

Cortico-subcortical visual, somatosensory, and motor activations for perceiving dynamic whole-body emotional expressions with and without striate cortex (V1)

Jan Van den Stock^{a,b}, Marco Tamietto^{a,c}, Bettina Sorger^d, Swann Pichon^e, Julie Grézes^f, and Beatrice de Gelder^{a,b,g,1}

^aCognitive and Affective Neuroscience Laboratory, Tilburg University, 5000 LE Tilburg, The Netherlands; ^bBrain and Emotion Laboratory Leuven, Department of Neurosciences, Katholieke Universiteit Leuven, 3000 Leuven, Belgium; ^cDepartment of Psychology, University of Torino, 10123 Torino, Italy; ^dDepartment of Neuropsychology, Maastricht University, 6200 MD Maastricht, The Netherlands; ^eLaboratory for Behavioral Neurology and Imaging of Cognition, Department of Neuroscience, Medical School, University of Geneva, Geneva 1211, Switzerland; ^fCognitive Neuroscience Laboratory, Institut National de la Santé et de la Recherche Médicale U960, Department for Cognitive Studies, Ecole Normale Supérieure, 75005 Paris, France; and ^gAthinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, MA 02129

Edited* by Richard M. Held, New England College of Optometry, Cambridge, MA, and approved August 8, 2011 (received for review May 5, 2011)

Patients with striate cortex damage and clinical blindness retain the ability to process certain visual properties of stimuli that they are not aware of seeing. Here we investigated the neural correlates of residual visual perception for dynamic whole-body emotional actions. Angry and neutral emotional whole-body actions were presented in the intact and blind visual hemifield of a cortically blind patient with unilateral destruction of striate cortex. Comparisons of angry vs. neutral actions performed separately in the blind and intact visual hemifield showed in both cases increased activation in primary somatosensory, motor, and premotor cortices. Activations selective for intact hemifield presentation of angry compared with neutral actions were located subcortically in the right lateral geniculate nucleus and cortically in the superior temporal sulcus, prefrontal cortex, precuneus, and intraparietal sulcus. Activations specific for blind hemifield presentation of angry compared with neutral actions were found in the bilateral superior colliculus, pulvinar nucleus of the thalamus, amygdala, and right fusiform gyrus. Direct comparison of emotional modulation in the blind vs. intact visual hemifield revealed selective activity in the right superior colliculus and bilateral pulvinar for angry expressions, thereby showing a selective involvement of these subcortical structures in nonconscious visual emotion perception.

blindsight | body expressions | consciousness

The visual system encompasses a number of parallel visual pathways (1) of which the primary geniculostriate system processes a wide range of stimulus attributes. Other extrageniculostriate visual routes likely have a much more narrowly specified function, as indicated by their sensitivity to a limited range of spatial frequencies (2), spectral components (3), or motion parameters (4). However, we do not yet have a clear understanding of how these different extrageniculostriate pathways and the visual attributes they process match. Some visual attributes can also be processed by both the geniculostriate pathway and a more specialized extrageniculostriate one.

One important example is movement perception. As originally discovered by Kohler and Held (5), movement perception elicits significant qualitative and quantitative differences at the neural as well as at behavioral level compared with static stimuli in the intact brain. These differences likely reflect the high evolutionary value of movement perception and may be especially important for understanding residual visual abilities in the case of striate cortex (V1) damage. In fact, after V1 damage, cortically blind patients retain a limited visual ability for movement discrimination (4, 6–9), akin to what has been previously observed in animals with V1 destruction (10, 11). This spared ability to process simple movement is probably based on the extrageniculostriate connections that motion-sensitive human middle temporal/V5 complex (hMT/V5) has with subcortical structures like the lateral geniculate nucleus (LGN) or pulvinar nucleus of the thalamus (Pulv), as

shown in humans and primates (12–14). However, compared with the perception of single moving dots or simple patches, perception of biological movement in healthy observers seems to recruit more temporal areas along the ventral visual stream, like the superior temporal sulcus (STS) (15, 16) and the fusiform gyrus (FG) (17), as well as subcortical and cortical areas related to visuomotor integration and action preparation, like the superior colliculus (SC), amygdala (Amg), and somatosensory, premotor, and motor areas (17, 18). Nevertheless, it is not yet known whether patients with cortical blindness may also process complex biological movement with social and emotional relevance and which of the various extrageniculostriate pathways underlie this residual function.

Interestingly, some of the brain structures activated by biological movement perception in the intact brain are also involved in nonconscious perception of emotions in healthy observers and cortically blind patients (19–23). Extrageniculostriate processing of affective information was first reported in the cortically blind patient GY, who was able to guess the emotional expression of faces presented in his blind right visual hemifield (RVF) above chance level (24) (a phenomenon termed “affective blindsight”). Follow-up studies using multiple methodologies in the same and other patients have since shed light on the neurophysiological correlates of this phenomenon. Multiple studies have indeed repeatedly shown functional connectivity and coactivation in the SC, Pulv, and Amg for facial as well as whole-body expressions presented in the blind visual hemifield (20, 25–27). Moreover, activity in these subcortical structures was often associated with enhancement in a few additional cortical areas. For example, presentation of static facial expressions in the blind hemifield of patient GY increased activity in the SC, Pulv, and Amg along with activity in the FG (26), whereas presentation of static whole-body expressions in the same patient elicited activity in the Pulv, in cortical area hMT/V5, in STS, and in the premotor cortex (25). Finally, a direct comparison of the behavioral and psychophysiological responses in GY and another patient with blindsight showed that unseen static facial and whole-body expressions were nonconsciously recognized with comparable accuracy and elicited spontaneous psychophysiological responses (i.e., facial mimicry and pupil dilation) that were faster and more intense than those recorded when the same stimuli were pro-

