

Physiological Responses to Verbally Inaccessible Pictorial Information in the Left and Right Hemispheres

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The present research was partially conducted while Kenneth Hugdahl was on sabbatical leave to UCLA.

Abstract

We investigated the effects of very brief pictorial information on transfer between the cerebral hemispheres through recordings of skin conductance responses. The pictorial stimuli had been judged previously as "neutral", "positive", or "negative" by an independent group of subjects. The verbally-available stimuli (VA) were neutral whereas the very brief, verbally-unavailable stimuli (VU) were positive or negative. The VA and VU stimuli were presented simultaneously, either in the same visual half-field (intra-

hemispheric interference) or in the opposite visual half-field (inter-hemispheric interference). In a third condition, there were only VA stimuli in either visual field (no interference). We found that the right hemisphere was especially sensitive to negative VU presentations, both in the inter-and intra-hemispheric interference groups. The left hemisphere showed a corresponding sensitivity to positive interference, but only in the inter-hemispheric interference group. These findings confirm the hemispheric roles in mediating positive versus negative emotions and they show that in the interplay between hemispheric specialization and commissural transfer, left to right transfer can take place without linguistic cognition.

Introduction

In investigations of hemispheric functional asymmetries, explicit knowledge of both the stimuli and the responses are typically available to the subjects (see Hellige, 1993 for a recent review of perceptual asymmetries). Specific verbal output or non-verbal motor responses, such as pressing a button are normally required. However, only a partial view of hemispheric asymmetry is gleaned from studies where there is explicit awareness of both stimulus contents and response. Investigating functional asymmetry when there is no explicit awareness of these parameters has the potential of augmenting our knowledge of functional asymmetry in the intact brain (cf. Brody, 1987).

The incompleteness of our understanding of the organization of the mind and brain from purely explicit behavioral measures has been amply demonstrated in the past. For example, patients suffering from "blindsight" can discriminate among visual stimuli, yet they deny explicitly having seen them (Weiskrantz, 1986). The damage is often bilateral and in the primary visual areas in the occipital lobe. What these patients demonstrate is that other cortical or subcortical regions must be functionally intact despite failure of

explicit vision. In another example, Tranel and Damasio (1985) found that two prosopagnosic patients who could not explicitly recognize familiar people by their faces alone, nevertheless showed larger electrodermal responses to pictures of familiar faces. Their study demonstrated that knowledge for familiar faces was intact despite bilateral damage to the temporo-occipital regions, but that this knowledge was unavailable to the patients' conscious awareness. In normal subjects, Marcel (e.g., 1983) has shown the effects of very brief stimuli of which subjects have been unaware on a supraliminal lexical decision task. The subjects were obviously influenced by the contents of the subliminal stimuli. In a similar way, Öhman (1985) demonstrated that normal subjects showed enhanced skin conductance responses to subliminal presentations of angry faces, after they had the faces paired with electric shock in a classical conditioning procedure. Following-up on Öhman's findings, Johnsen and Hugdahl (1991, see also Hugdahl & Johnsen, 1993) showed that evidence of conditioned autonomic responses after subliminal presentations of facial expressions occurred only when the faces were presented to the right hemisphere.

It seems clear that unified perception and subsequent processing of a stimulus is achieved through the constant flow of information between the hemispheres via the forebrain commissures. The role of hemispheric specialization in this process is not completely known, with contradictory findings regarding right versus left hemisphere superiority for emotional processing (Davidson & Tomarken, 1989; Ley & Bryden, 1979). On the other hand, left hemisphere specialization for language is well established. Controlling the accessibility of a stimulus to verbal awareness should help determine if left to right hemisphere transfer can take place without linguistic cognition.

