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Enhanced Extrastriate Activation during Observation of Distorted Finger Postures

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and Riitta Hari^{1,2}

Abstract

■ Hand and finger postures of other people are important body language cues that strongly contribute to the observer's decision about the person's intentions, thoughts, and attentional state. We compared neuromagnetic cortical activation elicited by color images of natural and distorted finger postures. The distorted postures contained computer-deformed joint

angles and thereby easily caught the observer's attention. From about 260 msec onwards, extrastriate occipital areas of both hemispheres were activated more strongly by distorted than natural finger postures. We interpret this result as an early top-down effect of emotional valence on the processing of unusual hand shapes in the extrastriate visual cortex. ■

INTRODUCTION

Humans are experts in evaluating other people's hand and finger postures. An intensive practice starts already at the age of 3–5 months and results in automatic recognition of various hand postures. Hand and finger postures are important social cues that contribute to our interpretation of another individual's intentions and thoughts. Pointing gestures are especially effective in influencing the decisions of other people's direction of attention (Langton & Bruce, 2000). Humans prefer to fixate their gaze on fingers during observation of finger, hand, and arm movements (Mataric & Pomplun, 1998).

Static views of faces and hands activate neurons in the monkey superior temporal sulcus (STS) (Desimone & Duncan, 1995; Perrett et al., 1989; Gross, Bender, & Rocha-Miranda, 1969). In humans, static hand images are processed in several occipital, parietal, and temporal brain regions, including areas near the superior temporal and intraparietal sulci, both considered as parts of the neuronal network involved in social perception (Downing, Jiang, Shuman, & Kanwisher, 2001; Langton & Bruce, 2000; McCarthy, Puce, Belger, & Allison, 1999).

In studying brain mechanisms underlying perception of socially valid body language cues, we wondered whether activations of visual cortical areas would differ when subjects observe natural versus distorted finger postures. Whole-scalp magnetoencephalographic (MEG) recordings were used to reveal cortical activation sequences (Hari, Levänen, & Raij, 2000) in 8 healthy subjects who were presented with images of natural and

distorted finger postures (see Figure 1 for examples). During observation condition, the subjects performed a one-back memory task, lifting the right index finger whenever the presented finger posture was identical to the previous one. During imitation condition, the subjects imitated the previous (natural) finger posture whenever an imperative stimulus appeared. Minimum current estimates (MCEs) (Uutela, Hämäläinen, & Somersalo, 1999), describing activations of the extrastriate cortices, were compared between natural and distorted finger postures.

RESULTS

None of our subjects reported any difficulties in following the tasks and many of them spontaneously described the images of the distorted fingers as unpleasant.

Figure 2 illustrates the mean source strengths across successive 100-msec periods at the back of the head of 1 subject. Natural and distorted postures activated rather similar cortical regions within the extrastriate occipital areas. However, activation tended to be stronger for the distorted than natural postures 300–600 msec after stimulus onset. The results were qualitatively similar in both observation and imitation conditions.

Figure 3 illustrates activation strengths as a function of time for the left and right occipital regions-of-interest (ROIs) in 2 subjects. In both subjects, similarly as in other 5 subjects, the sources were strongest during the transient evoked responses at 100–200 msec. Within this time window, the responses to distorted versus natural hand postures did not differ systematically in either condition.