Author contributions: J.V.d.S., M.T., S.P., J.G., and B.d.G. designed research; J.V.d.S., M.T., B.S., and B.d.G. performed research; J.V.d.S., M.T., and S.P. analyzed data; and J.V.d.S., M.T., and B.d.G. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

¹To whom correspondence should be addressed. E-mail: degelder@nmr.mgh.harvard.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1107214108/-DCSupplemental.

jected to the intact visual hemifield and were therefore consciously perceived (28).

The precise role of the SC and Pulv in emotion processing is as yet unclear, although there are indications that these subcortical structures do not merely operate as relay stations of visual information to the Amg. For example, direct stimulation of the SC in rats induces freezing and flight reactions (29). In healthy human observers, one study combining magnetoencephalography with functional magnetic resonance imaging (fMRI) found that event-related synchronization in response to fearful faces occurred in the Pulv after only 10–20 ms after stimulus onset (30). This activity could not be attributed to, and could not be modulated directly by, Amg activity because synchronization in the Amg took place later in time (20–30 ms after stimulus onset), and because the connections between Pulv and Amg are unidirectional (31). Finally, selective damage to the human Pulv impairs emotion processing even when the Amg is intact and can receive detailed and fully processed visual information from the inferotemporal cortex through the ventral continuation of the geniculostriate system (32). Altogether, these findings suggest that the SC and Pulv are to some extent directly involved in nonconscious emotional processing and can implement emotion-related functions such as reorienting attention, directing saccades, and initiating reflex-like behavioral reactions.

To investigate the neural systems involved in the conscious and nonconscious perception of biological movement, short video clips displaying dynamic whole-body emotional actions were presented in the intact and blind visual hemifields of patient GY. As it happens, patient GY offers a unique opportunity in this respect because his unilateral destruction of left V1, resulting in blindness over the RVF, enables a direct within-subject comparison of the neural basis of biological movement perception in the intact vs. the blind hemifield, while keeping the stimulus properties identical. Dynamic whole-body angry expressions were contrasted against instrumental neutral actions because the former are easily recognizable emotional stimuli, signal threat unambiguously, and trigger adaptive actions in the observers (17). Moreover, the same contrast between angry and instrumental whole-body actions has already been investigated in healthy subjects and revealed activity in all areas characteristically involved in the perception of socially significant movement and emotions, thereby enabling a direct comparison with previous findings gathered in the intact brain (17, 18).

Results

Behavioral Results. The results of the behavioral experiment performed a few months after the fMRI experiment are shown in Fig. 1. This experiment was performed to collect behavioral data about nonconscious recognition in GY of dynamic whole-body expressions. Correct categorization in a two-alternative forced-choice (2AFC) task of neutral and angry dynamic whole-body actions projected in the (intact) left visual hemifield (LVF) was near ceiling ($47/48 = 98\%$, $P < 0.0001$ by binomial test). Correct categorization of the same stimuli in the (blind) RVF was also significantly above chance level ($33/48 = 69\%$, $P < 0.013$ by binomial test).

GY's eye movements were monitored online by an experimenter, and, based on this evidence, none of the trials had to be discarded because of unsteady fixation or excessive movement during stimulus presentation. Furthermore, GY was questioned about his visual awareness for stimuli projected in the (blind) RVF on a trial-by-trial basis, and he reported no visual awareness of stimulus presence, onset, or offset and claimed that his responses were entirely based on "blind guessing."

fMRI Results. We first compared perception of angry and neutral whole-body expressions separately for each visual hemifield. Then, we directly investigated neural activity specific for the

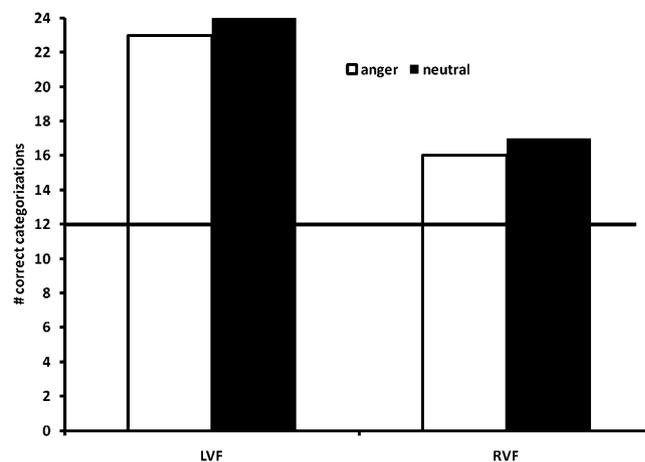


Fig. 1. Behavioral performance of GY in the categorization of neutral and angry dynamic whole-body expressions in the 2AFC task for (intact) LVF and (blind) RVF presentation. The horizontal bar represents chance level (12/24 for each condition and side of presentation, corresponding to 50% correct).