In the present study we investigated the effects of non-verbal information on intra- and inter-hemispheric processes through recordings of skin conductance responses (SCRs). Explicit knowledge of the transfer stimuli was manipulated by very brief presentations (30 msec) of pictorial stimuli, too brief for subjective awareness of the

pictures. Moreover, no explicit cognitive or behavioral tasks were required of the subject, they were merely told to look at a series of pictures projected for 180 msec durations in either the left or right visual half-fields (see McKeever, 1986 for an explanation of the visual half-field technique). This has not been studied previously. SCRs are sensitive indicators of changes in orienting and arousal (Raskin, 1972; Siddle, Stephenson & Spinks, 1983). The use of an autonomic indicator of hemisphere-specific arousal and interhemispheric transfer protects against confounding hemisphere stimulus-effects with response-effects, as when using a verbal response to assess hemisphere-specific effects of non-verbal stimuli.

The main purpose of the present study was to investigate the intra-and inter-hemispheric nature of knowledge not immediately available to conscious awareness. We have used "emotional" stimuli as a probe. It has previously been shown that affect and emotional activation are related to left and right hemisphere activation depending on the affective nature of the stimulus (e.g. Davidson & Tomarken, 1989). However, how positive and negative emotional stimuli interact with neutral stimuli has not been previously investigated in the hemispheres.

A final issue to be investigated in the present study was any differences in response magnitudes between the left and right hand skin conductance recording. SCRs are caused by increased hydration in the eccrine sweat glands in the digits. The eccrine sweat glands are exclusively innervated by the sympathetic branch of the autonomic nervous system. Previous research has shown that activation of the autonomic nervous system is differentially controlled from the left and right hemispheres (cf. Werntz, Bickford, Bloom, & Shannahoff-Khalsa, 1983). Moreover, electrodermal responses have frequently been used in efforts to reveal the asymmetric regulation of autonomic function by the hemispheres (see Hugdahl, 1984 for a review). For example, Lacroix and Comper (1979) showed smaller responses in the hand contralateral to the left hemisphere when verbal

stimuli were used, while smaller responses were observed in the hand contralateral to the right hemisphere to visuo-spatial stimuli.

Method

Subjects.

Thirty-three female subjects, recruited from the University of Bergen, participated in the study. The mean age was 20.6 years (range 19 - 23 years). All subjects were right-handed according to the Raczkowski, Kalat and Nebes (1974) handedness-questionnaire. Criterion for inclusion in the study was a preference for using the right hand on 11 out of 15 items on the questionnaire. In addition, the subjects had to show a minimum of .05 μ S skin conductance response to a 30 ms test trial slide.

Apparatus.

Skin conductance responses (SCR) from the left and the right hand were recorded digitally using PSYLAB[©] software equipped with two Contact Precision Instrument SC4 SCR couplers. Each of the couplers supplied a constant voltage of .6 V. Beckman 8 mm Ag/AgCl cup-electrodes filled with Unibase 0.05 molar NaCl electrolyte were used in the SCR recordings (Fowles et al., 1981).

The visual half-field (VHF) apparatus consisted of a 75 x 70 x 72 cm viewing chamber made out of plywood. A rubber-mask opening was placed int he anterior wall of the VHF-apparatus. The posterior wall consisted of a milk-glass screen on to which the slides were back-projected. The VHF-apparatus was placed in a sound attenuating chamber inside the laboratory. A 2 mm light emitting diode (LED) was placed in the centre of the milk-glass screen as focusing point.

The slides were presented from two Kodak Carousel S-AV 1030 slide projectors. Each projector had a Compur high-speed shutter mounted on the lens. Opening and closing time for the shutters was 5.5 ms. The shutters were controlled by two Hampton

electronics shutter-drivers. Timers activated by pre-recorded 1000 Hz tones, that were played from a stereo cassette recorder, controlled the duration of the slide presentations.

Stimuli.

The experimental stimuli consisted of 10 positive, 10 negative and 20 neutral pictures. They were all familiar to people in Western cultures and had previously been rated either as "positive", "neutral", or "negative" by a group of 23 right-handed (11 males, 12 females) undergraduate students in psychology at UCLA (see below). The stimuli consisted of simple black and white familiar line drawings of common objects, simple situations, and faces taken from several sources: Peabody Picture Vocabulary Test, Atlas of Human Expression, and Peabody Individual Achievement Test. Examples of the types of stimuli used in the experiment are seen in Figure 1.

