparatus

Participants sat in a dimly lit booth, 70 cm away from a 19-inch computer screen (resolution 1024×768 pixels, refresh rate 100 Hz). They viewed stimuli through CrystalEye liquid crystal shutter goggles (Real D Inc., Beverly Hills, California, USA), synchronized by infrared signal to the monitor's vertical retrace. This enabled monocular presentation of selected stimuli by addressing every odd frame to one eye and every even frame to the other. The experiment was programmed and run in Matlab (Mathworks, Natick, Massachusetts, USA) with Psychtoolbox on a MacPro (Apple, Cupertino, California, USA).

Stimuli and procedure

We used upright and inverted schematic face-like patterns (visual angle of $4.5 \times 6.4^\circ$ or 5.5×7.8 cm), which consisted of three black square blobs ($0.8 \times 0.8^\circ$, 1×1 cm), corresponding to the location of the eyes and mouth, overlaid on a plain grey oval (20% black). The fixation stimulus was a black star (1° or 1.26 cm radius).

Each trial begun with a central fixation point, presented to both the eyes for 700–1200 ms, followed by an upright or an inverted face-like pattern flashed peripherally for 200 ms at the eccentricity of 8° , either on left or right side of the screen. Each stimulus was addressed either to the left or to the right eye. Each of the eight different trial types (2 stimuli \times 2 sides \times 2 eyes) was presented in a fully random order with equal probability. The inter-trial interval varied between 700 and 900 ms. The stimuli were displayed on a uniform grey background (50% black). In total, 320 trials were run, grouped in eight blocks of 40 trials with short breaks between blocks.

A practice block consisted of 10 trials with a black-and-white square checkerboard (visual angle of 5.14° , 6.3 cm) as the saccade target. The participants' task on each trial was to make a speeded saccade (Experiment 1), or to press a button under the corresponding index finger (Experiment 2) as soon as the peripheral target appeared on the left or right side of the screen, and then to refixate again in the centre when they saw the fixation stimulus reappear. In most trials in Experiment 1, the target stimulus had already disappeared by the time the participants foveated its location.

Response recording

In Experiment 1 SRTs were measured through electro-oculography using the Electrical Geodesics (EGI) acquisition system (500 Hz sampling rate, 0.1–200 Hz band-pass filter) (NetAmps 200, Electrical Geodesics Inc., Eugene,

Oregon, USA). The electrooculographic signal was collected with a 128-channel Hydrocel Net against vertex reference. SRTs were calculated offline on the basis of an existing protocol [21]. In Experiment 2 manual reaction times were collected with EGI button box, connected to the EGI amplifier (500 Hz sampling rate). We applied this unusual method of reaction time measurement to achieve a temporal resolution of the manual reaction time measurement comparable with that of SRTs in Experiment 1.

Median saccadic (Experiment 1) or manual (Experiment 2) reaction times for upright and inverted face-like stimulus in the temporal and nasal hemifield were calculated.

Results

Experiment 1

The SRTs in response to an upright and an inverted face-like pattern were submitted to a two-way (face orientation \times temporal/nasal hemifield) repeated-measures analysis of variance (Fig. 1a). Saccades were initiated faster towards the temporal than towards the nasal hemifield [temporal/nasal main effect: $F(1,11) = 9.99$, $P = 0.009$], and a main effect of orientation indicated shorter reaction times to upright than to inverted faces [face orientation main effect: $F(1,11) = 13.02$, $P = 0.004$]. A significant interaction of factors revealed that face orientation had a different effect in the two hemifields [$F(1,11) = 5.21$, $P = 0.043$]. As predicted, we found faster saccade initiation by upright than inverted faces in the temporal [$t(11) = 3.87$, $P = 0.003$] but not in the nasal hemifield [$t(11) = 1.47$, $P = 0.17$]. Similarly, shorter latencies were recorded in response to the upright stimulus in the temporal than nasal field [$t(11) = 3.88$, $P = 0.03$]. To conclude, a schematic face presented in the visual periphery with only the basic face-like configuration elicits faster saccadic responses in the temporal visual field, compared with an identical stimulus in the nasal visual field, or inverted stimulus in the temporal visual field.

