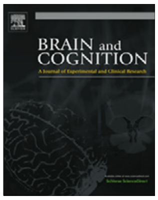
Brain and Cognition 78 (2012) 7–13

Contents lists available at SciVerse ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c



Hemisphere-dependent holistic processing of familiar faces

Meike Ramon *, Bruno Rossion

Institute of Psychology (IPSY) & Institute of Neuroscience (IoNS), Université catholique de Louvain, Belgium

ARTICLE INFO

Article history:
Accepted 19 October 2011
Available online 17 November 2011

Keywords:
Face perception
Holistic processing
Hemispheric asymmetries
Composite face effect
Personal familiarity

ABSTRACT

In two behavioral experiments involving lateralized stimulus presentation, we tested whether one of the most commonly used measures of holistic face processing—the composite face effect—would be more pronounced for stimuli presented to the right as compared to the left hemisphere. In experiment 1, we investigated the composite face effect in a verbal identification task, similar to its original report (Young, Hellawell, & Hay, 1987). Aligning top and bottom halves of composite face stimuli led to performance decreases irrespective of hemifield, indicating holistic processing of comparable magnitude for inputs provided separately to either hemisphere. However, when matching of the same top parts was required in experiment 2, an alignment-dependent performance decrease was found for stimuli presented in the left, but not right visual field. These observations suggest that the right hemisphere dominates in early stages of holistic processing, as indexed by the composite face effect, but that later processes such as face identification and naming are based on unified representations that are independent of input lateralization. Moreover, the composite face effect may not rely on the exact same representation(s) when measured in matching and identification tasks.

1. Introduction

The well-known human right hemisphere superiority in face processing has been inferred from studies of brain-damaged patients (e.g., Bouvier & Engel, 2006; Hécaen & Anguelergues, 1962; Landis, Regard, Bliestle, & Kleihues, 1988; Levy, Trevarthen, & Sperry, 1972; Michel, Poncet, & Signoret, 1989; Sergent & Signoret, 1992), divided visual field studies of normal observers (e.g., Hillger & Koenig, 1991; Rizzolatti, Umiltà, & Berlucchi, 1971), neuroimaging (e.g., Sergent, Ohta, & MacDonald, 1992) and electrophysiological studies (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996). This right hemisphere superiority for face processing has also been found in studies of non-human primates and other mammals (e.g., Peirce, Leigh, & Kendrick, 2000; Zangenehpour & Chaudhuri, 2005). Consequently, the two hemispheres' processing of faces is considered as being functionally distinct in that they are assumed to process faces in a qualitatively different manner (Hellige, Jonsson, & Michimata, 1988; Sergent, 1982). Holistic/configural processing is thought to be preferentially executed by the right hemisphere, while the left hemisphere is regarded as more involved in analytical or part-based processing (Hillger & Koenig, 1991; Rossion et al., 2000; Sergent, 1984, 1988).

In the field of face processing, holistic/configural processing refers to the simultaneous integration of the facial features into a unified perceptual representation (e.g., Maurer, Grand, & Mondloch, 2002; McKone et al., 2003; Rossion, 2008; Sergent, 1984; Young et al., 1987). With respect to faces, there is evidence that holistic processing can occur at two levels of visual categorization (see e.g., Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Rossion, Dricot, Goebel, & Busigny, 2011). The first entails face detection. For instance, deciding whether a two-tone "Mooney" stimulus represents a face or not relies on the global configuration of the stimulus, since the local elements of the stimulus are usually not interpretable as being face-like (Mooney, 1957). There is evidence that this type of processing is carried out relatively more efficiently by the right hemisphere. For instance Parkin and Williamson (1987), as well as Newcombe (1974) found that Mooney faces were detected more quickly when presented within the left visual field. Neuroimaging studies have also reported exclusive or increased right lateralization during perception of such Mooney or "Arcimboldo" face stimuli as compared to fully visible face photographs (Dolan et al., 1997; Rossion et al., 2011).

Holistic processing is also involved in a finer-grained level of categorization of faces at the individual level, e.g. when face discrimination/matching, or identification of previously seen pictures of faces is required (e.g., Hole, 1994; Sergent, 1984; Tanaka & Farah, 1993; Young et al., 1987). Findings from neuroimaging (e.g.,

---

* Corresponding author. Address: Institute of Psychology (IPSY) & Institute of Neuroscience (IoNS), Université Catholique de Louvain, 10, Place du Cardinal Mercier, 1348 Louvain-la-Neuve, Belgium. Fax: +32 10 47 37 74.

E-mail addresses: meike.ramon@uclouvain.be (M. Ramon), bruno.rossion@uclouvain.be (B. Rossion).

