Eye preferences in capuchin monkeys (Sapajus apella)

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Abstract This study explored whether capuchin monkey eye preferences differ systematically in response to stimuli of positive and negative valence. The ‘valence hypothesis’ proposes that the right hemisphere is more dominant for negative emotional processing and the left hemisphere is more dominant for positive emotional processing. Visual information from each eye is thought to be transferred faster to and primarily processed by the contralateral cerebral hemisphere. Therefore, it was predicted capuchin monkeys would show greater left eye use for looking at negative stimuli and greater right eye use for looking at positive stimuli. Eleven captive capuchin monkeys were presented with four images of different emotional valence (an egg and capuchin monkey raised eyebrow face were categorised as positive, and a harpy eagle face and capuchin monkey threat face were categorised as negative) and social relevance (consisting of capuchin monkey faces or not), and eye preferences for viewing the stimuli through a monocular viewing hole were recorded. While strong preferences for using either the left or right eye were found for most individuals, there was no consensus at the population level. Furthermore, the direction of looking, number of looks and duration of looks did not differ significantly with the emotional valence of the stimuli. These results are inconsistent with the main hypotheses about the relationship between eye preferences and processing of emotional stimuli. However, the monkeys did show significantly more arousal behaviours (vocalisation, door-touching, self-scratching and hand-rubbing) when viewing the negatively valenced stimuli than the positively valenced stimuli, indicating that the stimuli were emotionally salient. These findings do not provide evidence for a relationship between eye preferences and functional hemispheric specialisations, as often proposed in humans. Additional comparative studies are required to better understand the phylogeny of lateral biases, particularly in relation to emotional valence.

Keywords Eye preferences · Behavioural laterality · Hemispheric specialisations · Emotion · Capuchin monkeys

Introduction

Behavioural laterality in primates has been widely and intensively studied for decades (Ward and Hopkins 1993; Fitch and Braccini 2013), such as hand preferences (e.g. Humle and Matsuzawa 2009), eye preferences (e.g. Westergaard and Suomi 1996b) and auditory preferences (e.g. Lemasson et al. 2010). Studies on these lateral biases are important because these are believed to be closely connected to cerebral hemispheric specialisations (Rogers et al. 2013). In mammals the left hemisphere appears to be relatively more important for focused attention to invariable stimuli, following learned rules and categorising stimuli, and can inhibit the right hemisphere (Rogers et al. 2013). The right hemisphere appears to be more important for face perception (Dahl et al. 2013; Tomonaga 1999), spatial cognition, non-focussed attention to novel stimuli, emergency responses involving intense emotions such as fear and rage, and negative cognitive bias (Rogers et al. 2013). These hemispheric specialisations are thought to be reflected in the contralateral side of the body in preferences.
How emotional processing is specialised in each hemisphere is still controversial. There are two main hypotheses: the ‘right hemisphere hypothesis’ proposes that the left hemisphere is more dominant for cognitive processing and the right hemisphere is more dominant for emotional processing (Borod et al. 1998). The ‘valence hypothesis’ proposes that the right hemisphere is more dominant for negative emotional processing and the left hemisphere is more dominant for positive emotional processing (Davidson 1995). In addition, the ‘motivational approach–withdrawal hypothesis’ complements the valence hypothesis and proposes the left hemisphere may play a greater role in approach behaviour towards stimuli, and the right hemisphere a greater role in withdrawal behaviour away from stimuli (Demaree et al. 2005).

In human and non-human primates, empirical evidence suggests the right hemisphere is more dominant for emotional processing (Lindell 2013). For example, in humans, Adolphs et al. (1996) found damage to the right hemisphere impairs the ability to identify and discriminate facial emotions, whereas damage to the left hemisphere does not. In non-human primates, Vermeire and Hamilton (1998) presented split-brain rhesus macaques with photographic slides of rhesus monkey faces with different emotional expressions. The split-brain procedure involves a midline bisection of the cerebral nerve fibres connecting the two brain hemispheres, and section of the optic chiasm so that visual input is restricted to one hemisphere of the brain when the opposite eye is covered (Vermeire and Hamilton 1998). They found the monkeys were significantly better at discriminating emotional facial expressions when presented through a single eyehole to the isolated right hemisphere than to the isolated left hemisphere.