This finding is consistent with our primary hypothesis that an extrageniculate route is mediating rapid orienting to face-like stimuli in the visual periphery. Our result closely resembles previous reports with newborns, where a similar asymmetry of preferential orienting to the upright schematic face was found [22,23]. To our knowledge, this is the first direct evidence that the orienting bias to faces is mediated by relatively primitive subcortical structures in the visual midbrain.

One primary function of the SC is to generate reflexive saccadic orienting to visual stimuli in the periphery [24]. We predicted that if the effect of preferential orienting to a face-like pattern were specific to the oculomotor system, it would not be present in the same task

but with manual responses required to the peripheral visual targets.

Experiment 2

A two-way analysis of variance (face orientation by temporal/nasal hemifield) on the manual reaction time data did not show any significant main effect, or an interaction [temporal/nasal field, $F(1,11) = 3.38$, $P = 0.093$; orientation $F(1,11) = 0.37$, $P = 0.553$; temporal/nasal visual field \times orientation $F(1,11) = 0.56$, $P = 0.472$]. Thus, consistent with our prediction, no support was found for preferential orienting effect towards the upright face-like pattern in Experiment 2 with manual responses.

Discussion

Our results support the hypothesis that subcortical structures along the extrageniculate pathway mediate rapid orienting to face-like stimuli. Our participants made saccades more rapidly towards an upright face-like pattern than to the same stimulus inverted when it was presented in the temporal but not in the nasal hemifield. This asymmetry is commonly recognized as a marker of subcortical mediation in visual orienting tasks.

To date, the ‘quick-and-dirty’ subcortical visual pathway, dependent on the retinal input to the colliculus, with further projections to pulvinar and amygdala, has been implicated in rapid detection and processing of threat-related social stimuli [6]. Our findings provide new insights into the role of this pathway and indicate that it is likely to be involved in rapid detection and coarse processing of human faces appearing in the periphery. Thus the role of this system lies not only in rapid detection of threat, but also in the orienting towards and processing of other socially and biologically important stimuli. Our data might inform the research on the early biases and developmental trajectory of the subcortical visual pathway and its role in fast processing of socially relevant stimuli [7,8,25].

Another important aspect of our finding is its evolutionary context. Compared with the visual areas in the neocortex, the extrageniculate visual pathway is a relatively ancient part of the mammalian visual system. The extrageniculate pathway through the SC is a homologue of the visual tectum in phylogenetically older vertebrates (e.g. amphibians), which evolved as a visual system for prey and predator detection. In mammals, this pathway mediates responses to biologically and socially relevant stimuli, in particular, the detection of predators or conspecifics. Our results suggest that subcortically-mediated orienting towards conspecifics remains active in the adult human brain, despite the elaborate cortical control over eye movements. This raises further questions about the interactions of this phylogenetically ancient pathway and more recent neocortical mechanisms supporting social

cognition. Our finding suggests that the extrageniculate pathway biases the processing of human faces to allow rapid foveation, which in turn, could engage fine-grained cortical mechanisms of visual processing [5]. In turn, this could lead to generating adaptive social behaviour, such as the deeper processing of faces with direct gaze to play an important role in human face-to-face communication.

Conclusion

Rapid orienting of saccades towards upright schematic face-like patterns shows temporal-nasal hemifield asymmetry. The presence of a similar asymmetry of the orienting bias in newborns supports the role of extrageniculate pathways in face detection throughout the life span.