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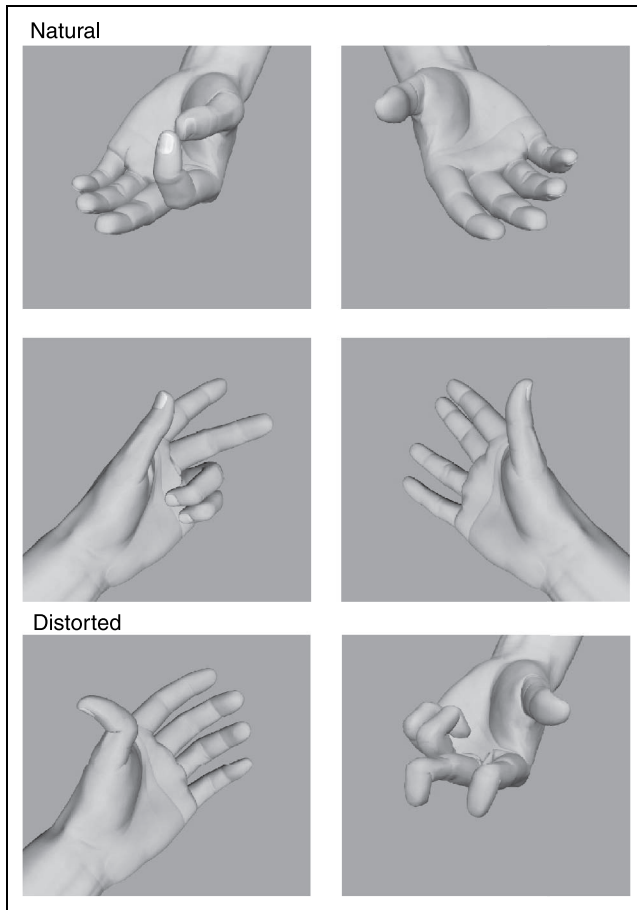
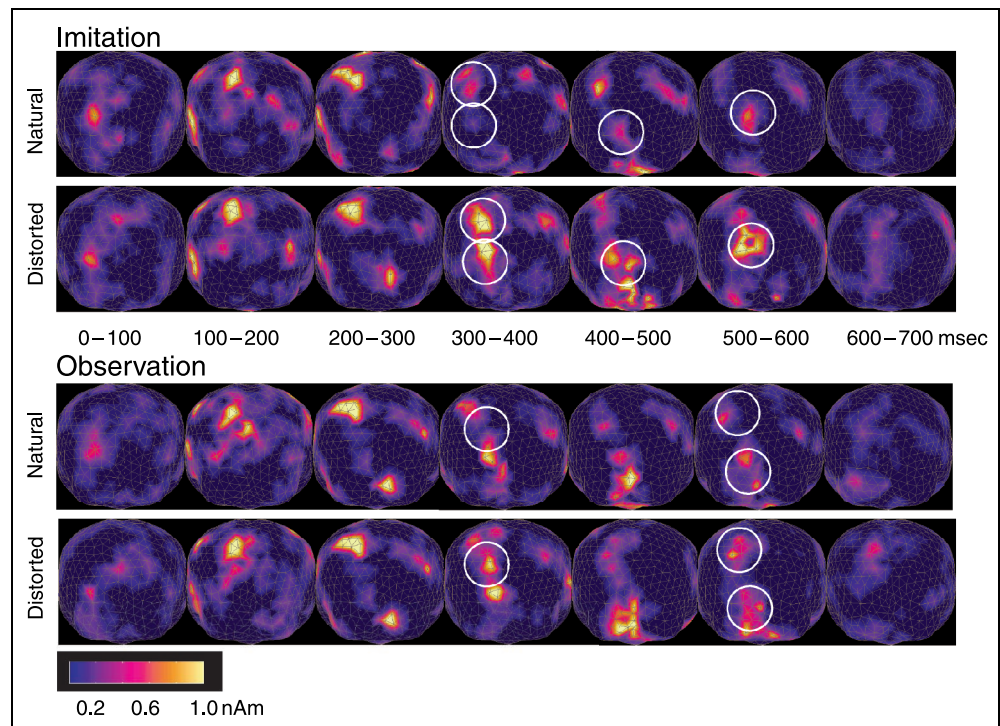


Figure 1. Examples of stimuli, comprising images of both natural and distorted finger postures.

Figure 2. MCEs at the back of the head of Subject 1 during imitation and observation conditions. The pictures illustrate mean source strengths of successive 100-msec periods. The circles indicate areas with the clearest differences between responses to distorted and natural postures.



At 250–700 msec, both subjects of Figure 3 showed stronger activation for distorted than natural postures, regardless of the task, as is indicated by the shaded areas between the activation curves. The insert in the middle of Figure 3 shows that in the whole group of subjects the difference between responses to distorted versus natural postures reached statistical significance ($p < .05$) about 260 msec after stimulus onset.