0278-2626/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2011.10.009

Jacques & Rossion, 2009; Schiltz & Rossion, 2006) and brain-damaged patients suffering from prosopagnosia (e.g., Barton, Press, Keenan, & O'Connor, 2002; Levine & Calvanio, 1989; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Sergent & Villemure, 1989; see Busigny et al., 2010; Ramon, Busigny, & Rossion, 2010, for a recent review and empirical evidence) also suggest a right hemisphere superiority for holistic processing of individual faces. However, there is a lack of consistent behavioral evidence from divided visual field studies with healthy observers supporting this view. For instance, while a right visual field/left hemisphere advantage has been found for detection of changes between faces differing in single local features, superior performance for left visual field/right hemisphere stimulus presentation is found when faces differ in terms of multiple features (Hillger & Koenig, 1991; Parkin & Williamson, 1987; Sergent & Bindra, 1981, experiment 1). Unfortunately, it remains unclear which of these manipulations taps relatively more into holistic processing. Indeed, feature-based processing could be efficient when all facial features are diagnostic, while holistic processing might be particularly important given only a single diagnostic feature the location/nature of which observers are unaware (Ramon & Rossion, 2010). Studies of hemispheric lateralization which have used the inversion effect (Yin, 1969) as a measure of holistic processing have also provided inconsistent results. For instance, Ellis and Shepherd (1975) investigated the efficiency with which participants matched upright/inverted faces flashed briefly within the right or left visual field to subsequently presented comparison faces. Their results indicated higher proficiency for stimuli presented in the left visual field, irrespective of orientation. Contrariwise, using longer presentation durations (120 and 150 ms) and bilateral stimulus presentation, Leehey, Carey, Diamond, and Cahn (1978) found no negative effect of inversion for right visual field presentation, but a pronounced inversion effect for faces presented in the left visual field.

A more direct and widely used measure of holistic processing is the composite face effect. Initially demonstrated in a famous face identification task (Young et al., 1987), it is more commonly used in the context of face matching tasks (since Hole, 1994). The composite face effect—the relative decline in recognizing top face parts when they are aligned, as opposed to misaligned with bottom parts—disappears or is strongly attenuated when stimuli are inverted (e.g., Hole, 1994; Rossion & Boremanse, 2008; Young et al., 1987) and is considered the most compelling evidence that faces are perceived holistically (Maurer et al., 2002).

In the present study, in a divided visual field paradigm we aimed to investigate the lateralization of holistic processing using the composite face effect. Composite face stimuli created from pictures of personally familiar individuals were briefly presented either in the left or right visual field and had to be verbally identified (experiment 1), or matched to previously presented face stimuli (experiment 2). This provided a promising means to probe the laterality of holistic processing under different task constraints. We hypothesized that holistic processing would be more pronounced for stimuli presented to the right as compared to the left hemisphere. Our aim was thus not to investigate the right hemisphere advantage in face processing *per se*. Rather, we sought to determine the extent to which the two hemispheres are involved in holistic processing of individual faces, as assessed by the performance decline associated with alignment of halves of composite face stimuli, i.e. the composite face effect.

The use of personally familiar faces is advantageous given limitations associated with the use of famous face stimuli. These do not only concern the wide range of inter-/intra-individual variation in degree of familiarity with famous faces, but also the potentially iconic nature of their representations (Carbon, 2008). Although the extent of familiarity with personally familiar faces may also vary, such differences are assumed to be less severe than for instance those involved when using famous faces from various fields/periods of time. Using personally familiar faces further ensures that robust representations have been acquired naturally, across a number of viewing conditions, in the absence of potentially unnatural processing strategies applied with experimental familiarization of previously unfamiliar faces.

2. Materials and methods

2.1. Participants

All participants (normal/corrected vision) were personally familiar with the individuals depicted by the stimuli (undergraduate students from the faculty of Psychology with the same major subject of study, attending various courses together). Twenty-two individuals (16 females; mean age: 23 ± 1; four left-handed, three of which were female), participated in experiment 1, 16 of which (11 females; mean age: 23 ± 1; two left-handed) participated in experiment 2 (~2.5 months later; two participants were rejected due to insufficient performance (see analysis), resulting in $n = 14$, 10 female, four male; one left-hander per gender). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).

2.2. Stimuli

Full frontal color photographs of 26 students were processed using Adobe Photoshop 7.0. After cropping hair/external features, top and bottom parts were created by inserting a five pixel gap just above the top of the nostril. Each top part was then paired with two bottom parts of the same gender, resulting in 52 composite faces; two misaligned versions were created for each one by horizontally offsetting bottom parts until the tip of the nose was located beneath the center of the left or right pupil. Offsetting to both sides was done so that the task relevant *top* parts would not differ in position across hemifields, as bottom parts were always misaligned towards the fovea so that top parts were located in exactly the same position for mis/aligned trials. In experiment 1 we selected the composite faces created from 23 of the original 26 photographs, thereby using 46 of the total of 52 composite stimuli. Each stimulus was presented twice per condition, resulting in 184 trials in total. At a 60 cm viewing distance, the stimuli comprised approximately $4 \times 6^\circ$ of visual angle (72 pixel/in. resolution). For experiment 2, the full set of composite faces was used to maximize the number of trials available for analyses. Furthermore, given that this experiment required delayed matching, the stimuli were converted to grayscale. This was done to circumvent participants engaging in color-based matching, rather than matching of the identity of the top parts to be attended. Importantly, although experiment 2 could have been carried out using unfamiliar face stimuli, we used (the same) personally familiar faces as in experiment 1, to ensure that potentially diverging findings could not be attributed to changes in familiarity across experiments.