nonconscious perception of dynamic angry expressions. For this second purpose, we calculated the interaction between the type of perception (RVF nonconscious vs. LVF conscious) and the expression (anger vs. neutral): $[(RVF\ anger - RVF\ neutral) > (LVF\ anger - LVF\ neutral)]$. As it happens, this contrast has not been reported before in studies on affective blindsight and highlights only those areas differentially active in the nonconscious perception of angry movements, whereas any activity equally present during neutral or emotion processing and during conscious or nonconscious perception (and thus of no interest for our present purposes) is discounted and goes undetected. Moreover, the use of a passive observation design, not requiring GY to perform any response during the presentation of neutral and angry whole-body expressions, warranted that the recorded neural activity was exclusively related to, and consequent upon, visual processing and was unaffected by voluntary action execution and button press (*Materials and Methods*). Results are displayed in Fig. 2 and Tables 1 and 2.

The contrast between seen (LVF) angry vs. neutral whole-body actions revealed activation in several areas related to biological movement perception (STS), motor execution and preparation (e.g., precentral gyrus as well as middle and superior frontal gyrus), somatosensation (postcentral gyrus), sensory and self-awareness (superior frontal gyrus and precuneus), and attention modulation (intraparietal sulcus and precuneus). At the subcortical level, activation was found only in the right (contralateral) LGN.

Comparing dynamic angry vs. neutral whole-body actions in the blind (RVF) hemifield revealed activity in the SC, Pulv, and Amg bilaterally, in the middle part of the right FG, and in the somatosensory (postcentral gyrus) and motor areas bilaterally (precentral gyrus), but more evident in the right hemisphere.

The direct comparison between nonconscious and conscious perception of angry whole-body actions $[(RVF\ anger - RVF\ neutral) > (LVF\ anger - LVF\ neutral)]$ revealed only subcortical activity in the right SC and, bilaterally, in the Pulv.

Also in this experiment, at the end of the whole fMRI scanning session, GY was questioned about his visual awareness for stimuli projected to his (blind) RVF. Consistent with previous reports, he claimed no visual awareness of stimulus presence, onset, or offset.

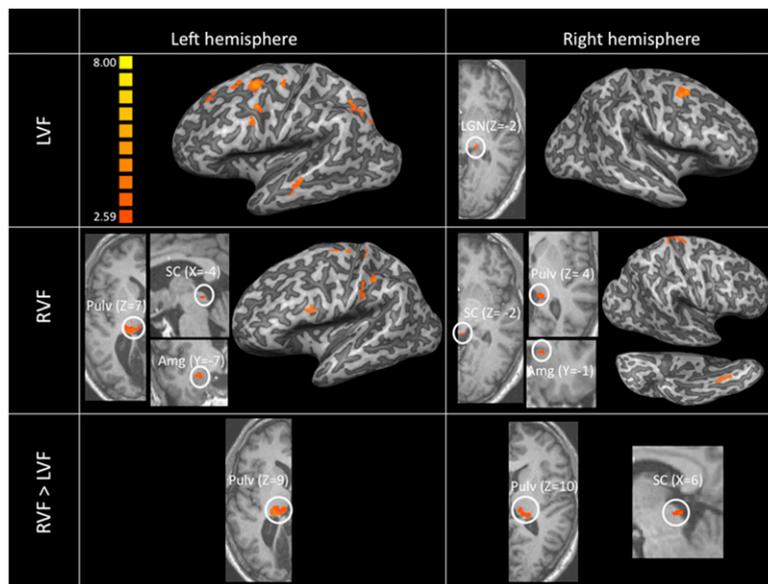


Fig. 2. Brain areas significantly more activated by angry compared with neutral dynamic whole-body expressions as a function of visual hemifield of presentation and hemisphere. X, Y, and Z refer to Talairach coordinates. The color bar on the top left reflects t values of the respective brain activation contrasts.

Discussion

The present results show that a cortically blind patient can discriminate between angry and neutral dynamic whole-body expressions without consciously perceiving them. In fact, in the behavioral experiment reported above, GY performed significantly above chance level in categorizing dynamic whole-body neutral and angry expressions presented in his blind visual hemifield, extending previous studies using static facial and bodily expressions (25, 28).

At the neural level, the SC, Pulv, and Amg, bilaterally, and the middle part of the right FG were significantly more activated by blind (RVF) presentation of angry compared with neutral whole-body actions. Enhanced activity in this subcortical pathway has been repeatedly reported during nonconscious perception of static facial and whole-body expressions of fear and joy in blindsight patients (20, 25, 27) as well as in healthy subjects in whom nonconscious perception was induced by experimental manipulations such as visual masking (19, 21, 23), binocular rivalry (33, 34), or flash suppression (35). Consistent with these data, recent anatomical studies revealed the existence of direct anatomical connections between the SC, Pulv, and Amg in nonhuman primates (36), and *in vivo* tractography found the same connections in healthy human subjects and in patient GY (37). The activation in the SC is in line with its role in triggering reflex-like emotional reactions (29) and with previous evidence showing its pivotal role in blindsight (3, 38). Pulv activity is consistent with the role of this structure in determining what is salient in the visual scene. Specifically, Pulv activity has been previously reported during nonconscious perception of emotional stimuli in blindsight (20, 26), including static whole-body expressions (25). Pulv activation is also in keeping with recent findings showing impaired automatic (i.e., preattentive) processing of emotions in a patient with Pulv damage (32).