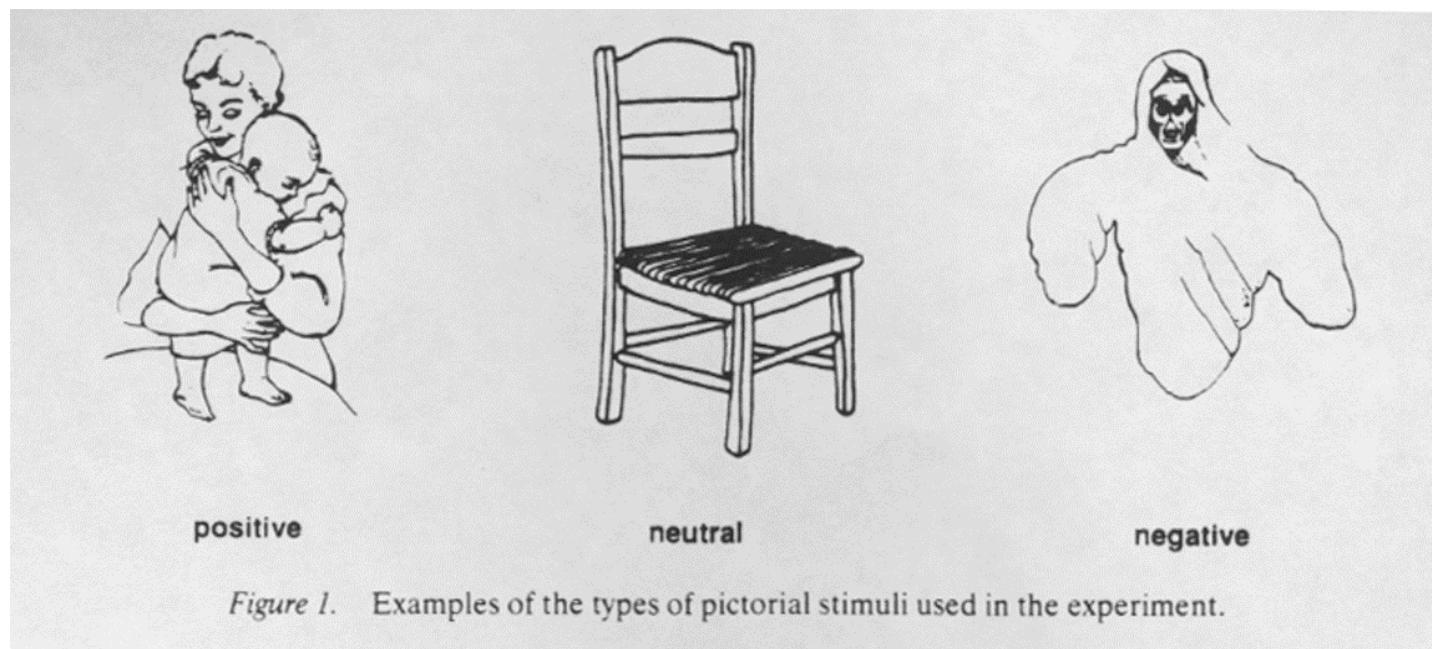


Figure 1. Examples of the types of pictorial stimuli used in the experiment.

The ratings of the pictures as positive, neutral, or negative was performed by subjects who saw 96 pictures one at a time as transparent overheads. These subjects were

instructed to spontaneously rate each of the pictures as either "positive" = a rating of 1, "neutral" = a rating of 2, or "negative" = a rating of 3, immediately after each picture was shown on the overhead projector. The subjects were not allowed to talk to each other during the ratings. Importantly, there were no sex differences in the responses. For the experimental trials, ten pictures which received a mean rating score in the range of 1.0 - 1.2 were chosen for the "positive" stimuli. Ten pictures with a mean rating score in the range of 3.0 - 3.0 were used as the "negative" stimuli, and 20 pictures with mean rating scores in the range of 2.0 - 2.2 were used as the "neutral" stimuli.