2.3. Procedure

Stimuli were presented on white background on a 17-in. PC monitor (60 Hz refresh rate; 1280 × 1024 pixel resolution) using E-prime 1.1. Participants were seated in a quiet, dimly lit room (viewing distance: 60 cm) and instructed to maintain central fixation; both experiments began with four randomly chosen practice trials (excluded from analysis).

2.3.1. Experiment 1

Participants identified top parts of briefly flashed composite stimuli by clearly pronouncing the first name into a microphone mounted on a tripod in front of them. On each trial a fixation cross was presented for 1000 ms, followed by a composite stimulus in a given hemifield for 200 ms (a presentation duration also used in other studies involving lateralized stimulus presentation, e.g., de Haan & van Kollenburg, 2005). Responses were recorded up to 5000 ms after the stimulus had disappeared; trials were separated by a 1000 ms ISI. Within each of the two blocks, stimuli appeared equally often within each visual field, with roughly the same number of mis/aligned trials per block. Stimuli presented within the left and right visual field were presented offset by 190 pixels left/right of the center of the screen (i.e. the borders of the laterally presented face stimuli were located 5° of visual angle from the screen center). Trials had been previously randomized and separated into blocks; stimuli were presented to participants in the same random order as the task required recording their performance on the identification task (errors included failure to respond, as well as erroneous identification). RTs were recorded via a SRBOX connected to the microphone and computer.

2.3.2. Experiment 2

Participants were instructed to judge (by button press) whether top parts of probe stimuli were different/identical to those of preceding target stimuli. On each trial a fixation cross was presented for 1000 ms, followed by a target presented centrally for 150 ms. After a 1200 ms blank, a probe stimulus appeared within a visual field for 150 ms (a presentation duration used by e.g., Leehey et al., 1978). Participants could respond up to 3500 ms after disappearance of the probe; trials were separated by a 1000 ms ISI. Targets and probes were either always both aligned or misaligned; in order to avoid visual field cueing, on misaligned trials, the bottom parts of targets and probes were offset at random either in the same or opposite directions (again, top parts were always presented in exactly the same location irrespective of alignment; see Fig. 1).

Participants completed two blocks differing only with respect to the order in which a given face pair was presented (i.e. targets in block 1 were probes in block 2; block order was randomly assigned). Each block contained 312 randomly presented trials, which were separated into 12 parts of equal length with interleaved pauses. Of these trials, 104 required a "different" response: targets and probes were random pairs of same sex composite faces with different tops and bottoms (52 misaligned, 26 presented per visual field). The 208 trials requiring a "same" response consisted of 104 catch trials which involved stimulus repetition (target = probe; 52 aligned, 26 per visual field) and 104 crucial trials, for which identical tops were paired with different bottoms. The latter were the trials of interest for analyses (208 in total); the remainder served to ensure sufficiently high performance.

2.4. Analyses

For both experiments, mean accuracy and correct RTs were computed individually per condition (for each subject trials with RTs > 3SDs of the average RT per condition were excluded). Additionally, further analyses were conducted on individual inverse efficiency scores (RT/Accuracy; Townsend & Ashby, 1978). This was done to consider potential speed-accuracy trade-offs and circumvent the possibility of effects being precluded due to individual differences in strategies (e.g., some participants showing effects for only one of the two measures). Repeated measures