Cortical activity for nonconscious emotion perception was found only in the right FG. Activity in this area is associated with conscious perception of facial expressions (39) but has also been associated with the processing of dynamic and static whole-body movements and emotional expressions in healthy subjects (40). FG activity during nonconscious perception of emotions has been reported only in one previous study on GY that used static facial expressions (26). However, in that study, the FG activity

was observed in the left hemisphere. Moreover, two different facial expressions were displayed simultaneously to both the intact and blind visual hemifield. It is thus possible that FG activity was partly related to conscious emotion perception occurring in the intact hemifield and attributable to feed-forward projections from the geniculostriate pathway to the FG, either directly or via interhemispheric cross-talk. In the present case, in which one single stimulus was delivered to one visual hemifield at a time, this possibility can be safely ruled out. Instead, FG activity likely reflects the modulatory action exerted by the Amg over the FG. In fact, projections from the Amg reach ipsilateral ventral visual cortices including the FG (31), and, accordingly, the ipsilateral (right) Amg was found to be active specifically during nonconscious perception of angry whole-body actions in our data. Therefore, the present findings support, and extend to the nonconscious domain, previous evidence about a mechanism of reentrant modulation from the Amg to the FG enhancing sensory processing that has been reported thus far only in the case of conscious perception of static facial and bodily expressions (41, 42).

Notably, none of the neural structures above were significantly active when the same contrast was performed on stimuli presented in the intact LVF. In fact, emotional modulation of subcortical structures induced by consciously seen stimuli was restricted to the right (contralateral) LGN. Activity in the right LGN for stimuli in the LVF is consistent with evidence that LGN neurons have receptive fields confined to the contralateral visual hemifield (43) and also provides an additional indication that GY kept steady fixation during the experiment, so that the stimuli fell only in the designated visual hemifield. This result is also in line with evidence that activation in the LGN of GY is related to consciously seen visual stimuli, but not to non-conscious visuomotor integration and blindsight (3), and probably reflects cortico-geniculate feedback from the ipsilateral V1.

Cortical activity specific for conscious perception of whole-body angry expressions was found in STS, whose role in the conscious perception of biological movement and dynamic bodily expressions has been reported in several neuroimaging studies with healthy observers (17, 44). Activation was also found in areas related to conscious information processing and sensory awareness, such as the prefrontal cortex and precuneus (45), and

Table 1. Brain regions significantly more activated by angry compared with neutral dynamic whole-body expressions (anger > neutral)

Brain region	Blind RVF					Intact LVF				
	BA	X	Y	Z	n	BA	X	Y	Z	n
Right hemisphere										
Amg		20	0	-10	15					
Pulv		14	-25	8	283					
SC		4	-30	-1	21					
LGN						18	-24	-1	44	
FG	37	26	-50	-17	522					
Postcentral gyrus (I)	5	28	-32	67	307					
Postcentral gyrus (II)	7	56	-15	43	399	7	52	-11	48	276
Precentral gyrus (I)	4	14	-26	68	926					
Precentral gyrus (II)	4	42	-16	52	446					
Middle frontal gyrus						6	39	4	49	715
Precuneus						7	5	-67	43	693
Left hemisphere										
Amg		-23	-5	-12	234					
Pulv		-15	-28	8	1,021					
SC		-3	-29	-2	18					
Superior frontal sulcus						8	-19	30	42	313
Superior frontal gyrus						6	-27	12	53	387
Orbitofrontal cortex	11	-26	21	-12	503					
Inferior frontal gyrus	6	-49	6	26	257					
Postcentral sulcus (I)	40	-54	-23	36	437					
Postcentral sulcus (II)	7	-42	-31	41	220					
Precuneus						7	-6	-66	39	393
Intraparietal sulcus						19	-33	-59	36	643
STS						21	-61	-16	2	311
Precentral gyrus						4	-42	-15	58	257
Precentral sulcus (I)						6	-26	-1	52	438
Precentral sulcus (II)						6	-36	-3	39	281
Inferior frontal gyrus						44	-48	12	27	119

Brain regions significantly activated when angry and neutral stimuli presented in the same visual hemifield were contrasted. X, Y, and Z refer to Talairach coordinates. BA, Brodmann area; n, number of voxels.

in areas involved in attention modulation, such as the intraparietal sulcus (46).

Altogether, the present results indicate that conscious and nonconscious perception of emotional whole-body movements rely on neural systems that are partly segregated. Conscious perception of emotions seems based predominantly on the geniculostriate system, including its continuation in extrastriate visual areas along the ventral stream, and in a number of other cortical regions. Conversely, nonconscious perception seems based on the extrageniculostriate and predominately subcortical pathway involving the SC, Pulv, and Amg. Whether and how these two neural systems can interact during normal (i.e., conscious) perception of emotions remains an open question. In fact, absence of significant activity in the SC, Pulv, and Amg during conscious perception of emotional movements does not necessarily mean that this subcortical system is not functioning under such conditions. Standard fMRI methods sample and average brain signal at relatively long time scales and do not enable a fine-grained distinction of the possibly different temporal profiles at which neural activity in various brain areas may occur. For example, investigation of conscious perception of fearful expressions by using the high temporal resolution of magnetoencephalography detected early activity in the Pulv (10–20 ms) and Amg (20–30 ms) (30), which is frequently reported only during nonconscious emotion perception with standard fMRI methods (22). This activity was then followed by cortical responses in the visual cortex (40–50 ms) and in prefrontal areas