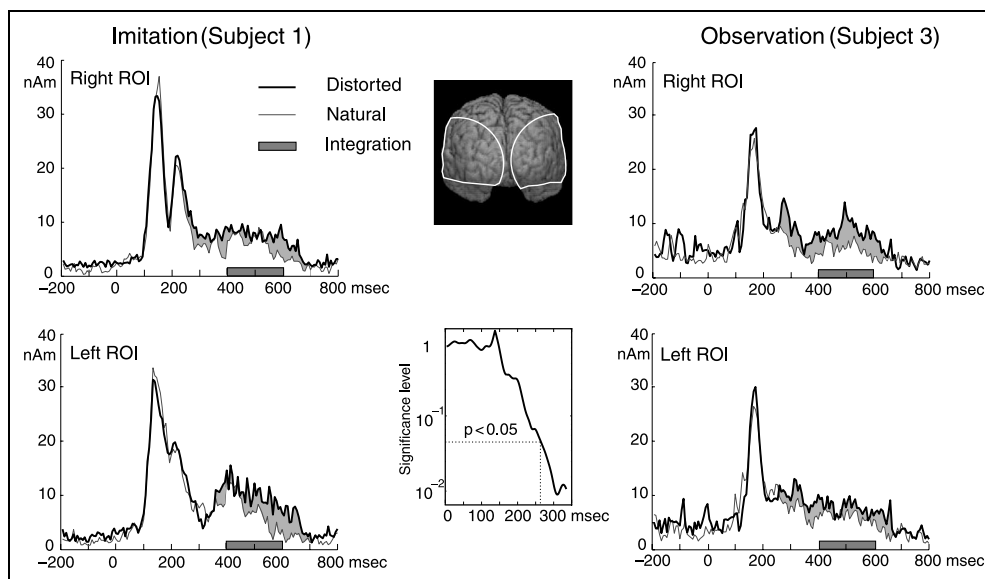
Figure 4 shows the individual source strengths in the left and right ROIs for distorted finger postures (mean at 400–600 msec) as a function of the corresponding source strengths for natural postures. In both observation and imitation conditions, the symbols tend to be above the diagonal, implying stronger activation for distorted than natural postures.

The source strengths were subjected to ANOVA with the within-subject factors hemisphere (left, right), condition (observation, imitation), and posture (natural, distorted). Because there was no significant condition effect, $F(1,6) = 2.0$, the data were collapsed across the two conditions. The activations were on average 19% stronger for the distorted than natural postures, $F(1,7) = 9.1$, $p = .02$, while the Hemisphere \times Posture interaction was not significant. The activation was on average 15% stronger in the left than the right hemisphere, regardless of posture, $F(1,7) = 9.4$, $p = .02$.

DISCUSSION

We demonstrated that the extrastriate cortices react more strongly to observation of distorted than natural

Figure 3. The mean amplitudes of occipital (left and right) ROIs as a function of time in 2 subjects to natural and distorted finger postures in imitation and observation conditions. The horizontal shaded bars indicate the time window used for quantification of the responses in all subjects. Middle (top): Schematic presentation of the two ROIs superimposed on the posterior view of a 3-D MRI of 1 subject. Middle (bottom): Significance levels for differences between the cumulative amplitudes of the responses to distorted versus natural postures (paired *t* test) plotted as a function of time to assess the onset time of the difference.



finger postures. The statistically significant difference between the responses started around 260 msec and was most consistent across subjects 400–600 msec after stimulus onset.

Voluntary attention affects processing throughout the visual pathways; the higher the cortical hierarchy level and the longer the response latency, the stronger is the effect (for a review, see Treue, 2001). However, the stronger responses to distorted than natural finger postures unlikely reflect stronger voluntary (sustained) attention paid to the distorted fingers: First, the natural and distorted postures were presented in a random order, which prevented anticipation of a specific stimulus type. Second, the processing loads were in the observation condition equal to both stimuli, since the subject performed a one-back recognition task for all stimuli. In the imitation condition, the load was even stronger for the natural than the distorted postures, because only the natural postures had to be imitated. Still in both conditions, the responses were stronger to the distorted than normal postures.

The earliest cortical visual processing most likely reflects mainly bottom-up activation, strictly bound to physical stimulus features, whereas responses at longer latencies in the same areas may reflect top-down modulation arising from other brain areas (Tanaka, 2001; Lamme & Roelfsema, 2000; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999; Roelfsema, Lamme, & Spekreijse, 1998). The rather late (250–300 msec) onset of the difference between distorted and natural postures would agree with top-down modulation.