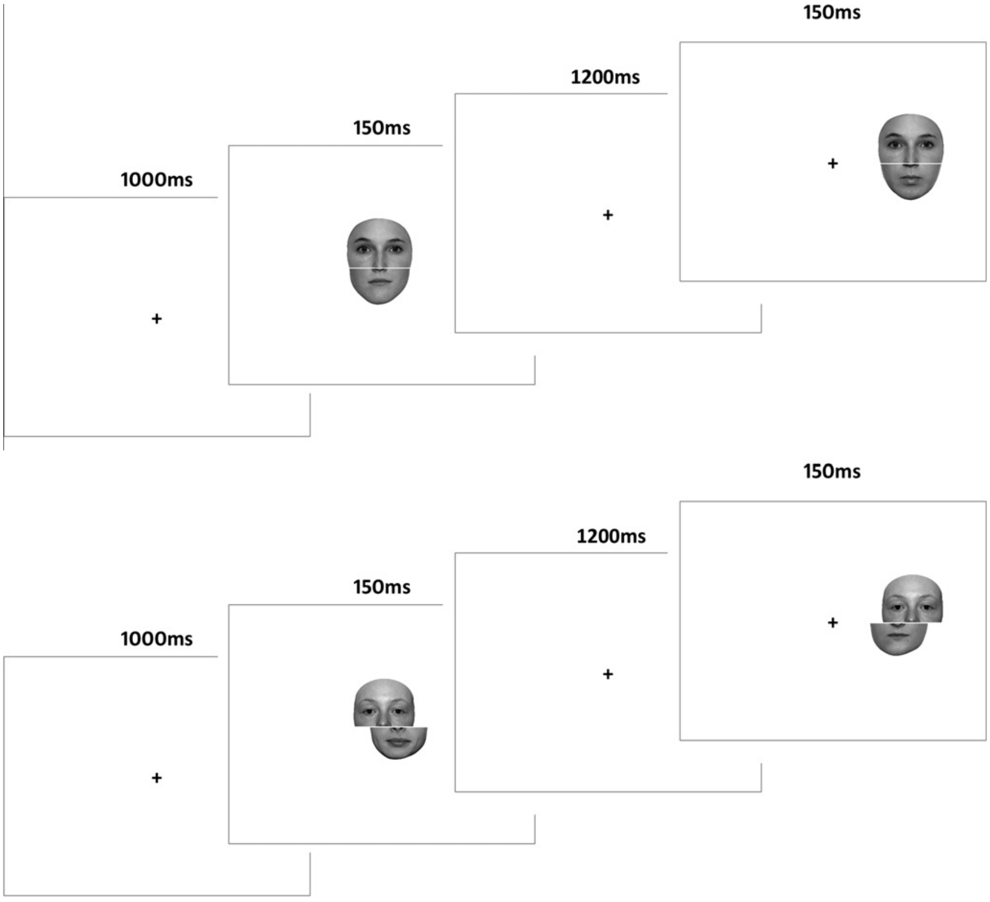


Fig. 1. Examples of trials presented in experiment 2. Shown here are two instances of "same" trials; top: aligned; bottom: misaligned, with bottoms offset in opposite directions.

ANOVAs with 2 within-subject factors (*visual field*, *alignment*) were conducted for all dependent measures; for both experiments Mauchley's test indicated no violations of sphericity. For experiment 2 (delayed matching) only participants who scored $\geqslant 75\%$ for the catch condition were considered (two participants—one male, both right-handed—were excluded); analyses were confined to crucial, i.e. "same" trials involving changes of bottom parts of consecutively presented targets/probes.

3. Results

Accuracy, RTs, and inverse efficiency scores (SDs) per condition and experiment are provided in Table 1; Fig. 2 demonstrates inverse efficiency scores for both experiments.

3.1. Experiment 1

For accuracy scores, there was a main effect of *visual field*, $F(1,21) = 9.38$, $p < .01$, given superior performance for stimuli presented within the right visual field, as well as a main effect of *alignment*, $F(1,21) = 10.67$, $p < .01$, due to higher accuracy for misaligned trials. There was no significant interaction between the two factors, $F(1,21) = 2.90$, $p = .10$. If anything, this trend was in the opposite direction as predicted: a non-significantly larger composite face effect for stimuli presented within the right visual field. For RTs, only a main effect of *alignment* emerged, $F(1,21) = 8.41$, $p < .01$, given longer RTs for aligned trials. Again no significant interaction was observed, $F(1,21) = .03$, *ns*. Regarding inverse efficiency, the results paralleled those obtained for accuracy, as only main effects of *visual field*, $F(1,21) = 5.54$, $p = .03$, and *alignment*, $F(1,21) = 8.72$, $p < .01$, emerged, with no significant interaction between the two factors, $F(1,21) = .27$, *ns*.

3.2. Experiment 2

Analyses of accuracy scores revealed no main effects (*alignment*: $F(1,13) = .72$, *ns*; *visual field*: $F(1,13) = .41$, *ns*), but a non-significant trend for an interaction between the two factors, $F(1,13) = 4.36$, $p = .057$. For RTs, the results paralleled those obtained for accuracy scores: no main effects (*alignment*: $F(1,13) = 2.81$, $p = .12$; *visual field*: $F(1,13) = .02$, *ns*) and no significant interaction between the two factors, $F(1,13) = 2.87$, $p = .11$. With respect to inverse efficiency, there were no main effects of *alignment*, $F(1,13) = 2.28$, $p = .16$, or *visual field*, $F(1,13) = .70$, *ns*. However, there was a significant interaction between *alignment* and *visual field*, $F(1,13) = 4.70$, $p < .05$.[1] Posthoc comparisons (adjusted for multiple comparisons) indicate that this interaction arose given superior performance for misaligned as compared to aligned trials for left, but not right visual field presentation ($t(1,13) = 2.44$, $p = .015$, and $t(1,13) = .23$, *ns*).

3.3. Analyses of right-handed subjects only

To ensure that the observed effects were not driven by left-handed subjects included in the tested sample(s), additional analyses were performed on only the right-handed subjects' IE scores. For experiment 1 ($n = 18$, 5 male), the repeated measures ANOVA yielded a main effect of *alignment*, $F(1,17) = 5.26$, $p < .05$, along with a trend for a main effect of *visual field*, $F(1,17) = 3.12$, $p = .095$, and no significant interaction, $F(1,17) = .39$, *ns*. For experiment 2, the ANOVA ($n = 12$, 3 male) yielded no main effect of *visual* field, $F(1,11) = .50$, *ns*, a non-significant trend for an effect of *alignment* ($F(1,11) = 3.58$, $p = .085$), and a trend for an interaction between the two factors, $F(1,11) = 4.30$, $p = .06$. Percentile bootstrap analyses were carried out to further investigate these differences (as the absence of main effects and interaction did not allow for posthoc comparisons). We sampled subjects with replacement, averaging the alignment-related differences in IE scores per visual field across participants. This process was repeated 999 times, leading to a distribution of bootstrapped estimates of the mean difference between the alignment related increases in IE per visual field, averaged across subjects. The 95% confidence interval ($\alpha = .05$) of the difference between the two sample means (i.e. the differences in IE due to alignment within each visual field separately) did not include zero, indicating a significant difference between the effect of alignment per visual field (CI: [9.21; 106.57]), i.e. a significant interaction between both factors. Considering the two sample means (effect of alignment per visual field) individually revealed that alignment was associated with a significant increase in IE scores for stimuli presented in the left visual field (CI: [16.64; 106.57]), but not those presented in the right visual field (CI: [−47.50; 38.93]).