(160–210 ms) typically observed in conscious perception (30). Moreover, functional connectivity data suggest that nonconscious emotion perception is supported by positive connectivity and coactivation in the subcortical pathway to the Amg, whereas conscious emotion perception is supported by negative cortico-subcortical connectivity along this pathway (47). Based on these and other behavioral findings in healthy participants indicating that nonconscious emotional perception can coexist and interfere with conscious perception (48), we have recently suggested that cortical feedback during conscious emotion perception might reflect inhibitory modulation over the subcortical SC–Pulv–Amg pathway (22). This proposal can explain the absence of subcortical activity during conscious emotion perception reported here. It is also in keeping with our data and with previous neuroimaging evidence in healthy observers showing that activity in Pulv and SC is significantly stronger (49, 50), rather than being unchanged or reduced, when nonconscious perception of emotions is directly contrasted with conscious perception, as revealed in the present case by the type of perception × expression interaction.

Aside from differences between the neural underpinnings of conscious and nonconscious perception, both consciously seen (LVF) and unseen (RVF) angry whole-body actions activated somatosensory as well as motor and premotor cortices. Although these cortical areas perform complementary functions related to sensory–motor integration, their conjoint activity has not been reported together in previous studies on patients with blindsight. The somatosensory cortex is involved in mapping the somatic changes typically triggered by emotion perception in healthy observers, such as increase in physiological arousal or spontaneous expressive modifications (51). Consistent with these data, lesions to the somatosensory cortex impair emotion recognition, and the severity of somatosensory impairment correlates with the severity of emotion recognition (52). Interestingly, emotional stimuli activate the somatosensory cortex in neurologically intact observers regardless of whether the stimuli are perceived implicitly or explicitly (53). Somatosensory activation for nonconscious perception of emotional stimuli has been previously reported in a sample of cortically blind patients with affective blindsight, and its intensity has been correlated with the intensity of startle-reflex potentiation as well as with the increase in the subjective reports of negative feelings (54).

Motor and premotor activity was reported in previous neuroimaging studies investigating conscious emotion recognition from static and dynamic facial expressions of fear and anger (55, 56) as well as for static and dynamic hand or whole-body angry actions (17, 57). The present study, however, reports activity in the premotor and motor cortices also during nonconscious perception of emotions in blindsight. The role of premotor and motor areas during emotion perception was initially related to a mechanisms of emotion recognition based on the internal simulation of the emotional state seen in others (58). Although this mechanism can play a role in emotion recognition, recent evidence suggests that these activations more likely reflect automatic preparation for action (17, 59). This interpretation is supported by significant

Table 2. Brain regions selectively activated by nonconscious perception of angry stimuli as revealed by the type of perception × expression interaction [(RVF anger – RVF neutral) > (LVF anger – LVF neutral)]

Brain region	X	Y	Z	n
Left Pulv	-15	-28	9	1,147
Right Pulv	15	-24	10	291
Right SC	5	-30	-1	63

X, Y, and Z refer to Talairach coordinates. n, number of voxels.

differences in premotor activity when static facial expressions of anger are contrasted to fearful faces (60) and by evidence that premotor and motor cortices are particularly active during processing of dynamic whole-body angry expressions (17). In fact, information concerning emotion and action are often equally prominent aspects of whole-body angry actions. Similar to facial expressions, bodily expressions communicate emotions through characteristic postural configurations, but, in addition to the former, they also evoke at the same time the adaptive reactions and motor responses related to defensive behaviors. In the case of conscious perception, information about emotional whole-body movements seems to reach somatosensory and motor areas through the geniculostriate pathway continuing to the ventral visual stream. However, the same areas can also receive movement information through direct and indirect connections from an extrageniculostriate pathway involving the SC, Pulv, and Amg during nonconscious perception.

To summarize, our data clearly show subcortical and cortical activations triggered by the emotional valence of dynamic whole-body actions presented in the blind visual hemifield of a cortically blind patient, and this finding is compatible with initial processing of such visual attributes in a subcortical extrageniculostriate pathway from the SC and Pulv to the Amg. At the same time, our data indicate that subcortical processes interact with cortical activations in the FG and primary somatosensory, premotor, and motor areas.

Materials and Methods

Participant. GY is a well-documented 53-y-old (at the time of testing) male patient who sustained a traumatic head injury at the age of 7, damaging the left V1 and resulting in a right homonymous hemianopia (for a detailed description of the anatomical and functional pathology, see ref. 3). Informed consent was obtained to participate in the study according to the Declaration of Helsinki.

Stimuli. Materials for the present experiment were derived from video recordings of 12 professional actors (6 females and 6 males), who were instructed by a professional director to perform different actions from daily life scenarios (e.g., walking, talking on the telephone, drinking, or opening a door) (see ref 17 for more details). Each action was performed with a different emotional valence, including a neutral one. For the scenario used in the present experiment, the actors were instructed to open the door, react to something or someone in front of them, and then close the door again. Continuous fragments of 3 s were selected from the raw materials, and the faces were subsequently blurred with a motion-tracking software (Adobe After Effects), so that only information from the body movements was visible (Movies S1 and S2 display one representative example of neutral and angry stimuli, respectively). The edited material was subjected to three different experiments that validated different dimensions and properties of the stimuli.