In the interference experiment, the projected size of the slides was 9 x 12 cm on the milk-glass screen. The visual angle from the LED mid-point to the nearest lateral edge of each picture during the VHF presentation was 2.29°, whereas the centre of the picture subtended 5.71° of visual angle. In the interhemispheric condition (see below), the emotional slide was presented immediately above the neutral slide, with the same lateral eccentricity from the fixation mid-point.

Design.

The study consisted of three groups. One group was presented with a neutral picture, in only one VHF, and simultaneously either a positive or negative picture in the opposite VHF. Both pictures were presented in a fixed location, specified above. This group was called the Interhemispheric interference group (InterHem).

A second group was shown the same neutral stimuli as the InterHem group, but they had both the emotional stimuli and the neutral stimuli simultaneously presented in the same VHF. This group was called the Intrahemispheric interference group (IntraHem). For the IntraHem group, the emotional slide appeared immediately above the neutral one.

A third group was presented only with the neutral slides. They were exposed randomly in oneVHF at a time. This was called the No Interference group (NoInt).

For each group, there were two Hemisphere conditions (left versus right VHF), and two Emotional valence conditions (positive versus negative emotional valence). Finally, a Trials-factor, and skin conductance recording sites, Hands (left versus right hand fingers) were added to the overall design of the experiment. Which VHF the neutral and emotional stimuli was presented to was randomized across trials, however, with the restriction that an equal number of trials appeared in the left and right half-fields.

Procedure

The subjects were randomly assigned to one of the three groups, and were placed inside the sound attenuating chamber. They were informed that they were to watch slides with different pictorial content. The skin conductance-sites were cleaned with distilled water and the electrodes were attached to the median phalanx of the second and third fingers of the right and left hand. The electrodes were fastened by means of adhesive collars. The subjects were instructed to focus on the LED that was going to be lit up on the screen 1 sec before the slides were presented and continued to be on during the slide presentation and until 1 sec after slide offset.

All subjects were presented with one 30 ms test-trial with similar contents with regard to the respective experimental condition and group. They were, furthermore, asked to try to identify the content of each slide. No subjects in the two interference groups identified both stimuli correctly. Only the 180 ms pictures were identified. Thus, the information in the 30 ms trials was verbally unavailable to the subjects. Those subjects who, at the end of the testing session, were asked to describe the two pictures, denied having seen two pictures on any given trial. The order of presentation of emotional valence and VHF was randomized across trials. The neutral slides were presented for 180 ms, and the emotional slides were presented for 30 ms. The brief 30 ms presentation was too quick for correct identification of the stimuli. The exposure onset of the neutral and emotional stimulus occurred at exactly the same time, projected simultaneously from two different slide-projectors and at the same location on the screen.

There were 20 trials in each group, with 10 positive and 10 negative trials in the two interference groups, and 20 neutral trials in the NoInterference group. The intertrial interval varied randomly between 10 and 20 sec in steps of 5 sec. The subjects filled out the handedness questionnaire and were debriefed regarding the purpose of the study before they left the laboratory.

Scoring of SCRs (skin conductance responses).

The SCRs were scored in the interval 1 to 5 sec after stimulus onset on each trial. All SCRs were based on accumulated response amplitudes, and the SCRs-scores were square-root transformed in order to obtain a normal distribution. Accumulated response amplitudes is the sum of all response amplitudes that occurred in the scoring interval, and that exceeded .05 μ S. That is, all phasic response amplitudes exceeding .05 μ S in the scoring interval were summed to yield an "accumulated amplitude". The data are also plotted as the average across trials.

Results

Mean SCR-magnitudes for the three interference groups, split for the positive and negative emotional stimulus valence condition, and left and right hemisphere presentation, are seen in Figure 2.