One plausible explanation for the enhanced extrastriate activation is related to the emotional valence of the unpleasant distorted postures. Amygdalar activation could thus be expected, in analogy to activations observed after threatening and fear-provoking stimuli (Tabert et al., 2001; Whalen et al., 1998; Breiter et al.,

1996; Cahill et al., 1996; Irwin et al., 1996). Amygdala receives direct thalamic projections from the pulvinar (Jones & Burton, 1976), and it is reciprocally connected to occipital visual areas (Amaral & Price, 1984). Consequently, amygdalar activation by visual stimuli can be associated with bilaterally enhanced activation of extrastriate cortices (Paradiso et al., 1999; Morris et al., 1998).

Finger and face stimuli resemble each other in many aspects: Recognition of both stimuli is overlearned during development, and distorted images evoke disgust, fear, and other negative emotions. Moreover, the natural and distorted finger stimuli, similarly as nonemotional and emotional faces, did not differ in physical salience. It is thus obvious that rather sophisticated visual processing is required before the emotional features (valence) of the stimuli become evident and before an “emotional capture” can occur.

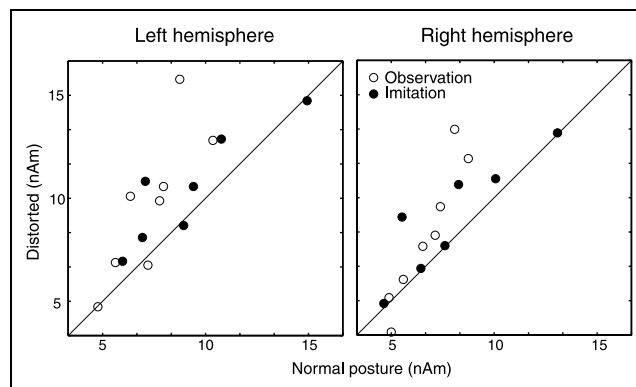


Figure 4. The mean source strengths at 400–600 msec for responses to distorted postures plotted as a function of the corresponding strengths to natural postures for both ROIs and for all subjects in observation and imitation conditions. If the responses to distorted and natural postures were equal in strength, all symbols would be on the diagonal.

Pessoa, McKenna, Gutierrez, and Ungerleider (2002) recently suggested that emotional face stimuli activate amygdala via the primary visual cortex and the extrastriate visual cortices. The distorted finger postures could be processed along similar pathways. Activation of amygdala has been observed already 120 msec after neutral faces (Halgren et al., 1994), and our results would agree with top-down modulation from amygdala to extrastriate areas via feedback signals (Amaral & Price, 1984), starting 250–300 msec after stimulus onset. The valence of the distorted postures would bias processing of stimuli in the extrastriate cortices for a few hundreds of milliseconds, as is suggested by the most consistent effect 400–600 msec after stimulus onset. The shorter latency to disgusting faces than finger postures supports the notion that faces are recognized more automatically than finger postures.

Because the distorted postures occurred, as a group, less frequently (1:3) than the natural postures, habituation could, in principle, have contributed to the observed differences. However, habituation would have required sophisticated processing of the emotional valence because the novelty was not based on differences in physical salience.

Thus, our results suggest that the stronger occipital activation to distorted than natural finger postures, starting around 260 msec after stimulus onset, is due to top-down modulation of the extrastriate visual cortices. Either attentional or emotion-related amygdalar influences, or both, could be involved.

METHODS

Subjects

Eight right-handed healthy subjects (5 females, 3 males; age 25.8 ± 1.2 years, range 23–33 years) were studied after informed consent. The study had prior approval by the Ethical Committee of the Hospital District of Helsinki and Uusimaa.

Stimuli and Tasks

The subjects viewed static color images of 48 different finger postures: 36 natural and 12 distorted postures, all designed by Poser 4.0 program. Figure 1 shows examples of the stimuli that comprised images of both left and right hands viewed from two different angles: one view similar to subject's own hands and the other resembling another person sitting in front of the subject. In the distorted finger postures, the distal phalanxes of different fingers were bent (by computer) into clearly unnatural positions. The $15^\circ \times 17^\circ$ stimuli were displayed in a random order to the center of a screen located 90 cm in front of the subject. The stimuli were presented once every 3.2 sec for 2 sec. All stimuli were similar in content complexity and luminance and they were displayed with equal probabilities (1/48) during the measurement.