Hemispheric laterality has also been studied in non-human primates with intact brains using non-invasive methods such as visual field use and eye preferences for looking through a monocular viewing hole. In some visual field use studies, the animal is trained to use a joystick to move a cursor over a central fixation point on a computer screen. Stimuli are then presented to the left or the right of the fixation point for a very brief period (shorter than the time it takes to make an eye saccade). This ensures the stimulus is restricted to only one visual half-field which directs information to the contralateral hemisphere (Hopkins et al. 1990; Vauclair et al. 1993; Wilde et al. 1994; Fagot and Deruelle 1997).

Measuring eye preferences, or “the consistent choice of one eye over the other in the monocular viewing situation” (Hook-Costigan and Rogers 1998, p. 110) is another non-invasive method of measuring hemispheric laterality. In primates, each eye provides sensory input via the optic fibres to both of the cerebral hemispheres. However, the contralateral optic fibres have larger diameter and more myelin, and transmit sensory information faster than the ipsilateral optic fibres (Jeffery 2001; Watson and Hanbury 2007). In addition, photoreceptor and ganglion cell density are higher in the nasal hemiretina compared with the temporal hemiretina (Curcio et al. 1987; Wässle et al. 1990), and so the contralateral hemisphere may receive monocular visual information of higher quality than the ipsilateral hemisphere (Bishop et al. 1953; Maddess 1975). Therefore, some researchers suggest that eye preferences for looking through a monocular viewing hole indicate lateralisation of the hemispheres for perceptual processing.

However, eye preferences have only been tested in a few non-human primate species, and the limited data are inconsistent; some studies found individual-level eye preferences, and others found group-level eye preferences, for which the direction varies between species (Chapelain and Blois-Heulin 2009). In addition, typically only one positive stimulus (i.e. food) is used (e.g. Kounin 1938; Westergaard and Suomi 1996b), and therefore support cannot be provided for either the right hemisphere or valence hypothesis.

In eye preference studies using stimuli of both positive and negative valence, Hook-Costigan and Rogers (1998) found support for the valence hypothesis in common marmosets: a right eye preference (left hemisphere dominance) for viewing food (banana), and a shift to left eye preference (right hemisphere dominance) for viewing a model snake. However, Rogers et al. (1994) found the opposite pattern of eye dominance in nocturnal small-eared bushbabies, which may be explained by anatomical differences of ganglion cell organisation in the retina between diurnal and nocturnal species (Hook-Costigan and Rogers 1998). More recently, Braccini et al. (2012) found support for the valence hypothesis when they examined eye preferences in captive adult chimpanzees for various positive and negative stimuli; the strongest right eye preference (greatest number of right eye looks relative to left eye looks) for viewing food (a banana) and the strongest left eye preference (greatest number of left eye looks relative to right eye looks) for viewing a plastic snake were found. In addition, the chimpanzees looked more frequently and for longer at the positive stimuli (approach behaviour), and less frequently and for shorter at the negative stimuli (withdrawal behaviour), consistent with the motivational approach–withdrawal hypothesis.

The aim of the present study was twofold. Firstly, we aimed to examine eye preferences in capuchin monkeys, a species popular for behavioural and cognitive research. There are some reports on eye preferences in capuchin monkeys for viewing food rewards (Kounin 1938), but the small sample size of three monkeys makes it difficult to
determine population-level, or species-level, eye preferences in this species. In a larger-scale study, Westergaard and Suomi (1996b) tested 40 capuchin monkeys and found individual-level but not group-level eye biases. However, only a single stimulus (a grape) was presented at the end of a tube. Therefore, secondly, we aimed to examine whether eye preferences were modulated by the emotional valence of the stimuli presented, including social stimuli not previously tested in this paradigm. In particular, we tried to test whether capuchin monkeys also show a pattern of eye preference consistent with the valence and motivational approach–withdrawal hypotheses. On this basis, we predicted they would prefer to view positively valenced stimuli with their right eye (more frequently and for a longer duration) and negatively valenced stimuli with their left eye (less frequently and for a shorter duration).