The results of the ANOVA, based on the design described above, showed a significant main-effect of emotional interference, with overall larger responses to the negative emotional interference condition compared to the positive condition, $F(1,30) = 6.705$, $MSerror = .114$, $p = .015$. The two-way interaction of Hemisphere x Emotional valence was also significant, $F(1,30) = 9.434$, $MSerror = .095$, $p = .005$. The interaction was followed-up with Tukey's HSD-test for multiple comparisons between means (Kirk, 1968). The HSD-test revealed larger responses from the right hemisphere during the negative emotional interference condition compared to the positive condition, while no significant differences were seen for left hemisphere trials. The two-way interaction is shown graphically in Figure 3.

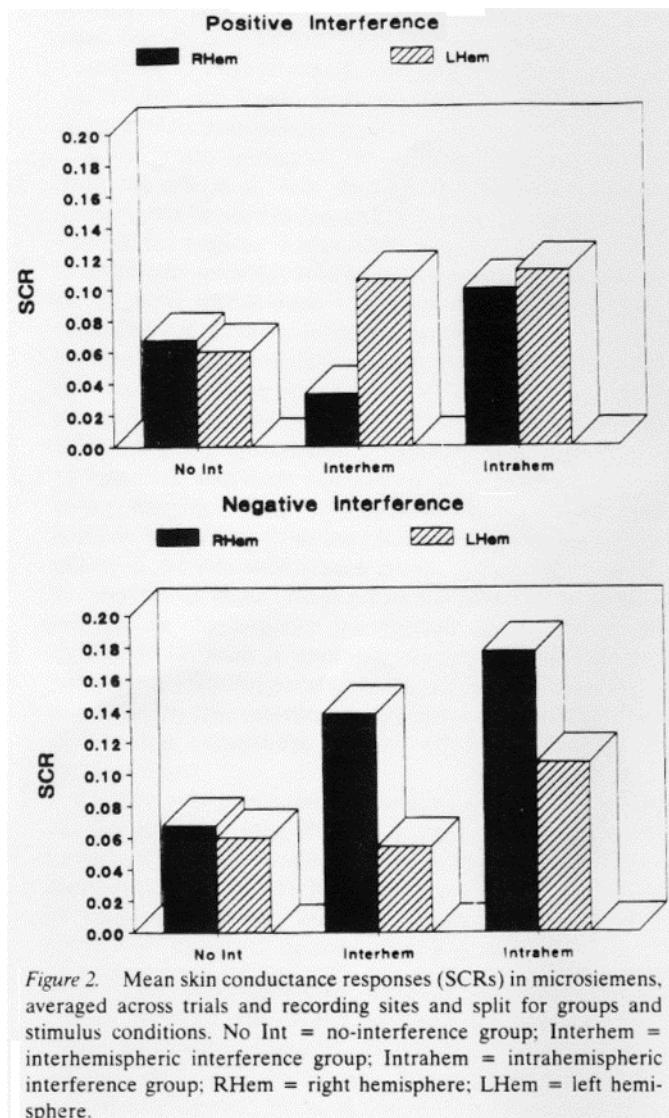


Figure 2. Mean skin conductance responses (SCRs) in microsiemens, averaged across trials and recording sites and split for groups and stimulus conditions. No Int = no-interference group; Interhem = interhemispheric interference group; Intrahem = intrahemispheric interference group; RHem = right hemisphere; LHem = left hemisphere.

The three-way interaction of Groups x Hemisphere x Emotional valence was also significant, $F(2, 30) = 4.611$, MSerror = .008, $p = .018$. This is shown in Figure 1. The significant three-way interaction was followed-up with Tukey's HSD-test which showed that it, in essence, was due to larger right than left hemisphere responses for both inter- and intrahemispheric interference on negative emotional trials, while there were larger left than right hemisphere responses on positive emotional trials only in the interhemispheric group (see Figure 2). Moreover, there were no differences between negative and positive trials for the NoInterference condition. There was also a

tendency towards larger responses to the negative stimuli presented to the right hemisphere for the Intrahemispheric condition (all $p < .05$).