Table 1

Accuracy scores (% correct), RTs and inverse efficiency (SD) for participants across conditions for (a) experiment 1 and (b) experiment 2. LVF: left visual field; RVF: right visual field.

	Accuracy (%)		RTs (ms)		Inverse efficiency	
	LVF	RVF	LVF	RVF	LVF	RVF
a. Experiment 1						
Aligned	64.2	66.7	1159	1135	1958	1804
	(14.9)	(13.0)	(252)	(266)	(813)	(670)
Misaligned	65.0	71.0	1076	1059	1806	1609
	(16.6)	(15.0)	(252)	(245)	(761)	(662)
b. Experiment 2						
Aligned	82.3	85.6	778	770	957	912
	(8.8)	(7.9)	(135)	(133)	(204)	(212)
Misaligned	85.6	84.8	755	765	896	917
	(8.7)	(8.0)	(128)	(132)	(209)	(218)

4. Discussion

Two experiments were conducted to investigate hemispheric lateralization of holistic processing by determining the extent to which the composite face effect (Young et al., 1987) varies as a function of visual field presentation, and thus hemispheric stimulation. Given previous findings of a right hemisphere dominance in face processing, we hypothesized that the composite face effect would be larger in magnitude for stimuli presented in the left visual field.

In keeping with the task employed in the original report of the composite face effect (Young et al., 1987), our initial experiment required naming top parts of composite stimuli, created from personally familiar individuals. With lateralized stimulus presentation we observed a clear composite face effect, a finding which, to our knowledge, has not been reported before. However, contrary to our hypothesis, we found that this effect did not differ as a function of visual field presentation, thereby precluding the conclusion that it varies as a function of hemispheric input.

We reasoned that this unexpected lack of difference in the magnitude of the composite face effect across visual field

---

[1] Note that using the inverse efficiency (IE) scores measure has been recently criticized (Bruyer and Brysbaert (2011), as this variable would generally increase variance, decreasing sensitivity as compared to when using RTs or accuracy rates alone. However, here, this is not the case: given the presence of a difference in the predicted direction for both accuracy rates and correct RTs that just fails to reach significance for each measure considered in isolation, the use of IE scores rather *increases* sensitivity. Indeed, in the composite face paradigm, the predicted difference may be observed for RTs for some subjects, and accuracy rates for other subjects. Combining the two measures thus allows the full effect to be explored. Irrespectively, as recommended by Bruyer and Brysbaert (2011), our analyses are not limited to IE scores, and one should note that in the second experiment the difference is in the predicted direction both for both accuracy rates and RTs.

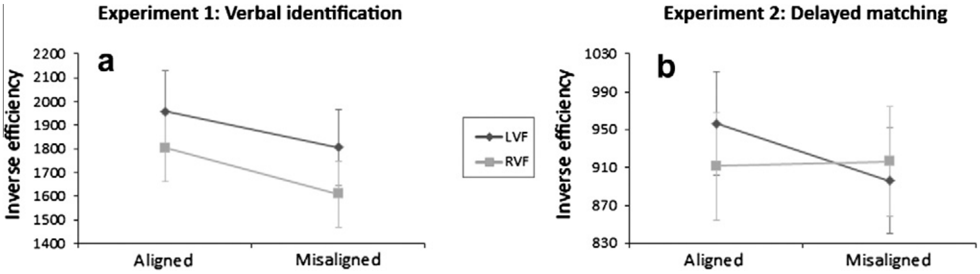


Fig. 2. Inverse efficiency scores (as computed by RT over accuracy) obtained for each condition in (a) experiment 1 and (b) experiment 2 (bars represent standard errors).

stimulation might be attributable to the nature of the task (verbal identification). Indeed, previous studies reporting greater holistic processing within the right as compared to left hemisphere involved tasks that were free of a verbal component (e.g., Jacques & Rossion, 2009; Schiltz & Rossion, 2006). Moreover, irrespective of the effect of alignment that was independent of visual field, there was a general advantage for stimuli presented in the right visual field. In experiment 2, using the same composite face stimuli and testing a sample of the participants who participated in the initial experiment, we investigated whether visual field dependent differences in holistic processing would arise provided a task devoid of explicit verbal requirements was used. In the realm of a delayed matching paradigm with laterally presented stimuli (names of the parts to be matched were task-irrelevant) we found a composite face effect for left, but not right visual field probe presentation.