Emotion validation experiment. A total of 141 edited video clips with different emotional expressions were presented to 12 naïve participants who were instructed to categorize the emotion expressed by each video in a 3AFC task (anger, fear, or neutral) without time limits. Average of correct recognition for anger scenarios was 76% (SD = 28) and for fearful scenarios was 97% (SD = 5). The 24 best-recognized angry movies (89%; SD = 15) and 24 best-recognized neutral movies (97%; SD = 15) were selected for the present experiment, resulting overall in 48 movies (12 actors \times 2 emotions \times 2 shootings).

Objective movement validation. To objectively quantify the amount of movement implied in the movies and to test possible quantitative differences in movement between neutral and anger stimuli, we estimated the movement in each video clip by calculating pixel-wise luminance variations between subsequent frames. These differences were then averaged across pixels that scored higher than 10 (highest possible value = 255), a value that corresponds to the noise level of the camera. Finally, these estimations were averaged for each movie. There was no significant difference in this movement index between the neutral and angry stimuli (two tailed t test, $P = 0.64$).

Subjective movement validation experiment. In addition to the analysis of objective movement, we ran a further validation experiment to quantify subjective ratings of global movement perception and to test possible differences in subjective movement perception between neutral and anger stimuli. The 48 stimuli were randomly displayed to 32 subjects who were instructed to indicate

the amount of movement perceived in each movie on a 5-point digital scale, ranging from 1, "very little movement," to 5, "a lot of movement." Mean rating of neutral movies was 2.48 (SD = 0.88), and mean rating of anger movies was 2.75 (SD = 0.68). Results showed no significant difference in subjective perception of global movement between angry and neutral stimuli [two-tailed paired-sample t test, $t(31) = 1.26$, $P = 0.216$].

Data about subjective and objective movement validation rule out the possibility that the present neurofunctional differences between angry and neutral whole-body actions are simply based on a specific objective or subjective differences in the amount of movement between stimuli. Instead, they suggest that the emotional dimension should be taken in account as the most relevant factor. Of course, this result does not exclude the possibility that more sophisticated analyses will be able to reveal differences in the type or amount of movement between neutral and angry whole-body actions in the future. However, these putative differences appear at present to be an intrinsic property of the emotional style by which a whole-body action is performed.

fMRI Experiment. The fMRI experiment consisted of a functional run in a 3.0-T MAGNETOM Allegra magnetic resonance head scanner (Siemens). A total of 570 brain volumes were scanned, each consisting of 42 slices, acquired in ascending interleaved order with no between-slice gap (2.5-mm slice thickness, 3.5 mm \times 3.5 mm in-plane resolution, repetition time = 2,250 ms, echo time = 25 ms).

In addition to the functional runs, a high-resolution T1-weighted anatomical image (voxel size = $1 \times 1 \times 1$ mm) was acquired with a 3D magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) sequence (repetition time = 2,250 ms, echo time = 2.6 ms, matrix size = 256 \times 256, 192 slices).

The stimulation protocol consisted of an orthogonal 2 emotions (neutral and angry) \times 2 visual hemifields (LVF and RVF) factorial design. Each video clip was presented once, first in the (blind) RVF and then in the (intact) LVF. Stimuli were centered vertically and presented with their innermost edge at 5° of horizontal eccentricity from the central fixation cross. They subtended a visual angle of 10.8° vertically \times 7.3° horizontally. A trial consisted of the presentation of a central fixation cross against a dark background (2,050 ms) followed by the presentation of a stimulus (3,000 ms). Stimulus presentation was synchronized with a change in the brightness of the central cross to facilitate fixation. Each of the four experimental conditions included 24 trials. Additionally, 76 null events and 30 oddball trials were included. Null events simply consisted of the dark background and were included to jitter intertrial intervals. Oddball trials consisted of an inverted neutral video clip.

GY was instructed to press the response button when an inverted stimulus was presented. This design enabled us to monitor GY's attention during the experiment while, at the same time, recordings of neural activity related to visual-stimulus processing was unaffected by spurious factors such as action execution and button press during presentation of the conditions of interest (i.e., neutral and angry whole-body expressions). It was, in fact, particularly important for the present purposes to avoid responses from GY during presentation of angry and neutral actions because, based on previous neuroimaging studies with dynamic and static whole-body expressions (17), we predicted enhanced activity in motor and premotor areas simply by following perception of angry expressions. The interpretation of this activity would have been problematic if it were concomitant with voluntary action execution.

Imaging data were analyzed using BrainVoyager QX software (Brain Innovation). The first five volumes of the functional run were discarded to allow for T1 equilibration. Preprocessing of the functional run included slice scan time correction, 3D motion correction, and temporal filtering. The structural scan was segmented to delineate white matter from gray matter; based on this segmentation, a cortical surface reconstruction was made. The functional data were coregistered with the anatomical scan and normalized to Talairach space (61). Four bilateral subcortical regions of interest were anatomically defined in the anatomical volume in native space: LGN, SC, Pulv, and Amg. The statistical analysis was based on the general linear model, with each condition defined as a predictor plus one predictor for the oddball condition. Two general linear model analyses were performed: one confined to the anatomically defined regions of interest and one to the whole cortex. The threshold level was set for the subcortical regions at $P < 0.05$ and for the cortex at $P < 0.01$, uncorrected.