Methods

Participants and housing

Eleven tufted capuchin monkeys (Sapajus apella) were tested at the Living Links to Human Evolution Research Centre located at the Royal Zoological Society of Scotland’s Edinburgh Zoo (UK). Nine males and two females took part in the experiment (age range 2–13 years old), and all but one monkey was captive born. The capuchin monkey’s indoor enclosure measured 32.5 m². The monkeys were habituated to the research cubicle environment and could voluntarily enter a test cubicle for short periods of isolation. The study was approved by the Research Ethics Review Committee at the University of Edinburgh, UK, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB 2012).

Apparatus

The experiment was conducted in research rooms, in which a set of eight research cubicles (0.5 m² each) were arranged. The monkeys voluntarily accessed the research cubicles through an entrance from their outdoor enclosure. Transparent or opaque slide doors allowed individual cubicles to be opened to or closed off from each other. Each cubicle had windows to allow the monkeys to be easily observed.

The viewing apparatus was a cardboard panel (37.0 cm × 33.8 cm) which slotted into the front of the research cubicle door with an 8-mm-diameter viewing hole (11 cm from the top of the panel). A 17-inch liquid-crystal display (LCD) monitor (Dell, E177FPc, Round Rock, TX, USA) was used to present stimuli using Microsoft PowerPoint. The monitor was placed on a 120-cm-high stand at a distance of 50 cm from the research cubicle door.

To record eye preferences, a video camera was placed directly on top of the research cubicle and angled downward to capture the position of the top of the monkey’s head in relation to the viewing hole. A second video camera was set at the far end of the research cubicles to record general behaviour and hand preferences when reaching for food rewards (Fig. 1).

Stimuli

Four stimuli (trimmed photographs against a black background) were presented per test session consisting of two positively and two negatively valenced stimuli, which were either social (featured capuchin monkey facial expressions) or non-social (did not feature capuchin monkeys). The non-social positively valenced stimulus was a boiled egg, a favourite food in their daily diet. The non-social negatively valenced stimulus was an open-mouth harpy eagle face, a natural predator (Fragaszy et al. 2004). The monkeys had been habituated to model snakes in previous studies, and so the harpy eagle was chosen as an alternative potentially emotive stimulus. The social positively valenced stimulus was a capuchin monkey raised eyebrow face, which is commonly displayed by all sex and age classes during social affiliative interactions and play (Fragaszy et al. 2004). The social negatively valenced stimulus was a capuchin monkey open-mouth threat face. The stimuli were presented successively, and presentation order was counterbalanced across monkeys.

Procedure

At the start of each session monkeys entered the research cubicles from outside. After the cubicle slide door was closed, and the monkeys became briefly accustomed to the inside of the cubicle, the stimuli were presented on a
The monkeys were never rewarded for looking into the viewing hole; monkeys were given food rewards and released. Participation handling the monkeys was blind to stimuli presentation order to avoid inadvertent cueing.

Each monkey was given up to 60 s to take an initial look at each stimulus. The experimenter would repeat the monkey’s name and tap at the hole at 15-s intervals until they took an initial look, or 1 min elapsed. After an initial look, the image was retained for an additional 30 s (without providing any cues). At the end of the trial, or if an initial look was not taken within 60 s, the next stimulus was presented. Therefore, the shortest length of time a monkey could be in the research cubicles on any one occasion was 2 min, and the longest time 6 min. If at any point the monkeys showed specific behaviours, such as pacing rapidly, vocalising excessively, or pushing the entrance slide door, the testing session was ended. After testing, the monkeys were given food rewards and released. Participants were never rewarded for looking into the viewing hole, as this may have reinforced the use of a particular eye (Chapelain and Blois-Heulin 2009).