Thus, comparing the results of experiments 1 and 2 reveals two major differences. In keeping with early neuropsychological findings (Levy et al., 1972), in experiment 1 we found superior performance for naming of composite faces presented in the right visual field (which was not the case in experiment 2). Additionally, in experiment 1 we found that the detrimental effect of alignment, i.e. the composite face effect, did not vary as a function of visual field presentation (Fig. 2a). In experiment 2, in the context of a complex visual face matching task without verbal component, a different pattern of performance was observed (Fig. 2b). Here, we found that alignment lead to inferior performance only for probes presented in the left visual field.

We would like to suggest that the present findings can be accounted for in terms of task-dependent, differential processing. While in delayed matching tasks, the demand is purely of a perceptual nature, verbal identification necessitates activation of the robust representations of individual, highly familiar identities to be named. The finding of a composite face effect for stimuli presented in the left but not right visual field in experiment 2 is in line with the view that the right hemisphere plays a dominant role in the perceptual aspects of face processing, notably in integrating individual facial features in healthy observers (see e.g., Hillger & Koenig, 1991; Schiltz & Rossion, 2006). Thus, the integrative capacities of both hemispheres are distinguishable provided task demands which emphasize perceptual processing. This is, however, not the case when task demands require semantic processing, as demonstrated by the finding of a visual field independent composite face effect in experiment 1. That is, hemispheric differences in the initial representation of information may be superseded if task demands require more than merely perceptual processing. This was the case in experiment 1, where holistic processing was measured in the context of a naming task. Although we attribute the right visual field advantage for naming composite face stimuli observed in the first experiment to the left hemisphere's dominance given verbal task demands, it remains to be determined whether this reflects name retrieval or production,[2] or reflects representational differences between both hemispheres (i.e. image-specific as opposed to abstract for the right and left hemisphere, respectively; e.g., Marsolek, 1995).

We believe that—although the faces to be matched in experiment 2 were personally familiar and had been previously presented—the results reflect hemispheric differences in perceptual processing and not the use of semantic cues (as pointed out by an anonymous reviewer). One could argue that the use of unfamiliar faces in experiment 2 would have been preferable to avoid or limit the potential use of semantic information. However, had we done so and found the same pattern of results across experiments as we reported here, one could have been inclined to simply attribute the divergent findings to the presence of underlying face representations, especially given findings that suggest that unfamiliar and familiar faces' identity is processed in a qualitatively different fashion (e.g., Megreya & Burton, 2006; Mohr, Landgrebe, & Schweinberger, 2002). Furthermore, the findings of experiment 2 are in line with previous observations of relatively larger right hemisphere involvement in holistic processing in studies that used unfamiliar face stimuli (e.g., Hillger & Koenig, 1991; Jacques & Rossion, 2009; Leehey et al., 1978; Rossion et al., 2000; Schiltz & Rossion, 2006; Sergent, 1984, 1988). Finally, we do not see why semantic processing as potentially at play in experiment 2 should have resulted in the absence of a composite effect for left visual field presentation, when it was found when the task (and stimuli) explicitly demanded the use of semantic information.

On a different note, the finding of a composite effect for stimuli presented in the left but not right visual field as observed in experiment 2 goes against the view that the effect measured in the composite paradigm as applied here has a decisional locus, as others have argued (Richler, Gauthier, Wenger, & Palmeri, 2008). Indeed, hemispheric differences in the composite face effect should not be observed if it resulted from a general decisional bias (see also Kuefner, Jacques, Prieto, & Rossion, 2010, for evidence of early

---

[2] This line of reasoning is consistent with previous findings and interpretations. Sergent (1985) reported an advantage for face recognition (academic vs. non-academic membership categorization), but no visual field difference during gender categorization, which renders two alternative interpretations. On the one hand, the task-dependent patterns of lateralization may be related to the task inherent visual demands, with recognition requiring more elaborate processing than gender categorization. On the other hand, verbal processing intrinsically engaged in while accessing individuals' names or semantic information required for membership categorization may have given rise to the observed visual field advantage for this task (Sergent, 1985; Sergent et al., 1992). Naturally, the present results require further corroboration. The nature of stimuli used here inevitably limited the population from which the samples were drawn. Future investigations would optimally involve larger populations to enable investigations of the effects of e.g. gender and handedness. Along the same line, additional experiments (which we were unable to conduct given participants' limited availability) could include e.g. a name-identity matching task involving a motor response to further investigate the nature of the right visual field advantage found on experiment 1.

composite face effects in event-related potentials without any decisional component).