Behavioral Experiment. A few months after the scanning session, a psychological experiment was conducted to investigate the behavioral recognition of whole-body dynamic expressions. GY was seated at ~60 cm from a computer screen and instructed to fixate on the central cross. The same stimuli and design used in the fMRI experiment were also used here with

only the following exceptions. The central cross lasted 500 ms (instead of 2,050 ms), and there was no null event or oddball trial. Stimulus offset was followed by the presentation of a question mark, and GY was instructed to indicate by button press whether the stimulus showed a neutral or angry expression in a 2AFC task. Response time was unlimited, and eye movements were monitored online by an experimenter throughout the whole session. Consistent with previous reports, GY showed extremely steady and reliable fixation on the central cross so that no trial had to be replaced. He was also questioned on

a trial-by-trial basis about visual awareness for RVF stimuli and never reported conscious perception of RVF stimuli.

ACKNOWLEDGMENTS. B.d.G., S.P., and J.G. were supported by European Commission Communication with Emotional Body Language (COBOL) Grant FP6-2005-NEST-Path Imp 043403-COBOL. J.V.d.S. is a postdoctoral researcher supported by Fonds voor Wetenschappelijk Onderzoek-Vlaanderen. M.T. was supported by Netherlands Organization for Scientific Research Postdoctoral Veni Grant 451-07-032 and partly by the Fondazione Carlo Molo, Turin, Italy.