A look was defined as the monkey’s head moving within at least 2 cm of the viewing hole and ended when the head moved 2 cm or more away. Eye use judgements were made by observing the position of the top of the monkey’s head in relation to cross-hairs transecting the viewing hole. Only one instance of switching the eye used to look at a stimulus between the first look and second look occurred, and so eye switching could not be examined in the subsequent analysis.

From initial video observations, four potential arousal behaviours were identified and recorded: a ‘hiccup’ vocalisation (e.g. Wheeler 2010), door-touching (often preceding pushing of the cubicle slide door), self-scratching (e.g. Yamanashi and Matsuzawa 2010; Dufour et al. 2011) and hand-rubbing (often preceded by sudden withdrawal from the viewing hole and accompanied by vocalisation). Arousal behaviours were recorded within the stimulus presentation period of each session.

In addition, hand preferences were preliminarily measured by recording which hand the monkeys used when reaching for food rewards given before the start of the experiment. Three or more hand reaches were used to determine hand preference.

**Inter-rater reliability**

Inter-rater reliability scores were obtained by asking a second rater to code the video recordings of three monkeys. Frequency and order of observed looks, and order of arousal behaviours were recorded. Kappa coefficients were calculated for the frequency of these measures (Bakeman and Gottman 1997). Inter-rater reliability for eye use scores was 0.77 (p < 0.001) indicating ‘substantial agreement’ between raters (Landis and Koch 1977). For arousal behaviours there was ‘fair agreement’ on the frequency of behaviours in a particular category (κ = 0.40, p < 0.001) and ‘perfect agreement’ on the category to which the behaviour belonged (κ = 1.0, p < 0.001).

**Statistical analysis**

The data were analysed using SPSS (version 19) and R (version 3.2.2). For each monkey, eye preferences were calculated using an eye use index measure. This was done by subtracting the total number of left eye uses (L) from the total number of right eye uses (R) and dividing by the total number, i.e. (R – L)/(R + L). Eye use index values ranged from 1.0 (complete preference for right eye use), through zero for no preference, to -1.0 (complete preference for left eye use) (Westergaard and Suomi 1996a). We also used binomial tests to evaluate the strength of eye preferences for each individual. Hand preference was calculated using the same method to generate a hand use index measure.

The mean scores for the duration of initial, and subsequent looks, and collated arousal behaviours (vocalisation, door touching, self-scratching and hand-rubbing) were not normally distributed. Square root transformations were performed, resulting in normally distributed scores (Shapiro–Wilk tests) for initial looks (S–W(28) = 0.97, p = 0.65), subsequent looks (S–W(28) = 0.98, p = 0.94) and arousal behaviours (S–W(44) = 0.97, p = 0.23). The square roots of the mean scores for all looking and behaviour dependent variables were then analysed using a 2 × 2 repeated-measures analysis of variance (ANOVA), with emotional valence and social relevance as independent variables. We also report the effect size for each statistical test, Cohen’s d for t tests and partial etas squared (η²) for ANOVAs.

**Results**

**Eye use**

The total number of looks at an individual stimulus ranged from 1 to 16. Figure 2 shows the median of the total number of looks (combined across right and left eyes) for each positively and negatively valenced category. Monkeys did not show any difference in total looks between valence categories (Wilcoxon signed-rank test, V = 8, N = 11,
or between social and non-social stimuli ($V = 14.5, N = 11, p = 1$).