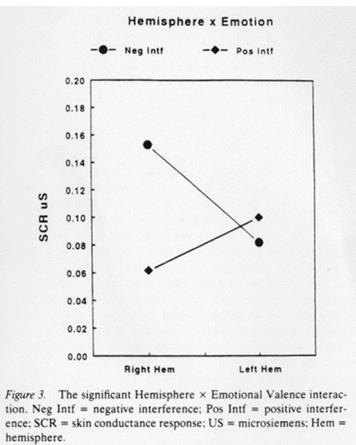


Figure 3. The significant Hemisphere \times Emotional Valence interaction. Neg Intf = negative interference; Pos Intf = positive interference; SCR = skin conductance response; US = microsiemens; Hem = hemisphere.

Finally, The three-way interaction of Hemisphere \times Hands \times Emotional valence was significant, $F(1,30) = 4.873$, MSerror = .008, $p = .035$. Looking specifically at the differences in response magnitudes between the left and right hand recordings, the interaction showed that responses were of equal magnitude from the left and right hands when the stimuli were presented to the left hemisphere. However, for right hemisphere stimulus presentations, left hand responses were larger on trials with negative emotional interference (Tukey's HSD, all p 's $< .05$). The mean SCRs for the left and right hands are presented in Table 1.

Table 1
Mean SCR Amplitudes Across Trials. Separated for Right- and Left-Hand Recordings

| SCR site | Right hemisphere | | Left hemisphere | |
|------------|------------------|----------|-----------------|----------|
| | Negative | Positive | Negative | Positive |
| Right hand | 0.133 | 0.063 | 0.099 | 0.087 |
| Left hand | 0.132 | 0.061 | 0.065 | 0.083 |

Note. SCR = skin conductance response.

There was a significant main-effect of trials, $F(9, 270) = 3.356$, MSerror = .067, $p = .006$. The trials-effect was due to larger responses on the first trial as compared to all later trials

(Tukey's HSD post-hoc test, $p < .05$). Moreover, there was a borderline significant interaction of Hemisphere x Emotion x Trials, $F(9, 270) = 1.820$, $MSerror = .062$, $p = .064$. Following-up the interaction with specific contrasts, using Tukey's LSD-test showed response decrement from the first to the two last trials in all three groups (all p' s $< .04$). The increase in SC response-magnitudes in the right hemisphere for negative interference was most pronounced during the initial trials, with virtually no difference between the groups on the last trials. Thus, habituation was demonstrated in all three groups, and particularly for right hemisphere presentations during negative interference.

Discussion

To summarize the major findings, the right hemisphere was especially sensitive to negative emotional brief presentations, both in the inter- and intra-hemispheric interference groups. The left hemisphere showed a corresponding sensitivity for positive interference but only in the inter-hemispheric interference group. Thus, a clear asymmetry in how a perceived but consciously-unavailable emotional stimulus has an effect on autonomic responding was demonstrated.

These findings shed light on the interplay between hemispheric specialization and interhemispheric communication that could not have been determined from behavioral measurements alone nor from explicit responses to explicit stimuli. They show that perceived stimuli have a selective effect on the specialized hemisphere, even when the information is initially perceived in the unspecialized hemisphere. A "master control switch" appears to relegate stimulus processing to the appropriate (specialized) hemisphere, which includes shuttling of information across the forebrain commissures. Moreover, we have learned through the control over the accessibility of a stimulus to verbal awareness (30 msec presentations) that left to right hemisphere transfer can take place without linguistic cognition. The use of stimuli with emotional valence has thus

illuminated one aspect of the interplay between hemispheric specialization and callosal transfer.