- Poppel E, Held R, Frost D (1973) Letter: Residual visual function after brain wounds involving the central visual pathways in man. *Nature* 243:295–296.
- Sahraie A, et al. (2003) Spatial channels of visual processing in cortical blindness. *Eur J Neurosci* 18:1189–1196.
- Tamietto M, et al. (2010) Collicular vision guides nonconscious behavior. *J Cogn Neurosci* 22:888–902.
- Morland AB, et al. (1999) Visual perception of motion, luminance and colour in a human hemianope. *Brain* 122:1183–1198.
- Kohler W, Held R (1949) The cortical correlate of pattern vision. *Science* 109:442.
- de Gelder B, et al. (2008) Intact navigation skills after bilateral loss of striate cortex. *Curr Biol* 18:R1128–R1129.
- Goebel R, Muckli L, Zanella FE, Singer W, Stoerig P (2001) Sustained extrastriate cortical activation without visual awareness revealed by fMRI studies of hemianopic patients. *Vision Res* 41:1459–1474.
- Huxlin KR, et al. (2009) Perceptual relearning of complex visual motion after V1 damage in humans. *J Neurosci* 29:3981–3991.
- Milner AD, Goodale MA (2006) *The Visual Brain in Action* (Oxford Univ Press, Oxford, UK).
- Girard P, Salin PA, Bullier J (1992) Response selectivity of neurons in area MT of the macaque monkey during reversible inactivation of area V1. *J Neurophysiol* 67:1437–1446.
- Humphrey NK, Weiskrantz L (1967) Vision in monkeys after removal of the striate cortex. *Nature* 215:595–597.
- Bridge H, Thomas O, Jbabdi S, Cowey A (2008) Changes in connectivity after visual cortical brain damage underlie altered visual function. *Brain* 131:1433–1444.
- Lyon DC, Nassi JJ, Callaway EM (2010) A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. *Neuron* 65:270–279.
- Sincich LC, Park KF, Wohlgenuth MJ, Horton JC (2004) Bypassing V1: A direct geniculate input to area MT. *Nat Neurosci* 7:1123–1128.
- Puce A, Perrett D (2003) Electrophysiology and brain imaging of biological motion. *Philos Trans R Soc Lond B Biol Sci* 358:435–445.
- Vangeneugden J, et al. (2011) Distinct mechanisms for coding of visual actions in macaque temporal cortex. *J Neurosci* 31:385–401.
- Pichon S, de Gelder B, Grèzes J (2008) Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Soc Neurosci* 3:199–212.
- Kret ME, Pichon S, Grèzes J, de Gelder B (2011) Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *Neuroimage* 54:1755–1762.
- Liddell BJ, et al. (2005) A direct brainstem-amygdala-cortical ‘alarm’ system for subliminal signals of fear. *Neuroimage* 24:235–243.
- Morris JS, DeGelder B, Weiskrantz L, Dolan RJ (2001) Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain* 124:1241–1252.
- Morris JS, Ohman A, Dolan RJ (1999) A subcortical pathway to the right amygdala mediating “unseen” fear. *Proc Natl Acad Sci USA* 96:1680–1685.
- Tamietto M, de Gelder B (2010) Neural bases of the non-conscious perception of emotional signals. *Nat Rev Neurosci* 11:697–709.
- Whalen PJ, et al. (1998) Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *J Neurosci* 18:411–418.
- de Gelder B, Vroomen J, Pourtois G, Weiskrantz L (1999) Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport* 10:3759–3763.
- de Gelder B, Hadjikhani N (2006) Non-conscious recognition of emotional body language. *Neuroreport* 17:583–586.
- de Gelder B, Morris JS, Dolan RJ (2005) Unconscious fear influences emotional awareness of faces and voices. *Proc Natl Acad Sci USA* 102:18682–18687.
- Pegna AJ, Khateb A, Lazeyras F, Seghier ML (2005) Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nat Neurosci* 8:24–25.
- Tamietto M, et al. (2009) Unseen facial and bodily expressions trigger fast emotional reactions. *Proc Natl Acad Sci USA* 106:17661–17666.
- Schenberg LC, et al. (2005) Functional specializations within the tectum defense systems of the rat. *Neurosci Biobehav Rev* 29:1279–1298.
- Luo Q, Holroyd T, Jones M, Hendlert T, Blair J (2007) Neural dynamics for facial threat processing as revealed by gamma band synchronization using MEG. *Neuroimage* 34:839–847.
- Whalen PJ, Phelps EA (2009) *The Human Amygdala* (Guilford, New York).
- Ward R, Danziger S, Bamford S (2005) Response to visual threat following damage to the pulvinar. *Curr Biol* 15:571–573.
- Pasley BN, Mayes LC, Schultz RT (2004) Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42:163–172.
- Williams MA, Morris AP, McGlone F, Abbott DF, Mattingley JB (2004) Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *J Neurosci* 24:2898–2904.
- Vizueta N, Patrick CJ, Jiang Y, Thomas KM, He S (July 14, 2011) Dispositional fear, negative affectivity, and neuroimaging response to visually suppressed emotional faces. *Neuroimage*, 10.1016/j.neuroimage.2011.07.015.
- Day-Brown JD, Wei H, Chomsung RD, Petry HM, Bickford ME (2010) Pulvinar projections to the striatum and amygdala in the tree shrew. *Front Neuroanat* 4:143.
- de Gelder B, van Honk J, Tamietto M (2011) Emotion in the brain: of low roads, high roads and roads less travelled. *Nat Rev Neurosci* 12:425.
- Leh SE, Ptilo A, Schönwiesner M, Chakravarty MM, Mullen KT (2010) Blindsight mediated by an S-cone-independent collicular pathway: An fMRI study in hemispherectomized subjects. *J Cogn Neurosci* 22:670–682.
- Sabatini D, et al. (2011) Emotional perception: Meta-analyses of face and natural scene processing. *Neuroimage* 54:2524–2533.
- de Gelder B, et al. (2010) Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions. *Neurosci Biobehav Rev* 34:513–527.
- Peelen MV, Atkinson AP, Andersson F, Vuilleumier P (2007) Emotional modulation of body-selective visual areas. *Soc Cogn Affect Neurosci* 2:274–283.
- Vuilleumier P, Richardson MP, Armony JL, Driver J, Dolan RJ (2004) Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nat Neurosci* 7:1271–1278.
- Kastner S, et al. (2004) Functional imaging of the human lateral geniculate nucleus and pulvinar. *J Neurophysiol* 91:438–448.
- Grèzes J, Pichon S, de Gelder B (2007) Perceiving fear in dynamic body expressions. *Neuroimage* 35:959–967.
- Kjaer TW, Nowak M, Kjaer KW, Lou AR, Lou HC (2001) Precuneus-prefrontal activity during awareness of visual verbal stimuli. *Conscious Cogn* 10:356–365.
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
- Williams LM, et al. (2006) Mode of functional connectivity in amygdala pathways dissociates level of awareness for signals of fear. *J Neurosci* 26:9264–9271.
- Tamietto M, de Gelder B (2008) Affective blindsight in the intact brain: Neural interhemispheric summation for unseen fearful expressions. *Neuropsychologia* 46:820–828.
- Anderson AK, Christoff K, Panitz D, De Rosa E, Gabrieli JD (2003) Neural correlates of the automatic processing of threat facial signals. *J Neurosci* 23:5627–5633.
- Bishop SJ, Duncan J, Lawrence AD (2004) State anxiety modulation of the amygdala response to unattended threat-related stimuli. *J Neurosci* 24:10364–10368.
- Craig AD (2009) How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci* 10:59–70.
- Adolphs R, Damasio H, Tranel D, Cooper G, Damasio AR (2000) A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J Neurosci* 20:2683–2690.
- Straube T, Miltner WH (2011) Attention to aversive emotion and specific activation of the right insula and right somatosensory cortex. *Neuroimage* 54:2534–2538.
- Anders S, et al. (2004) Parietal somatosensory association cortex mediates affective blindsight. *Nat Neurosci* 7:339–340.
- Kilts CD, Egan G, Gideon DA, Ely TD, Hoffman JM (2003) Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *Neuroimage* 18:156–168.
- Sato W, Kochiyama T, Yoshikawa S, Naito E, Matsumura M (2004) Enhanced neural activity in response to dynamic facial expressions of emotion: An fMRI study. *Brain Res Cogn Brain Res* 20:81–91.
- Grosbras MH, Paus T (2006) Brain networks involved in viewing angry hands or faces. *Cereb Cortex* 16:1087–1096.
- Adolphs R (2002) Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behav Cogn Neurosci Rev* 1:21–62.
- de Gelder B, Snyder J, Greve D, Gerard G, Hadjikhani N (2004) Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proc Natl Acad Sci USA* 101:16701–16706.
- Whalen PJ, et al. (2001) A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion* 1:70–83.
- Talairach J, Tournoux P (1988) *Co-Planar Stereotaxic Atlas of the Human Brain* (Thieme, New York).