Figure 3 shows the eye use index scores for each monkey. All monkeys significantly preferred using either their left or right eye (binomial tests, all $p < 0.05$). However, there was no significant population-level eye preference; seven monkeys had an overall left eye preference, and four monkeys had an overall right eye preference, irrespective of stimulus valence (binomial test, $p = 0.27$). The mean eye use index scores for valence categories based on total number of looks did not differ significantly from zero; for positively valenced stimuli the score was $-0.18$ ($t_{(10)} = 0.65, p = 0.53, d = 0.20$), and for negatively valenced stimuli $-0.30$ ($t_{(10)} = 1.08, p = 0.31, d = 0.33$). There was also no significant difference between valence categories ($t_{(10)} = 1.27, p = 0.23, d = 0.13$). This tendency was consistent when analysed on the basis of initial looks and subsequent looks.

Four monkeys did not take subsequent looks at all four stimuli, and so were excluded from the initial and subsequent look duration analyses. For initial looks the duration ranged from 0.1 to 5.4 s. Mean duration was 1.38 s (egg), 1.33 s (eagle face), 1.37 s (monkey raised eyebrow face) and 1.86 s (monkey threat face). A $2 \times 2$ repeated-measures ANOVA on the duration of initial look means found no significant main effects of valence and social stimuli type (valence: $F_{(1,6)} = 0.85, p = 0.39, \eta^2_p = 0.12$; social type: $F_{(1,6)} = 2.28, p = 0.18, \eta^2_p = 0.28$) and no interaction ($F_{(1,6)} = 1.09, p = 0.34, \eta^2_p = 0.15$). For subsequent looks the duration ranged from 0.2 to 3.6 s. Mean duration was 0.58 s (egg), 0.55 s (eagle face), 0.44 s (monkey raised eyebrow face) and 0.75 s (monkey threat face). Subsequent looks were significantly shorter than first looks ($t_{(6)} = 5.84, p = 0.001, d = 3.01$). A $2 \times 2$ repeated-measures ANOVA on the duration of subsequent looks means found no significant main effects of valence and social stimuli type (valence: $F_{(1,6)} = 1.10, p = 0.33, \eta^2_p = 0.16$; social type: $F_{(1,6)} = 0.05, p = 0.94, \eta^2_p = 0.00$) and no interaction ($F_{(1,6)} = 3.42, p = 0.11, \eta^2_p = 0.36$).

### Arousal behaviours

Figure 4 shows the mean number of observed arousal behaviours per session as a function of stimulus condition. Given the low frequency of arousal behaviours in some sessions, all arousal behaviours were combined across sessions, and an overall mean score calculated for each individual. The analysis found a significant main effect of valence ($F_{(1,10)} = 5.74, p = 0.04, \eta^2_p = 0.37$), which reflects more total arousal behaviours in response to viewing the negatively valenced stimuli ($M = 0.66$).
observed differences in eye preferences was not statistically significant (M = 0.40 observations per session).

Relationship between eye and hand preference

Figure 3 also shows hand use index scores for each monkey. Three monkeys did not make three or more hand reaches for food and so were excluded from the analyses. Left hand preferences were shown by three monkeys, and right hand preferences were shown by five monkeys. However, as clearly shown in this figure, there was no significant correlation between eye and hand use index scores (r(6) = −0.17, p = 0.69).

Discussion

This study found that eye preferences in capuchin monkeys were strongly lateralised at the individual level; all of the monkeys looked at all the stimuli consistently with either their left or right eye. There are only two previous studies which have investigated capuchin monkey eye preferences (Kounin 1938; Westergaard and Suomi 1996b). Our results are consistent with Westergaard and Suomi (1996b), who also showed individual level, but not group level, eye preferences using a similar monocular viewing task; 14 monkeys (41 %) showed a left eye bias, 13 monkeys (38 %) showed a right eye bias, and seven monkeys (21 %) showed no eye bias. In comparison, our study found seven monkeys (64 %) had a left eye bias and four monkeys (36 %) had a right eye bias. In both studies there was also no relationship between hand and eye preference. This is consistent with studies in both non-human primates (Braccini et al. 2012; Fitch and Braccini 2013) and humans (e.g. Papousek and Schuler 1999; Pointer 2001; Mapp et al. 2003).