A consistent finding in the present study was the more profound effects of inter- as compared to intra-hemispheric interference. As can be seen in Figure 2, there was an almost complete reversal for negative versus positive interference in the interhemispheric group; with larger right hemisphere responses on negative interference trials, and larger left hemisphere responses on positive interference trials. However, in the intrahemispheric group, the only significant hemisphere difference was for negative interference. At the same time, with only the present set of data and the current state of knowledge on left hemisphere information processing, it is difficult to say with certainty why there was no increase in SCRs for ipsilateral presentations of neutral and positive stimuli.

Comparing the two interference groups to the no-interference "control"-group (see Figure 2), reveals that the addition of the very brief interference stimulus had different effects in the two interference-groups depending on whether the interfering stimulus was positive or negative in emotional valence. In the negative interference-group, there was a significant increase in response-magnitudes only for right hemisphere stimulus presentations, while the opposite was true in the positive interference-group, i.e. largest increase in response-magnitudes for left hemisphere stimulus presentations.

The decreasing response-magnitudes across trials, or stimulus presentations (Figures 2 and 3), is probably best interpreted as habituation of the autonomic orienting response (OR) (cf. Siddle, 1991). Habituation occurs as a consequence of stimulus repetition (Sokolov, 1963), where an incoming stimulus is "matched" against a stored memory template. The template is gradually built up as a function of stimulus repetitions, and habituation occurs when there is a perfect "match" between the stored template in memory and the incoming sensory stimulus. Habituation of autonomic responses, like SCRs, requires the allocation of processing resources (Dawson, Filion, & Schell, 1989; Ohman, 1979), possibly related to activation of fronto-parietal areas in the brain. The habituation-

effect in the present study indicates that the stimuli were actively processed in the brain, despite not being consciously acknowledged by the subject. This is an important observation since it links the present findings regarding unconscious events to existing theories regarding consciously perceived events, like the elicitation and habituation of the autonomic orienting response. Thus, there are similarities in processing mode between unconsciously and consciously perceived sensory events.

The significant interaction with SCR recording sites showed larger responses from the left hand to right hemisphere negative interference. This result may be interpreted within the conceptual framework of a contralateral inhibitory circuitry linking cortical to peripheral autonomic activation (Lacroix & Comper, 1979). Some authors, e.g. Checetto and Saper (1990) have suggested that the medial prefrontal cortex, including the infralimbic parts, may act as an autonomic motor cortex. From animal studies it is known that skin conductance responses are controlled from two different cortical systems (see Boucsein, 1992). One system is ipsilateral, including the limbic structures and the hypothalamus. Another system is contralateral, including the prefrontal cortex and the basal ganglia. From the present findings of a contralateral SCR- effect, it could perhaps be argued that right hemisphere prefrontal areas are particularly involved in control of the electrodermal system.

The present results extend the view on hemispheric specialization for affect proposed by Davidson based on EEG recordings of cortical activity (e.g. 1984; Davidson, Ekman, Saron, et al., 1990) to also have peripheral consequences. That is, eliciting right and left hemisphere activation results in increased sympathetic outflow to the digits of the hands, even when the subject is not consciously aware of the particular cortical affective stimulus presentation. Thus, the present findings contribute to a better understanding of the dynamic and intricate interplay between central and peripheral physiological events, an interplay that to a large extent exists in parallel to conscious awareness. The prediction that positive and negative emotional brief stimuli should interact selectively and

asymmetrically with other stimuli that are simultaneously consciously processed received empirical support here.

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Figure Legends

Figure 1: Examples of the type of pictorial stimuli used in the experiment.

Figure 2: Mean skin conductance responses (SCRs) in microSiemens, averaged across trials and recording sites, and split for groups, and stimulus conditions. NoInt = No Interference group, Interhem = Interhemispheric interference group, Intrahem = Intrahemispheric interference group. RHem = Right hemisphere, LHem = Left hemisphere.

Figure 3: Graphic illustration of the significant hemisphere x emotional valence interaction. NegIntf = negative interference, PosIntf = Positive interference.