In keeping with the assumption of different characteristics of inter-hemispheric transfer depending on task requirements (Moscovitch, 1986; Sergent, 1985), which is corroborated by studies indicating right hemisphere superiority when delayed matching of face stimuli is required (e.g., Schweinberger & Sommer, 1991), we believe that the change in task type can be held responsible for the changes in performance profile observed here. The task differences between experiments 1 and 2 inevitably necessitated some procedural differences. While in experiment 1 a single stimulus was presented in a given visual field, in experiment 2 the laterally presented probes requiring a decision were preceded by centrally presented target stimuli, as required for the delayed matching task employed. The lack of a general RVF advantage in experiment 2 (as found for experiment 1) might be related to the applied dual presentation mode. However, this factor does not explain the more theoretically important interaction between visual field and alignment. In experiment 2 we further used a relatively decreased exposure duration, as compared to experiment 1. If anything, this should have further minimized unwanted saccades towards the laterally presented probes, which given the fully randomized design, however, cannot account for the present findings. Lastly, in experiment 2 grayscaled stimuli were used. This was done intentionally to minimize the possibility of participants focusing exclusively on color information, especially given the high demands posed due to the extremely short durations of the extrafoveally presented probes. Had we anticipated the outcome of experiment 1, which motivated the subsequent experiment, we would have used grayscaled stimuli in the initial experiment as well. Note also, that due to the specific population sampled here (personally familiar individuals who were senior year university students), unfortunately, we were unable to call back participants or simply test additional ones. However, we do not see any theoretical reason to assume that the use of grayscaled, instead of color, stimuli would have lead to the effects observed here.

Naturally, lateralized stimulation does not preclude information transfer in the normal brain. Therefore, the final output as observed behaviorally could be based on holistic processing or representations that are bi- or contra-lateral in nature. Theoretically, assessing the individual contribution or holistic processing capacities of each hemisphere *in isolation* would only be possible by testing split-brain and/or congenital acallosal patients, although the extent to which heir face processing skills can be directly compared to those of healthy individuals remains questionable.

To summarize, the present experiments add to a growing body of evidence that suggests that holistic processing in early perceptual processing stages is more pronounced in the right hemisphere. Furthermore, the extent to which holistic processing manifests itself as being lateralized depends on the specific task demands in a given experimental setting.

Acknowledgments

We thank Aurelie Dewulf for assistance during stimulus preparation, all participants for their cooperation and three anonymous reviewers for their helpful and constructive comments. MR and BR are supported by the Belgian National Foundation for Scientific Research (FNRS).

References

Barton, J. J. S., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology, 58*, 71–78.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*, 551–565.

Bouvier, S. E., & Engel, S. A. (2006). Behavioral deficits and cortical damage loci in cerebral achromatopsia. *Cerebral Cortex, 2*, 183–191.

Bruyer, R., & Brysbaert, M. (2011). Combining speed and accuracy in cognitive psychology: Is the Inverse Efficiency Score (IES) a better dependent variable than the mean Reaction Time (RT) and the Percentage of Errors (PE)? *Psychologica Belgica, 51*, 5–13.

Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: Evidence from an extensive case study of acquired prosopagnosia. *Neuropsychologia, 48*, 4057–4092.

Carbon, C. C. (2008). Famous faces as icons. The illusion of being an expert in the recognition of famous faces. *Perception, 37*, 801–806.

de Haan, E. H., & van Kollenburg, E. N. (2005). Lateralised processing of the internal and the external facial features of personally familiar and unfamiliar faces: A visual half-field study. *Cognitive Processing, 6*, 189–195.

Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R. S., et al. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature, 389*, 596–599.

Ellis, H. D., & Shepherd, J. W. (1975). Recognition of upright and inverted faces presented in the left and right visual fields. *Cortex, 11*, 3–7.

Hécaen, H., & Anguelergues, R. (1962). Agnosia for faces (prosopagnosia). *Archives of Neurology, 7*, 92–100.

Hellige, J. B., Jonsson, J. E., & Michimata, C. (1988). Processing from LVF, RVF and BILATERAL presentations: Examinations of metacontrol and interhemispheric interaction. *Brain and Cognition, 7*, 39–53.

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience, 3*, 42–58.

Hole, G. J. (1994). Configurational factors in the perception of unfamiliar faces. *Perception, 23*, 65–74.

Jacques, C., Rossion, B. (2009). The initial representation of individual faces in the right occipito-temporal cortex is holistic: Electrophysiological evidence from the composite face illusion. *Journal of Vision 9(6)*, 1–16. <http://journalofvision.org/9/6/8/>. doi: 10.1167/9.6.8.

Kuefner, D., Jacques, C., Prieto, E. A., & Rossion, B. (2010). Electrophysiological correlates of the composite face illusion: Disentangling perceptual and decisional components of holistic face processing in the human brain. *Brain and Cognition, 74*, 225–238.

Landis, T., Regard, M., Bliestle, A., & Kleihues, P. (1988). Prosopagnosia and agnosia for noncanonical views. An autopsied case. *Brain, 111*, 1287–1297.

Leehey, S., Carey, S., Diamond, R., & Cahn, A. (1978). Upright and inverted faces: The right hemisphere knows the difference. *Cortex, 14*, 411–419.

Levine, D. N., & Calvanio, R. (1989). Prosopagnosia, a defect in visual configural processing. *Brain and Cognition, 10*, 149–170.

Levy, J., Trevarthen, C., & Sperry, R. W. (1972). Reception of bilateral chimeric figures following hemispheric deconnexion. *Brain, 95*, 61–78.

Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 375–386.

Maurer, D., Grand, R. L., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6*, 255–260.