There was no difference in the direction of eye preference according to the emotional valence or social relevance of the stimuli. Eye preferences did not change between the first look and subsequent looks (when the monkeys had knowledge of the stimuli). Therefore, our results do not provide support for either the valence hypothesis or the right hemisphere hypothesis of emotional processing. More frequent looking and for a longer duration at the positively valenced stimuli (approach behaviour) and less frequent looking and for a shorter duration at the negatively valenced stimuli (withdrawal behaviour) was predicted (Braccini et al. 2012). Although subsequent looks were significantly shorter than first looks, possibly due to habituation, there was no difference in looking frequency or duration in regards to the stimuli valence. Overall, these results do not provide any support for the motivational approach–withdrawal hypothesis.

Previous eye preference studies providing support for the valence hypothesis in non-human primates have used real objects as stimuli (e.g. Hook-Costigan and Rogers 1998; Braccini et al. 2012). In the present study we presented stimuli as two-dimensional images on a monitor screen, to allow for greater control of social stimuli presentation, and to maintain consistency across all stimuli. One possibility is that two-dimensional representation has a weaker emotional salience than three-dimensional (real) representation (cf. Fagot et al. 2000). However, our monkeys showed more arousal behaviours in response to viewing the negatively valenced stimuli than the positively valenced stimuli, suggesting the images did have a degree of emotional salience. Despite this, emotional valence did not impact upon eye preference, and instead the monkeys demonstrated consistent individual eye preferences across stimuli.

Another explanation is that, although visual information from each eye is transferred faster to and primarily processed by the contralateral hemisphere, there is no systematic causal relationship between eye preference and hemispheric specialisations in non-human primates. If mammals with greater crossing of optic fibres than primates (50 % decussation) such as horses (80–90 % decussation) are tested (Brooks et al. 1999), hemispheric specialisation for emotional processing may affect eye preference more directly. However, after reviewing the previous literature in humans, Mapp et al. (2003) concluded that the sighting-dominant eye (the eye used for monocular viewing tasks) is determined by the constraint of the monocular viewing task itself, and “the habit or ease of using the chosen eye” (p. 314), independently of hemispheric specialisations. The strong individual left or right eye lateralisation found in this study may simply be a reflection of this constraint, which is a possible explanation for not finding a valence effect. Therefore, eye preferences may not be a good measure for testing the valence hypothesis. A better approach to examine hemispheric specialisations of emotional processing of visual stimuli may be to measure visual field use following the procedure outlined above (Hopkins et al. 1990; Vauclair et al. 1993; Wilde et al. 1994; Fagot and Deruelle 1997), although this requires more extensive training and specialist equipment.

Finally, we must acknowledge the general limitations of our study. As only four stimuli were presented, a larger battery of stimuli with both positive and negative valence would be needed to rule out findings specific to these stimuli. In addition, testing eye preferences in a larger number of capuchin monkeys with more trials may help to draw clearer conclusions. In conclusion, the findings from the data obtained in this study do not provide convincing support for eye preferences as a measure of hemispheric specialisation for emotional processing in captive capuchin monkeys.
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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The study was approved by the Research Ethics Review Committee at the University of Edinburgh, UK, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB 2012).

References


Fagot J, Deruelle C (1997) Processing of global and local visual information and hemispheric specialization in humans (Homo sapiens) and baboons (Papio papio). J Exp Psychol Hum Percept Perform 23(2):429


Hopkins WD, Washburn DA, Rumbaugh DM (1990) Processing of form stimuli presented unilaterally in humans, chimpanzees (Pan troglodytes), and monkeys (Macaca mulatta). Behav Neurosci 104(4):577


Westergaard GC, Suomi SJ (1996a) Hand preference for bimanual task in tufted capuchins (Cebus apella) and rhesus macaques (Macaca mulatta). J Comp Psychol 110:406–411
Wilde J, Vauclair J, Fagot J (1994) Eye movements in baboons performing a matching-to-sample task presented in a divided-field format. Behav Brain Res 63(1):61–70