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References

- 1 Ro T, Friggel A, Lavie N. Attentional biases for faces and body parts. *Vis Cogn* 2007; **15**:322–348.
- 2 Johnson MH, Dziurawiec S, Ellis H, Morton J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 1991; **40**:1–19.
- 3 Valenza E, Simion F, Macchi Cassia V, Umiltà C. Face preference at birth. *J Exp Psychol Hum Percept Perform* 1996; **22**:892–903.
- 4 Tomalski P, Csibra G, Johnson MH. Rapid orienting toward face-like stimuli with gaze-relevant contrast information. *Perception* 2009; **38**:569–578.
- 5 Johnson MH. Subcortical face processing. *Nat Rev Neurosci* 2005; **6**:766–774.
- 6 De Gelder B. Towards the neurobiology of emotional body language. *Nat Rev Neurosci* 2006; **7**:242–249.
- 7 De Gelder B, Vroomen J, Pourtois G, Weiskrantz L. Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport* 1999; **10**:3759–3763.
- 8 Morris JS, de Gelder B, Weiskrantz L, Dolan RJ. Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain* 2001; **124**:1241–1252.
- 9 Morris JS, Ohman A, Dolan RJ. A subcortical pathway to the right amygdala mediating unseen fear. *Proc Natl Acad Sci U S A* 1999; **96**:1680–1685.
- 10 Pasley BN, Mayes LC, Schultz RT. Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 2004; **42**:163–172.
- 11 Conley M, Lachica EA, Casagrande VA. Demonstration of ipsilateral retinocollicular projections in tree shrew. *Brain Res* 1985; **346**:181–185.
- 12 Perry VH, Cowey A. The ganglion cell and cone distribution in the monkey's retina: implications for central magnification factors. *Vision Res* 1985; **25**:1795–1810.
- 13 Williams C, Azzopardi P, Cowey A. Nasal and temporal retinal ganglion cells projecting to the midbrain implications for blindsight. *Neuroscience* 1995; **65**:577–586.
- 14 Posner MI, Cohen Y. Attention and control of movements. In: Stelmach GE, Region J, editors. *Tutorials in motor behavior*. Amsterdam: North Holland Publishing; 1980. pp. 243–258.
- 15 Kristjansson A, Vandenbroucke MW, Driver J. When pros become cons for anti- versus prosaccades: factors with opposite or common effects on different saccade types. *Exp Brain Res* 2004; **155**:231–244.
- 16 Rafal R, Henik A, Smith J. Extrageniculate contributions to reflex visual orienting in normal humans: a temporal hemifield advantage. *J Cogn Neurosci* 1991; **3**:322–328.
- 17 Berger A, Henik A. The endogenous modulation of IOR is nasal-temporal asymmetric. *J Cogn Neurosci* 2000; **12**:421–428.
- 18 Shulman GL. An asymmetry in the control of eye movements and shifts of attention. *Acta Psychol (Amst)* 1984; **55**:53–69.
- 19 Simion F, Valenza E, Umiltà C, Dalla Barba B. Inhibition of returns in newborns is temporo-nasal asymmetrical. *Infant Behav Dev* 1995; **18**:189–194.
- 20 Sylvester R, Josephs O, Driver J, Rees G. Visual fMRI responses in human superior colliculus show a temporal-nasal asymmetry that is absent in lateral geniculate and visual cortex. *J Neurophysiol* 2007; **97**:1495–1502.
- 21 Csibra G, Johnson MH, Tucker LA. Attention and oculomotor control: a high-density ERP study of the gap effect. *Neuropsychologia* 1997; **35**:855–865.
- 22 Simion F, Valenza E, Umiltà C, Dalla Barba B. Preferential orienting to faces in newborns: a temporal-nasal asymmetry. *J Exp Psychol Hum Percept Perform* 1998; **24**:1399–1405.
- 23 Johnson MH, Farroni T, Brockbank M, Simion F. Preferential orienting to faces in 4-month-olds: analysis of temporal-nasal visual field differences. *Dev Sci* 2000; **3**:41–45.
- 24 May PJ. The mammalian superior colliculus: laminar structure and connections. *Prog Brain Res* 2006; **151**:321–378.
- 25 Ward R, Calder AJ, Parker M, Arend I. Emotion recognition following human pulvinar damage. *Neuropsychologia* 2007; **45**:1973–1978.