In the observation condition, the subjects were asked to respond by lifting their right index finger when the image was identical to the previous one. In the imitation condition, the subjects were asked to imitate the previous natural finger posture whenever an imperative stimulus (an image of a small ball) appeared; the imperative stimuli occurred at the times when the subsequent stimulus should have appeared and one sequence of 100 stimuli contained on average 10 imperative stimuli. Data were collected from 7 out of the 8 subjects in the observation condition (1 subject's data were lost due to technical problems) and from all 8 subjects in the imitation condition. The subjects were instructed to avoid eye movements while looking at the images but no exact fixation point was given.

MEG Recording

MEG signals were recorded within a magnetically shielded room with a whole-scalp 306-channel superconducting quantum interference device (SQUID) neuromagnetometer (Vectorview, Neuromag, Helsinki). During the measurement, the subject sat relaxed, with the head supported against the bottom surface of the helmet-shaped neuromagnetometer. At each of the device's 102 sensor positions, two orthogonally oriented planar figure-of-eight gradiometers and one magnetometer picked up three independent measures of the magnetic field outside the head. The signals from all these flux transformers were then led to SQUIDS for detection.

Signals from four indicator coils attached to the scalp were used for determining the exact position of the head within the sensor helmet. The coil locations with respect to anatomical landmarks were found with a 3-D digitizer that allowed alignment of the MEG and magnetic resonance image (MRI) coordinate systems. Head MRIs were acquired with a 1.5-T Siemens Magnetom device from all subjects.

The recording passband was 0.1–200 Hz and the sampling rate was 600 Hz. Vertical and horizontal electro-oculograms were recorded to reject on-line epochs coinciding with blinks and excessive eye movements. At least 60 single responses were averaged for natural and distorted finger postures in each condition. The analysis started 200 msec before and ended 800 msec after the stimulus onset, covering the time window showing significant occipital activity.

Because natural postures, as a group, occurred three times more frequently than the distorted postures, averages to natural postures were computed off-line from a matching number of single epochs, randomly distributed over the whole session. Responses that were associated with motor activity (finger lift during observation or finger posture imitation during imitation conditions) were excluded from the analysis. The signals were pre-processed by omitting noisy channels and the baseline

for amplitude measurements was determined as the mean amplitude during a prestimulus 200-msec period and a 150-msec period at 650–800 msec.

MEG Analysis

The preprocessed data were analyzed with MCE based on L1 norm (Uutela et al., 1999). The estimate gives the current distribution in which the total sum of currents is as small as possible, while it still explains most of the measured signals. Initial analysis showed wide interindividual scatter of the MCEs within the occipital cortex of both hemispheres. Therefore, two large ROIs (see inset of Figure 3) covering the individual source areas were used in further analysis. Both ROIs covered approximately 40 cm² of cortex.

Differences between cortical activation strengths in response to natural and distorted finger postures, for the two ROIs and for each individual, were averaged within 100-msec time windows. The resulting values were subjected to *t* tests. As the most marked and consistent differences were observed in all subjects at 400–600 msec, the mean activation strengths were computed across this time window for both ROIs and for both natural and distorted postures, and then subjected to ANOVA.

The exact onset time of the difference between responses to distorted and natural postures was evaluated as follows. First, “areal mean” responses were computed for each subject and condition (natural and distorted stimuli, left and right occipital cortices) by averaging responses across left (*N* = 12) and right occipital channels (*N* = 12). The cumulative amplitudes of the areal means were then computed as a function of time. Next, difference curves between responses to distorted and natural postures were computed between the cumulative amplitudes, both for left and right occipital cortices and the two conditions; this procedure resulted in four difference curves per subject and in altogether 30 difference curves (as mentioned previously, data were not available for 1 subject in the observation condition). For each subject, the difference curves were then averaged across conditions and areas, and *t* tests at each point along the time axis served to probe the deviance of the mean from zero. The results of the *t* tests were plotted as a function of time to indicate the onset of the consistent statistically significant difference between natural and distorted stimuli.

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