McKone, E., Martini, P., & Nakayama, K. (2003). Isolating holistic processing in faces (and perhaps objects). In M. Peterson & G. Rhodes (Eds.), *Perception of faces, objects, and scenes: Analytic and holistic processes* (pp. 92–119). Oxford, UK: Oxford University Press.

Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. *Memory & Cognition, 34*, 865–876.

Michel, F., Poncet, M., & Signoret, J. L. (1989). Are the lesions responsible for prosopagnosia always bilateral? *Revue Neurologique, 145*, 764–770.

Mohr, B., Landgrebe, A., & Schweinberger, S. R. (2002). Interhemispheric cooperation for familiar but not unfamiliar face processing. *Neuropsychologia, 40*, 1841–1848.

Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology, 11*, 219–226.

Moscovitch, M. (1986). Afferent and efferent models of visual perceptual asymmetries: Theoretical and empirical implications. *Neuropsychologia, 24*, 91–114.

Newcombe, F. (1974). Selective deficits after focal cerebral injury. In S. J. Dimond & J. G. Beaumont (Eds.), *Hemisphere function in the human brain* (pp. 311–334). New York: Halsted Press.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9*, 97–113.

Parkin, A. J., & Williamson, P. (1987). Cerebral lateralisation at different stages of facial processing. *Cortex, 23*, 99–110.

Peirce, J. W., Leigh, A. E., & Kendrick, K. M. (2000). Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia, 38*, 475–483.

Ramon, M., Busigny, T., & Rossion, B. (2010). Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. *Neuropsychologia, 48*, 933–944.

Ramon, M., & Rossion, B. (2010). Impaired processing of relative distances between features and of the eye region in acquired prosopagnosia – two sides of the same holistic coin? *Cortex, 46*, 374–389.

Richler, J. J., Gauthier, I., Wenger, M. J., & Palmeri, T. J. (2008). Holistic processing of faces: Perceptual and decisional components. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 34*, 328–342.

Riddoch, M. J., Johnston, R. A., Bracewell, R. M., Boutsen, L., & Humphreys, G. W. (2008). Are faces special? A case of pure prosopagnosia. *Cognitive Neuropsychology, 25*, 3–26.

Rizzolatti, G., Umiltà, C., & Berlucchi, G. (1971). Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material. *Brain, 94*, 431–442.

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica, 128*, 274–289.

Rossion, B., Boremanse, A. (2008). Nonlinear relationship between holistic processing of individual faces and picture-plane rotation: Evidence from the face composite illusion. *Journal of Vision, 8(4)*, 1–13. <http://journalofvision.org/8/4/3/>. doi: 10.1167/8.4.3.

Rossion, B., Dricot, L., Devolder, A., Bodart, J. M., Crommelinck, M., De Gelder, B., et al. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 12*, 793–802.

Rossion, B., Dricot, L., Goebel, R., & Busigny, T. (2011). Holistic face categorization in higher order visual areas of the normal and prosopagnosic brain: Toward a non-hierarchical view of face perception. *Frontiers in Human Neuroscience, 10*(4), 225.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *Neuroimage, 32*, 1385–1394.

Schweinberger, S. R., & Sommer, W. (1991). Contributions of stimulus encoding and memory search to right hemisphere superiority in face recognition: Behavioural and electrophysiological evidence. *Neuropsychologia, 29*, 389–413.

Sergent, J. (1982). About face: Left-hemisphere involvement in processing physiognomies. *Journal of Experimental Psychology: Human Perception and Performance, 8*, 1–14.

Sergent, J. (1984). Configural processing of faces in the left and the right cerebral hemispheres. *Journal of Experimental Psychology: Human Perception and Performance, 10*, 554–572.

Sergent, J. (1985). Influence of task and input factors on hemispheric involvement in face processing. *Journal of Experimental Psychology: Human Perception and Performance, 11*, 846–861.

Sergent, J. (1988). Face perception and the right hemisphere. In L. Weisskrantz (Ed.), *Thought without language* (pp. 108–131). Oxford: Clarendon Press.

Sergent, J., & Bindra, D. (1981). Differential hemispheric processing of faces: Methodological considerations and reinterpretation. *Psychological Bulletin, 89*, 541–554.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain, 115*, 15–36.

Sergent, J., & Signoret, J. L. (1992). Varieties of functional deficits in prosopagnosia. *Cerebral Cortex, 2*, 375–388.

Sergent, J., & Villemure, J. G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain, 112*, 975–995.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology. A, Human experimental psychology, 46*, 225–245.

Townsend, J. T., & Ashby, F. G. (1978). Methods of modeling capacity in simple processing systems. In N. J. Castellan & F. Restle (Eds.), *Cognitive theory* (pp. 199–239). Hillsdale, NJ: Erlbaum.

Yin, R. (1969). Looking at upside down faces. *Journal of Experimental Psychology, 81*, 141–145.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception, 16*, 747–759.

Zangenehpour, S., & Chaudhuri, A. (2005). Patchy organization and asymmetric distribution of the neural correlates of face processing in monkey inferotemporal cortex. *Current Biology, 15*, 993–1005.